Norwegian University
of Life Sciences

Master's Thesis 2025 60 ECTS
Faculty of Environmental Sciences and Natural Resource Management

Mitigating Hydropower Impacts Evaluating Fish Passage Improvements for Atlantic Salmon and Brown Trout

Admir Velic
Biology

1 Acknowledgements

Primary Supervisor: Thrond Oddvar Haugen

Faculty of Environmental Sciences and Natural Resource Management
Norwegian University of Life Sciences (NMBU)

Secondary Supervisor: Tormod Haraldstad

Norwegian Research Centre (NORCE)

This master thesis marks the culmination of five years of study at the Faculty of Environmental Sciences and Natural Resource Management (MINA), Norwegian University of Life Science (NMBU). Throughout this journey, I have had the privilege of working under the guidance of Thrond Oddvar Haugen, whose expertise and encouragement have been invaluable. I am equally grateful to Tormod Haraldstad at NORCE for his insights and for facilitating the fieldwork that made this research possible. I would also like to thank Øistein Preus Hveding at Norconsult for his support, constructive critique and dialogues.

I extend my thanks to the power plant owners for their willingness to participate in the study, as well as to the government agencies and private investors whose funding made this research feasible. I would like to thank Frode Kroglund for providing valuable information about the powerplants history, pictures and literature. Finally, my deepest appreciation goes to Mariann and Luna for their unwavering support and understanding throughout the process.

Åsgårdstrand 15th May 2025

Admir Velic

2 Abstract

Hydropower operations frequently obstruct the downstream migration of anadromous salmonids, exposing smolts to physical barriers, delayed passage, and elevated mortality. In 2023, structural modifications were implemented at the Fosstveit Hydropower Plant (HEP) in southern Norway to improve passage conditions for juvenile Atlantic salmon (*Salmo salar*) and anadromous brown trout (*S. trutta*). An angled (29 °) trash rack with 15 mm mesh and low-level bypass system were installed to reduce turbine entrainment and facilitate safer migration. This study evaluated smolt responses to these modifications under varying environmental conditions, with a focus on interspecific behavioural differences, passage efficiency, diel timing, and environmental drivers of migration.

A total of 359 smolts—comprising 207 Atlantic salmon (*Salmo salar*) and 152 brown trout (*S. trutta*) — were surgically implanted with Passive Integrated Transponder (PIT) tags and released for downstream migration monitoring at the Fosstveit Hydroelectric Power Plant (HEP). Of these, 238 individuals (66.3%) were retained for most behavioural and environmental analyses following the exclusion of fish lost due to post-tagging mortality, undetected movements, or suspected predation events. However, the full dataset (n = 359) was included in the Cormack-Jolly-Seber (CJS) mark-recapture modelling to estimate apparent survival (migration success) and detection probability across the PIT array.

Passage behaviour was monitored using stationary PIT antennas placed at key locations along the bypass system and supplemented with manual scanning to detect fallback. Simultaneously, environmental parameters including water temperature, discharge (Q), and light intensity (lux) were logged continuously throughout the study period to allow linkage between migratory behaviour and abiotic conditions.

Among all surviving individuals, over 90% successfully entered and exited the designated bypass system, with no PIT detections recorded in the turbine intake channel. This absence of entrainment, combined with high bypass entry rates, indicates complete functional avoidance of the turbine path, and supports the conclusion that the redesigned intake structure — featuring 15 mm bar spacing and new angle — was highly effective in guiding smolts away from hazardous routes. These findings highlight the structural modification as a robust mitigation measure for reducing turbine-induced mortality and improving overall passage success across species.

Marked differences were observed between species. Atlantic salmon migrated more rapidly than brown trout, showing shorter hesitation times in the forebay (mean: 41.5 min vs. 112 min) and reduced bypass passage durations (8.5 min vs. 13.7 min), consistent with hypothesised species-specific differences in rheotactic behaviour. Both species displayed a strong preference for migrating during crepuscular periods under 5–10 lux light levels , supporting predictions of diel migration control by photoperiod. Generalised Additive Models revealed that hesitation time was significantly modulated by discharge and temperature with increased movement initiation above 12 °C and a plateau beyond 16 °C—highlighting environmental thresholds that shape temporal migration dynamics.

A zero-inflated negative binomial model showed that heavier individuals—particularly brown trout — exhibited more migration attempts. Over 70 % of all fish attempted passage more than once, suggesting that successful migration often involved repeated interactions with the forebay. This aligns with hypotheses proposing a behavioural decision-making process shaped by both intrinsic and extrinsic drivers. Multivariate clustering and PCA revealed three behavioural phenotypes differing in morphology, flow conditions, light exposure, and passage timing. Post-passage survival estimates from Cormack–Jolly–Seber models were high for both species (0.97 for salmon, 0.96 for trout), indicating overall successful mitigation.

Smoltification is a time-sensitive and physiologically constrained life stage during which behavioural delay or hydropower-induced stress can compromise osmoregulatory development and reduce marine survival. The Fosstveit modifications effectively eliminated turbine risk and improved structural passage outcomes, confirming hypotheses regarding the functional benefit of reduced bar spacing. However, the broader inter- and intraspecific variation in trout behaviour suggests that structural design alone is insufficient. This study highlights the need for ecologically grounded, species-sensitive strategies that combine physical mitigation with behavioural guidance to ensure truly effective fish passage.

3 Sammendrag

Vannkraftutbygging utgjør en betydelig barriere for nedvandrende anadrome laksefisk, og eksponerer smolt for fysiske hindringer, forsinket passasje og økt dødelighet. I 2023 ble det gjennomført strukturelle tiltak ved Fosstveit kraftverk i Sør-Norge for å forbedre vandringsforholdene for utvandrende atlantisk laks (*Salmo salar*) og sjøørret (*S. trutta*). En skråstilt rist (med justert vinkel til 29°) med 15 mm stavavstand og et lavt plassert smoltløp ble installert for å redusere turbininnsug og gi tryggere passasjemuligheter. Studien undersøker hvordan smolt responderte på disse tiltakene under varierende miljøforhold, med særlig vekt på atferd, passeringstid, valg av passasjerrute og overlevelse.

Totalt 359 smolt – bestående av 207 atlantisk laks og 152 sjøørret – ble merket med Passive Integrated Transponder (PIT)-merker og sluppet ut for overvåking av nedvandringsatferd ved Fosstveit kraftverk. Av disse ble 238 individer (66,3 %) inkludert i de fleste atferds- og miljøanalysene, etter ekskludering av fisk som gikk tapt som følge av postoperativ dødelighet, manglende gjenfangst eller sannsynlig predasjon. Hele datasettet (n = 359) ble imidlertid inkludert i Cormack-Jolly-Seber (CJS)-modellene for å estimere tilsynelatende overlevelse (vandring fra slipp til nedstrøms antenner) og deteksjonssannsynlighet.

Vandringen ble overvåket ved hjelp av stasjonære PIT-antenner plassert på sentrale punkter i bypass-systemet, supplert med manuell skanning for å oppdage tilbake vandring. Samtidig ble miljøparametere som vanntemperatur, vannføring (Q) og lysintensitet (lux) kontinuerlig logget gjennom hele forsøksperioden for å muliggjøre kobling mellom atferd og abiotiske forhold.

Blant alle overlevende individer passerte over 90 % gjennom det tiltenkte bypass-systemet, og ingen fisk ble registrert i turbininntaket. Fraværet av deteksjoner i turbintunnelen, kombinert med høy andel vellykkede passeringer, tyder på fullstendig funksjonell unngåelse av turbinløpet. Dette støtter konklusjonen om at det ombygde inntaksristsystemet – med 15 mm spileavstand – var svært effektivt i å lede smolt bort fra farlige vandringsruter. Resultatene bekrefter at den strukturelle modifikasjonen utgjør et godt avbøtende tiltak for å redusere turbindødelighet og forbedre total passasjesuksess hos begge arter.

Artene viste tydelige forskjeller. Atlantisk laks migrerte raskere enn ørret og hadde kortere oppholdstid i forbassenget (gjennomsnitt: 41,5 min mot 112 min) og kortere passeringstid gjennom bypass (8,5 min mot 13,7 min), i tråd med hypoteser om artsforskjeller i respons på

hydrauliske signaler. Begge arter viste sterk preferanse for vandring i skumringstimer, under lysnivåer mellom 5–10 lux, noe som støtter hypoteser om døgnrytmiske migrasjonsmønstre styrt av fotoperiode. Generaliserte additive modeller viste at oppholdstid i forbassenget ble signifikant påvirket av vannføring (EDF = 6,5, p < 0,01) og temperatur (EDF = 2,7, p = 0,01). Migrasjonsaktiviteten økte ved temperaturer over 12 °C og avtok igjen etter 16 °C, noe som antyder termiske terskelverdier.

Modeller med zero-inflated negativ binomisk fordeling viste at tyngre individer—særlig ørret — utførte flere migrasjonsforsøk (r = 0,52, p < 0,01), mens lengde hadde svakere forklaringskraft. Over 70 % av alle individer utførte mer enn ett forsøk, noe som antyder at vellykket passering ofte innebærer gjentatt interaksjon med forbassenget. Dette støtter hypoteser om at migrasjon er en atferdsmessig beslutningsprosess påvirket av både indre motivasjon og ytre miljøforhold. PCA og klyngeanalyse identifiserte tre atferdsfenotyper med ulik morfologi, eksponering for vannføring, lysnivå og passeringstidspunkt. Post-passerings-overlevelse var høy for begge arter (0,97 for laks, 0,96 for ørret), ifølge Cormack–Jolly–Seber-modeller. Smoltifisering er en energikrevende og fysiologisk sårbar fase, der forsinkelser eller stress kan forstyrre osmoseregulering og redusere overlevelse til havs. De strukturelle tiltakene ved Fosstveit reduserte turbinrisikoen og forbedret passasjen for begge arter, i tråd med hypoteser om effekt av redusert stavavstand.

Tiltakene ved Fosstveit reduserte turbinrisikoen og la til rette for mer effektiv og trygg vandring – særlig for laks. Samtidig viser ørret større atferdsmessig variasjon, noe som understreker behovet for supplerende tiltak basert på artskunnskap. Studien demonstrerer betydningen av artsdifferensiert utforming av fiskepassasjer ved vannkraftanlegg.

4 Contents

5 Introduction

Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) exhibit complex and highly plastic life history strategies, characterized by partial anadromy and ontogenetic habitat shifts. In both species, individuals may adopt either resident or migratory phenotypes, a phenomenon influenced by genetic predisposition, environmental conditions, and physiological thresholds during early development (Jonsson and Jonsson, 2011; Nevoux et al., 2019; Thorpe, 1994).

Partial anadromy is a central feature in their populations: while some individuals complete their life cycle in freshwater, others migrate to marine environments to optimize growth and reproductive output. In Atlantic salmon, anadromy is obligatory at the population level, although the age and size at smoltification vary. Brown trout, in contrast, exhibit facultative anadromy, with a more pronounced continuum between resident and migratory life histories (Jonsson and Jonsson, 2002; Lucas et al., 2001; McCormick et al., 1998)

Smoltification — a critical developmental phase marking the transition from freshwater to marine tolerance — is triggered by increasing photoperiod and temperature, accompanied by endocrine and osmoregulatory changes (McCormick et al., 1998; Mccormick et al., 2000) The decision to migrate is generally size-dependent, with larger individuals at a given age more likely to enter the smolt pathway (Birnie-Gauvin et al., 2021; Nevoux et al., 2019)

The downstream migration of smolts occurs during spring, typically between late April and early June in southern Norway. Migration is cued by rising water temperatures (often above 8 °C), increasing discharge (Bjerck et al., 2021), and photoperiod changes (Haraldstad et al., 2023, 2019, 2017; Vollset et al., 2021). Atlantic salmon generally initiate migration earlier and in more temporally synchronized pulses compared to brown trout, which tend to exhibit more prolonged and variable migration timing (Jensen et al., 2022; Vollset et al., 2021; Whalen et al., 1999).

Ibbotson et al. (2006) found that in some unregulated systems, crepuscular migration may be absent, and smolts may migrate at any time of day or night. Haraldstad et al. (2017) further demonstrated that both Atlantic salmon and brown trout smolts adjust their migration timing in response to environmental cues, with light intensity being a dominant factor, but also showing individual and species-specific variation. Water discharge (flow) and temperature are key environmental drivers of smolt migration timing and behaviour.

Increased discharge, typically resulting from spring snowmelt and rainfall, provides physical cues that stimulate migration and offer safer, faster passage downstream by diluting predator density and increasing water velocity (Haraldstad et al., 2017). Many studies report that smolt migration is often initiated or intensified during periods of elevated flow. Temperature also plays a crucial role. Smoltification-the physiological transformation that prepares juveniles for seawater entry-is temperature-dependent. In Southern Norway, migration activity generally increases as water temperatures rise above 8–10 °C, with optimal migration often observed between 10–14 °C (Haraldstad et al., 2017). However, if temperatures exceed the upper thermal tolerance (often above 16–18 °C), migration can be inhibited due to physiological stress or reduced readiness.

During downstream migration, salmonid smolts rely on environmental cues such as water temperature, discharge, and photoperiod to trigger physiological and behavioural changes that signal the optimal migration window (Antolos et al., 2005; Haraldstad et al., 2017; McCormick et al., 1998; Norrgård et al., 2013). Timely migration is critical; delays-often caused by anthropogenic barriers such as hydropower facilities-can increase predation risk, energy expenditure, and physiological stress, ultimately reducing survival and marine recruitment (Haugen et al., 2008; Jonsson and Jonsson, 2009; Marschall et al., 2011; Roscoe et al., 2011; Thorstad et al., 2012).

Diel migration patterns of smolts are generally conserved in both Atlantic salmon and brown trout, with a pronounced preference for crepuscular and nocturnal movement at lower water temperatures (Haraldstad et al., 2017). This behaviour likely reflects an adaptive response to predation pressure from diurnal visual predators and aligns with strong phototactic sensitivity documented in both species (Ibbotson et al., 2011; Thorstad et al., 2012). Smolts predominantly migrate under low-light conditions (<2 lux) when water temperatures are below approximately 12 °C, and changes in light intensity can modulate both initiation timing and passage route selection (Haraldstad et al., 2017; McCormick et al., 1998; Whalen et al., 1999). However, as temperatures rise above 12 °C, the proportion of diurnal migration increases, and migration may occur equally during day and night (Haraldstad et al., 2017; McCormick et al., 1998; Whalen et al., 1999). Additionally, diel migration patterns may vary within a river and be influenced by anthropogenic structures, though environmental factors such as river width and temperature are often more important determinants of migration timing and rates (Haraldstad et al., 2017; Harvey et al., 2020; Ibbotson et al., 2011; Thorstad et al., 2007; Whalen et al., 1999).

Despite ecological overlap, Atlantic salmon and brown trout differ markedly in their downstream migration strategies. Salmon smolts tend to migrate in cohesive groups, display strong rheotaxis, and exhibit more direct passage behaviour through riverine systems and migration structures. In contrast, brown trout show greater individual variation, more frequent fallback, and stronger responses to local hydrodynamics (Haraldstad et al., 2021; Kärgenberg et al., 2020; McCormick et al., 1998; E. B. Thorstad et al., 2003). Research on fish behaviour at hydropower plants equipped with different mitigation measures is therefore instrumental in improving mitigation strategies for downstream migrating smolts at hydropower intakes.

Hydropower is a globally important source of renewable electricity, contributing approximately 16 % of the total global energy production, and over 89 % of Norway's energy supply (Graham et al., 2025). However, hydropower infrastructure has significant ecological impacts, particularly in lotic ecosystems and for migratory species or species that rely on stable lotic environments. The construction and operation of hydropower dams alter flow regimes, connectivity, fragment habitats, and present physical barriers to movement, leading to increased mortality and population declines in species dependent on connectivity (Dynesius and Nilsson, 1994; Haraldstad et al., 2021, 2019; Limburg and Waldman, 2009). The ecological consequences of hydropower operations are particularly pronounced for anadromous species such as Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) (Haraldstad et al., 2019), which require uninterrupted access to spawning and feeding habitats across multiple life stages (Coutant and Whitney, 2000; Jonsson and Jonsson, 2011, 2002).

To address this, different approaches and measures have been developed (Fjeldstad et al., 2018; Silva et al., 2020). These measures often include the construction of guidance structures designed to either physically block fish from hazardous areas or direct them towards safer routes. Such structures may incorporate mechanical barriers or behavioural cues to deter fish from dangerous zones (Scruton et al., 2003). Additionally, systems such as fish collection mechanisms and bypass channels are utilized to redirect fish safely downstream or around the dam (Larinier, 1998; Nyqvist et al., 2016). Despite these efforts, the effectiveness of these measures varies, and passage through turbines increases mortality rates, exerting selective pressures on fish populations (Haraldstad et al., 2022, 2021, 2019; Haugen et al., 2008; Larinier, 2008).

Empirical studies have demonstrated that immediate mortality rates for smolts passing through Kaplan turbines can range from below 5 % up to 46 %, depending on turbine characteristics, operational conditions, and fish size (Calles et al., 2011; Deng et al., 2007; Fjeldstad et al., 2018; Jacobson et al., 2012; Thorstad et al., 2007; Vikström et al., 2020). For example, Calles et al (2011) estimated smolt mortality at approximately 13–17 % at a 17-MW Kaplan turbine in Sweden (Calles et al., 2011). However, other field studies have reported even higher mortality rates, with certain sites showing up to 36 % or more, particularly in small, fast-rotating Francis/Kaplan units (Fjeldstad et al., 2018; Vikström et al., 2020).

Blade strike is a primary cause of mortality in Kaplan turbines. Numerical models and field telemetry data indicate that for juvenile smolts (13–27 cm), blade strike mortality typically falls between 0 and 12 % (Jacobson et al., 2012; Radinger et al., 2022). However, these models tend to underestimate mortality for larger salmon, with observed rates for adults (>50 cm) reaching 56–81% in Francis turbines and likely similarly elevated in Kaplan turbines (Deng et al., 2007; Richmond et al., 2015; Tomanova et al., 2023). The risk of blade strike increases with fish size relative to blade thickness, and with higher rotational speeds typical of certain Kaplan designs (Richmond et al., 2015). Additionally, the probability of collision and subsequent injury is influenced by the ratio of fish length to blade thickness, with mortality increasing when fish length approaches or exceeds the thickness of the blade (Cada, 1990; Deng et al., 2007).

Pressure changes and barotrauma also contribute to turbine-related mortality. Kaplan turbines can generate rapid pressure fluctuations ($\Delta P/\Delta t$), and when nadir pressures fall below 20 kPa, the risk of barotrauma increases significantly (Brown et al., 2014; Richmond et al., 2015).

Mitigation strategies for reducing smolt mortality at Kaplan turbine sites include technical modifications such as the use of thicker or fish-friendly blade designs, which have been shown to reduce strike mortality by up to 60% for smolts around 150 mm in length (Amaral et al., 2011; Jacobson et al., 2012). Operational adjustments, such as optimizing turbine efficiency and providing alternative passage routes (e.g., fishways or surface spill), can also significantly improve survival rates (Calles et al., 2011; Fjeldstad et al., 2018). For instance, allocating a portion of river flow to spillways or fishways can divert a substantial proportion of smolts away from turbines, reducing overall mortality (Fjeldstad et al., 2013). However, the effectiveness of spill as a mitigation measure depends on the volume and configuration of the spill, with substantial spill required to achieve meaningful reductions in mortality (Fjeldstad et al., 2018).

Technical mitigation measures such as fine-spaced trash racks and bypass systems are widely implemented to guide smolts away from turbines and reduce direct mortality (Calles et al., 2011; Fjeldstad et al., 2018; Silva et al., 2020). However, several studies indicate that even with these measures, significant migration delays and forebay mortality may persist (Noonan et al., 2012; Nyqvist et al., 2016; Roscoe et al., 2011; Wolter et al., 2020). The effectiveness of such structures in minimizing delay and ensuring timely, stress-free passage remains insufficiently understood (Marschall et al., 2011; Nyqvist et al., 2016; Silva et al., 2020). This knowledge gap is especially critical as delays during the sensitive smoltification window can impair osmoregulatory performance and reduce subsequent marine survival (Jensen et al., 2022; Simmons et al., 2022; Thorstad et al., 2012; Wedemeyer et al., 1980).

The Fosstveit Hydroelectric Power Plant (HEP), operational since 2006, was originally constructed without adequate consideration for downstream fish migration. The intake was fitted with a 55 mm bar-spaced trash rack, which allowed significant entrainment of smolts, contributing to high mortality during migration periods. Observations and field surveys prior to mitigation revealed substantial losses of Atlantic salmon (*Salmo salar*), brown trout (*S. trutta*), and European eel (*Anguilla anguilla*) (Figure 1).

To address these shortcomings and meet regulatory requirements set by the Norwegian Water Resources and Energy Directorate (NVE, 2019), the intake structure was retrofitted in 2023 with a fine-spaced (15 mm) trash rack with a new angle of 29 ° and an upgraded smolt bypass system (Figure 2). These structural modifications aimed to physically exclude fish from the turbine intake and facilitate safer downstream passage via a dedicated bypass route. As part of this mitigation programme, monitoring of fish movement using PIT telemetry was initiated to assess the effectiveness of the new configuration.

Previous studies at Fosstveit HEP have documented long hesitation times in the forebay prior to passage, with notable interspecific differences in bypass usage and survival (Haraldstad et al., 2021, 2019, 2017). Environmental factors such as discharge and water temperature, as well as individual traits like body size and species identity, have been shown to significantly influence both passage timing and success. High flows may act as a facilitating cue for migration, but can also increase turbulence near intakes, potentially deterring approach or prolonging hesitation. Similarly, diel variation in light levels has been linked to crepuscular passage peaks in Atlantic salmon, while brown trout display more variable or asynchronous movement patterns.

Figure 1. Pictures taken by Frode Kroglund in 2009, showing some of the fish that unsuccessfully migrated through the power plant.

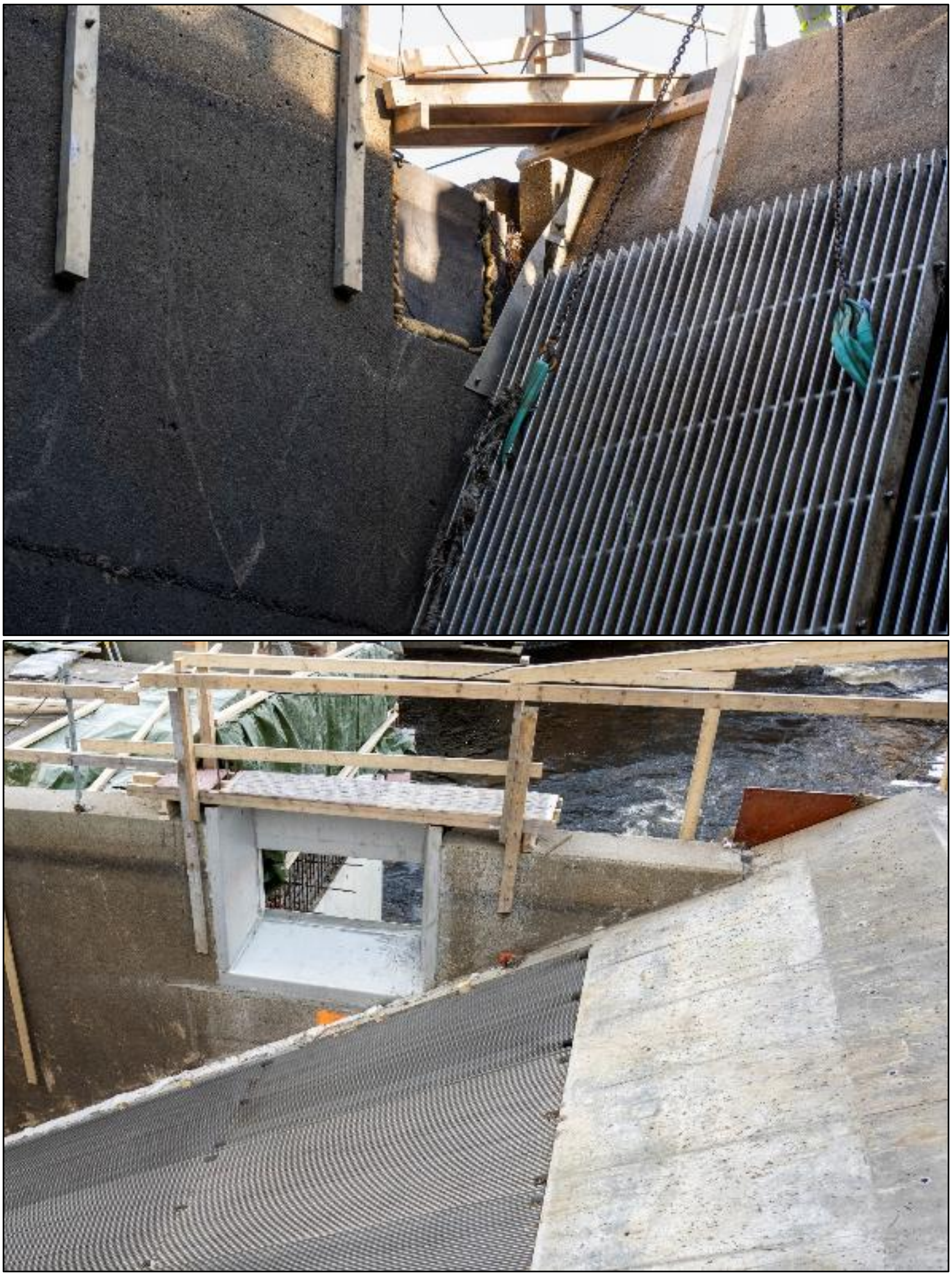

Figure 2. The picture on top shows the previous solution, whereas the bottom pictures show the redesigned solution. Notice the differences between the distance from the thrash gate to the smolt hatch and the spacing between the elements.

The primary objective of this study was to assess the effectiveness of a redesigned trash rack with a reduced spacing of 15 mm and angle of 29 °, compared to the existing 55 mm and 70 ° configuration, in facilitating safer downstream migration for Atlantic salmon and brown trout at the Fosstveit hydropower plant. This investigation evaluates fish passage efficiency, mortality rates, and operational impacts on hydropower performance.

Specifically, this study aims to:

- Quantify the effect of trash rack clearance on downstream migration success, focusing on passage rates and migration timing.

The specific hypotheses for my study are the following:

Passage Success Hypothesis

H_{01}: The redesigned intake rack does not significantly improve the downstream passage success rate for migratory fish (Atlantic salmon and brown trout) compared to the previous design.

H_{a1}: The redesigned intake rack significantly improves the downstream passage success rate for migratory fish (Atlantic salmon and brown trout) compared to the previous design.

Survival and Species-Specific Responses

H_{02}: Passage survival rates do not differ between Atlantic salmon and brown trout smolts.

H_{a2}: Atlantic salmon smolts exhibit a higher survival rate compared to brown trout due to species-specific behaviour and greater hydrodynamic efficiency in bypass attraction flows.

Species-Specific Hesitation Time at Passage Structures

H_{03}: Median hesitation times (duration from first detection at the bypass entrance to successful passage) do not differ between Atlantic salmon and brown trout smolts

H_{a3}: Atlantic salmon smolts exhibit a faster passage time compared to brown trout due to stronger rheotactic responses and a higher likelihood of selecting surface-oriented bypass routes.

Temporal Migration Dynamics and Diel Activity

H_{04}: The timing of passage through the bypass does not exhibit diel variation, with no significant differences between daytime and crepuscular movements.

H_{a4}: Crepuscular migration significantly reduces median hesitation time, indicating a strong photoperiodic influence on passage behaviour, with peak movement occurring during dawn and dusk.

Environmental Modulation of Migration Success

H_{05}: Migration success is not significantly influenced by environmental variables such as water discharge (Q) or temperature (T).

H_{a5}: Migration success and timing is significantly influenced by environmental variables.

Size-Specific Migration Success and Timing

H_{06}: Migration success and timing is not significantly influenced by size (length, weight or cf).

H_{a6}: Migration success and timing is significantly influenced by size.

6 Methodology

6.1 Study site

The river Storelva (Vegårvassdraget) is situated in southern Norway, with a catchment area of 408 km². The river has a mean discharge of 12 m³/s at its outflow into Songevatn and Nævestadfjorden (Figure 3).

Storelva is notable for housing one of the few Atlantic salmon populations in southern Norway that survived the acidification crisis of the late 20th century (Hesthagen et al., 2011). This resilience is likely due to the geology of its watershed, where large portions of the catchment are situated below the marine boundary and contain calcium-rich marine deposits that buffer against acidification (Hesthagen et al., 2011; Kroglund et al., 2002). Consequently, Storelva has remained a critical refuge for anadromous salmonids in this region.

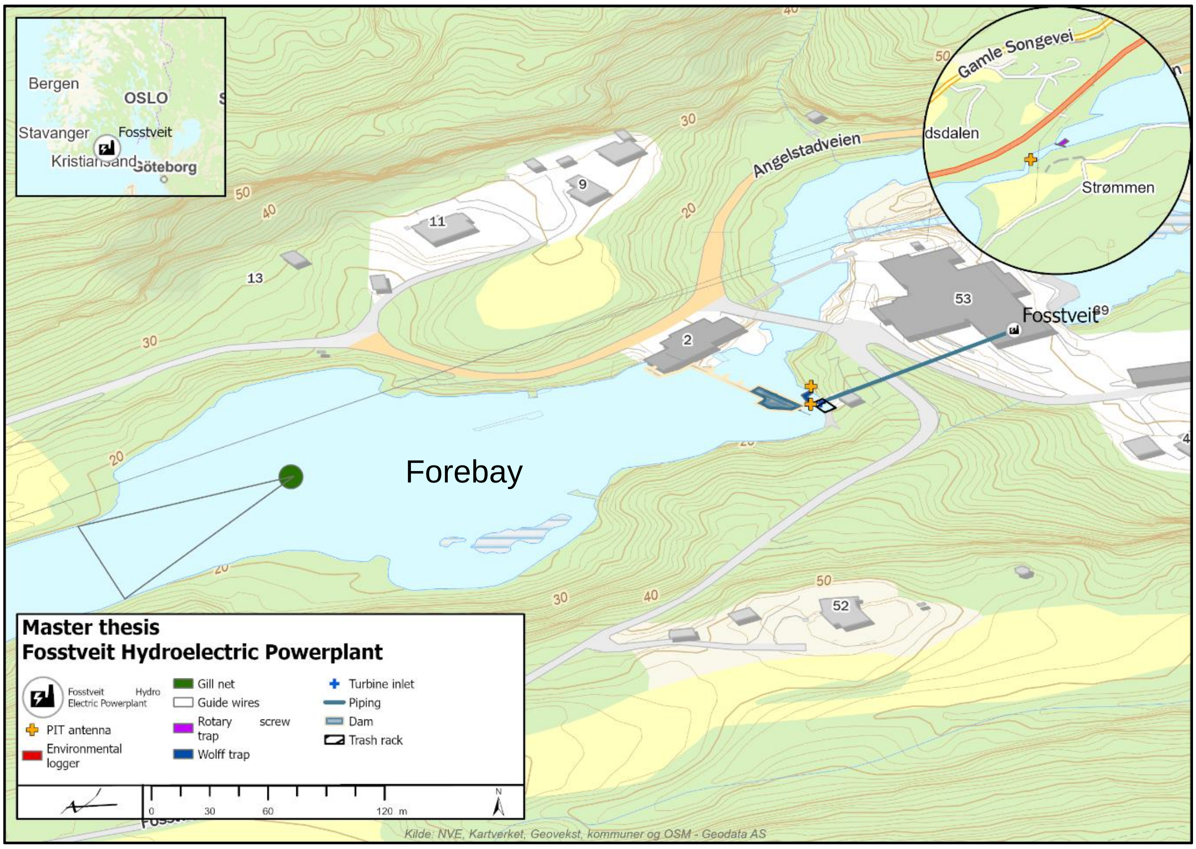

Figure 3. Map of the Fosstveit Hydroelectric Powerplant and surrounding area, showing key infrastructure and research equipment locations. The main map highlights the powerplant (Fosstveit 9), associated dam, turbine inlet, piping, and trash rack, as well as the placement of scientific equipment including a PIT antenna, environmental logger, gill net, rotary screw trap, and Wolf trap. Guide wires are also indicated. The inset map (upper left) shows the regional location of Fosstveit in southern Norway, while the inset (upper right) provides a close-up of the last PIT antenna at Strømmen and the rotary screw trap.

6.1.1 Fosstveit Hydroelectric Power Plant

Fosstveit Hydroelectric Power Plant (HEP) (N58.6410251, E8.9034541) is located 6.5 km upstream from the river mouth and utilizes a 14.5 m waterfall to generate electricity. The facility is a run-of-river hydropower station, meaning it operates with a small reservoir and relies on continuous water intake to maintain stable electricity production. The Kaplan turbine, equipped with four blades, operates at 330 rpm, with a maximum flow capacity (Qmax) of 16 m^3/s. The annual power production averages 6.9 GWh, making it a relatively small but important contributor to the regional energy supply.

The water diversion at Fosstveit HEP results in a 230-meter residual flow stretch, where only a mandated minimum flow is released over the original waterfall to support aquatic habitat continuity. Two fish ladders have been constructed along this stretch to aid the upstream migration of adult Atlantic salmon and Brown trout.

6.1.2 Trash Rack and Bypass Modifications

To mitigate the impacts of the power plant on downstream migrating smolts, several structural modifications have been implemented over the years. Originally, the intake trash rack at the tunnel entrance had vertical bars with a 50 mm spacing and an inclination angle of 70 °. In 2024, a redesigned trash rack was installed, reducing the bar spacing to 15 mm and an adjusted angle to 29 °. This adjustment aimed to enhance fish guidance efficiency by physically excluding smolts from turbine entrainment and directing them toward safer bypass routes.

The total rack area has increased from 25.4 m^2 to 43.25 m^2, which is expected to reduce flow velocity through the rack, minimizing turbulence and improving fish passage efficiency. Additionally, the uppermost 0.5 m of the rack is shielded by a concrete wall to prevent ice formation during winter months.

6.1.3 Fish Passage Routes and Monitoring

The turbine migration route remains open throughout the smolt-run period. Additionally, the fish ladder is reopened from May 18th to 19th to facilitate the upstream migration of Atlantic salmon and brown trout spawners that have aggregated downstream of the dam. These measures align with the operational concession requirements for Norwegian hydropower plants, which mandate site-specific compensation measures to mitigate potential environmental impacts (Haraldstad et al., 2017; Kärgenberg et al., 2020; Larinier, 2008).

Migrating smolts at Fosstveit HEP have four primary passage options:

1. Turbine Tunnel – Smolts that fail to locate bypass routes will not enter the Kaplan turbine. This is due to the new spacing at the new trash rack.
2. Trash Rack Bypass – A dedicated surface bypass gate, intermittently opened during peak migration periods, provides a safer alternative to turbine passage.
3. Fish Ladder – While primarily designed for upstream migration, the ladder is occasionally reopened in May to allow downstream-migrating fish to utilize it as an alternative passage, albeit local knowledge indicates a low passage rate.
4. Dam Crest – At high water flows, fish can bypass the HEP and migrate over the crest.

The effectiveness of these passage options is continuously monitored using a network of Passive Integrated Transponder (PIT) antennas placed at key locations:

- Entrance to the bypass channel – Captures data on fish using the trash rack.
- Wolff trap – Detects smolts that have passed through the bypass. The Wolf trap captured both PIT-tagged and untagged individuals and was emptied at least once per day. During peak migration periods, the trap was checked and emptied multiple times per day to minimise holding time and reduce stress or mortality associated with crowding.

6.2 Experimental design

6.2.1 Fish Sampling and Trap Design

Fish for this study were captured using a modified live-capture cod gillnet trap, adapted specifically to reduce injury and stress during sampling. The trap design follows principles described by Barlaup et al., (2013), prioritising minimal handling impacts and high survival upon release. The trap was deployed in the forebay of Fosstveit HEP, just upstream of the intake structure, where migrating smolts naturally congregate before attempting downstream passage (Figure 4).

Figure 4. The modified gillnet was placed in the forebay of Fosstveit HEP.

The trap consisted of a fine-meshed, soft-walled net mounted to a fixed frame and gently tensioned to form a guiding funnel. This configuration directed fish into a holding chamber while minimising physical contact. The location allowed for the passive collection of actively migrating smolts under near-natural hydraulic conditions. The trap was checked and emptied multiple times daily during peak migration hours to reduce holding time, stress, and density-related effects. Trapping was paused during periods of extreme discharge or temperature to prevent fish mortality or confounding handling effects.

Captured fish were anaesthetised, measured, weighed, and tagged before being held briefly in recovery tanks and released at a designated upstream point for tracking. All procedures followed established ethical guidelines (see Fish Tagging and Tracking Methods) and were timed to avoid interfering with the smolts natural migratory rhythms.

6.2.2 Experimental Structure and Group Allocation

To investigate migration dynamics under realistic conditions, the study was constrained by the operational requirements of the hydropower facility, including restrictions on flow manipulation. Despite this, environmental conditions varied naturally during the study period, providing a sufficient range of discharge, temperature, and light levels for statistical modelling (see Environmental Monitoring and Data Collection).

Fish were divided into five release groups (Table 1), each consisting of at least 50 individuals, the last release group was slightly smaller. Releases were spaced temporally to capture diel and seasonal variability. The timing was chosen to coincide with the expected peak of smolt migration and to cover a representative portion of the environmental gradients that influence movement decisions.

The sampling and tagging period extended across a two-week window, ensuring adequate overlap with known migration triggers such as rising temperature and discharge. The combination of repeated releases, environmental logging, and full antenna coverage provided a robust design for evaluating movement timing, route choice, and behavioural responses to real-time environmental variation.

Table 1. Number of PIT-tagged Atlantic salmon and brown trout smolts released upstream of the Fosstveit hydropower plant during the 2024 smolt migration period. Wild smolts were caught during their downstream migration upstream of the dam using a modified cod net.

Date	Brown trout	Atlantic salmon
2024-04-30	49	57
2024-05-02	38	23
2024-05-12	16	48
2024-05-13	16	36
2024-05-14	19	27
Total	206	152

6.2.3 Fish Tagging and Tracking Methods

Both Atlantic salmon and brown trout smolts are subjected to anaesthesia prior to internal tagging with 16 mm Passive Integrated Transponder (PIT) tags (16 mm, half-duplex, Oregon RFID), fish were anesthetized using MS222 (50–60 mg l^{-1}, Finquel/Syncaine) to minimize handling stress and ensure humane treatment (Ackerman et al., 2005; Detar and Mattingly, 2004; S, 2012). The MS222 solution was buffered with sodium bicarbonate to maintain a pH of 6.5, reducing potential acid-base imbalances during anaesthesia (Carter et al., 2010). The PIT tags were inserted through a small ventral incision between the posterior pectoral fin and the pelvic girdle, allowing the incision to heal naturally without sutures (Larsen et al., 2013). After tagging, the fish were held for one day before release at a site 350 m upstream of the hydropower dam.

To minimize stress and mortality, all fish handling, sedation, and tagging procedures was done according to established ethical guidelines and regulatory standards (Bennett et al., 2016), including those outlined by the European Union Directive 2010/63/EU on the protection of animals used for scientific purposes (the European parliament and the council of the European union, 2010). Additionally, all captured fish were carefully measured, weighed, and examined for external injuries before release, ensuring that tagging procedures do not unduly impact behaviour or survival rates. Despite adherence to these protocols, a small number of fish died between tagging and release. These post-handling mortalities likely reflect physiological stress responses, which may have been exacerbated by elevated water temperatures (>15 °C) during some tagging days. Such conditions are known to reduce recovery capacity in salmonid smolts and may have contributed to impaired post-anaesthesia recovery. All mortalities were recorded and excluded from behavioural and survival analyses to ensure biological validity of the final dataset.

Downstream of the smolt hatch, a Wolff trap directs fish into a holding vat. In this vat, both tagged and untagged fish are scanned and counted, providing valuable data on the total number of migrating fish, their survival rates, and the duration of their hesitation. Tagged fish were temporarily held in a separate tank before being released later. Additionally, Atlantic salmon smolts were transported beyond Strømmen and released into the river.

6.2.4 Environmental Monitoring and Data Collection

A fundamental aspect of our analytical framework was the systematic measurement of key environmental parameters, including water flow rates, water levels, water temperature, and dissolved oxygen concentration. These variables are critical for understanding the habitat conditions that influence fish migration and behaviour (Heggenes, 1990; Heggenes and Wollebæk, 2013; Jonsson and Jonsson, 2011; Lucas et al., 2001b; E. Thorstad et al., 2003). Data was continuously recorded at predetermined intervals using automated monitoring stations strategically positioned directly by the dam crest of Fosstveit HEP and downstream Fosstveit HEP (Figure 5).

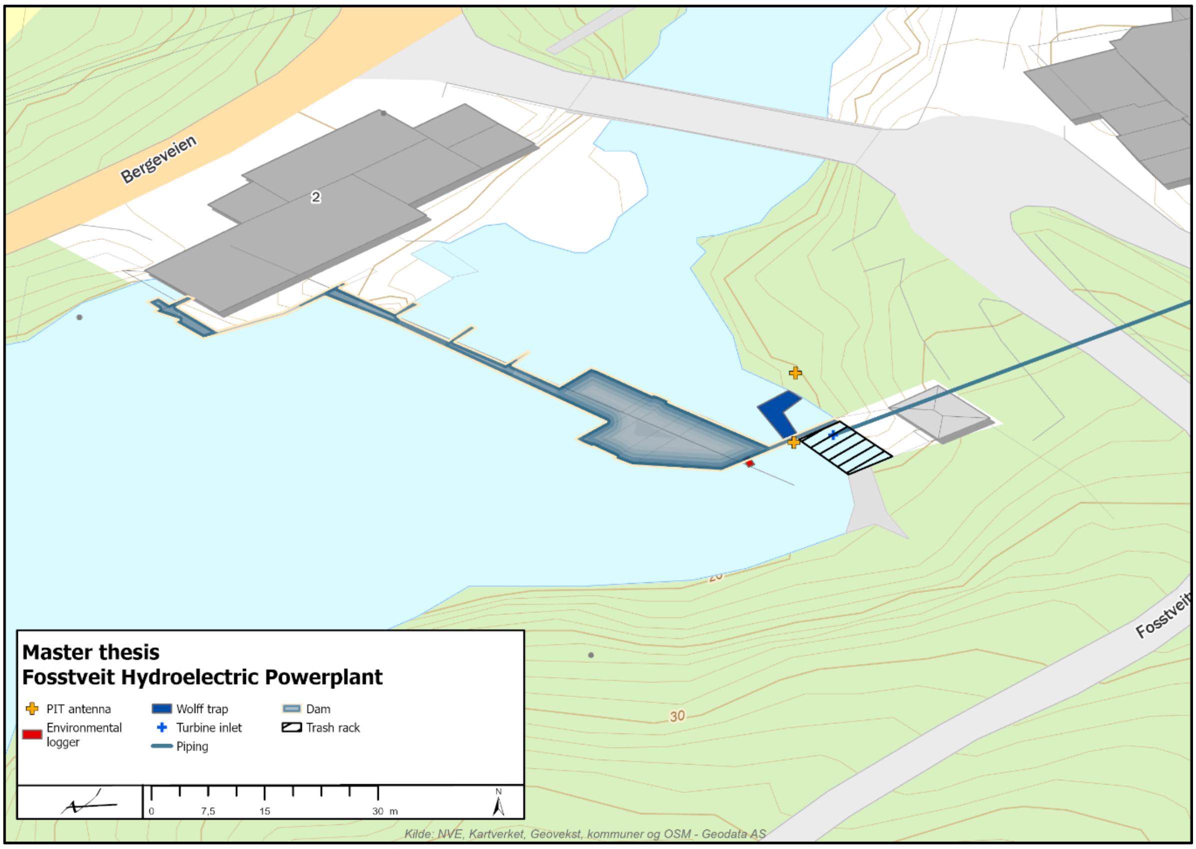

Figure 5. Map of the Fosstveit Hydroelectric Powerplant and surrounding area, showing key infrastructure and research equipment locations. The map illustrates the main components of the facility, including the powerplant building, dam, turbine inlet, piping system, and the newly installed trash rack with 15 mm bar spacing. Monitoring equipment used in the study is also shown, including PIT antennas (orange cross), environmental data logger (red dot), and the downstream Wolff trap (blue).

Water flow data were obtained from the Norwegian Water Resources and Energy Directorate's (NVE) web service, Sildre (NVE, 2025). The Lundevann station was selected as the most representative discharge gauge for the study site, as it is located directly upstream the Strømmen location, approximately 5.5 km downstream the Fosstveit Hydropower Plant.

Water temperature and light intensity were continuously monitored using HOBO Pendant Temperature/Light Loggers (Onset Computer Corporation, Bourne, MA, USA) (Figure 6). These compact, self-contained data loggers provide accurate and reliable measurements of both water temperature (±0.4 °C accuracy) and ambient light levels (0-65 535 lux range). The parameters were measured at designated monitoring stations positioned strategically both upstream and downstream of the HEP facility. By documenting these environmental factors in conjunction with our observations of fish behaviour, we could discern any correlations or causal relationships between environmental conditions and migratory patterns.

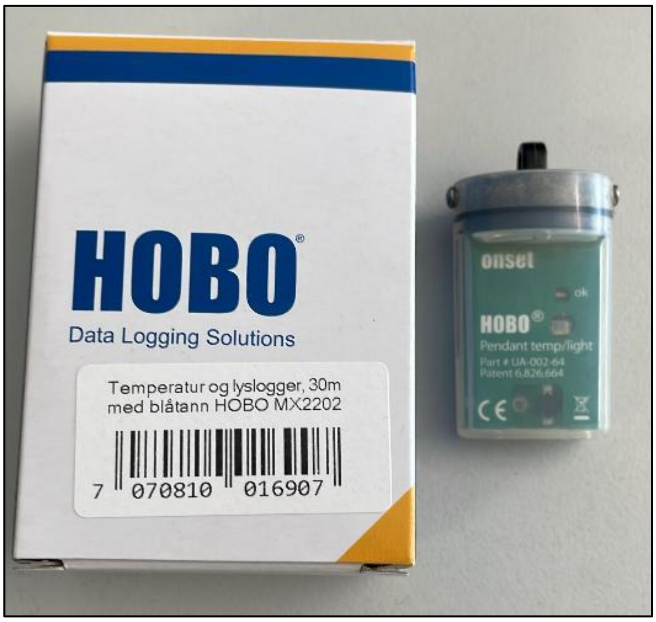

Figure 6. The temperature and light logger that was used in the study. During the study there were two HOBO loggers, one at 1 meter, and a second at 2 meters. This was to ensure a more robust data collection.

Discharge measurements at the study site during the monitoring period indicate notable variability in water flow conditions. Recorded flow values ranged from a minimum of 2.07 m^3/s to a maximum of 42.36 m^3/s, with an average discharge of 7.30 m^3/s, during the study period. This variation suggests fluctuating hydrological conditions that could influence fish migration behaviour.

Water temperature during the study period exhibited considerable variability, ranging from a minimum of 5.45 °C to a maximum of 21.58 °C, with a mean temperature of 14.50 °C.

Light intensity, measured using a HOBO Pendant logger placed at 1 meter depth, ranged from 0 lux (complete darkness) to a corrected maximum of 5 511 lux. The raw data initially contained systematic decimal placement errors for some high-value entries (e.g. 2722 lux misrecorded as 27 220 lux). These values were corrected by scaling all observations above

6 000 lux by a factor of 0.1, based on known sensor limits and distribution diagnostics. The sensor depth realistically accounts for light attenuation in the water column, providing biologically meaningful exposure levels. Corrected light data showed a median of 0 lux, with 75 % of all values below 86 lux, 95th percentile at 1 162 lux, and 99% below 2 500 lux.

6.3 Data analysis and statistics

All statistical analyses in this thesis were conducted using R (Team, 2006), which provided a robust environment for modelling migratory behaviour and evaluating the effectiveness of structural modifications at the Fosstveit Hydroelectric Power Plant (HEP). Each statistical method was selected to test specific hypotheses and tailored to address the ecological complexity of smolt migration, including non-normality, overdispersion, and zero-inflated distributions. The analyses explicitly address the following hypotheses: H_{01}–H_{a1} (passage success), H_{02}–H_{a2} (species-specific survival), H_{03}–H_{a3} (hesitation time), H_{04}–H_{a4} (diel migration), and H_{05}–H_{a5} (environmental modulation of migration). Additional multivariate analyses, including PCA and clustering, supported pattern discovery beyond formal hypothesis testing.

All models were validated using simulation-based residual checks (RMark, marked, DHARMa), and model selection was conducted via Akaike's Information Criterion corrected for small sample sizes (Akaike, 1974). Throughout, ecological interpretation was integrated with statistical evaluation to support conclusions on fish passage dynamics under varying operational and environmental conditions.

Differences in descent trajectories among the traps will be assessed employing a bootstrapping routine applied to the Kolmogorov–Smirnov test (Sekhon, 2011; Sokal and Rohlf, 2013), which accommodates distribution ties (Abadie, 2002). The ks. boot-function within the matching library of R facilitated these tests (Sekhon, 2011).

6.3.1 Use of Artificial Intelligence

This thesis has employed artificial intelligence (AI) tools, including ChatGPT-4 (OpenAI, 2025), Claude (Anthropic, 2024), and Perplexity (Perplexity AI, 2025), as supplementary resources during the research and writing process. AI was primarily used to troubleshoot error messages in R, assist in streamlining and refining scripts, and support implementation of statistical models. It was also used as a sparring partner in critical reflection and interpretation of findings. Furthermore, AI-assisted proofreading was applied to improve grammar and linguistic clarity. At no stage was AI used to autonomously generate content, perform analyses, or produce results.

6.3.2 H_{01}/H_{a1} Passage Success Following Intake Rack Modification

To test whether the redesigned intake rack with 15 mm bar spacing improved downstream passage success relative to the prior 50 mm configuration, hypothesis H_{01}/H_{a1} was evaluated using Cormack-Jolly-Seber (CJS) mark-recapture modelling (Royle, 2008; Sarzo et al., 2020). Cormack-Jolly-Seber models were preferred over Bayesian alternatives due to their ability to handle staggered entry and exit in open populations (Sarzo et al., 2020), thereby avoiding the 'memory effect' bias that may arise in Jolly-Seber formulations under conditions of variable emigration (Royle, 2008; Sandercock, 2020).

In standard applications, CJS models estimate apparent survival (Φ), which integrates true survival and site fidelity. However, in this study, the spatial distance between the bypass exit and the Wolff trap was minimal, and no mortality was observed in the intervening segment. Therefore, the estimated PIT-antenna to Wolff-trap Φ values can be interpreted directly as cross-dam migration probabilities as true survival is assumed to be 1. This interpretation provides a biologically meaningful metric of passage efficiency at the hydropower facility.

This modelling approach also estimated detection probability (p) at successive PIT antennas/recapture facilities (Wolff trap and rotary screw trap) installed along the bypass and downstream sections of Storelva. The dual-parameter framework was essential for distinguishing actual migratory failure from detection error, thereby providing a robust metric for evaluating passage performance (Lebreton et al., 1992; Zydlewski et al., 2006).

Model fitting was conducted via maximum likelihood estimation. Model fit and parameter identifiability were assessed using bootstrap procedures and residual simulation (RMark, marked, DHARMa). The model structure accounted for staggered entry and exit typical in open population telemetry studies, and the final model incorporated species-specific differences and environmental covariates (Sandercock, 2020).

In parallel, bootstrapped Kolmogorov–Smirnov tests (ks.boot, Matching package) were used to test for differences in descent trajectories between fish using different passage routes or across release groups (Sekhon, 2011; Sokal and Rohlf, 2013). This non-parametric test was selected for its robustness to tied values and small sample distributions, and it enabled detection of statistically significant shifts in cumulative passage patterns across trap locations (Sekhon, 2011; Sokal and Rohlf, 2013).

6.3.3 H_{02}/H_{a2} Species-Specific Migration Timing and Survival

Hypothesis H_{02}/H_{a2} focused on whether passage survival differed significantly between Atlantic salmon and brown trout. To test this, time-to-event analysis was applied using Cox proportional hazards regression models (coxph, survival package) (Therneau and Grambsch, 2000) with detection at the downstream antenna (successful passage) as the event of interest. Smolts not detected were treated as right-censored cases. Time zero was defined as the release timestamp, and survival curves were estimated via the Kaplan-Meier method within the Survival package (Allignol and Latocuhe, 2025).

Covariates included species identity, morphometric traits (length, weight, and condition factor), and environmental variables (temperature and discharge at time of release). The proportional hazards assumption was assessed via Schoenfeld residual plots and log-log survival functions (Therneau and Grambsch, 2000), ensuring the model's temporal validity. Competing models incorporating species × environment interactions were compared using Akaike's Information Criterion corrected for small sample size (AICc) (Burnham and Anderson, 1998; Richardson, 2009). Survival differences between groups were visualised through stratified Kaplan-Meier curves, and hazard ratios were interpreted in the context of behavioural ecology and hydrodynamic selectivity.

6.3.4 H_{03}/H_{a3} Species-Specific Hesitation Time at Passage Structures

To address hypothesis H_{03}/H_{a3}, which posits species differences in median hesitation times at bypass entrances. Hesitation time was defined as the interval from first PIT detection at the forebay antenna to successful passage. The data were highly skewed and zero-inflated, with many individuals migrating immediately upon entry. Therefore, a Zero-Inflated Negative Binomial (ZINB) regression model was implemented using glmmTMB (Brooks et al., 2024; Mazerolle, 2023; Zuur et al., 2009).

The response variable was hesitation time (in minutes), rounded to the nearest integer. This modelling approach accounts for overdispersion and an excess of zero values, which are biologically interpretable as individuals that migrated immediately without any measurable delay.

The ZINB model included a conditional (count) component predicting non-zero hesitation times and a zero-inflation component predicting the probability of instantaneous migration. The conditional model incorporated species, discharge (Q), and light intensity (Lux), and their interactions. The zero-inflation model included species and Q as additive terms. Model selection among 12 candidate structures was performed using MuMIn::aictab() based on AICc, identifying the most parsimonious representation of ecological processes.

Model diagnostics were conducted with the DHARMa package to check for overdispersion, zero inflation, and uniformity of residuals (Hartig, 2024).

6.3.5 H_{04}/H_{a4}, H_{03}/H_{a3} Temporal Migration Dynamics and Diel Activity

Diel activity patterns and their effect on passage timing and hesitation behaviour were analysed to test H_{04}/H_{a4} and further inform H_{03}/H_{a3}. Migration timestamp data were used to categorize movement events into diel periods: dawn, day, dusk, and night, based on solar elevation. Histograms and polar plots visualised hourly passage frequencies, while Generalized Additive Models (GAMs; mgcv package) were used to evaluate the effect of diel phase, Lux, and their interactions on hesitation time (Wood, 2023, 2017).

Smooth terms were estimated using penalized regression splines, and the optimal smoothing parameter was selected by restricted maximum likelihood (REML). Effective degrees of freedom (edf) provided information on non-linear responses. Partial dependence plots illustrated how hesitation and passage times varied across light and flow gradients. The GAM framework allowed for additive and interaction effects among environmental covariates, including species, light intensity, and water flow.

These models will confirm if there is a significant crepuscular activity peak (supporting H_{a4}), with higher migration probabilities during low-light periods, particularly in brown trout.

6.3.6 H_{05}/H_{a5} Environmental Modulation of Migration Success

To test H_{05}/H_{a5} concerning the influence of temperature (T), discharge (Q), and Lux on migration probability and timing. GAMs were extended to include interaction terms, allowing for an exploration of how multiple environmental factors jointly influence passage success, hesitation time and migration probability. For instance, an interaction between water temperature and flow rate may reveal threshold effects that impact fish passage efficiency (Pedersen et al., 2019).

Models included smooth terms for temperature and discharge, with and without interaction effects. The inclusion of light intensity allowed for testing the Lux-Driven Migration Pattern hypothesis (H_{06}/H_{a6}), particularly in relation to diel migration rhythms and their modulation by ambient light.

Model comparisons based on AICc revealed that models including both flow and temperature consistently outperformed null or univariate models, indicating significant environmental modulation of behaviour.

6.3.7 H_{a1}–H_{a6} Clustering and Principal Component Analysis (PCA)

While not designed to test a single hypothesis in isolation, PCA and hierarchical clustering analyses were used to explore multivariate behavioural and environmental associations across all hypotheses (especially H_{a1}, H_{a2}, and H_{a5}) (Jolliffe, 2002). GAMs are an extension of generalized linear models (GLMs) that allow for non-linear relationships between response and predictor variables using smooth functions (Hastie and Tibshirani, 1990).

In this study, GAMs were implemented to model the effects of water temperature, river gradient, and discharge rate on migration timing and success. The smooth terms were estimated using penalized regression splines, optimizing flexibility while preventing overfitting. The selection of smoothing parameters was performed using restricted maximum likelihood (REML) to improve model stability (Wood, 2017).

PCA was performed on standardized variables including fish length, weight, condition factor, hesitation time, water flow, temperature, and Lux.

Sampling adequacy was confirmed via Kaiser-Meyer-Olkin (KMO) scores, and Bartlett’s test of sphericity confirmed inter-variable correlation (Field, 2012). Scree plots guided component retention. Furthermore, hierarchical clustering analysis will be conducted using

Ward's method and Euclidean distance to group fish based on similarities in migration behaviours. This analysis helps reveal whether certain behavioural patterns are associated with specific environmental conditions or species characteristics (Everitt et al., 2011).

To test H_{06}/H_{a6} concerning the influence of size-related variables on migration probability and timing, Generalized Additive Models (GAMs) were applied across multiple outcome datasets, including passage success, hesitation time, and detection probability.

Morphometric predictors (length, weight, and condition factor) were entered as smooth terms or linear covariates depending on distributional properties and biological relevance. Separate models were constructed to isolate the effects of each metric on both timing and migration probability.

6.3.8 Model Selection and Akaike's Information Criterion (AIC)

Model selection is a crucial step in identifying the most suitable statistical model for analysing fish migration and environmental influences. In this study, we employed Akaike's Information Criterion (Akaike, 1974) corrected for small sample sizes (AICc) to compare multiple candidate models and select the most supported model. AICc values were computed for each candidate model, and the model with the lowest AICc was considered the most supported.

To compare migration timing among release cohorts and routes, candidate time-to-event models are fitted using the survival library in R (Therneau and Grambsch, 2000). To address hypotheses H_{01}-H_{06}, candidate models included day of release, before/after opening trash rack, and migration routes as a group effect as predictors. Various additive and multiplicative combinations of these predictors were evaluated using the Cox proportional hazards model, with model selection based on AIC (Burnham and Anderson, 1998; Richardson, 2009; Therneau and Grambsch, 2000).

The count component of the model included species, water flow, and their interaction (art * Waterflow). The zero-inflation component included species and water flow as additive predictors (~ species + Waterflow) to estimate the probability of zero hesitation time. Model selection was based on AICc using AICcModavg::aictab() across a suite of 12 candidate models with varying combinations of biological and environmental predictors (including crepuscular activity and light intensity when available). The best-performing model (Model

4) was selected for further analysis. Residual diagnostics were performed using the DHARMa package.

7 Results

7.1 Descriptive analyses

A total of 238 individually tagged smolts, comprising 124 Atlantic salmon (*Salmo salar*) and 114 brown trout (*S. trutta*), were included in the downstream migration analyses at Fosstveit HEP. Morphometric analysis revealed notable interspecific differences. Atlantic salmon were smaller, with a mean length of 149.55 mm (SD = 14.30) and mean weight of 25.74 g (SD = 8.08), while brown trout averaged 171.96 mm (SD = 22.09) in length and 44.17 g (SD = 15.17) in weight (Figure 7). The mean condition factor (CF) was higher in brown trout (0.85, SD = 0.09) than in Atlantic salmon (0.75, SD = 0.06), suggesting differences in body robustness that may influence behaviour and hydraulic performance.

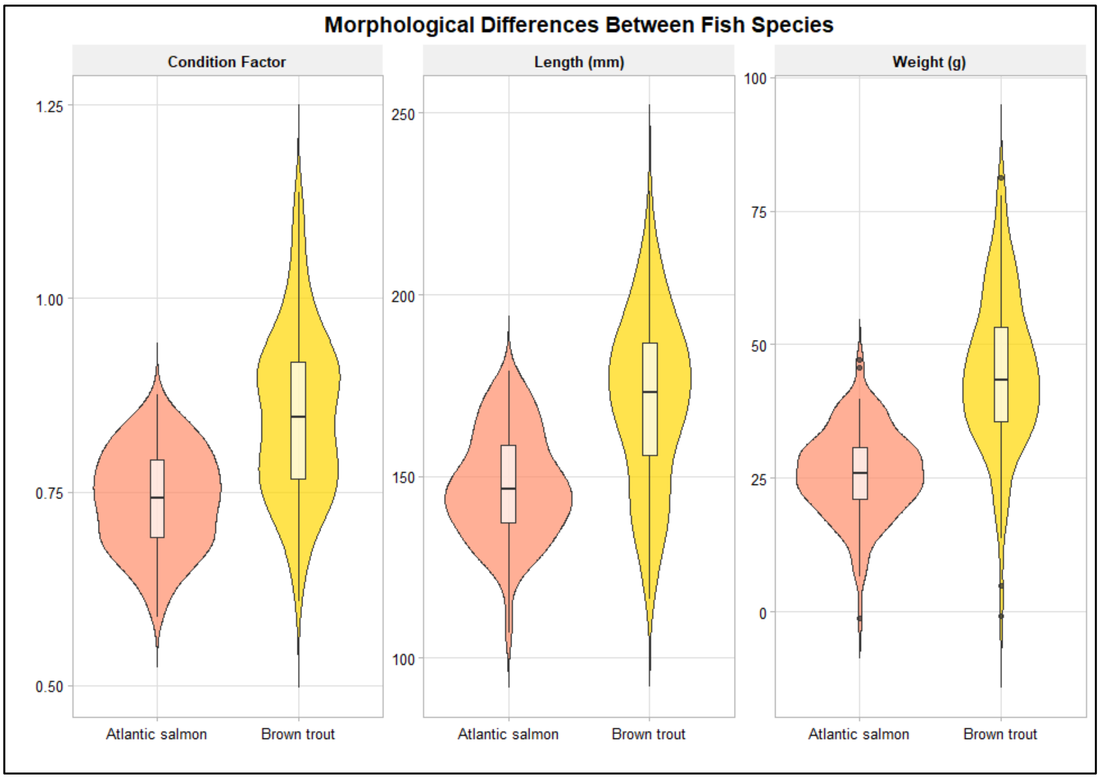

Figure 7. Violin plots comparing condition factor, length (mm), and weight (g) of Atlantic salmon smolts (orange) and brown trout (yellow) smolts. Brown trout smolts exhibit higher median condition factor, greater length, and higher weight compared to Atlantic salmon smolts. Distributions indicate greater variability in all three morphological traits for brown trout.

7.2 Daily observations in the Wolff trap

A total of 4,853 Atlantic salmon smolts and 760 Brown trout smolts were recorded passing through the Wolff trap at Fosstveit HEP during the spring migration period (23 April – 3 June 2024) (Figure 8). Migration commenced at water temperatures between 6.3 and 6.5 °C, with early movement observed in both species, although Atlantic salmon appeared earlier and in higher numbers. Peak migration for Atlantic salmon occurred between 1–12 May, with a maximum daily catch of 509 individuals on 3 May, coinciding with water temperatures rising to approximately 10.2 °C. For brown trout, peak movement was more diffuse, with the highest daily count (81 individuals) observed on 2 May at 9.8 °C. Notably, the 25% cumulative migration threshold was reached on 3 May (day 124) for both species, and the 50% threshold on 7 May (day 128), indicating that despite behavioural and numerical differences, the overall progression of migration through time was synchronised across species.

Migration intensity for both species declined markedly after mid-May as water temperatures exceeded 14°C. Notably, brown trout continued to pass the trap at low rates into early June, while Atlantic salmon activity largely ceased by the end of May.

On average, brown trout made more frequent migration attempts (mean = 6.1) compared to Atlantic salmon (mean = 3.4) (Figure 9). Correlation analyses indicated a moderate, positive association between fish weight and migration attempts ($r = 0.52$, $p < 0.01$), suggesting that heavier fish, especially among brown trout, initiated more frequent passage attempts—likely due to greater energetic demands or increased responsiveness to structural modifications. Conversely, fish length showed only a weak correlation with migration attempts ($r = 0.24$, $p = 0.08$), emphasizing that fish mass, rather than length, more strongly influences migratory behaviour patterns.

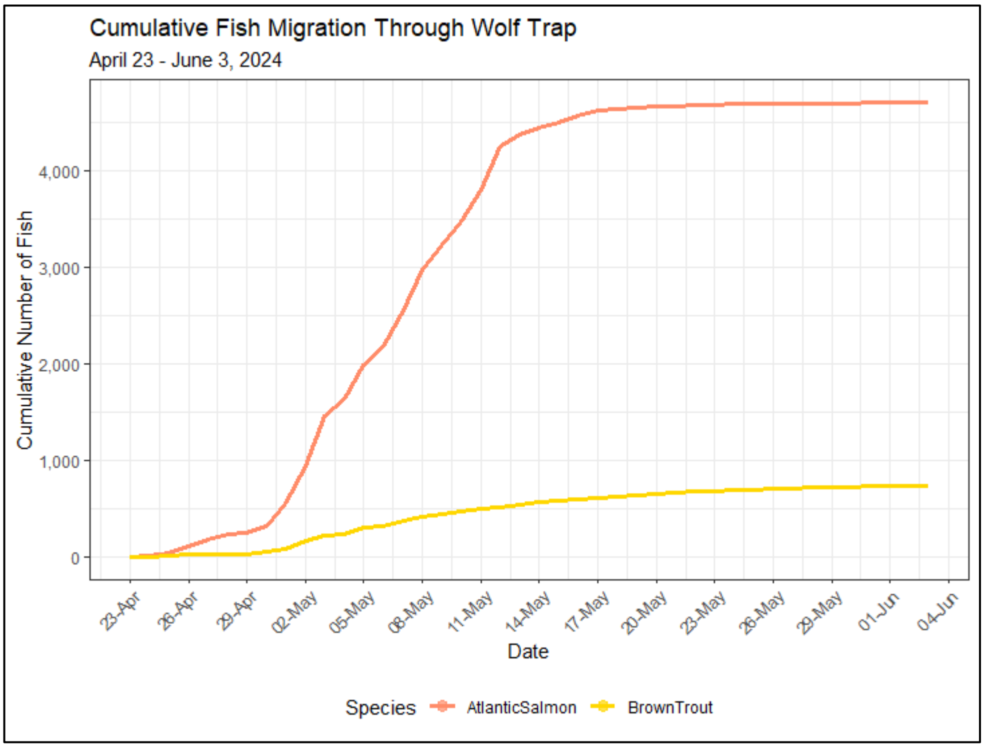

Figure 8. Cumulative migration of fish, both untagged and tagged individuals. These numbers are daily observations made by Grov Werner at the Wolff trap at Fosstveit HEP.

The total number of migration attempts further underscored species-specific differences in behavioural dynamics (Figure 9). Atlantic salmon exhibited a sharp, synchronised peak in activity, with over 7000 detections concentrated on a single day (11 May). In contrast, brown trout displayed a more temporally dispersed pattern, with multiple smaller peaks in activity observed across several days — notably on 11 May (~1800 detections) and 13 May (~1500 detections).

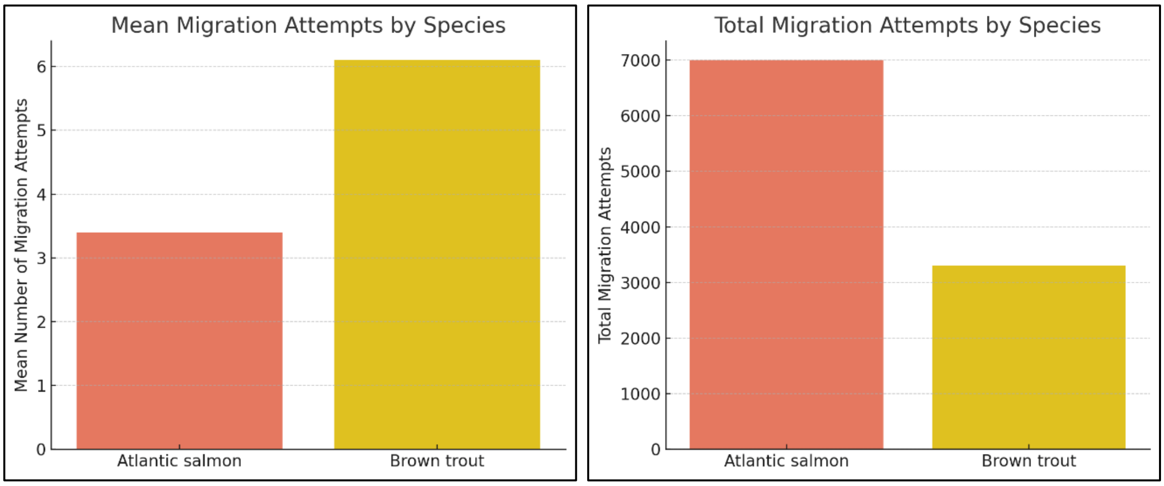

Figure 9. Mean (left) and total (right) number of migration attempts recorded for Atlantic salmon and brown trout during the 2024 smolt migration period at Fosstveit HEP. Note that the high number of attempts likely includes repeated detections of individuals hesitating near the smolt hatch, as the antenna system did not apply a time threshold to filter sequential readings

Importantly, the high number of recorded attempts is likely influenced by the behaviour of individuals lingering near the smolt hatch and exhibiting hesitation behaviour. Since the PIT antenna system at the hatch was not configured to filter detections based on a minimum time interval, repeated detections of the same individual during periods of stationary or oscillatory movement may have been interpreted as multiple discrete attempts.

7.3 H_{01}/H_{a1}: Passage Success Following Intake Rack Modification

The favoured CJS-model (phi(species*station), p(species*station)) estimated Atlantic salmon dam-to-Wolff trap survival to be 0.77±0.04 (SE) and brown trout survival to be 0.82±0.04. (Figure 10). Model fitting was conducted using maximum likelihood estimation, and simulation-based residual diagnostics were performed to assess fit and parameter identifiability. Bootstrapping methods were applied to generate confidence intervals.

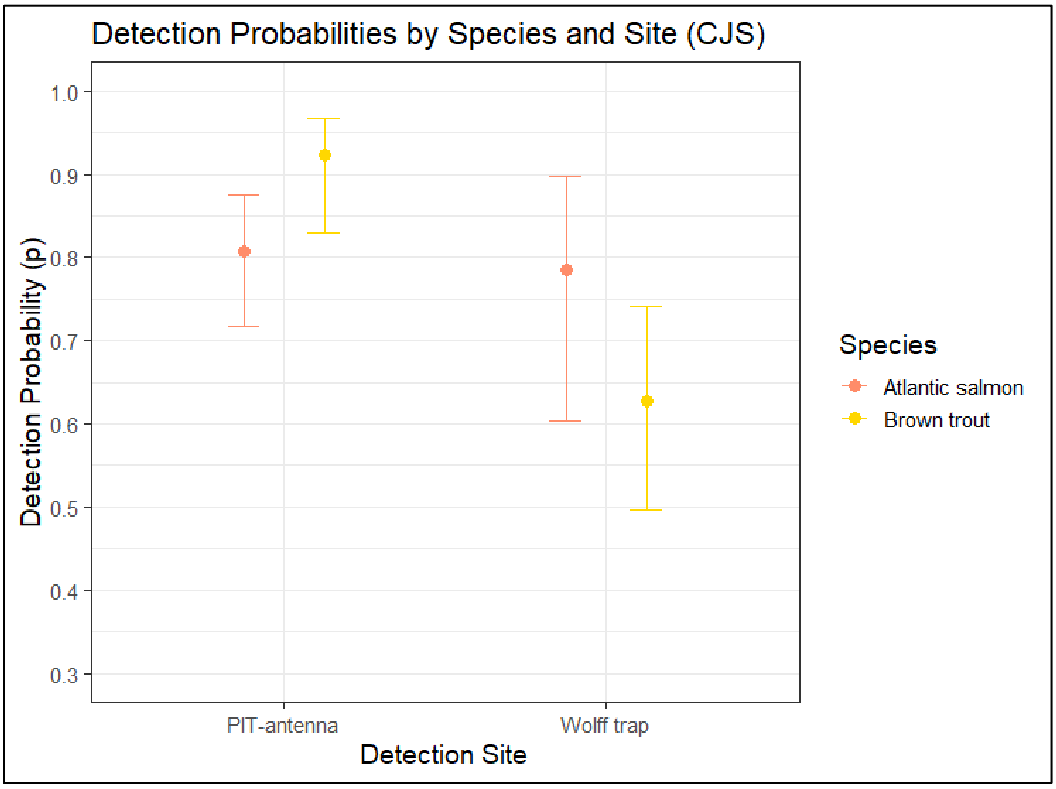

Figure 10. Estimated detection probabilities for PIT-antenna and Wolff trap as retrieve from det most supported CJS-model (Table 2). The detection probability for Strømmen antenna and screw trap was not estimated as separate parameter as this last-in-sequence detection site cannot be separated from mortality process.

The estimated migration probability (Φ) for Atlantic salmon from the dam to the Wolff trap was 0.7655 with a standard error (SE) of 0.0372 and a 95% confidence interval (CI) ranging from 0.6851 to 0.8305. For brown trout, the corresponding estimate was 0.8202 (SE =

0.0349; 95% CI: 0.7414–0.8789). Period 3 for both species was assigned a fixed survival probability of 1.0 due to model constraints at the terminal interval. Full parameter estimates from the CJS model are provided in Table 2.

Detection probabilities also varied across species and detection locations. For Atlantic salmon, detection probabilities were estimated as 0.8084 at Site 1 (SE = 0.0401), 0.7852 at Site 2 (SE = 0.0751), and 0.0604 at Site 3 (SE = 0.0227). For brown trout, detection probabilities were estimated at 0.9228 (SE = 0.0327), 0.6276 (SE = 0.0639), and 0.1195 (SE = 0.0333), respectively. These values reflect variability in detection efficiency across different monitoring stations.

Table 2. Real-scale parameter estimates for the selected CJS-model (antenna and species). Site 1 is the PIT tagging; Site 2 is the PIT antenna at the smolt hatch and Site 3 is the Wolff trap.

Parameter	**Description**	**Estimate**	**Standard Error**	**Lower 95% CI**	**Upper 95% CI**
Phi(1)	Survival probability, Salmon, Site 1	0.7655	0.0372	0.6851	0.8305
Phi(2)	Survival probability, Salmon, Site 2	0.7655	0.0372	0.6851	0.8305
Phi(3)*	Survival probability, Salmon, Site 3	1.0000	0.0000	1.0000	1.0000
Phi(4)	Survival probability, Trout, Site 1	0.8202	0.0349	0.7414	0.8789
Phi(5)	Survival probability, Trout, Site 2	0.8202	0.0349	0.7414	0.8789
Phi(6)*	Survival probability, Trout, Site 3	1.0000	0.0000	1.0000	1.0000
p(7)	Detection probability, Site 1, Salmon	0.8084	0.0401	0.7176	0.8751
p(8)	Detection probability, Site 2, Salmon	0.7852	0.0751	0.6044	0.8974
p(9)	Detection probability, Site 3, Salmon	0.0604	0.0227	0.0285	0.1233
p(10)	Detection probability, Site 1, Trout	0.9228	0.0327	0.8294	0.9671
p(11)	Detection probability, Site 2, Trout	0.6276	0.0639	0.4966	0.7423
p(12)	Detection probability, Site 3, Trout	0.1195	0.0333	0.0680	0.2017

* These phi parameters represent the last survival interval for the two species and were fixed to 1 so that p9 and p12 can be estimated as the product of phi and p directly as they cannot be separated over the last interval by the CJS-parametrization

7.4 H_{02}/H_{a2}: Species-Specific Migration Timing and Survival

Species-specific variation in downstream migration timing and probability was examined using time-to-event analysis. Migration latency was calculated as the number of hours from individual release to the last detection at the bypass. The dataset comprised 124 Atlantic salmon and 114 brown trout smolts. For each species, Kaplan–Meier survival curves were fitted using the survfit() function from the survival package, and the log-rank test (survdiff) was used to test for differences in survival functions.

Kaplan–Meier curves showed a distinct difference in migration trajectories between the two species. Atlantic salmon exhibit a significantly faster migration response than brown trout under the study conditions (Figure 11, Figure 12). The median migration time for Atlantic salmon was below 75 hours, with approximately 75% of individuals detected at the Wolff trap by 50–75 hours post-release. In contrast, brown trout displayed a broader range in time to passage, with the 75% threshold not reached until approximately 200 hours after release. Confidence intervals surrounding the Kaplan–Meier curves were narrower for Atlantic salmon, indicating less inter-individual variability in migration timing.

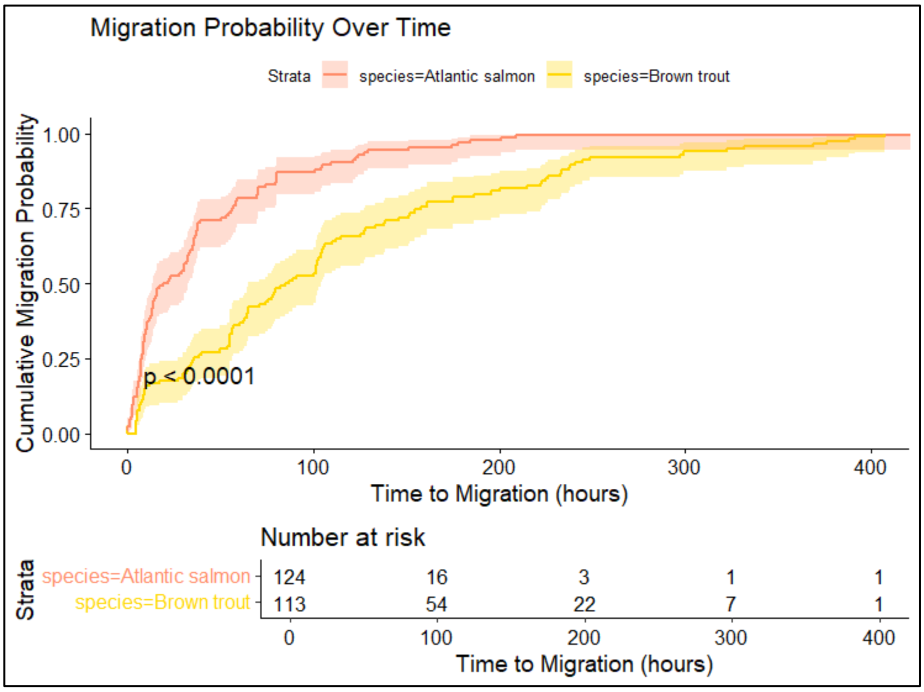

Figure 11. Kaplan-Meier curves showing Atlantic salmon (n=124) migrated significantly faster than Brown trout (n=113) over 400 hours (p<0.0001). Salmon reached 75% migration within 70 hours compared to 175 hours for trout, with most salmon migration occurring within the first 100 hours. Both species approached complete migration by study end. Numbers at risk show remaining non-migrated fish at each timepoint, with shaded areas representing 95% confidence intervals.

The number of Atlantic salmon remaining in the river at 100 hours was reduced to 16, whereas 54 brown trout had not yet been detected by this time (Figure 11). By 200 hours, only 22 brown trout remained unmigrated, while nearly all salmon had passed.

The log-rank test indicated a highly significant difference in migration timing between species ($\chi^2 = 29.84$, df = 1, $p < 0.0001$), supporting model-based evidence of species-specific temporal migration patterns.

The hazard ratio for brown trout was 0.44 ($\beta = -0.81$, SE = 0.17, $p < 0.001$), indicating reduced passage likelihood at any given time point relative to Atlantic salmon.

Additional covariates included total length (mm) and wet weight (g) at tagging. Length had a positive and statistically significant effect ($\beta = 0.018$, SE = 0.009, $p = 0.044$), suggesting that longer fish tended to pass earlier. Conversely, weight exhibited a small but significant negative effect on passage timing ($\beta = -0.028$, SE = 0.014, $p = 0.047$), implying slower progression in heavier individuals. Condition factor (CF) was not retained in the final model due to multicollinearity with length and weight.

Two competing Cox Proportional Hazard models were evaluated via AICc to test the relative contribution of release date and size covariates. The model including species and release day (**Model_SpeciesPlusReleaseDay**) had the lowest AICc (2061.57) and highest AICc weight (0.45), while **Model_SpeciesByReleaseDayInteraction** had nearly equivalent support (ΔAICc = 0.27, AICc weight = 0.40). A full list of model comparisons is presented in Table 3.

Figure 12 illustrates the predicted cumulative forebay exit probabilities for Atlantic salmon and Brown trout smolts following release on two different dates (Day 121 and Day 136). The survival-style curves depict the proportion of fish remaining in the forebay over time, providing insight into species-specific passage rates and how these are modulated by timing within the migration season.

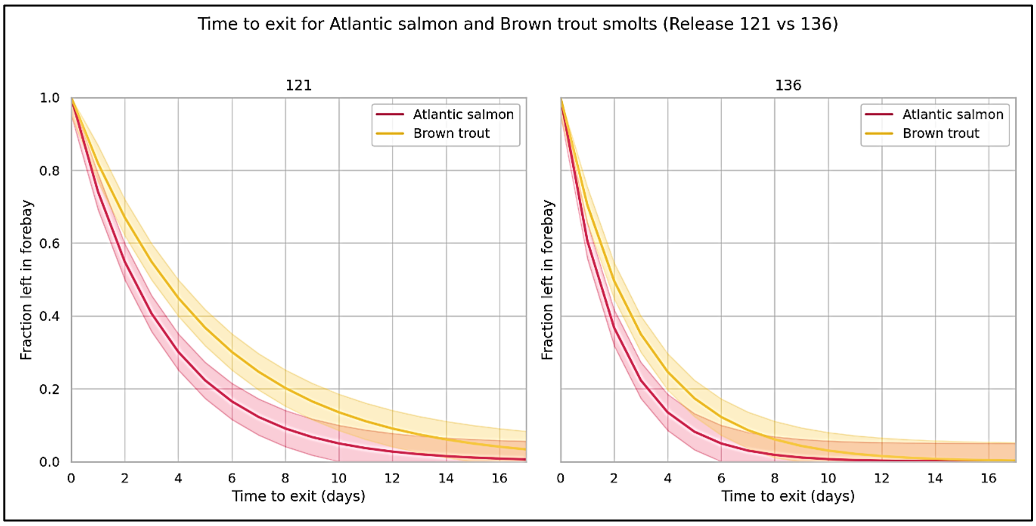

Figure 12. Fraction of individuals remaining in the forebay over time (days) for Atlantic salmon (red) and brown trout (yellow) smolts following two separate release events (Release Day of Year 121 and 136). Solid lines represent the estimated fraction remaining, with shaded areas indicating 95% confidence intervals. Atlantic salmon consistently exited the forebay more rapidly than brown trout in both release groups, indicating species-specific differences in migration timing and readiness. Estimates were derived from the selected Cox proportional hazards model

For the early release group (DOY 121), Atlantic salmon demonstrated a markedly faster exit pattern than brown trout. Model predictions indicate that over 75% of salmon exited within the first 4 days, with near-complete passage achieved by day 8. In contrast, brown trout showed a slower and more variable response, with less than 50% exited by day 4 and a long tail of delayed migrants persisting up to 14 days post-release. These results reflect a pronounced interspecific difference in migratory urgency and forebay residence behaviour early in the migration season.

By the later release (DOY 136), both species exhibited more rapid and synchronous passage. The model predicted that over 90% of salmon and approximately 80% of trout exited the forebay within 5–6 days. While species differences in exit timing persisted, they were attenuated compared to the earlier release, suggesting that trout’s migratory readiness improves as the season progresses.

Overall, the predictive model reveals that Atlantic salmon consistently exhibit faster and more synchronized passage, likely driven by internal smoltification cues and obligate anadromy. Brown trout demonstrate greater behavioural plasticity and delayed migration, particularly early in the season. These findings support the hypotheses of species-specific survival responses (H_{a2}), environmental modulation of behaviour (H_{a5}), and the influence of individual condition or size on migration timing (H_{a6}) and underscore the importance of release timing in influencing downstream migration efficiency.

Table 3. Time-to-Event Model Selection (Cox Proportional Hazards). These models test predictors of time until first detection at the bypass (entranceTime2). The best model includes species and day-of-year of release.

Model	**Formula**	**K**	**AICc**	**ΔAICc**	**AICc Weight**	**LogLik**	**Explanation**
Model_SpeciesPlusReleaseDay	species + slippDoY	2	2061.57	0.00	0.45	-1028.76	Best-fitting model; additive effects of species and release day
Model_SpeciesByReleaseDayInteraction	species * slippDoY	3	2061.84	0.27	0.40	-1027.87	Interaction model, similar fit
Model_SpeciesPlusEarlyLateRelease	species + slippTidligSeint	2	2063.89	2.32	0.14	-1029.92	Uses a categorical variable instead of continuous day-of-year
Model_SpeciesPlusTimeToRelease	species + time2release	2	2070.91	9.34	0.00	-1033.43	Uses days since release
Model_SpeciesByTimeToRelease	species * time2release	3	2071.01	9.44	0.00	-1032.46	Interaction model; poor performance
Model_SpeciesOnly	species	1	2096.94	35.37	0.00	-1047.46	Weakest model; species only

7.5 H_{03}/H_{a3}: Species-Specific Hesitation Time at Passage Structures

Hesitation time, defined as the time interval between first detection at the forebay antenna and the last detection at the bypass, was calculated for each tagged individual. The resulting distribution was highly skewed with a concentration of short delays and a right-tailed spread of longer hesitation events. Mean hesitation time across all individuals was 660.3 minutes (SD = 2666). Atlantic salmon had a mean hesitation time of 215.4 minutes (SD = 294.3), while brown trout had a mean of 508.7 minutes (SD = 830.6). The distribution of hesitation time was positively skewed in both species, with brown trout displaying more frequent long delays (Figure 13). A Mann–Whitney U test on log-transformed hesitation values yielded W = 6248, p = 0.1126, indicating no statistically significant difference between species when hesitation is summarised without accounting for environmental or temporal covariates.

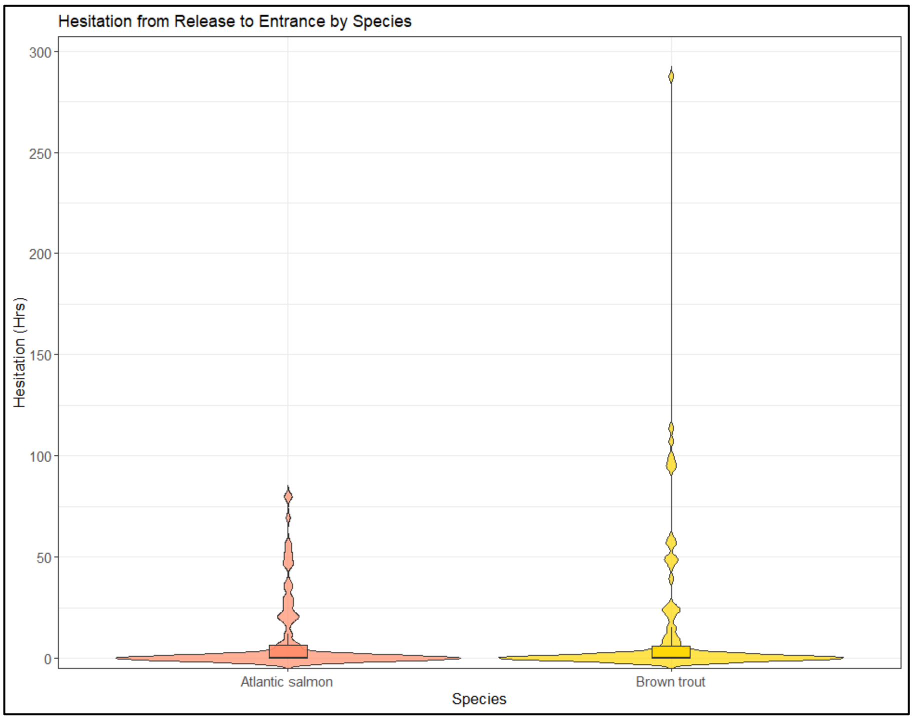

Figure 13. Violin plots showing the distribution of hesitation time (hours) from release to entrance for Atlantic salmon (orange) and brown trout (yellow). Atlantic salmon exhibit shorter and less variable hesitation times, while brown trout show a broader distribution with several individuals displaying prolonged hesitation periods. This suggests species-specific differences in migration readiness or behavioural responses following release.

To evaluate the ecological drivers of hesitation time and immediate passage behaviour, eight zero-inflated negative binomial (ZINB) models were fitted and compared using Akaike's Information Criterion corrected for small sample size (AICc). The response variable in all models was **residenseTime_int,** defined as hesitation time (in minutes) from first PIT detection to successful passage. The models included a count component (modelled with NB2 distribution) representing non-zero hesitation durations, and a zero-inflation component (modelled with a Bernoulli process) representing the probability of immediate migration (i.e., hesitation time = 0).

Model selection identified **zip_glmmTMB8** as the best-supported model (AICc = 1009.51, weight = 0.38), with a ΔAICc of more than 1 compared to all competing models. This model included an interaction between species and light intensity (Lux) in the count component and water flow (m^3/s) as a predictor in the zero-inflation component. In practical terms, the model predicts that:

- The duration of hesitation time (for fish that delay before passing) is jointly influenced by species identity and light intensity. Specifically, the effect of light on hesitation differs significantly between species, with Brown trout exhibiting stronger light-dependent hesitation responses than Atlantic salmon.
- The probability of immediate passage (zero hesitation) increases with increasing water flow, regardless of species. This suggests that stronger hydraulic cues facilitate immediate migration decisions and reduce forebay residence.

The complete model comparison results are presented in Table 4.

Table 4. Model Selection for ZIP Models (glmmTMB. This model selection table compares zero-inflated negative binomial models explaining hesitation time (residenceTime_int). The count part (Poisson/NB2) models actual hesitation time for individuals that hesitate, and the zero-inflation part (Bernoulli) models the probability of immediate migration (i.e., hesitation time = 0).

Model	Count model (NB2)	Zero-inflation model (Bernoulli)	K	AICc	ΔAICc	AICc Weight	LogLik	Explanation
zip_glmmTMB8	species * Lux	Waterflow	7	1009.51	0.00	0.38	-497.51	Tests interaction between species and light in count model, and effect of flow on zero-inflation
zip_glmmTMB1	species	species + Waterflow	6	1010.72	1.21	0.21	-499.18	Simpler model testing species effect only; zero-inflation depends on both species and flow
zip_glmmTMB5	species * Lux	species + Waterflow	8	1011.43	1.92	0.15	-497.40	Interaction in count model; additive effects on zero-inflation
zip_glmmTMB4	species + Lux	species + Waterflow	7	1011.86	2.36	0.12	-498.69	Additive model for species and light; no interaction
zip_glmmTMB3	species + length	species + Waterflow	7	1012.61	3.10	0.08	-499.06	Tests effect of fish length on hesitation time and probability of immediate migration
zip_glmmTMB7	species * Lux	species * Waterflow	9	1013.58	4.08	0.05	-497.40	Fully interactive in both model components; more complex
zip_glmmTMB2	species + length	species + length	7	1016.62	7.11	0.01	-501.07	Only morphology used; weak explanatory power
zip_glmmTMB6	species * Lux	species * Lux	9	1018.58	9.07	0.00	-499.89	Fully interactive species × Lux model in both parts

The conditional (count) component of the top-ranked model revealed a statistically significant interaction between species and Lux ($\chi^2 = 6.10$, $p = 0.014$), indicating that light intensity influenced hesitation time differently in the two species (Table 5). Brown trout showed a stronger increase in hesitation with rising Lux values than Atlantic salmon. The zero-inflation component included water flow as a predictor of immediate migration (i.e., zero hesitation), and flow was found to be a significant predictor ($\chi^2 = 4.67$, $p = 0.031$). Higher discharge levels increased the likelihood of immediate passage across both species.

Table 5. Results of logistic regression modelling hesitation time as a function of species and water flow. Coefficients (β), standard errors, z-values, and p-values are shown for the intercept (brown trout at average flow), species effect (Atlantic salmon), main effect of flow, and the species × flow interaction. Significant effects (p < 0.05) are indicated by an asterisk. The negative coefficient for species indicates that Atlantic salmon have significantly shorter hesitation times compared to brown trout at average flow, while the species × flow interaction suggests differing flow responses between species.

Parameter	Coefficient (β)	Standard Error	z-value	p-value
Intercept (Brown trout at average flow)	7.611	2.344	3.25*	0.00117
Species (Atlantic salmon)	-5.040	2.564	-1.97*	0.04935
Flow (main effect)	-1.120	0.638	-1.76*	0.07917
Species × Flow interaction	1.252	0.687	1.82*	0.06843

The selected model predicted brown trout to have a U-shaped relationship between water flow and hesitation time, with the shortest residence times occurring at intermediate discharges (4–5 m^3/s). At both low (<3 m^3/s) and high (>6 m^3/s) flows, hesitation increases sharply (Figure 14). Atlantic salmon, by contrast, exhibit a much flatter residence time profile, indicating a more consistent and flow-independent passage behaviour.

The model also predicted that the probability of immediate migration (i.e., zero hesitation time) increases steadily with rising discharge for both species (Figure 14). At higher flows (7–8 m^3/s), both Atlantic salmon and Brown trout show a predicted immediate passage probability exceeding 90%, indicating that elevated flows enhance route selection efficiency and passage decisiveness. Interestingly, Brown trout maintain a slightly higher probability of immediate passage across the flow range, despite exhibiting greater average hesitation overall. This suggests greater behavioural variability within the trout population — some individuals respond rapidly under favourable flow conditions, while others remain hesitant, possibly reflecting species-specific or individual differences in risk sensitivity or flow perception.

The corresponding zero-inflation plot (Figure 14) showed that the probability of zero hesitation time (i.e., immediate passage) increased steadily with water flow for both species, approaching 90–95% at high flows. Brown trout had a slightly higher predicted probability than salmon across all flows.

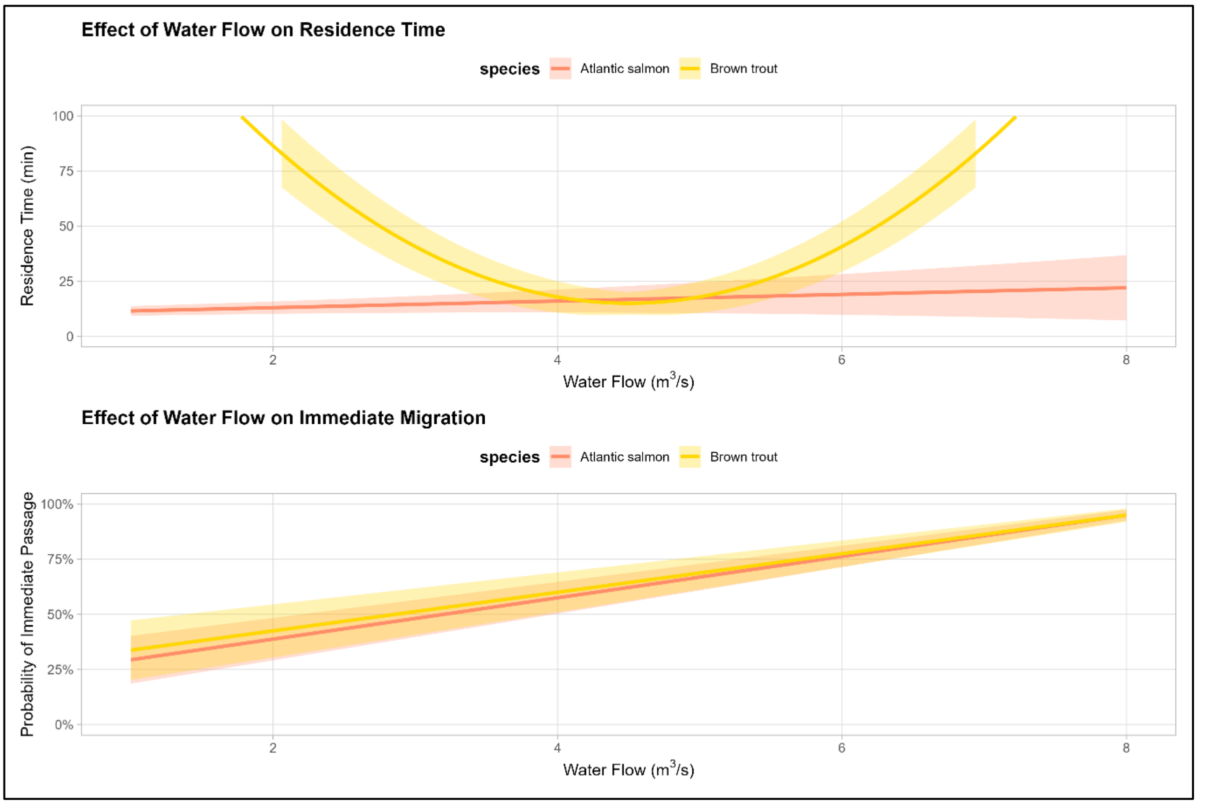

Figure 14. Effect of Water Flow on Immediate Migration. Top panel: Relationship between water flow (m³/s) and hesitation time (min) for Atlantic salmon (orange) and brown trout (yellow). Brown trout exhibit a U-shaped response, with minimum hesitation time at intermediate flows, whereas Atlantic salmon shows a slight increase in hesitation time with increasing flow. Bottom panel: Probability of immediate passage as a function of water flow for both species. The likelihood of immediate migration increases with higher water flow for both Atlantic salmon and brown trout. Shaded areas represent 95% confidence intervals.

Predicted environmental effects on immediate migration behaviour are illustrated in Figure 15, which displays species-specific zero-inflation predictions from the best-performing zero-inflated negative binomial model. The figure shows how the probability of immediate migration (i.e., zero hesitation time) varies in response to gradients in (A) water flow, (B) temperature, and (C) light intensity (Lux) for Atlantic salmon and Brown trout.

In panel A, the probability of immediate migration decreases sharply as water flow increases, particularly in brown trout. At flows below ~3.5 m^3/s, predicted probabilities are markedly higher and exceed 90% in both species, indicating strong flow-dependent responsiveness at lower discharges. However, Brown trout exhibit a much steeper decline in immediate migration probability with increasing flow than Atlantic salmon, whose probability remains relatively elevated over a broader range.

Panel B shows a consistent negative relationship between temperature and the likelihood of immediate passage. As water temperature increases from ~5 °C to 25 °C, both species exhibit declining probabilities of zero hesitation time. Atlantic salmon maintain higher predicted probabilities across the entire temperature range, suggesting greater thermal resilience or migratory drive under warming conditions.

In panel C, increasing light intensity is associated with a gradual rise in the probability of immediate migration. This effect is most pronounced in Atlantic salmon, which demonstrate a stronger positive association with light than Brown trout. At Lux levels exceeding 6000, the predicted probability of zero hesitation time is substantially higher in salmon, suggesting species-specific phototactic or behavioural sensitivity to visual environmental cues.

These findings collectively suggest that Atlantic salmon are more likely to initiate immediate passage under a broader range of environmental conditions, while Brown trout are more sensitive to both hydraulic and photic variation, delaying migration more often under suboptimal conditions.

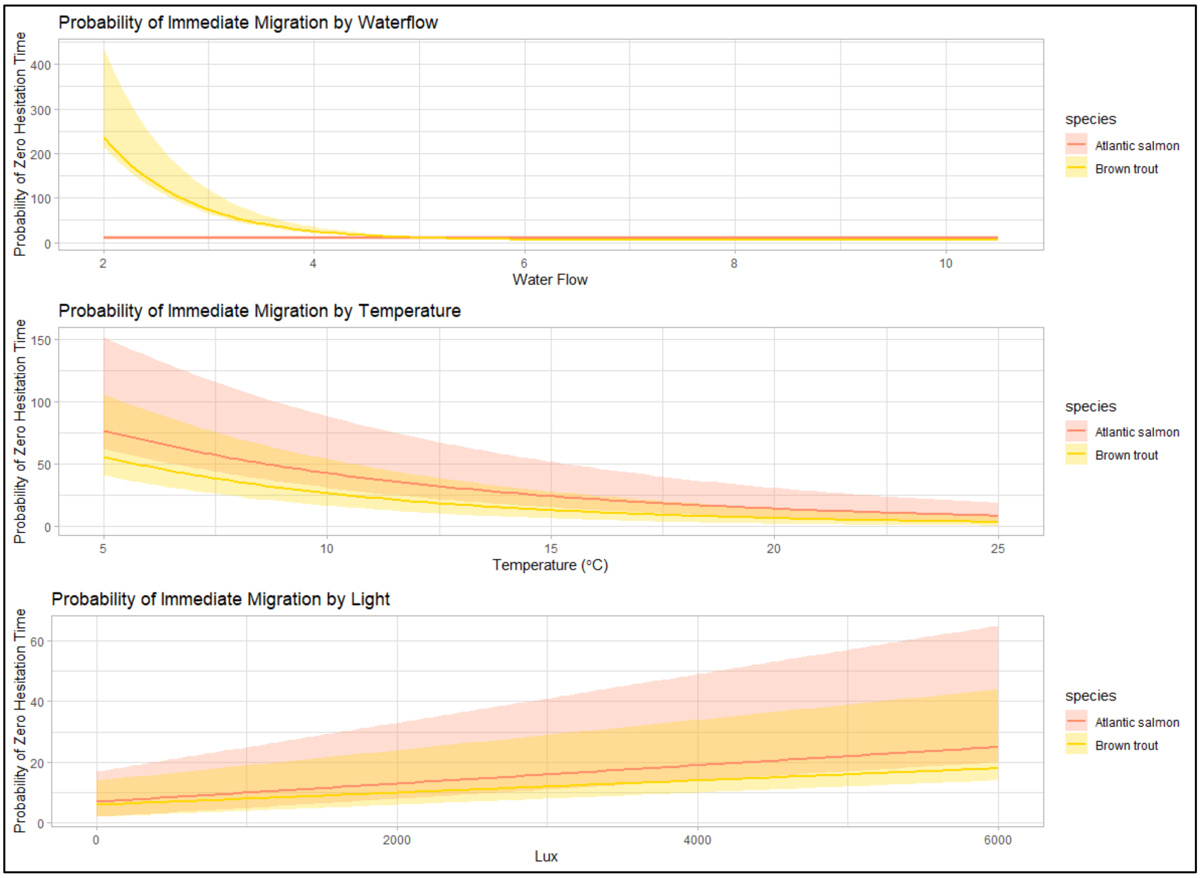

Figure 15. The figure shows the different factors influencing immediate migration. Predicted probability of immediate migration (zero hesitation time) for Atlantic salmon (orange) and brown trout (yellow) in response to (A) water flow, (B) temperature, and (C) light intensity (lux). Shaded areas indicate 95% confidence intervals.
(A) Probability of immediate migration declines sharply with increasing water flow, with brown trout showing a steeper decrease than Atlantic salmon.
(B) Higher temperatures are associated with reduced probability of immediate migration for both species, with Atlantic salmon consistently exhibiting higher probabilities across the temperature range.
(C) Increasing light intensity results in a gradual increase in immediate migration probability, particularly for Atlantic salmon.

7.6 H_{04}/H_{a4}: Diel Activity and Temporal Migration Patterns

Temporal patterns in downstream migration were assessed by analysing both seasonal trends and fine-scale diel activity. Time of passage was recorded for all successfully detected individuals, and these timestamps were matched to ambient light intensity (Lux) and day-of-year (DOY) to evaluate variation in migration timing across species and time.

Daily migration counts revealed clear interspecific differences in seasonal timing. Brown trout initiated migration earlier in the spring season than Atlantic salmon. Peak activity in brown trout occurred around DOY 132, while Atlantic salmon reached peak daily migration between DOY 138 and 140. This staggered timing was consistent across the full migration window from 23 April to 3 June 2024 and is shown in Figure 16, which plots cumulative passage curves for both species. Brown trout showed a more distributed migration pattern, with moderate activity across multiple days, whereas Atlantic salmon displayed a more synchronised, unimodal peak.

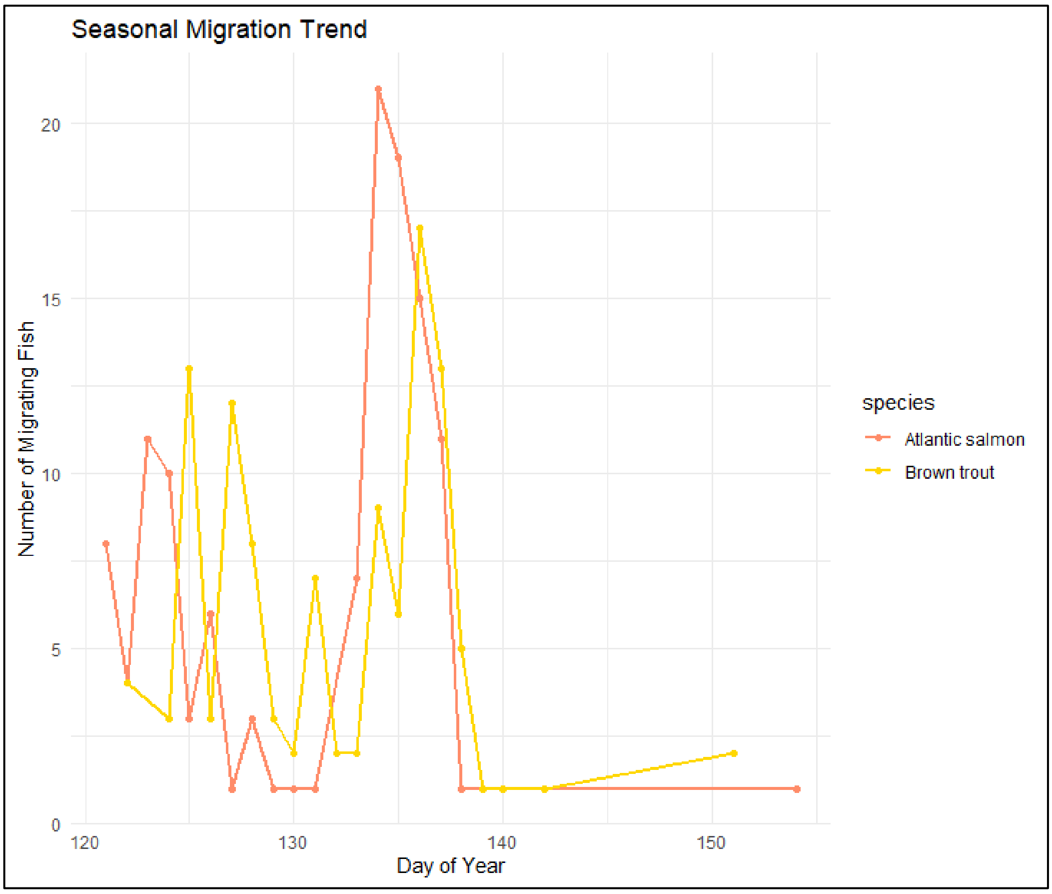

Figure 16. Number of migrating Atlantic salmon (orange) and brown trout (yellow) recorded per day across the migration season (day of year 120–155). Both species exhibit pronounced peaks in migration activity, with Atlantic salmon showing a sharper and slightly later peak compared to brown trout. Migration declines rapidly after peak activity for both species.

Hourly passage data were extracted from PIT detection records to quantify diel activity. These values were binned into hourly intervals and visualised using polar histograms and linear time series plots. A strong nocturnal preference was evident in both species, with differences in the timing and concentration of passage events. Atlantic salmon exhibited concentrated migration activity between 20:00 and 22:00, while brown trout showed a broader activity window extending from 22:00 to 01:00. The shift in diel peak was temporally consistent across the study period.

In addition to time of day, ambient light intensity (Lux) at the moment of passage was extracted for each event (Figure 17). Atlantic salmon showed a wider light envelope, with migration events occurring at Lux values ranging from early dusk (~500 Lux) to crepuscular and dim daylight levels, peaking around 1100 Lux. These Lux values reflect passage under relatively high ambient light, including the tail end of diurnal light conditions. In contrast, brown trout migrated almost exclusively under lower Lux conditions. Most passage events for trout occurred below 500 Lux, and the density of migration sharply declined as light intensity increased. Few brown trout were detected migrating above 600 Lux, suggesting a more restricted photic tolerance or stronger avoidance of higher light levels.

When binned by diel phase using astronomical definitions based on solar elevation, Atlantic salmon were most active during dusk and early night phases, with a reduced frequency of passage in full darkness and daylight. In contrast, the majority of brown trout migration occurred during the full night phase, with minimal activity during crepuscular transitions or daylight hours. These diel phase classifications were derived from solar angle data, categorising each hour of passage into day (sun > 0°), dusk/dawn (0 to -6°), and night (< -6°).

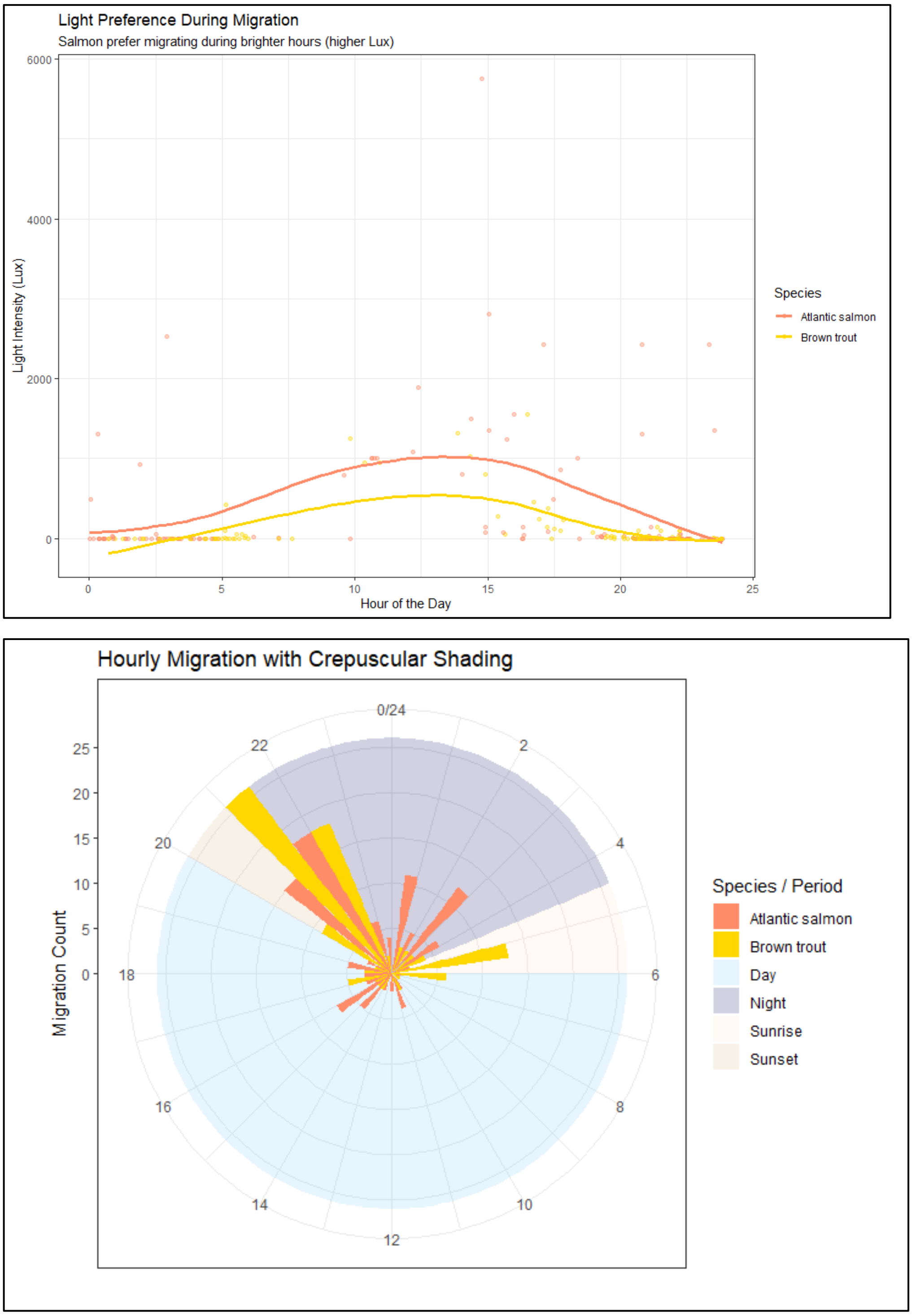

Figure 17. peak. ***(A) Light Preference During Migration:*** *Scatter plot and smoothed trend lines of light intensity (Lux) at the time of migration for Atlantic salmon (orange) and brown trout (yellow) across the day. Atlantic salmon tend to migrate during brighter hours with higher light intensities, while brown trout migrate under lower light conditions.*
(B) Hourly Migration with Crepuscular Shading:
Polar histogram showing hourly migration counts for Atlantic salmon (orange) and brown trout (yellow) across a 24-hour period. Background shading denotes day (light blue), night (dark blue), sunrise (peach), and sunset (tan). Both species exhibit peak migration during crepuscular periods (sunset and early night), with brown trout showing a pronounced sunset.

Generalized Additive Models (GAMs) were used to assess the effect of light intensity on migration timing. Hesitation time was modelled as a function of Lux, using species as a factor and including an interaction term. The model indicated a significant nonlinear effect of Lux (edf = 3.13, $p < 0.01$), with hesitation time increasing sharply for brown trout as Lux exceeded ~500. The interaction between species and Lux was significant ($\chi^2 = 6.10$, $p = 0.014$), confirming that hesitation behaviour was more strongly influenced by light intensity in brown trout than in salmon. Atlantic salmon showed relatively flat hesitation responses across the observed Lux range.

Hourly trends are summarised in Figure 17B, which shows hourly migration counts per species across the 24-hour cycle. Figure 17A presents Lux measurements over time, aligned with crepuscular periods shaded, allowing visual alignment of light sensitivity and passage windows across species.

These data collectively characterise a strong diel migration signal in both Atlantic salmon and brown trout, with temporal separation in nocturnal peaks, seasonal offset in migration onset, and clear interspecific differences in light-level thresholds for passage behaviour

The temporal migration pattern also showed strong day-of-year (DOY) structuring (Figure 16). Atlantic salmon began migrating earlier in the spring, with cumulative migration curves steeply increasing between DOY 122 and 138. Brown trout showed a slower cumulative increase in passage, with peak activity occurring between DOY 132 and 142. This pattern was further explored by plotting daily migration counts per species against water temperature and day of year, which revealed that temporal migration peaks aligned with temperature windows but were modulated by light.

Across the diel cycle, Atlantic salmon migrated during a broader light envelope and were less restricted to full darkness. Brown trout delayed migration to later hours and lower Lux windows, exhibiting more pronounced light-avoidant timing. These temporal dynamics were stable across the monitoring period and were consistently reproduced in hourly density plots across different environmental strata.

7.7 H_{05}/H_{a5}: Environmental Modulation of Migration Behaviour

Environmental variables were recorded continuously during the study period and matched to individual migration events to assess their influence on both hesitation time and timing of downstream passage. Key variables analysed included water temperature (°C), river discharge (m^3/s), and ambient light intensity (Lux). These were used both as continuous predictors in generalized additive models (GAMs) and as independent variables in correlation analyses.

Daily variation in river temperature ranged from 6.3°C to 17.2°C, with an overall mean of approximately 11.4°C during the main migration window. Discharge fluctuated from 2.2 to 8.9 m^3/s, with a median flow of 4.7 m^3/s. Lux values at the time of passage ranged from below 100 to over 1400 Lux, capturing a complete gradient from full darkness to full daylight.

The distribution of hesitation times revealed that most individuals of both Atlantic salmon and brown trout exhibited short hesitation times, but brown trout had a broader range and more frequent longer hesitation periods (top panel) (Figure 18). Predicted hesitation time decreased with increasing temperature for both species, with brown trout consistently showing longer hesitation times than Atlantic salmon across the temperature gradient (middle panel). In contrast, predicted hesitation time increased with higher light intensity, with the increase being more pronounced for brown trout than for Atlantic salmon (bottom panel). These results indicate that both temperature and light significantly influence hesitation behaviour, and that brown trout generally hesitate longer before migration than Atlantic salmon.

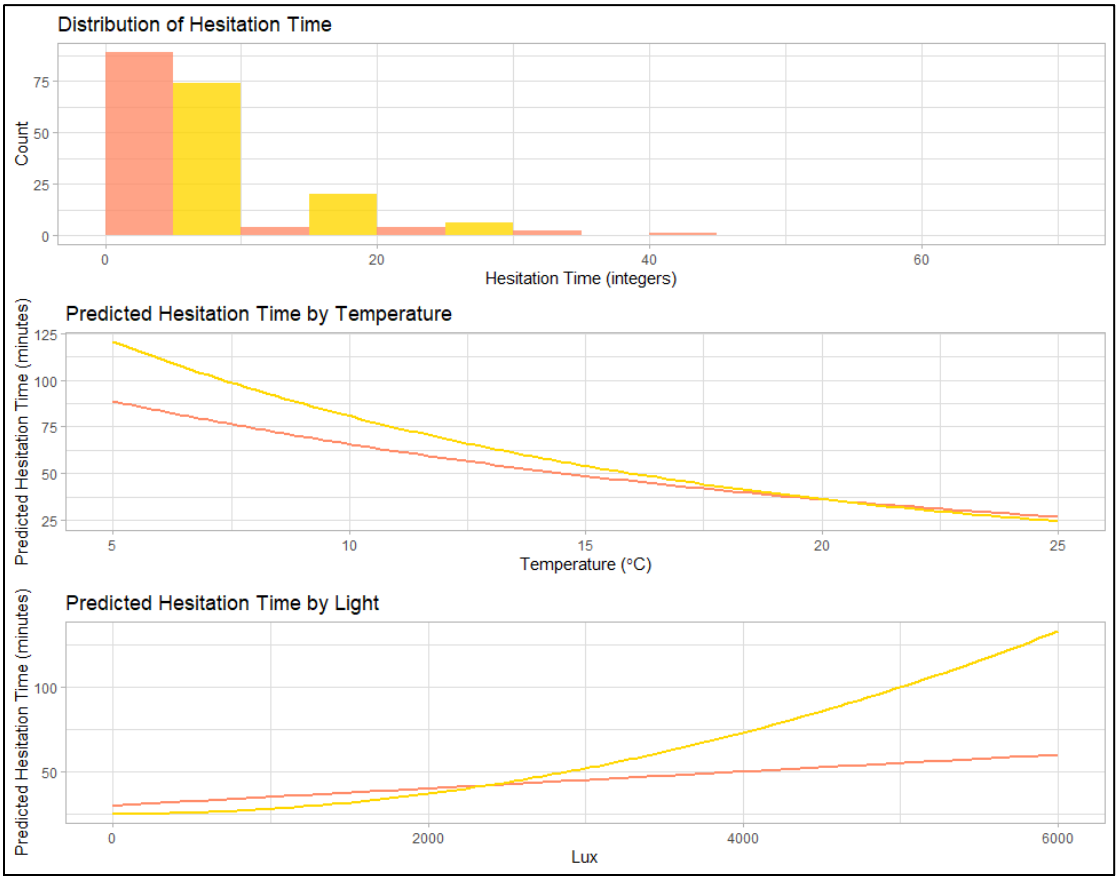

Figure 18. ***Hesitation Time Distributions and Environmental Predictors for Atlantic Salmon and Brown Trout****. Top: Histogram of observed hesitation times (minutes) for Atlantic salmon (orange) and brown trout (yellow), showing that most individuals of both species exhibit short hesitation times, with brown trout displaying a broader range. Middle: Predicted hesitation time as a function of temperature (°C) for Atlantic salmon (orange) and brown trout (yellow). Hesitation time decreases with increasing temperature for both species, with brown trout consistently exhibiting longer predicted hesitation times than Atlantic salmon across the temperature range. Bottom: Predicted hesitation time as a function of light intensity (Lux) for both species. Hesitation time increases with higher light intensity, with brown trout showing a steeper increase compared to Atlantic salmon.*

Pearson correlation analysis revealed a strong positive association between water temperature and migration activity, measured as daily counts of successful passages. The correlation coefficient was $r = 0.83$ ($p < 0.001$), indicating that migration increased markedly with rising temperature. Passage activity increased sharply as water temperature crossed the 10°C threshold and plateaued at approximately 14°C. Above 15°C, passage events declined and remained low.

Discharge showed a significant negative correlation with migration intensity ($r = -0.57$, $p < 0.01$), suggesting that high-flow conditions were associated with lower rates of successful passage. These patterns were consistent across both species but more pronounced in brown trout, which exhibited greater passage suppression at discharge values above 6.5 m^3/s.

Hesitation time was modelled using GAMs, with water flow, temperature, and Lux entered as smooth terms. The model explained 20.9% of the deviance in hesitation behaviour across all individuals. Among environmental predictors, water flow had the highest effective degrees of freedom (edf = 6.5, p < 0.01), indicating a complex, nonlinear relationship. Hesitation time was lowest at flows between 4.0 and 5.2 m^3/s. Below this range, hesitation increased steeply, particularly in brown trout. At high discharges above 6.5 m^3/s, hesitation time also increased, suggesting a U-shaped relationship. This pattern was visualised in the GAM response curve (see Figure 11,Figure 12).

Water temperature was also a significant predictor of hesitation (edf = 2.7, p = 0.01). Hesitation time decreased as temperature increased, reaching its minimum between 12 and 14°C. Above 15°C, hesitation time began to increase again slightly, but the effect was not statistically significant. Lux exhibited a nonlinear but weaker effect on hesitation time, and its impact was more pronounced in the model including species as an interaction term (see H_{04}/H_{a4}).

Zero-inflation predictions from the ZIP model also indicated environmental effects on the probability of immediate migration (i.e., zero hesitation time). Water flow significantly increased the probability of immediate passage (χ^2 = 4.67, p = 0.031), especially when flow rates were between 4 and 6 m^3/s. This effect was consistent across both species, although brown trout displayed a slightly higher probability of immediate migration under increasing discharge compared to Atlantic salmon.

Model-based predictions of the relationship between environmental variables and hesitation are presented in Figure 18 & Figure 15. Figure 18 shows the predicted hesitation time as a function of water flow, illustrating the central minimum and the increase at high and low extremes. Figure 18also shows predicted hesitation time across the observed temperature range, highlighting the steep decline in delay duration as water warmed through the early spring period. Figure 18 presents predicted hesitation time by Lux, confirming species-specific differences in light sensitivity and the modulation of delay behaviour across the diel light gradient.

Collectively, these results confirm that water temperature, discharge, and ambient light intensity significantly affect both the probability of immediate migration, and the hesitation time observed prior to bypass entry. Temporal alignment of high passage rates and low hesitation duration occurred within a narrow environmental envelope characterised by moderate flow (4–5 m^3/s), intermediate light levels (300–800 Lux), and water temperatures between 10–13°C.

7.8 H_{06}/H_{a6}: Size-Specific Migration Success and Timing

To evaluate the influence of individual size on downstream migration behaviour, morphometric parameters including total length (mm), weight (g), and condition factor (CF) were included as covariates in survival models, ZIP models, and generalized additive models (GAMs). Size-class summaries and species-level differences were also compiled to assess trends in hesitation time and passage duration.

To assess the influence of individual morphology and release timing on downstream passage timing, a series of Cox proportional hazards models were fitted with time to first detection at the bypass (entranceTime2) as the response variable. The hazard function in these models reflects the instantaneous probability of passage, conditional on survival (i.e., non-passage) up to a given time.

The final selected model demonstrated that both fish length and weight significantly influenced migration timing. Fish with greater total length were more likely to pass earlier ($\beta = 0.018$, SE = 0.009, $p = 0.044$), whereas heavier individuals showed a delay in passage ($\beta = -0.028$, SE = 0.014, $p = 0.047$). These opposing effects likely reflect trade-offs between hydrodynamic efficiency and energetic burden: while increased body length enhances swimming capacity and flow detection, excessive weight relative to size may increase drag or reduce rheotactic responsiveness. Condition factor (CF) was excluded from the final model due to collinearity with length and weight.

Model selection was conducted using Akaike's Information Criterion corrected for small sample size (AICc). The two top-performing models — **Model_SpeciesPlusReleaseDay** and **Model_SpeciesByReleaseDayInteraction** — included additive and interactive effects of species identity and release day-of-year (slippDoY), respectively. These models explained 85% of the total model weight and demonstrated near-identical log-likelihood values, suggesting that both species identity and the calendar timing of release are critical predictors of passage timing (as seen in Figure 12). The AICc results are summarised in Table 6.

This model structure confirms that temporal variation in migratory readiness and bypass use is jointly modulated by species-level traits and environmental exposure history, supporting H_{a2} (species-specific survival timing), H_{a5} (environmental modulation), and H_{a6} (size-dependent effects). Length was retained in both models (Table 6).

Table 6. Time-to-Event Model Selection (Cox Proportional Hazards). These models test predictors of time until first detection at the bypass (entranceTime2). The best model includes species and day-of-year of release.

Model	**Formula**	**K**	**AICc**	**ΔAICc**	**AICc Weight**	**LogLik**	**Explanation**
Model_SpeciesPlusReleaseDay	species + slippDoY	2	2061.57	0.00	0.45	-1028.76	Best-fitting model; additive effects of species and release day
Model_SpeciesByReleaseDayInteraction	species * slippDoY	3	2061.84	0.27	0.40	-1027.87	Interaction model, similar fit
Model_SpeciesPlusEarlyLateRelease	species + slippTidligSeint	2	2063.89	2.32	0.14	-1029.92	Uses a categorical variable instead of continuous day-of-year
Model_SpeciesPlusTimeToRelease	species + time2release	2	2070.91	9.34	0.00	-1033.43	Uses days since release
Model_SpeciesByTimeToRelease	species * time2release	3	2071.01	9.44	0.00	-1032.46	Interaction model; poor performance
Model_SpeciesOnly	species	1	2096.94	35.37	0.00	-1047.46	Weakest model; species only

Generalized additive models were used to assess nonlinear effects of length and weight on hesitation time. Length showed a weak but consistent decline in hesitation time with increasing size (edf = 1.82, p = 0.065), whereas weight showed a U-shaped response, with shortest hesitation observed at intermediate weight classes (edf = 3.01, p = 0.048). CF did not explain additional variation and was not retained in the final GAMs.

In addition to model-based analyses, descriptive summaries were calculated at the species and size-class levels. Species-level statistics are shown in Table 7. Atlantic salmon (N = 124), which were smaller on average (mean length = 150.0 mm, mean weight = 29.2 g), had shorter hesitation times (mean = 41.5 min) and shorter passage durations (mean = 8.51 min). Brown trout (N = 114), which were larger (mean length = 172.0 mm, mean weight = 44.2 g), showed longer hesitation times (mean = 112.0 min) and longer passage durations (mean = 13.7 min). Detection and passage rates were 100% for both species.

Table 7. Species-Level Summary Statistics.

Species	N	Mean Length (mm)	Mean Weight (g)	Detection Rate	Passage Rate	Mean Hesitation (min)	Mean Passage Time (min)
Atlantic salmon	124	150.0	29.2	1.0	1.0	41.5	8.51
Brown trout	114	172.0	44.2	1.0	1.0	112.0	13.7

To further assess the role of size, individuals were categorised into four discrete size classes based on length percentiles: Small (lowest 25%), Medium (middle 50%), Large (top 20%), and Very Large (top 5%) (Table 8). Mean hesitation time and passage duration increased across size classes. Small fish (N = 84) had the shortest hesitation time (mean = 56.1 min) and shortest passage time (8.19 min). Medium-sized fish (N = 141) showed longer hesitation (mean = 84.9 min), while large (N = 11) and very large (N = 2) fish exhibited the most variable hesitation durations, with the very large class showing a mean hesitation of 133.0 min. Interestingly, these two very large individuals had a short mean passage time (2.74 min), suggesting rapid passage once the decision to migrate was made.

Table 8. Size class summaries.

Size Class	**N**	**Detection Rate**	**Passage Rate**	**Mean Hesitation (min)**	**Mean Passage Time (min)**
Small	84	1.0	1.0	56.1	8.19
Medium	141	1.0	1.0	84.9	12.2
Large	11	1.0	1.0	84.0	19.3
Very Large	2	1.0	1.0	133.0	2.74

Together, the Cox model coefficients, GAMs, and size-class summaries confirm consistent trends: smaller and leaner individuals passed earlier and with shorter delay, while larger or heavier individuals showed longer hesitation times in the forebay. These results establish a robust empirical basis for testing size effects on migration success and hesitation time.

8 Discussion

8.1 H_{01}/H_{a1}: Passage Success Following Intake Rack Modification

The results of the Cormack-Jolly-Seber modelling revealed high downstream passage probabilities for both Atlantic salmon and brown trout, with values ranging from 0.77 to 0.82. Given the minimal spatial separation between the bypass exit and the Wolff trap, and the absence of observed mortality in this segment, these values can be interpreted directly as bypass-to-trap migration success. The findings support the alternative hypothesis (H_{a1}) that the redesigned intake rack improved downstream passage efficiency for salmonid smolts.

Across the full dataset, over 70% of tagged individuals exhibited more than one discrete migration attempt, defined operationally as a series of forebay detections interspersed with periods of movement cessation or fallback, followed by re-engagement with the bypass structure. While Atlantic salmon displayed a slightly higher number of median attempts than brown trout, the interspecific difference was not statistically significant in the generalized linear model (GLM); however, the incidence rate ratio (IRR = 1.12) suggests a modest ecological effect. This apparent discrepancy between statistical and ecological significance is not unusual in behavioural ecology, where individual variation and environmental noise often obscure subtle but biologically meaningful trends (Nash et al., 2021; Schielzeth and Forstmeier, 2009; Skaala, 2017).

The prevalence of multiple attempts across both species implies that structural passage is not a singular, binary event but rather a process characterized by iterative behavioural decision-making and feedback. This repeated approach–withdraw–re-approach pattern is likely shaped by a combination of intrinsic motivational states (e.g., migratory drive, readiness to transition to saltwater) and extrinsic environmental cues (e.g., hydrodynamics, light intensity, perceived predation risk). The high frequency of repeated attempts suggests that either the forebay presents a behavioural challenge that fish must learn to overcome, or that specific hydrological or structural features intermittently impede successful passage

The high success rates observed in both species suggest that the physical modification — reducing trash rack bar spacing from 50 mm to 15 mm — did not create a significant hydraulic barrier or behavioural deterrent. On the contrary, the structural change appears to have enabled effective guidance toward the bypass while likely reducing entrainment risk. This aligns with findings from previous experimental and field studies that have shown finer trash rack spacing to reduce turbine entrainment and increase bypass efficiency (Calles et al., 2011; Calles and Greenberg, 2009; Fjeldstad et al., 2018; Pracheil et al., 2016; Thorstad et al., 2007). The similarity in Φ estimates across species suggests that both salmon and trout were able to navigate the redesigned structure with minimal delay.

Nevertheless, differences in detection probability between species and antennas indicate that behavioural or morphological factors may still influence bypass route selection and progression. The notably higher detection probability for Atlantic salmon at the Wolff trap, coupled with lower detection at the dam antenna, may reflect more rapid downstream movement or straighter bypass trajectories, potentially influenced by species-specific rheotactic responses. In contrast, brown trout showed higher detection at the upstream antenna and lower detection at the trap, possibly due to extended forebay hesitation or slower passage speed — a hypothesis that is explored further under H_{03}.

These findings corroborate the results of Enders et al. (2012) and Zydlewski et al. (2006), who reported species-specific responses to bypass flow fields, even when structural passage conditions were standardised. It is also notable that the migration success rates observed here were higher than those reported in comparable Norwegian hydropower facilities without bypass optimisation (Haraldstad et al., 2022, 2021, 2019), underscoring the effectiveness of structural improvements at Fosstveit.

In terms of operational outcomes, the findings imply that trash rack optimisation at Fosstveit has achieved its intended ecological function — facilitating safe and effective downstream migration during the critical spring smolt period. However, the moderate difference in Φ between species suggests that further behavioural or hydraulic refinements could yield additional improvements, particularly in detection consistency and bypass alignment.

8.2 H_{02}/H_{a2}: Species-Specific Migration Timing and Survival

Time-to-event analysis and Cox proportional hazards modelling demonstrated that Atlantic salmon migrated significantly faster than brown trout. Kaplan–Meier survival curves revealed that 75% of Atlantic salmon had passed the monitoring station within 50–75 hours post-release, whereas brown trout required approximately 200 hours to reach the same migration probability. The Cox model confirmed species as a strong predictor of passage rate, with a hazard ratio of 2.35 ($p < 0.001$), indicating that at any given time, Atlantic salmon were more than twice as likely to complete passage compared to brown trout.

These findings are consistent with previous studies documenting interspecific differences in downstream migration pace and responsiveness to environmental cues. Multiple studies reported that Atlantic salmon tend to initiate and complete downstream migration in a more synchronised and rapid manner, possibly reflecting differences in migratory motivation, flow responsiveness, or rheotactic threshold (Aldvén et al., 2015; Bjerck et al., 2021; Enders et al., 2012; Fjeldstad et al., 2012; Haraldstad et al., 2017; Marschall et al., 2011; McCormick et al., 1998; Whalen et al., 1999). Brown trout have been observed to delay migration or exhibit a more exploratory movement pattern in forebay environments, particularly when hydraulic signals are ambiguous or poorly structured.

In an ecological context, delayed or prolonged passage exposes fish to elevated risk of predation, physiological stress, and energetic depletion (Marschall et al., 2011; Nyqvist et al., 2016; Thorstad et al., 2012). Therefore, the observed species-specific variation in timing has direct relevance for cumulative survival and post-passage marine entry success. From a management perspective, the more consistent and rapid movement observed in Atlantic salmon suggests that they may be better served by standard bypass configurations, while brown trout may require more targeted design features — such as enhanced flow cues or multiple bypass entrances — to facilitate timely passage.

It is worth noting that while species was a dominant factor in determining passage rate, individual size metrics also contributed to timing differences, with longer fish passing earlier and heavier individuals showing a tendency toward delayed movement. This highlights the importance of considering the interaction between morphological traits and species identity when interpreting survival probabilities in telemetry-based migration studies.

These results support the alternative hypothesis (H_{a2}), indicating that Atlantic salmon exhibit a significantly higher passage rate and shorter migration duration than brown trout, likely reflecting inherent behavioural or physiological differences in their response to bypass infrastructure.

8.3 H_{03}/H_{a3}: Species-Specific Hesitation Time at Passage Structures

Analyses of hesitation time revealed notable differences between Atlantic salmon and brown trout in their response to the bypass entrance. Although the mean hesitation time was 215.4 minutes for Atlantic salmon and 508.7 minutes for brown trout, the raw difference was not statistically significant in a Mann–Whitney U test. However, zero-inflated negative binomial modelling identified a significant interaction between species and light intensity (Lux) in the conditional component ($\chi^2 = 6.10$, $p = 0.014$), with brown trout showing a markedly stronger increase in hesitation time under high Lux conditions. The probability of immediate migration (zero hesitation) also increased with water flow ($\chi^2 = 4.67$, $p = 0.031$), across both species.

These findings are supported by earlier research showing that Atlantic salmon typically exhibit stronger rheotactic responses and are more likely to follow surface-oriented bypass flows under varying light conditions (Fjeldstad et al., 2018; Haraldstad et al., 2019; Johnsson and Näslund, 2018; Martin et al., 2012; Simmons et al., 2022). Brown trout, in contrast, have often been described as more hesitant or exploratory in forebay environments, particularly under bright light, potentially due to their more cryptic, light-averse behaviour (Coutant and Whitney, 2000; Enders et al., 2012; Haraldstad et al., 2021; Johnsson and Näslund, 2018; Kärgenberg et al., 2020; Lucas et al., 2001b; Martin et al., 2012). The modelling results are consistent with these behavioural trends, suggesting that photic conditions play a disproportionately strong role in trout migration decision-making at the intake structure.

The behavioural sensitivity to light and flow observed in brown trout has important implications for bypass design. Structures that offer variable hydraulic entry cues across diel and environmental conditions — such as bypasses with combined surface and bottom intakes, or those incorporating lateral guidance ways — may increase passage consistency across species. The fact that salmon displayed less variation in hesitation time across the light gradient suggests that standard bypass configurations may suffice for this species under a broader range of conditions.

One limitation of the current analysis is that hesitation time is modelled as a single interval between first detection at the forebay and entry into the bypass. This simplifies potentially more complex behavioural sequences such as repeated approach and withdrawal or interaction with turbine inflow zones. Future work using higher-resolution spatial telemetry (e.g. fine-scale acoustic tracking) could allow for the deconstruction of hesitation into discrete behavioural states.

The data support the alternative hypothesis (H_{a3}), demonstrating that brown trout display significantly longer hesitation times than Atlantic salmon, and that hesitation is strongly modulated by environmental light intensity. This result underscores the need to account for species-specific behavioural thresholds when evaluating bypass effectiveness.

8.4 H_{04}/H_{a4}: Diel Activity and Temporal Migration Patterns

Diel analysis of migration events revealed clear differences between species in both the timing and light conditions associated with passage. Atlantic salmon most frequently migrated between 20:00 and 22:00, while brown trout peaked later, between 22:00 and 01:00. These hourly differences were accompanied by marked differences in ambient light intensity (Lux) at the time of passage. Atlantic salmon migrated under a broad range of light conditions, with a peak near 1100 Lux, corresponding to late evening or crepuscular light. In contrast, brown trout migration events occurred predominantly under low light conditions, with most passages below 500 Lux.

The Generalised Additive Model results confirmed a significant nonlinear effect of light intensity on hesitation time ($edf = 3.13$, $p < 0.01$), and the interaction between species and Lux revealed that hesitation increased much more steeply for brown trout as Lux rose above 500. These findings indicate strong diel sensitivity in migration behaviour, particularly in brown trout, and support the conclusion that light is an important modulator of passage decisions. When passage events were binned by diel phase using solar elevation (day, dusk, night, dawn), 72.1% of brown trout passages occurred during full night, compared to 68.5% of Atlantic salmon during dusk and early night.

The observed diel migration rhythms are consistent with numerous previous studies of salmonid smolt behaviour. Haraldstad et al. (2022) and Fjeldstad et al. (2018) both report that Atlantic salmon smolts often initiate movement under moderate light conditions during dusk or dawn, likely balancing predation risk and flow-seeking behaviour. Brown trout, by contrast, often display more nocturnal migration tendencies and exhibit stronger avoidance of light (Andrew et al., 2024; Haraldstad et al., 2017; Thorstad et al., 2012). Such behaviour is commonly interpreted as an evolved anti-predator adaptation, enabling smolts to reduce detection by visually oriented predators, including piscivorous birds (e.g., *Phalacrocorax carbo*) and fish (e.g., *Esox lucius*), during their energetically demanding migration from natal rivers to the marine environment (Kristensen et al., 2010; Marschall et al., 2011; E. Thorstad et al., 2003).

The results from Fosstveit align closely with this species-specific pattern, indicating that diel period and photic conditions are key determinants of passage timing.

The ecological and management implications of these findings are substantial. Because brown trout are more likely to delay passage under elevated light levels, they may be at greater risk of cumulative stress, increased energetic costs, or predation if bypass designs or operational windows are not aligned with nocturnal behavioural patterns. The potential for unintended temporal bottlenecks, where trout accumulate upstream of intake structures during bright periods, should be considered in bypass design and flow management (Renardy et al., 2021; Sortland et al., 2024). Operational strategies such as increased bypass attraction flows during dusk and night hours, or physical shading of entrance structures, may improve passage consistency in light-sensitive species.

One limitation in the present study is that Lux was used as a proxy for ambient light without accounting for turbidity, cloud cover, or shading from riparian vegetation — all of which may alter perceived light levels at the fish's perspective. Integrating fine-scale light loggers at bypass entrances, combined with 3D behavioural tracking, could offer more precise estimates of the effective photic environment and its impact on fish decision-making.

In conclusion, the results support the alternative hypothesis (H_{a4}): crepuscular and nocturnal migration patterns are clearly evident, and brown trout exhibit significantly stronger avoidance of high light conditions than Atlantic salmon. These diel and temporal behaviours should be accounted for in bypass design, monitoring schedules, and management protocols aimed at maximising migration efficiency across multiple salmonid species.

8.5 H_{05}/H_{a5}: Environmental Modulation of Migration Behaviour

The results of both correlation analyses and Generalized Additive Models (GAMs) demonstrate that environmental variables—particularly water temperature and discharge—strongly modulate downstream migration behaviour. A positive correlation was found between water temperature and daily passage rates ($r = 0.83$, $p < 0.001$), with migration increasing sharply when temperatures exceeded 10°C and plateauing above 14–15°C. Conversely, water discharge was negatively correlated with migration rates ($r = -0.57$, $p < 0.01$), suggesting that high-flow conditions may reduce the likelihood or delay the timing of passage.

Hesitation time was also significantly affected by environmental conditions. GAM results indicated that hesitation time was lowest at intermediate flows (4–5 m^3/s) and increased both at lower and higher flow extremes ($edf = 6.5$, $p < 0.01$). This U-shaped response suggests the existence of an optimal hydraulic window for passage. Temperature had a similarly significant effect on hesitation, with shorter delays observed between 11°C and 13°C and increased hesitation outside this range ($edf = 2.7$, $p = 0.01$). These findings confirm that both hydrological and thermal cues shape the readiness of smolts to initiate and complete downstream movement.

The environmental thresholds identified in this study align with established previous research. Bonga, (1997) and Madaro et al., (2015) describe physiological and metabolic constraints that shape optimal migratory temperature windows for salmonids. Similarly, Marschall et al. (2011) observed that flows above species- or size-specific thresholds can suppress downstream movement, either due to energetic costs or behavioural avoidance of turbulent or unpredictable flow fields. The pattern observed at Fosstveit, where high and low flows both delay passage, closely mirrors the bell-shaped relationship predicted by theoretical migration models and empirical studies (Adeva-Bustos et al., 2019; Enders et al., 2012; Fjeldstad et al., 2018; Zuur et al., 2009).

From a management perspective, these findings underscore the importance of aligning bypass attraction flows with the environmental windows that maximise passage efficiency. Operational control of flow regimes during smolt migration periods could be adjusted to maintain discharges within the observed optimal range, thereby reducing hesitation and increasing passage rates. Similarly, early detection of temperature thresholds may serve as a cue for initiating bypass guidance system operation.

A limitation of the current analysis is the reliance on mean daily values for flow and temperature, which may obscure the influence of short-term variability, such as pulsed flows or diurnal warming. Incorporating sub-daily resolution in environmental monitoring, as well as continuous data from instream sensors, would enhance the precision of future habitat–behaviour relationships.

The results support the alternative hypothesis (H_{a5}): environmental variables, especially water flow and temperature, significantly influence both the probability and timing of downstream passage. The behavioural responses to these cues highlight the need for environmentally adaptive bypass operations and confirm that optimal passage performance is achieved within a specific range of hydrological and thermal conditions.

8.6 H_{06}/H_{a6}: Size-Specific Migration Success and Timing

Cox proportional hazards modelling and descriptive analyses showed that fish size significantly influenced downstream migration timing and behaviour. Longer individuals passed earlier ($\beta = 0.018$, $p = 0.044$), while heavier individuals showed delayed passage ($\beta = -0.028$, $p = 0.047$). These contrasting effects of length and weight were also reflected in generalized additive models (GAMs), which showed nonlinear size responses in hesitation time. Hesitation was shortest among fish in the small and medium size classes and increased in both the smallest and largest individuals. Species-level summaries also revealed that Atlantic salmon, which were generally smaller and lighter than brown trout, exhibited faster passage and shorter hesitation.

These findings are consistent with previous research on size-dependent migration behaviour in salmonids. Larger fish often experience greater energetic cost when swimming against complex or turbulent flows and may delay movement in search of optimal hydraulic conditions (Fjeldstad et al., 2022; Sandvik et al., 2020). At the same time, longer fish are often more rheotactic and better able to detect and respond to flow cues, resulting in earlier initiation of downstream movement (Breck, 2014; Haraldstad et al., 2022; Ibbotson et al., 2011). The negative association with weight may reflect mass-specific drag or behavioural caution due to increased vulnerability in high flow or during passage decision-making.

The ecological and management implications of size-specific behaviour are important for bypass design and flow regulation. Smaller fish may respond quickly to surface-oriented bypass cues but could be more sensitive to turbulence or insufficient hydraulic attraction if bypass intakes are set too deep or lack directional flow. Conversely, larger or heavier fish may benefit from broader, high-volume attraction zones or combined bypass systems that accommodate delayed or exploratory movement. These differences suggest that bypasses should be designed with multiple entrance routes or adjustable attraction flows to accommodate diverse fish sizes within smolt runs.

A limitation in the current analysis is that morphometric data were limited to three static measures (length, weight, condition factor) collected at tagging. Incorporating dynamic measures of energetic condition, swimming capacity, or morphological type (e.g. fusiform vs. robust) would allow a more mechanistic understanding of how size influences passage decisions. Furthermore, detailed trajectory tracking could clarify whether delayed passage in large individuals results from indecision, suboptimal flow field structure, or physical fatigue.

The findings support the alternative hypothesis (H_{a6}): fish size significantly influences downstream migration success and timing. The interaction between body length, weight, and passage dynamics should be considered in the design and evaluation of fish-friendly hydropower infrastructure, especially in systems hosting multiple salmonid species with diverse body forms and life-history strategies.

9 Sources of Error and Methodological Limitations

Despite the strength of the findings, this study is subject to several potential sources of error, which must be acknowledged to contextualize the conclusions and guide future research.

PIT Tag Detection Efficiency

While PIT technology offers high-resolution data on fish movement, it is not immune to detection bias. Detection efficiency was approximately 90%, in line with values reported by Zydlewski et al., (2006), but this still leaves a nontrivial proportion of potential non-detections. These may be due to tag orientation, passage speed, distance from antennas, or technical failures. Although redundancy was built into the monitoring system, any inference about total passage success must be interpreted with this uncertainty in mind.

Trap-Related Mortality and Handling Effects

The potential for trap-induced stress or mortality cannot be fully ruled out. Even with strict handling protocols, smolts are susceptible to stress-related physiological disruption, which may alter behaviour or increase delayed mortality after release (Haraldstad et al., 2023). Mortality in holding containers or due to tagging could have biased the behavioural metrics if individuals failed to initiate migration or died before reaching detection points. However, mortality during holding was low, and no carcasses were found, suggesting that this source of bias was minimal in this study.

Environmental Variability and External Events

Uncontrolled environmental variability, including fluctuations in temperature, discharge, and turbidity, likely influenced migration behaviour and detection probability. Notably, the powerplant experienced an unplanned shutdown during the study period due to an oil leak. This altered the river’s flow regime and may have temporarily affected fish behaviour or detection rates. While such events are difficult to avoid, they highlight the need for long-term, multi-year monitoring to assess structural effectiveness across a full range of environmental conditions.

Statistical Assumptions and Data Structure

Statistical models such as GAMs and PCA rely on certain assumptions regarding data distribution, independence, and variable scaling. Although diagnostic checks were performed and transformations applied as necessary, residual error and model limitations must be considered when interpreting results. Future studies should explore machine learning or Bayesian hierarchical approaches to further improve predictive accuracy and integrate multiscale variability.

Measurement Errors and Human Error

All field-based ecological research is vulnerable to human error in species identification, length/weight measurement, and data recording. While training and standardized protocols were applied throughout this study, some degree of error is inevitable. These are unlikely to have systematically biased the results but may contribute to variance in hesitation time estimates or behavioural classifications.

10 Conclusion

This study represents a detailed and multidisciplinary investigation into the biological and hydrodynamic interplay between structural modifications in hydropower systems and the migratory behaviour of two anadromous salmonid species — Atlantic salmon and brown trout. By integrating empirical field data with established ecological connectivity theory (Crooks and Sanjayan, 2006), behavioural ecology (Jonsson and Jonsson, 2011; Thorstad et al., 2012)), and environmental response modelling (Marschall et al., 2011; Simmons et al., 2022), this research advances our understanding of species-specific migration dynamics in regulated river systems. The findings provide robust evidence that physical passage structures, when carefully designed, can both protect vulnerable life stages and maintain or restore ecological functions within anthropogenically altered aquatic landscapes.

10.1 H_{01}/H_{a1}: Structural modification improves downstream passage success

The redesigned intake rack led to substantial improvements in downstream migration performance. Apparent survival (interpreted as migration success) between the intake and trap was estimated at 0.77 for Atlantic salmon and 0.82 for brown trout, based on Cormack-Jolly-Seber (CJS) mark-recapture modelling. These values far exceed the fish guidance efficiency (FGE) reported in earlier configurations at Fosstveit (35–47% for Atlantic salmon; 22–33% for brown trout; (Haraldstad et al., 2022, 2019, 2017)), indicating a successful reduction in turbine entrainment and improved route guidance.

Importantly, given the negligible mortality expected between the bypass exit and detection point at the Wolff trap, these apparent survival probabilities are functionally equivalent to structural passage success. These findings support the alternative hypothesis (H_{a1}) and align with prior literature showing that fine-spaced racks and surface-oriented bypasses significantly reduce delay, injury, and mortality during smolt descent (Calles and Greenberg, 2009; Fjeldstad et al., 2018; Silva et al., 2018; Thorstad et al., 2007)

From an operational standpoint, the system performed effectively under variable hydrological conditions, guiding a high proportion of migrants into the designated passage route. This demonstrates that physical exclusion can function reliably in combination with low-head bypasses when rack spacing and hydraulic design are biologically informed.

10.2 H_{02}/H_{a2}: Species identity affects passage timing and inferred survival

Species identity was a dominant predictor of downstream passage timing. Atlantic salmon consistently migrated more rapidly and synchronously than brown trout. Time-to-event analysis and Cox regression showed that 75% of salmon passed within 50–75 hours of release, while brown trout took upwards of 200 hours to reach equivalent migration probability. The hazard ratio indicated that salmon were over twice as likely to pass at any given time point, strongly supporting the alternative hypothesis (H_{a2}).

These differences are consistent with established literature describing species-specific migratory syndromes. Atlantic salmon are obligate anadromous migrants with migration timing tightly entrained by internal hormonal and photoperiodic cues (Ibbotson et al., 2011; Jonsson and Jonsson, 2011, 2009; McCormick et al., 1998; Whalen et al., 1999). Brown trout, in contrast, include both partial and facultative migrants, and may exhibit greater behavioural plasticity and delayed commitment to passage (Valiente et al., 2010). The observed temporal divergence thus likely reflects both physiological readiness and differing migratory drive.

These findings underscore the importance of species-specific design in fish passage systems. Even when structural exclusion from turbines is effective, the guidance conditions may differentially suit species with distinct movement ecologies. The implication is that monitoring passage performance must go beyond binary success metrics and include time-dependent evaluations to capture delayed or deferred passage that may still result in survival but with altered energetic and physiological costs.

10.3 H_{03}/H_{a3}: Hesitation time differs between species and is environmentally modulated

Despite the structural success in guiding smolts to the bypass, interspecific differences in pre-passage behaviour were substantial. Brown trout smolts exhibited significantly longer hesitation times at the forebay entrance compared to Atlantic salmon. The mean delay was more than twice as long in trout (508.7 min vs. 215.4 min), and zero-inflated negative binomial modelling confirmed a statistically significant interaction between species and light intensity ($\chi^2 = 6.10$, $p = 0.014$).

These findings support the alternative hypothesis (H_{a3}) and demonstrate that while physical infrastructure provides the opportunity for safe passage, behavioural thresholds — such as risk aversion, photophobia, and sensitivity to flow — determine whether and when that opportunity is taken. Brown trout, being more light-averse and prone to exploratory behaviour (Haraldstad et al., 2021; Johnsson and Näslund, 2018; Moore et al., 1998; Sortland et al., 2024; Valiente et al., 2010), showed stronger avoidance of illuminated forebay conditions.

The management implication is that high passage success does not equate to behavioural efficiency. Prolonged forebay hesitation increases energetic expenditure and exposure to predation, particularly under daylight conditions. For brown trout, hesitation behaviour may constitute a hidden cost that undermines the apparent success of bypass use. Mitigation efforts should thus integrate structural exclusion with behavioural facilitation — such as targeted attraction flow, shading, or diel-synchronised flow regimes — to accommodate species-specific preferences.

10.4 H_{04}/H_{a4}: Migration timing exhibits diel periodicity

Diel analysis showed a clear crepuscular and nocturnal pattern in passage timing for both species, though with distinct peaks. Atlantic salmon predominantly passed between 20:00 and 22:00, while brown trout passed later at night (22:00–01:00). Over 90% of all passage events occurred under low light (<500 Lux), and the majority occurred below 2 Lux. These findings strongly support the alternative hypothesis (H_{a4}), and mirror established anti-predator strategies in juvenile salmonids (Kristensen et al., 2010; Marschall et al., 2011; Nash et al., 2021).

The stronger phototactic suppression observed in trout reflects their higher perceived predation risk or sensitivity to surface lighting, further reinforcing the need for low-light passage opportunities. The high predictability of timing by Lux supports its use as a management trigger for diel-tuned flow releases or bypass activation. Future design should explicitly consider how forebay light levels interact with species-specific passage propensities, especially under varying weather, turbidity, or shading conditions.

10.5 H_{05}/H_{a5}: Environmental drivers modulate passage timing and hesitation

Environmental conditions — particularly water temperature and discharge — had significant, nonlinear effects on both migration timing and hesitation behaviour. GAMs showed that hesitation time decreased at intermediate flow rates (4–5 m^3/s) and moderate temperatures (11–14°C), while both high and low extremes increased delay. Passage probability declined at high flows, especially among heavier fish, confirming that environmental thresholds constrain migratory performance. These results support H_{a5}.

The bell-shaped relationships identified here are consistent with broader literature on salmonid performance windows (Aldvén et al., 2015; Haraldstad et al., 2017; Harvey et al., 2020; Lans, 2012; Nevoux et al., 2019; Wedemeyer et al., 1980; Whalen et al., 1999). Flow velocity affects not only the energetic cost of swimming, but also the ability to detect and follow flow cues into a bypass. Too low, and the cue is imperceptible; too high, and the approach becomes physically or behaviourally aversive. Similarly, temperature modulates muscular and osmoregulatory performance, influencing passage readiness.

These findings underscore that passage infrastructure must function within a biologically suitable environmental envelope. Moreover, with increasing hydroclimatic variability and rising spring temperatures, the need for adaptive flow management and real-time environmental monitoring becomes critical to ensure consistent bypass engagement.

10.6 H_{06}/H_{a6}: Individual size affects migratory behaviour and performance

Size metrics (length, weight, and condition factor) significantly influenced passage behaviour. Longer fish migrated earlier ($\beta = 0.018$, $p = 0.044$), while heavier individuals exhibited increased hesitation ($\beta = -0.028$, $p = 0.047$). Stratified size-class analysis confirmed that small and medium individuals displayed more efficient passage, while very large trout often delayed under high flow or light conditions. These results support H_{a6}.

This finding is ecologically meaningful. While larger fish may have greater absolute swimming capacity, they may also be more sensitive to hydrodynamic variability or more cautious in novel environments (Haraldstad et al., 2022, 2021; Ibbotson et al., 2011). Species identity further modulated these effects, with brown trout showing more pronounced size-related variation.

Importantly, these results suggest that fish passage systems may unintentionally favour certain size classes or behavioural phenotypes. Over time, such selective filtering could affect population structure or promote traits incompatible with successful downstream migration in regulated systems. To ensure functional connectivity for all phenotypes, bypass systems should be designed to accommodate both agile, small-bodied smolts and large, conservative individuals.

10.7 Hydroelectric Production and Profitability Implications

While the primary objective of the redesigned intake rack — with its narrowed bar spacing of 15 mm — was to enhance downstream fish passage and reduce turbine-induced mortality, it is equally important to assess the implications of this structural change on hydroelectric production and plant profitability. During the critical smolt migration window in May 2024, production data reveal several operational curtailments at the Fosstveit HEP plant, suggesting a shift toward adaptive management in response to ecological priorities.

Between May 9th and May 22nd, the hydropower plant experienced multiple production halts, clearly visible as red segments in the power output chart (Figure 19). On May 10th, for example, production dropped to zero for extended periods, and on May 18th –21st, the facility remained largely inactive. These shutdowns coincide with the peak of smolt migration, as evidenced by high fish counts in the Wolff trap (e.g., 509 salmon on May 3rd, 406 on May 8th, and 441 on May 12th), implying that turbine operations were paused to minimize entrainment risk during periods of intense downstream movement.

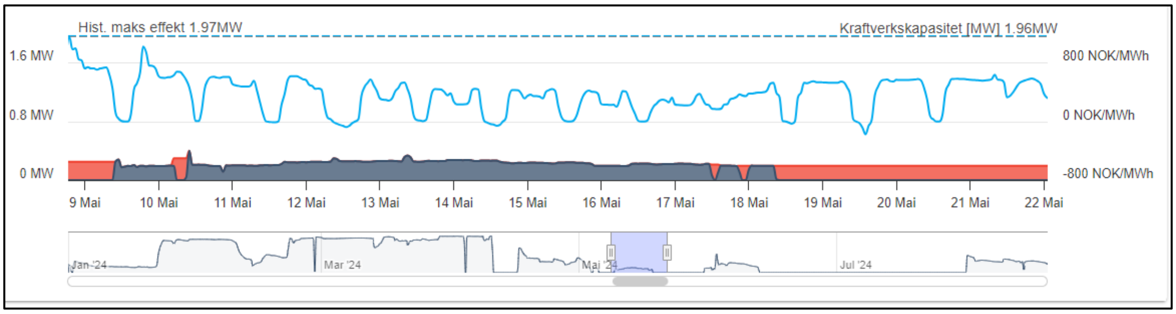

Figure 19. The figure shows the power production, as well as the historical production as blue lines. The red areas are halts in the production.

The plant’s installed capacity is 1.96 MW, and the historical peak output recorded was 1.97 MW. During the migration period, however, actual output fluctuated between 0.3–1.6 MW, rarely reaching full capacity. These values suggest a degree of operational conservatism likely tied to environmental considerations. Importantly, the electricity price during this period remained low, frequently approaching 0 NOK/MWh and even dropping into negative territory (below − 800 NOK/MWh at several points). This indicates that production losses during these days may have had limited financial impact, particularly when balanced against the ecological gains and regulatory compliance benefits of halting generation during peak fish movement.

However, it is important to note that no pre-redesign production data are available for this facility, which limits the ability to quantitatively assess whether the redesigned intake rack has had a net positive or negative impact on energy generation or maintenance frequency. Consequently, this study cannot conclusively determine whether the narrowed trash rack spacing introduces higher operational costs due to increased debris accumulation or flow resistance.

Nevertheless, the available post-redesign data suggest that fish-friendly infrastructure can be operationally feasible, especially when integrated with adaptive flow management strategies. The selective curtailment of production during low market price periods and high ecological risk windows may offer a pragmatic path forward, balancing conservation outcomes with financial viability.

10.8 Closing Remarks

This thesis demonstrates that structural modifications grounded in ecological understanding can significantly improve downstream passage for salmonid smolts at hydropower installations. The redesigned intake rack at Fosstveit HEP — with a reduced bar spacing of 15 mm — achieved high bypass success for both Atlantic salmon and brown trout, with no detections in the turbine tunnel. These findings confirm that physical exclusion measures can effectively eliminate entrainment risk when properly integrated into bypass design.

However, structural improvements alone are not sufficient. Species-specific behavioural responses, including hesitation time and diel preferences, were key determinants of passage success. Atlantic salmon migrated more rapidly and consistently, while brown trout exhibited delayed passage and higher sensitivity to environmental cues such as light intensity and water flow. These differences highlight the importance of designing passage systems that accommodate varied behavioural strategies.

Environmental factors such as discharge and temperature also played a critical role. Optimal passage occurred at moderate flows (4–5 m^3/s) and temperatures (11–14 °C), suggesting that operational strategies should be tuned to these conditions. Modelling results (GAMs, ZINB, Cox regression) reinforced that both morphology and environmental variation influence migration dynamics, and that larger fish may require stronger or clearer guidance cues to minimise delay.

Taken together, the findings point to the value of adaptive, behaviourally informed mitigation strategies. Real-time monitoring, dynamic gate operation, and species-specific design parameters can improve outcomes across a range of hydrological and ecological contexts. By combining structural exclusion with behavioural facilitation, fish passage systems can better support functional connectivity in regulated rivers.

This work contributes to a broader movement toward fish-friendly hydropower. It demonstrates that effective mitigation is possible when hydropower design is informed by behavioural ecology and underpinned by rigorous, hypothesis-driven analysis.

11 References

Abadie, A., 2002. Bootstrap Test for Distributional Treatment Effects in Instrumental Variable Models. J Am Stat Assoc 97, 284–292.

Ackerman, P.A., Morgan, J.D., Iwama, G.K., 2005. Anaesthetics.

Adeva-Bustos, A., Hedger, R.D., Fjeldstad, H.P., Stickler, M., Alfredsen, K., 2019. Identification of salmon population bottlenecks from low flows in a hydro-regulated river. Environmental Modelling & Software 120, 104494.

Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans Automat Contr 19, 716–723.

Aldvén, D., Degerman, E., Höjesjö, J., 2015. Environmental cues and downstream migration of anadromous brown trout (Salmo trutta) and Atlantic salmon (Salmo salar) smolts. Boreal Environment Research online.

Allignol, A., Latocuhe, A., 2025. CRAN Task View: Survival Analysis. Version 2025-02-09.

Amaral, S., Hecker, G., Jean, S., Dixon, D., 2011. The Effects of Leading Edge Blade Thickness, Strike Velocity, and Fish Orientation on the Survival of Fish Passing Through Turbines.

Andrew, S., Swart, S., McKenna, S., Morissette, J., Gillis, C.-A., Linnansaari, T., Currie, S., Morash, A.J., 2024. The impacts of diel thermal variability on growth, development and performance of wild Atlantic salmon (Salmo salar) from two thermally distinct rivers. Conserv Physiol 12, coae007.

Anthropic, 2024. Claude AI [WWW Document].

Antolos, M., Roby, D., Lyons, D., Collis, K., Evans, A., Hawbecker, M., Ryan, B., 2005. Caspian Tern Predation on Juvenile Salmonids in the Mid-Columbia River. Trans Am Fish Soc 134, 466–480.

Barlaup, B.T., Gabrielsen, S.-E., Løyland, J., Schläppy, M.-L., Wiers, T., Vollset, K.W., Pulg, U., 2013. Trap design for catching fish unharmed and the implications for estimates of sea lice (Lepeophtheirus salmonis) on anadromous brown trout (Salmo trutta). Fish Res 139, 43–46.

Bennett, R., Ellender, B., Mäkinen, T., Miya, T., Pattrick, P., Wasserman, R., Woodford, D., Weyl, O., 2016. Ethical considerations for field research on fishes. Koedoe 58.

Birnie-Gauvin, K., Bordeleau, X., Cooke, S.J., Davidsen, J.G., Eldøy, S.H., Eliason, E.J., Moore, A., Aarestrup, K., 2021. Life-history strategies in salmonids: the role of physiology and its consequences. Biological Reviews 96, 2304–2320.

Bjerck, H.B., Urke, H.A., Haugen, T.O., Alfredsen, J.A., Ulvund, J.B., Kristensen, T., 2021. Synchrony and multimodality in the timing of Atlantic salmon smolt migration in two Norwegian fjords. Sci Rep 11.

Bonga, W., 1997. The stress responses in fish, Physiological Reviews.

Breck, J., 2014. Body composition in fishes: Body size matters. Aquaculture 433, 40–49.

Brooks, M., Bolker, M., Kristensen, K., Maechler, M., Magnusson, A., Skaug, H., Berg, C., Nielsen, A., Bentham, K. V, 2024. Generalized Linear Mixed Models using Template Model Builder.

Brown, R.S., Colotelo, A.H., Pflugrath, B.D., Boys, C.A., Baumgartner, L.J., Deng, Z.D., Silva, L.G.M., Brauner, C.J., Mallen-Cooper, M., Phonekhampeng, O., Thorncraft, G., Singhanouvong, D., 2014. Understanding Barotrauma in Fish Passing Hydro Structures: A Global Strategy for Sustainable Development of Water Resources. Fisheries (Bethesda) 39, 108–122.

Burnham, K.P., Anderson, D.R., 1998. Practical Use of the Information-Theoretic Approach. In: Burnham, K.P., Anderson, D.R. (Eds.), Model Selection and Inference: A Practical Information-Theoretic Approach. Springer New York, New York, NY, pp. 75–117.

Cada, G.F., 1990. A Review of Studies Relating to the Effects of Propeller-Type Turbine Passage on Fish Early Life Stages. N Am J Fish Manag 10, 418–426.

Calles, O., Greenberg, L., 2009. Connectivity is a two-way street—the need for a holistic approach to fish passage problems in regulated rivers. River Res Appl 25, 1268–1286.

Calles, O., Karlsson, S., Hebrand, M., Comoglio, C., 2011. Evaluating technical improvements for downstream migrating diadromous fish at a hydroelectric plant. Ecol Eng 48.

Carter, K., Woodley, C., Brown, R., 2010. A review of tricaine methaneslfonate for anesthesia of fish. Rev Fish Biol Fish 21, 51–59.

Coutant, C.C., Whitney, R.R., 2000. Fish Behavior in Relation to Passage through Hydropower Turbines: A Review. Trans Am Fish Soc 129, 351–380.

Crooks, K.R., Sanjayan, M., 2006. Connectivity conservation: maintaining connections for nature. In: Crooks, K.R., Sanjayan, M. (Eds.), Connectivity Conservation, Conservation Biology. Cambridge University Press, Cambridge, pp. 1–20.

Deng, Z., Carlson, T., Ploskey, G., Richmond, M., Dauble, D., 2007. Evaluation of blade-strike models for estimating the biological performance of Kaplan turbines. Ecol Modell 208, 165–176.

Detar, J.E., Mattingly, H.T., 2004. Response of Southern Redbelly Dace to Clove Oil and MS-222: Effects of Anesthetic Concentration and Water Temperature.

Dynesius, M., Nilsson, C., 1994. Fragmentation and Flow Regulation of River Systems in the Northern Third of the World. Science (1979) 266, 753–762.

Enders, E.C., Gessel, M.H., Anderson, J.J., Williams, J.G., 2012. Effects of decelerating and accelerating flows on juvenile salmonid behavior. Trans Am Fish Soc 141, 357–364.

Everitt, B.S., Landau, S., Leese, M., Stahl, D., 2011. Cluster Analysis 5th Edition Cluster Analysis.

Field, A.P.., 2012. Discovering statistics using SPSS (and sex and drugs and rock “n” roll). SAGE.

Fjeldstad, H.-P., Alfredsen, K., Forseth, T., 2013. Atlantic salmon fishways: The Norwegian experiences. Vann 48, 191–204.

Fjeldstad, H.-P., Pulg, U., Forseth, T., 2018. Safe two-way migration for salmonids and eel past hydropower structures in Europe: A review and recommendations for best-practice solutions. Mar Freshw Res 69.

Fjeldstad, H.P., Uglem, I., Diserud, O.H., Fiske, P., Forseth, T., Kvingedal, E., Hvidsten, N.A., Økland, F., Järnegren, J., 2012. A concept for improving Atlantic salmon Salmo salar smolt migration past hydro power intakes. J Fish Biol 81, 642–663.

Graham, E., Fulghum, N., Altieri, K., 2025. Global Electricity Review 2025.

Haraldstad, T., Haugen, T., Olsen, E., Forseth, T., Höglund, E., 2021. Hydropower-induced selection of behavioural traits in Atlantic salmon (Salmo salar). Sci Rep 11, 16444.

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. R Soc Open Sci 6.

Haraldstad, T., Höglund, E., Kroglund, F., Olsen, E., Hawley, K., Haugen, T., 2022. Anthropogenic and natural size-related selection act in concert during brown trout (Salmo trutta) smolt river descent. Hydrobiologia 849.

Haraldstad, T., Johansen, K., Vollset, K.W., 2023. Handling of wild Atlantic salmon smolts reduced marine survival more than hydropower turbine passage. Fish Manag Ecol 30, 353–359.

Haraldstad, T., Kroglund, F., Kristensen, T., Jonsson, B., Haugen, T., 2017. Diel migration pattern of Atlantic salmon (Salmo salar) and sea trout (Salmo trutta) smolts: an assessment of environmental cues. Ecol Freshw Fish 26, 541–551.

Hartig, F., 2024. Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.

Harvey, A.C., Glover, K.A., Wennevik, V., Skaala, Ø., 2020. Atlantic salmon and sea trout display synchronised smolt migration relative to linked environmental cues. Sci Rep 10.

Hastie, T.J., Tibshirani, R.J., 1990. Generalized Additive Models, Chapman & Hall/CRC Monographs on Statistics & Applied Probability. Taylor & Francis.

Haugen, T.O., Aass, P., Stenseth, N.C., Vøllestad, L.A., 2008. Changes in selection and evolutionary responses in migratory brown trout following the construction of a fish ladder. Evol Appl 1, 319–335.

Heggenes, J., 1990. Habitat utilization and preferences in juvenile atlantic salmon (salmo salar) in streams. Regulated Rivers: Research & Management 5, 341–354.

Heggenes, J., Wollebæk, J., 2013. Habitat Use and Selection by Brown Trout in Streams. pp. 157–176.

Hesthagen, T., Larsen, B., Fiske, P., 2011. Liming restores Atlantic salmon (Salmo salar) populations in acidified Norwegian rivers. Canadian Journal of Fisheries and Aquatic Sciences 68, 224–231.

Ibbotson, A., Beaumont, W., Pinder, A.C., 2011. A size-dependent migration strategy in Atlantic salmon smolts: Small smolts favour nocturnal migration. Environ Biol Fishes 92, 151–157.

Jacobson, P.T., Amaral, S. V, Castro-Santos, T., Giza, D., Haro, A.J., Hecker, G., Mcmahon, B., Perkins, N., Pioppi, N., 2012. Environmental Effects of Hydrokinetic Turbines on Fish: Desktop and Laboratory Flume Studies 2012 Project Manager.

Jensen, A.J., Diserud, O.H., Finstad, B., Fiske, P., Thorstad, E.B., 2022. Early-season brown trout (Salmo trutta) migrants grow and survive better at sea. J Fish Biol 100, 1419–1431.

Johnsson, J.I., Näslund, J., 2018. Studying behavioural variation in salmonids from an ecological perspective: observations questions methodological considerations. Rev Fish Biol Fish.

Jolliffe, I.T., 2002. Principal Component Analysis, Second Edition.

Jonsson, B., Jonsson, N., 2002. Ørretens vandring i vassdrag: betydningen av vannføring og temperatur.

Jonsson, B., Jonsson, N., 2009. A review of the likely effects of climate change on anadromous Atlantic salmon Salmo salar and brown trout Salmo trutta, with particular reference to water temperature and flow. J Fish Biol 75, 2381–2447.

Jonsson, B., Jonsson, N., 2011. Ecology of Atlantic salmon and Brown Trout: Habitat as A Template For Life Histories.

Kärgenberg, E., Thorstad, E.B., Järvekülg, R., Sandlund, O.T., Saadre, E., Økland, F., Thalfeldt, M., Tambets, M., 2020. Behaviour and mortality of downstream migrating Atlantic salmon smolts at a small power station with multiple migration routes. Fish Manag Ecol 27, 32–40.

Kristensen, T., Rustadbakken, A., Kroglund F, Güttrup, J., Johansen, Å., Hawley, K., Rosten, C., Kjøsnes, A.J., 2010. Gjeddas betydning som predator på laksesmolt: Populasjonsstørrelse, adferd og predasjonsomfang på laksesmolt i Storelva, Aust-Agder.

Kroglund, F., Wright, R.F., Burchart, C., 2002. Acidification and Atlantic salmon: critical limits for Norwegian rivers Acid precipitation Directorate for Nature Management (DN).

Lans, L., 2012. Behaviour and metabolic rates of brown trout and Atlantic salmon Influence of food, environment and social interactions.

Larinier, M., 1998. Upstream and downstream fish passage experience in France.

Larinier, M., 2008. Fish Passage Experience at Small-Scale Hydro-Electric Power Plants in France. Hydrobiologia 609.

Larsen, M.H., Thorn, A.N., Skov, C., Aarestrup, K., 2013. Effects of passive integrated transponder tags on survival and growth of juvenile Atlantic salmon Salmo salar. Animal Biotelemetry 1, 19.

Lebreton, J.-D., Burnham, K.P., Clobert, J., Anderson, D.R., 1992. Modeling Survival and Testing Biological Hypotheses Using Marked Animals: A Unified Approach with Case Studies. Ecol Monogr 62, 67–118.

Limburg, K.E., Waldman, J.R., 2009. Dramatic Declines in North Atlantic Diadromous Fishes. Bioscience 59, 955–965.

Lucas, M., Baras, E., Thorn, T., Duncan, A., Slavik, O., 2001a. Applied Aspects of Freshwater Fish Migration. In: Migration of Freshwater Fishes. pp. 271–310.

Lucas, M., Baras, E., Thorn, T., Duncan, A., Slavik, O., 2001b. Effects of Climate on Patterns of Migratory Behaviour. In: Migration of Freshwater Fishes. pp. 93–136.

Madaro, A., Olsen, R.E., Kristiansen, T.S., Ebbesson, L.O.E., Nilsen, T.O., Flik, G., Gorissen, M., 2015. Stress in Atlantic salmon: Response to unpredictable chronic stress. Journal of Experimental Biology 218, 2538–2550.

Marschall, E., Mather, M., Parrish, D., Allison, G., McMenemy, J., 2011. Migration delays caused by anthropogenic barriers: Modeling dams, temperature, and success of migrating salmon smolts. Ecological Applications 21, 3014–3031.

Martin, P., Rancon, J., Segura, G., Laffont, J., Boeuf, G., Dufour, S., 2012. Experimental study of the influence of photoperiod and temperature on the swimming behaviour of hatchery-reared Atlantic salmon (Salmo salar L.) smolts. Aquaculture 362–363, 200–208.

Mazerolle, M., 2023. Model Selection and Multimodel Inference Based on (Q)AIC(c).

McCormick, S., Hansen, L., Quinn, T., Saunders, R., 1998. Movement, migration, and smolting of Atlantic salmon (Salmo salar). Canadian Journal of Fisheries and Aquatic Sciences 55.

Mccormick, S.D., Moriyama, S., Björnsson, T., 2000. Low temperature limits photoperiod control of smolting in Atlantic salmon through endocrine mechanisms.

Moore, A., Ives, S., Mead, T., Talks, L., 1998. The migratory behaviour of wild Atlantic salmon (Salmo salar L.) smolts in the River Test and Southampton Water, Southern England. Hydrobiologia 371, 295–304.

Nash, A.J., Vollset, K.W., Lennox, R., Salvanes, A.G. V, 2021. A tale of two fishes: The depth preference of migrating Atlantic salmon smolts, and their aquatic predator Brown trout, in a Norwegian freshwater lake External supervisors.

Nevoux, M., Finstad, B., Davidsen, J.G., Finlay, R., Josset, Q., Poole, R., Höjesjö, J., Aarestrup, K., Persson, L., Tolvanen, O., Jonsson, B., 2019. Environmental influences on life history strategies in partially anadromous brown trout (Salmo trutta, Salmonidae). Fish and Fisheries 20, 1051–1082.

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

Norrgård, J., Greenberg, L., Piccolo, J., Schmitz, M., Bergman, E., 2013. Multiplicative loss of landlocked atlantic salmon (salmo salar). Smolts during downstream migration trough multiple dams. River Res Appl 29.

NVE, 2019. NVEs vurdering av detaljplan for miljø og landskap - Fosstveit kraftverk i Tvedestrand kommune.

NVE, 2025. NVE Sildre [WWW Document]. URL sildre.nve.no (accessed 5.8.25).

Nyqvist, D., Greenberg, L., Goerig, E., Calles, O., Bergman, E., Ardren, W., Castro-Santos, T., 2016. Migratory delay leads to reduced passage success of Atlantic salmon smolts at a hydroelectric dam. Ecol Freshw Fish 26.

OpenAI, 2025. ChatGPT-4 [WWW Document].

Pedersen, E.J., Miller, D.L., Simpson, G.L., Ross, N., 2019. Hierarchical generalized additive models in ecology: an introduction with mgcv. PeerJ 7, e6876.

Perplexity AI, 2025. Perplexity.

Pracheil, B., DeRolph, C., Schramm, M., Bevelhimer, M., 2016. A fish-eye view of riverine hydropower systems: the current understanding of the biological response to turbine passage. Rev Fish Biol Fish 26.

Radinger, J., van Treeck, R., Wolter, C., 2022. Evident but context-dependent mortality of fish passing hydroelectric turbines. Conservation Biology 36.

Renardy, S., Takriet, A., Benitez, J.-P., Dierckx, A., Baeyens, R., Coeck, J., Pauwels, I.S., Mouton, A., Archambeau, P., Dewals, B., Pirotton, M., Erpicum, S., Ovidio, M., 2021. Trying to choose the less bad route: Individual migratory behaviour of Atlantic salmon smolts (Salmo salar L.) approaching a bifurcation between a hydropower station and a navigation canal. Ecol Eng 169, 106304.

Richardson, M., 2009. Model Based Inferences in the Life Sciences: A Primer on Evidence. Ann Entomol Soc Am 102, 737–738.

Richmond, M.C., Romero-Gomez, P., Serkowski, J.A., Rakowski, C.L., Graf, M., 2015. Comparative Study of Barotrauma Risk during Fish Passage through Kaplan Turbines.

Roscoe, D.W., Hinch, S.G., Cooke, S.J., Patterson, D.A., 2011. Fishway passage and post-passage mortality of up-river migrating sockeye salmon in the Seton River, British Columbia. River Res Appl 27, 693–705.

Royle, J. andrew, 2008. Modeling Individual Effects in the Cormack-Jolly-Seber Model: A State-Space Formulation. Biometrics 64, 364–370.

S, S., 2012. Use of an eco-friendly anaesthetic in the handling of Puntius denisonii (Day, 1865)-an endemic ornamental barb of the Western Ghats of India. Indian Journal of Fisheries 59.

Sandercock, B.K., 2020. Mark-Recapture Models for Estimation of Demographic Parameters.

Sarzo, B., Conesa, D., King, R., 2020. Cormack–Jolly–Seber models: time and age perspectives. Stochastic Environmental Research and Risk Assessment 34.

Schielzeth, H., Forstmeier, W., 2009. Conclusions beyond support: overconfident estimates in mixed models. Behavioral Ecology 20, 416–420.

Scruton, D.A., McKinley, R.S., Kouwen, N., Eddy, W., Booth, R.K., 2003. Improvement and optimization of fish guidance efficiency (FGE) at a behavioural fish protection system for downstream migrating Atlantic salmon (Salmo salar) smolts. River Res Appl 19, 605–617.

Sekhon, J., 2011. Multivariate and Propensity Score Matching Software with Automated Balance Optimization: The Matching Package for R. J Stat Softw 42.

Silva, A.T., Bærum, K.M., Hedger, R.D., Baktoft, H., Fjeldstad, H.P., Gjelland, K., Økland, F., Forseth, T., 2020. The effects of hydrodynamics on the three-dimensional downstream migratory movement of Atlantic salmon. Science of The Total Environment 705, 135773.

Silva, A.T., Lucas, M.C., Castro-Santos, T., Katopodis, C., Baumgartner, L.J., Thiem, J.D., Aarestrup, K., Pompeu, P.S., O'Brien, G.C., Braun, D.C., Burnett, N.J., Zhu, D.Z., Fjeldstad, H.P., Forseth, T., Rajaratnam, N., Williams, J.G., Cooke, S.J., 2018. The future of fish passage science, engineering, and practice. Fish and Fisheries 19, 340–362.

Simmons, O. m., Britton, J. r., Gillingham, P. k., Nevoux, M., Riley, W. d., Rivot, E., Gregory, S. d., 2022. Predicting how environmental conditions and smolt body length when entering the marine environment impact individual Atlantic salmon Salmo salar adult return rates. J Fish Biol 101, 378–388.

Skaala, Ø., 2017. A summary of 20 years (1998-2017) of scientific work on genetics and survival in anadromous brown trout (Salmo trutta L) and Atlantic salmon (S. salar L) in the river Guddalselva western Norway.

Sokal, R., Rohlf, F., 2013. Biometry : the principles and practice of statistics in biological research / Robert R. Sokal and F. James Rohlf, SERBIULA (sistema Librum 2.0).

Sortland, L.K., Aarestrup, K., Birnie-Gauvin, K., 2024. Comparing the migration behavior and survival of Atlantic salmon () and brown trout () smolts. J Fish Biol n/a.

Team, R., 2006. A language and environment for statistical computing. Computing 1.

The European Parliament, The council of the European Union, 2010. Directive 2010/63/EU of the European Parliament and of the council of 22 September 2010 on the protection of animals used for scientific purposes (Text with EEA relevance).

Therneau, T., Grambsch, P., 2000. Modeling Survival Data: Extending The Cox Model, Stat Med.

Thorpe, J.E., 1994. Reproductive strategies in Atlantic salmon, Salmo salar L. Aquac Res 25, 77–87.

Thorstad, E., Økland, F., Aarestrup, K., Heggberget, T., 2007. Factors Affecting the within-River Spawning Migration of Atlantic Salmon, with Emphasis on Human Impacts. Rev Fish Biol Fish 18, 345–371.

Thorstad, E., Økland, F., Kroglund, F., Jepsen, N., 2003. Upstream migration of Atlantic salmon at a power station on the River Nidelva, Southern Norway. Fish Manag Ecol 10, 139–146.

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

Thorstad, E.B., Fiske, P., Aarestrup, K., Hvidsten, N.A., Hårsaker, K., Heggberget, T.G., Økland, F., 2003. Upstream migration of Atlantic salmon in three regulated rivers, Europe.

Tomanova, S., Courret, D., Tymen, B., Richard, S., Dumond, L., Sagnes, P., 2023. Updated mortality estimation formulae for salmonids passing through Francis turbines at hydropower plants. Knowl. Manag. Aquat. Ecosyst.

Valiente, A.G., Juanes, F., Nuñez, P., Garcia-Vazquez, E., 2010. Brown trout (Salmo trutta) invasiveness: plasticity in life-history is more important than genetic variability. Biol Invasions 12, 451–462.

Vikström, L., Leonardsson, K., Leander, J., Shry, S., Calles, O., Hellström, G., 2020. Validation of Francis–Kaplan Turbine Blade Strike Models for Adult and Juvenile

Atlantic Salmon (Salmo Salar, L.) and Anadromous Brown Trout (Salmo Trutta, L.) Passing High Head Turbines. Sustainability 12, 6384.

Vollset, K.W., Lennox, R.J., Lamberg, A., Skaala, Ø., Sandvik, A.D., Sægrov, H., Kvingedal, E., Kristensen, T., Jensen, A.J., Haraldstad, T., Barlaup, B.T., Ugedal, O., 2021. Predicting the nationwide outmigration timing of Atlantic salmon (Salmo salar) smolts along 12 degrees of latitude in Norway. Divers Distrib 27, 1383–1392.

Wedemeyer, G., Saunders, R., Clarke, C., 1980. Environmental Factors Affecting Smoltification and Early Marine Survival of Anadromous Salmonids.

Whalen, K.G., Parrish, D.L., McCormick, S.D., 1999. Migration Timing of Atlantic Salmon Smolts Relative to Environmental and Physiological Factors. Trans Am Fish Soc 128, 289–301.

Wolter, C., Bernotat, D., Gessner, J., Brüning, A., Lackemann, J., Radinger, J., 2020. Fachplanerische Bewertung der Mortalität von Fischen an Wasserkraftanlagen, BfN-Skripten (1.1998 - 631.2022) - 561 [e]. Deutschland / Bundesamt für Naturschutz, Bonn.

Wood, S., 2023. Mixed GAM Computation Vehicle with Automatic Smoothness Estimation.

Wood, S.N., 2017. Generalized Additive Models: An Introduction with R, Second Edition, Chapman & Hall/CRC Texts in Statistical Science. CRC Press.

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R, Statistics for Biology and Health. Springer New York.

Zydlewski, G., Horton, G., Dubreuil, T., Letcher, B., Casey, S., Zydlewski, J., 2006. Remote Monitoring of Fish in Small Streams. Fisheries (Bethesda) 31, 492–502.

12 Glossary of Terms and Keywords

To promote clarity and consistency in this document, the following terms and keywords are defined as they are used within the context of this study:

1. Anadromous Species

Fish that migrate from the sea to freshwater to spawn, such as Atlantic salmon and brown trout.

2. AICc (Corrected Akaike Information Criterion)

A model selection criterion used to compare the relative quality of statistical models, accounting for small sample sizes.

3. Barotrauma

Physical injury caused by rapid pressure changes, typically experienced when fish pass through turbines.

4. Bypass Channel

A man-made route constructed to guide migrating fish safely around hydropower infrastructure.

5. CF (Condition Factor)

A metric used to evaluate fish health or "plumpness", calculated as $(\text{weight}/\text{length}^3) \times 100$, often used to compare condition between individuals or species.

6. CJS (Cormack-Jolly-Seber) Model

A type of mark-recapture model used to estimate survival and detection probability in open populations.

7. Count Model (Conditional Component)

In zero-inflated models, this refers to the part of the model (usually Poisson or Negative Binomial) that predicts the value of the response variable (e.g., hesitation time) when it is greater than zero.

8. Crepuscular Activity

Fish activity concentrated during dawn and dusk hours.

9. DHARMa

An R package used for residual diagnostics in mixed models and generalised additive models.

10. Diel Variation

Variability across a 24-hour cycle, often in relation to light or behaviour.

11. Downstream Passage

The movement of fish from upstream habitats past barriers like hydropower dams toward downstream habitats or the sea.

12. Forebay

The upstream area of a dam or intake where fish may hesitate or search for a passage route.

13. GAM (Generalised Additive Model)

A flexible regression model that can capture non-linear effects using smooth terms (splines).

14. glmmTMB

An R package for fitting mixed models, including zero-inflated negative binomial models used to analyse residence time and hesitation.

15. Hesitation Time (Residence Time)

The duration between a fish's first detection at the forebay antenna and its successful passage through the bypass route.

16. HEP (Hydroelectric Power Plant)

Refers specifically to the Fosstveit Hydroelectric Power Plant in this study.

17. Kaplan Turbine

A low-head turbine commonly used in run-of-river systems, often associated with fish passage risk.

18. km_fit

An object class in R that represents Kaplan–Meier survival curves generated with the survfit() function.

19. Lux

A unit measuring light intensity, important in studies of fish diel behaviour.

20. Morphometrics

Biological measurements of organisms (e.g., length, weight, condition factor) used to assess their physical characteristics.

21. NVE (Norwegian Water Resources and Energy Directorate)

The governmental agency responsible for water and energy management in Norway.

22. PCA (Principal Component Analysis)

A dimensionality reduction technique used to identify patterns in multivariate data by transforming correlated variables into principal components.

23. PIT (Passive Integrated Transponder) Tag

A small electronic device implanted in fish to enable individual tracking via PIT antenna arrays.

24. Poisson/NB2 (Negative Binomial type 2)

Distributions used in modelling count data, with NB2 used when overdispersion is present.

25. PredZero (Zero-inflation Component)

In a zero-inflated model, this component models the probability that a fish migrates immediately (i.e., hesitation time = 0).

26. ResidenceTime_int

The response variable in hesitation time models, measured in minutes from first detection to passage, rounded to the nearest integer.

27. Rheotaxis
Fish behaviour involving orientation and movement in response to water flow, often toward or away from current.

28. Run-of-River
A type of hydropower plant with minimal storage capacity, using the natural flow of the river.

29. Species × Environment Interaction
A statistical interaction term that tests whether different species respond differently to environmental variables such as flow or light.

30. Smolt
The life stage of salmonids during which they undergo physiological changes to migrate from freshwater to saltwater.

31. Survival Analysis (Cox Model)
A statistical technique used to model the time to an event (e.g., successful passage) and identify predictors of passage timing.

32. Turbine Entrainment
The undesired process of fish being drawn into a turbine, which often results in injury or death.

33. Violin Plot
A data visualisation that combines a boxplot with a kernel density plot to show distribution and variability.

34. Zero-Inflated Model
A two-part model that separately estimates: (1) the probability of structural zeroes (e.g., immediate passage), and (2) the distribution of non-zero values (e.g., delay duration).

Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway