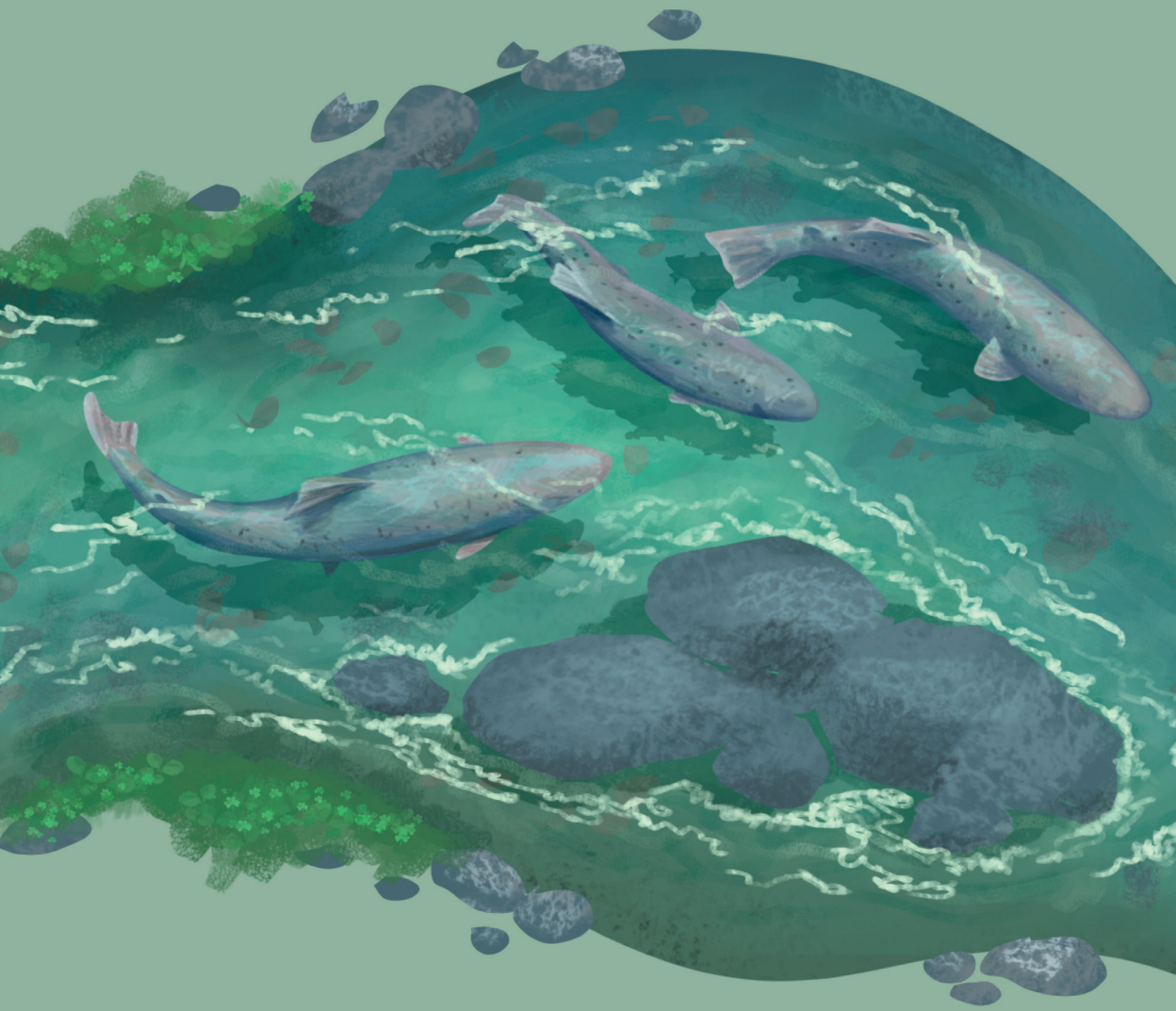
Samuel Shry



Anadromy in Fragmented Rivers

Downstream Passage Challenges for Migrating Salmonids

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Faculty of Health, Science and Technology

Biologi

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“Unless someone like you cares a whole awful lot, nothing is going to get better. It’s not.”
-Dr. Seuss

“One of the penalties of an ecological education is that one lives alone in a world of wounds.”
-Aldo Leopold

Abstract

Migration is a fundamental ecological process, and for anadromous salmonids, successful movement between freshwater and marine environments is essential for growth, survival, and reproduction. River fragmentation from hydropower development has severely disrupted these movements, with dams creating hazardous downstream passage conditions for both smolts and post-spawned adults (kelts). Delays, increased predation risk, altered hydraulic conditions, and dam-related injuries can reduce survival and threaten population viability, in particular in rivers containing multiple barriers. Downstream fish passage solutions at dams can mitigate these negative effects, but the performance of most solutions remain rarely evaluated.

The overarching aim of this thesis was to evaluate downstream passage performance of dams for salmonids in fragmented rivers, identify environmental and behavioral drivers that impact passage rates, and assess the efficiency of existing mitigation measures. Acoustic telemetry was used to quantify movement patterns, route choice, passage efficiency and success, migration speeds, and instantaneous loss rates for smolts and kelts across river sections fragmented by hydroelectric power stations (HEPs) compared to free-flowing sections.

Atlantic salmon smolt passage success at HEPs ranged from 71–95%, whereas passage success in free-flowing sections ranged from 75–100%. Smolt migration speeds in HEP sections ranged from 0.6-9.5 km·day^{-1}, whereas migration in free-flowing sections ranged from 1.5-24.2 km·day^{-1}. In the river Mörrumsån, smolt passage success across the study area averaged 61% across release groups (passage 2xHEPs: 52.6%, passage 1xHEP: 61.5%, control: 69.2%), and losses were mainly observed in lentic habitats and reservoir forebays of the two small-scale HEPs evaluated. Restored free-flowing sections exhibited the fastest smolt migration speeds, and removal of the Marieberg HEP more than doubled migration speeds. Smolts released downstream of the HEPs in river Mörrumsån, acting as a control group, exhibited similar passage success and migration speeds as the HEP-passage groups, highlighting limited effects associated with longer migrations and/or HEP passage. When approaching the HEPs, downstream migrating smolts were

strongly influenced by hydraulic conditions, preferentially selecting high-velocity areas while avoiding strong velocity gradients, with increased spill discharge promoting spill gate use and influencing overall route selection. In river Dalälven, passage success across the study area and the two large-scale HEPs remained relativity stable over three years, averaging 57% (2019: 53%, 2020: 61%, 2021: 58%), corresponding to a mean loss rate of 2.0 % km-1. Smolt passage success were lowest through lentic habitats and HEP sections, where migration speeds were also slowest, suggesting potential migratory bottlenecks. Smolts released downstream of the HEPs in river Dalälven, acting as a control group, exhibited migration speeds more than twice as fast as those of the HEP-passage group, highlighting indirect effects associated with longer migrations and/or HEP passage. In both rivers, water temperature and diel period were the most influential predictors of passage rates, with increasing temperatures and nighttime periods associated with increased passage rates.

In river Emån, kelt return rates to the Baltic Sea were on average 39%, with only overwintering individuals that out-migrated in the spring successfully reaching the river mouth. Overwintering was observed in 56% of salmonid spawners, with the majority overwintering as kelts in the upper reaches of available river habitat (>30km upstream from river mouth). Downstream migration was initiated by 69% of tagged individuals, with passage success across HEP and free-flowing river sections ranging from 81–93% and migration speeds of 0.6–6.2 km·day^{-1}. Downstream passage was faster and more efficient at HEP facilities equipped with designated downstream passage solutions.

Results demonstrate that while localized passage success within river sections can be high, river-scale passage success remains strongly constrained by lentic bottlenecks, hydraulic alterations, and cumulative barrier effects. However, restored free-flowing habitats and HEPs equipped with downstream passage solutions substantially improved connectivity and reduced migration delays. Together, these findings highlight the critical importance of implementing site-specific and functional downstream passage solutions for maintaining viable anadromous salmonid populations in fragmented rivers.

Populärvetenskaplig sammanfattning

Vandring är en grundläggande ekologisk process, och för anadroma laxfiskar är en framgångsrik förflyttning mellan sötvatten- och havsmiljöer avgörande för tillväxt, överlevnad och reproduktion. Fragmentering av vattendrag till följd av vattenkraftsutbyggnad har haft en starkt negativ påverkan på vandrande fiskpopulationer eftersom det föreligger en förhöjd skaderisk för laxfiskar, både juvenila (smolt) och utlekta vuxna (kelt), vid nedströmspassage av vattenkraftverk. Fördröjningar, ökad risk för predation, förändrade hydrauliska förhållanden och skador relaterade till dammpassage minskar överlevnaden och hotar därmed vandrande fiskpopulationers långsiktiga resiliens, i synnerhet i vattendrag med flera hinder. Passagelösningar för nedströmsvandrande fiskar kan mildra dessa negativa effekter, men det är fortfarande ovanligt med utvärdering av sådana miljöförbättrande åtgärders funktion.

Det övergripande syftet med denna avhandling var att studera laxfiskars nedströmsvandring i fragmenterade vattendrag, samt att utvärdera funktionen hos befintliga passagelösningar. Vidare undersöktes vilka miljöfaktorer som påverkade fiskarnas beteende och passageframgång. Akustisk telemetri användes för att kvantifiera rörelsemönster, vägval, passerbarhet, migrationshastighet och förlustfrekvens för smolt och kelt i vattendrag som fragmenterats av vattenkraftverk (HEP), men även längs fritt strömmande sektioner.

Atlantlaxsmoltens passageframgång vid vattenkraftverk varierade mellan 71 och 95 %, medan överlevnaden i de fritt strömmande sektionerna varierade mellan 75 och 100 %. Smoltens vandringshastighet i de fragmenterade sektionerna varierade mellan 0,6 och 9,5 $km \cdot dag^{-1}$, medan vandringen i fritt strömmande sektioner varierade mellan 1,5 och 24,2 $km \cdot dag^{-1}$. I Mörrumsån var passageframgången jämförbar förbi de två utvärderade småskaliga vattenkraftverken, 87 respektive 86 %, och total passageframgång i studieområdet var i genomsnitt 61 % för alla utsättningsgrupper (passage av två kraftverk: 52,6 %, passage av ett kraftverk: 61,5 %, kontroll: 69,2 %). Vandringshastigheten var högst i de fritt strömmande sektionerna, efter restaurering, och vid platsen för Mariebergs vattenkraftverk mer än fördubblades vadringshastigheten

efter att kraftverket tagits bort. Förluster av smolt observerades främst i långsamflytande (lentiska) habitat och i de uppdämda områdena uppströms de två vattenkraftverken som utvärderades. Smolt som satts ut nedströms vattenkraftverken i Mörrumsån, och fungerade som kontrollgrupp, uppvisade liknande passageframgång och vandringshastigheter som grupperna som passerat vattenkraftverken. Nedströmsvandrande smolt påverkades starkt av de hydrauliska förhållandena i området uppströms kraftverken, och valde framför allt att simma till områden med hög flödeshastighet samtidigt som de undvek platser med starka hastighetsgradienter. Ökad tappning av spillvatten resulterade i att fler smolt passerade kraftverket genom spilluckorna och påverkade därmed det övergripande vägvalet. I det betydligt större vattendraget Dalälven, var passageframgången förbi de två storskaliga vattenkraftverken relativt stabil under tre år, där i genomsnitt 57 % av smolten framgångsrikt nådde till havet (2019: 53 %, 2020: 61 %, 2021: 58 %), vilket motsvarar en genomsnittlig förlust på 2 km·dag^{-1}. Passageframgång och vandringshastighet var lägst förbi långsamflytande habitat och förbi vattenkraftverken, vilket tyder på potentiella flaskhalsar för överlevnad. En kontrollgrupp, i form av märkta smolt som sattes ut nedströms kraftverken, uppvisade en vandringshastighet som var mer än dubbelt så hög som för de fiskar som tvingades passera vattenkraftverken. Skillnaderna mellan dessa två grupper tyder på indirekta, negativa effekter av långa vandringssträckor och/eller kraftverkspassage. I båda vattendragen var vattentemperatur och tid på dygnet de faktorer som hade störst betydelse för vandringsframgång, där stigande temperatur och nattaktivitet var indikatorer på hög överlevnad.

I Emån var keltöverlevnaden till Östersjön i genomsnitt 39 % och endast individer som övervintrande i vattendraget och vandrade ut på våren lyckades nå havsmynningen. Övervintring observerades hos 56 % av de lekvandrande laxfiskarna, där majoriteten övervintrade i de övre delarna av den tillgängliga delen av vattendraget (mer än 30 km uppströms från mynningen i Östersjön). Totalt initierade 69 % av de märkta fiskarna nedströmsvandring, med en passageframgång förbi vattenkraftverk och i fritt strömmande sektioner på mellan 81 och 93 % och en vandringshastighet på 0,6–6,2 km·dag^{-1}. Nedströmsvandringen var snabbare och effektivare vid de två vattenkraftverk som var

utrustade med nedströmspassager, än det kraftverk som saknade passageförbättrande åtgärder.

Sammanfattningsvis visar resultaten att även om passageöverlevnaden var hög inom vissa vattendragssektioner, begränsades passagefram-gången på vattendragnivå av platsspecifika flaskhalsar för överlevnad och inte minst kumulativa barriäreffekter. Det finns dock en stor förbättringspotential i form av återställandet av fritt strömmande sträckor och vattenkraftverk utrustade med nedströmspassagelösningar, vilka i kombination med andra miljöförbättrande åtgärder kan rehabilitera korridorfunktionen i reglerade vattendrag. Sammantaget understryker dessa resultat den avgörande betydelsen av en bred implementering av platsspecifika och väl fungerande passageåtgärder, för att bibehålla livskraftiga anadroma laxfiskpopulationer i fragmenterade vattendrag.

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List of chapters

This doctoral thesis is based on the following papers, which are referred to by their roman numerals.

I. **Shry, S.**, Harbicht, A., Forsberg, H., Nilsson, P.A., Hellström, G., Österling, M., & Calles, O. (2024). Challenges in downstream dam passage and the effect of dam removal on Atlantic salmon (*Salmo salar*) smolt migrations. *Journal of Fish Biology*, *106*(5), 1440-1451.

II. **Shry, S.**, Campbell, J., Hansson, M., Nilsson, P.A., Hellström, G., Österling, M., Calles, O. Hydraulic influences on Atlatntic salmon (*Salmo salar*) smolt movement behavior and route selection in dam forebays. (Manuscript)

III. **Shry, S.**, Harbicht, A., Gullberg, K., Hellström, G., Calles, O. Multi-year assessment of smolt migrations in a large, fragmented river: hydropower and the remnant wild Atlantic salmon (*Salmo salar*) of the River Dalälven. (In Revision)

IV. **Shry, S.**, Harbicht, A., Nordahl, O., Tibblin, P., Österling, M., Hellström, G., Nilsson, P.A., Calles, O. Spawning, overwintering, and downstream migration of salmonids in a fragmented river with varying bypass solutions. (Manuscript)

Author contributions

Conceptualization, formal analysis, methodology, supervision, writing & editing, Resources, funding acquisition

I. Conceptualization: SS, AN, GH, MÖ, OC, Data curation: SS, HF, Formal analysis: SS, HF, AH, Methodology: SS, HF, AH, AN, OC, GH, Supervision: AN, GH, MÖ, OC, Writing & editing: SS, HF, AH, AN, MÖ, OC, Resources: GH, OC, Funding: OC

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S. Shry (SS), O. Calles (OC), M. Österling (MÖ), G. Hellström (GH), P. A. Nilsson (AN), H. Forsberg (HF), M. Hansson (MH), J. Campbell (JC), O. Nordahl (ON), P. Tibblin (PT), Karl Gullberg (KG), Andrew Harbicht (AH)

Publications not included

List of publications during doctoral studies not included in this thesis.

V. 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*) and anadromous brown trout (*Salmo trutta*) passing high head turbines. *Sustainability*, *12*(16), 6384.

VI. Campbell, J. A., **Shry, S.**, Calles, O., & Hölker, F. (2023). Application of animal movement models to acoustic telemetry positioning. In *International School of Hydraulics* (pp. 29-41). Cham: Springer Nature Switzerland.

VII. Campbell, J. A., **Shry, S. J**., Lundberg, P., Calles, O., & Hölker, F. (2025). A population Monte Carlo model for underwater acoustic telemetry positioning in reflective environments. *Methods in Ecology and Evolution*, *16*(4), 775-785.

VIII. Brand, J. A., Michelangeli, M., **Shry, S. J.**, Moore, E. R., Bose, A. P., Cerveny, D., ... & Bertram, M. G. (2025). Pharmaceutical pollution influences river-to-sea migration in Atlantic salmon (*Salmo salar*). *Science*, *388*(6743), 217-222.

Introduction

Importance of migration

Migration is a widespread ecological phenomenon occurring across nearly all animal taxa. It represents an adaptive movement pattern expressed over diverse spatial and temporal scales, characterized by persistent and directional movement of individuals or entire populations between habitats (Dingle & Drake 2007, Lucas & Baras 2008). The magnitude and distance of these movements vary across species and environment s, from diel vertical migrations of zooplankton that can span only a few meters per day, to annual migration of Arctic terns who can move up to 670 km·day^{-1} (Hansson & Hylander 2009, Egevang et al. 2010). In terrestrial animals, migrations are often visible and follow well-defined, species-specific routes across landscapes. In contrast, aquatic migrations occur beneath the water surface, restricted spatially to aquatic environments, and therefore generally unseen. The adaptive value of migrations comes from the stabilizing forces of costs and benefits: energy expenditure, increased predation risk and mortality must be offset by advantages such as growth, survival, and reproductive success (Gross et al. 1988, Thorpe 1988, Chapman et al. 2012). Large-scale migrations are often connected with a species' life history strategies, as individuals move between habitats to exploit seasonal or habitat-specific resources, avoid unfavorable conditions, or improve reproductive advantages (Fleming 1979, Dingle 2014). For example, humpback whales migrate between high-latitude feeding grounds and low-latitude breeding and calving areas (Rizzo & Schulte 2009). These strategies can enhance population resilience to environmental variation and promote local adaptation (Holt & Gomulkiewicz 1997, Nakazawa & Yamamura 2007). A clear example of this is found in iteroparous and anadromous fish species, like Atlantic salmon (Salmo salar) and certain populations of brown trout (Salmo trutta), which migrate repeatedly between freshwater and marine environments to optimize growth and reproductive success throughout their lifecycle (Thorpe et al. 1998, Dodson et al. 2013).

Salmonid migrations

Atlantic salmon and anadromous brown trout begin their lifecycle in freshwater, where juveniles remain for one to four years before migrating downstream to marine environments, or lacustrine environments in the case of landlocked populations (McCormick & Saunders 1987, Mills 1991) (Figure 1). During this transition phase from freshwater to marine environments, juveniles undergo a series of physiological and behavioral changes, driven in part by environmental cues, that prepare them for survival at sea (Hoar, 1988, Thorpe 1988). This process, known as smoltification, is regulated by both intrinsic factors (such as age, size, and growth rate) and external environmental cues (such as water temperatures, discharge, or photoperiod) (Wedemeyer et al. 1980, Thorpe 1989, Hvidsten et al. 1995, McCormick 1998). The interaction and timing of these cues influence not only the initiation of smoltification, but also migratory success, which typically varies between years (Hvidsten et al. 1995, Haraldstad et al. 2017).

Downstream migration of smolt represents one of the most critical and hazardous stages in the salmonid life cycle. At this stage, individuals are relatively small (10 – 20 cm), energetically constrained, and exposed to high mortality risks (Thorstad et al. 2011). Predation pressure can vary based on biological traits (e.g., body size, condition factor), environmental conditions (e.g., photoperiod, water temperature), and anthropogenic modifications such as flow regulation, barriers, and the presence of turbines (Thorstad et al. 2012, Hostetter et al. 2023, Mensinger et al. 2023). Furthermore, smolts must navigate unfamiliar environments, often traveling hundreds to thousands of kilometers before reaching productive marine feeding habitats (Davidsen et al. 2009, Friedland et al. 2017).

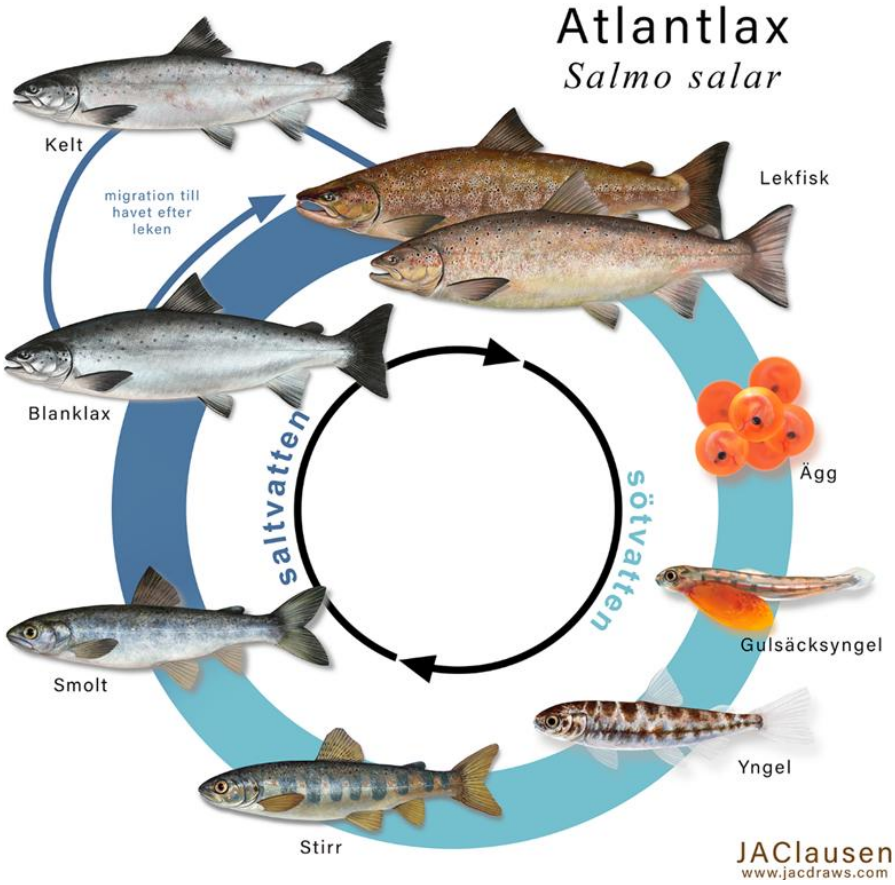


Figure 1. Diagram of the Atlantic salmon life cycle. Illustrations by Jennifer Clausen.

Once post-smolts migrate to marine environments for feeding, they grow and eventually return to their natal freshwater habitat for spawning after one to five years at sea (Klemetsen et al. 2003). Mortality at sea is substantial, with only a small proportion successfully returning to their native rivers as adults for spawning (Hubley et al. 2008, Chaput 2012). In iteroparous species like Atlantic Salmon and anadromous brown trout, this reproductive migration may occur several times during an individual's lifetime, and their ability to repeat spawning contributes substantially to population stability and resilience (Seamons & Quinn 2010, Moore et al. 2014). After spawning, post-spawned individuals, commonly called kelts, either remain in freshwater over winter or migrate directly downstream toward estuarine and marine environments (Bendall et al. 2005). Mortality during the spawning migration can be substantial, ranging between 10-80% and is influenced by multiple factors including migration distance, water temperature, river discharge, individual physiological differences, and presence of barriers

(Cooke et al. 2006, Keefer et al. 2008, Macdonald et al. 2010, Birnie-Gauvin et al. 2019). Kelt mortality is also variable, but generally lower, with rates typically ranging 0-40 %, and may differ between sexes and species (Nyqvist et al. 2016, Haraldstad et al. 2018, Babin et al. 2021).

Differentiating mortality vectors and timing between the spawning and post-spawning phases is challenging because spawning is seldom directly observed and often inferred from telemetry data or capture history (Martins et al. 2012, Gauld et al. 2016).The timing of downstream kelt migration can be influenced by factors such as species, sex, body size, and condition, and usually most strongly associated with hydrological and thermal conditions such as river discharge and water temperature (Kraabøl et al. 2008, Östergren & Rivinoja 2008, Calles & Greenberg 2009). Migration may occur both during the day and night, and individuals can show location-specific diel preferences of migration (Bendall et al. 2005, Östergren & Rivinoja 2008). The interval between successive spawning events varies widely, from several months to multiple years, with repeat spawning generally being more common among brown trout than Atlantic salmon (Bendall et al. 2005). The success of these repeated migrations and spawning events depends on unhindered access between freshwater and marine environments, making migratory salmonids particularly vulnerable to fragmented river systems.

Fragmentation and ecological consequences

River fragmentation and other human-induced pressures have dramatically altered freshwater ecosystems, contributing to an estimated 84% decline in freshwater species abundance since the 1970's (Almond et al. 2020). Currently, more than 60 % of the world's large rivers (exceeding 1000 km in length) are fragmented by dams (WWF 2006), and an additional 800,000 smaller dams estimated to exist globally (McCully 1996). The construction of these barriers fundamentally transforms rivers, creating new ecosystems and disrupting riverine connectivity. These alterations modify flow regimes, hydraulic conditions, water temperature, sediment transport, habitat structure, and even influence diurnal conditions (i.e., homogenize thermal variability, photoperiod disruptions) (Baxter 1977, Fuller et al. 2015, Perkin et al. 2021, Chan et al. 2025). Because anadromous fish species depend on unimpeded

access to both freshwater and marine environments to complete their life cycles, river fragmentation represents one of the most severe anthropogenic threats to their survival (Verhelst et al. 2021, Chan et al. 2025). Barriers can cause migratory delays, increase energetic costs, restrict access to essential habitats, and degrade the environmental conditions necessary for successful reproduction (Karlsson and Karlström 1994, Northcote 1998, Larinier 2000, Lucas & Baras 2001). By dividing rivers into a series of disconnected segments, fragmentation creates artificial isolation that disrupts populations connectivity, reduces gene flow, and alters metapopulation dynamics (Castric et al. 2001, Jager et al. 2001, Costello et al. 2003, Taylor et al. 2003). Over time, these processes can drive population declines or even local extirpation of migratory fish populations dependent on habitat located upstream of impassable barriers (Rolls 2011, Press et al. 2014).

For downstream migrating fish, the disruption of natural flow patterns at barriers poses navigation challenges that can delay migration, increase energetic costs and predation risk (Larinier 2000, Marschall et al. 2011, Mensinger et al. 2023). Altered flow regimes, hydraulic conditions, and water temperature can further compromise survival by interfering with the environmental cues smolts and kelts rely on to initiate and follow for migration, while also transforming flowing (lotic) habitats into still (lentic) zones that favor piscivorous predators (McCormick 1998, Renardy et al. 2022, Mensinger et al. 2023). These changes can shift or prolong migration, which is often optimized within populations to ensure juveniles arrive in marine environments when feeding conditions are favorable (McCormick et al. 1998, Hvidsten et al. 1997, 2009). Passage at barriers can also be behaviorally selective, where certain movement behaviors may be preferential for passage, such as migrating along channel margins, diving to locate bottom-fed spillway openings, or responding to specific flow cues (Arnekleiv et al. 2007, Scruton et al. 2007, Nyqvist et al. 2017). While smolts face high predation pressure during their migration, post-spawning kelts are equally vulnerable due to depleted energy reserves as a result of significant reproductive investments. The cumulative effects of migration delays, sub-lethal passage injuries, and elevated water temperatures can induce a physiological stress response that increases susceptibility to disease and secondary infections, often leading to mortality (Teffer

et al. 2017, Bordeleau et al. 2018, Elmer et al. 2023). Without a dedicated downstream passage solution, smolts and kelts may be forced to pass through hydropower turbines, where exposure to blade strikes, shear forces, rapid pressure changes, and disorientation can cause substantial direct and indirect mortality (Östergren and Rivinoja 2008, Nyqvist et al. 2016, Algera et al. 2020, Vikström et al. 2020). Migration delays and survival are often species- and site-specific, with bypass design and operational strategy being critical factors of passage efficiency (Calles et al. 2012, Nyqvist et al. 2017). For the long-term viability of anadromous salmonid populations, downstream migration requires safe and efficient riverine passage. To achieve this, site-specific characteristics of each barrier must be evaluated to determine passage performance, and appropriate mitigation measures must be implemented.

The scale and technical characteristics of a hydroelectric power plant (further referred to as HEP) strongly influence downstream passage success. Small-scale HEPs (≤10 MW) are more numerous and, when equipped with bypass solutions, their small size and lower vertical drops (low-head) are often easier for fish to pass. In contrast, large-scale HEPs occur less frequently but generally pose greater passage challenges due to larger vertical drops (high-head) and/or simply being physically larger (Kosnik 2010, Larinier 2008). However, in the absence of bypass solutions, turbine passage at small-scale HEPs may be particularly hazardous, as smaller turbines often operate at higher rotational speeds (Larinier 2008). The specific turbine-type further affects passage risk, as mortality rates vary widely among designs (e.g., Pelton, Kaplan, Francis) and are influenced by site-specific factors such as dam height, discharge, rotational speed, number of turbines, as well as fish species and life stage (Bell 1981, Hadderingh & Bakker 1998, Larinier 2008, Vikström et al. 2020). Consequently, maintaining adequate downstream passage across diverse HEP configurations requires effective, site-specific mitigation strategies that address the underlying causes of passage failure.

Fish passage solutions, also known as fishways or fish passes, are engineered structures designed to facilitate the safe and efficient movement of fish past river barriers (Silva et al. 2018). Among the various passage strategies, dam removal is the most effective means of re-establishing

longitudinal connectivity, as it allows rivers to return as closely as possible to their natural, free-flowing state (Silva et al. 2018, Birnie-Gauvin et al. 2019). While dam removal is most commonly applied to small barriers (<2 meters), large hydroelectric power stations have also been decommissioned in recent years where ecological benefits have outweighed the energy production value (Gowan et al. 2006). Given the diversity of migratory behaviors among fish species, passage solutions are often tailored to specific species, life stages, and site conditions, which complicates full-river connectivity (Seliger & Zeiringer 2018, Birnie-Gauvin et al. 2019). Historically, most passage design and management efforts have focused on upstream migration, particularly for salmonids, where development of effective solutions has a relatively long history. In contrast, downstream passage solutions have only more recently received attention, and relatively few have been evaluated for performance (Whitney et al. 1997, Larinier et al. 2002, Calles et al. 2013, Nyqvist 2017) To be successful, solutions must not only enable individuals to locate the entry point of the fish passage solution (attraction efficiency), but also allow them to pass the barrier in a safe and timely manner (passage efficiency) (Aarestrup et al. 2003, Silva et al. 201 8). Ensuring both components' function effectively is crucial for maintaining migratory connectivity and population resilience in fragmented river systems.

Downstream fish passage solutions

Historically, downstream passage solutions have been lacking in most regulated rivers, forcing fish to migrate through hydropower turbines as the primary route (Katopodis & Williams 2012) However, in recent decades, several types of downstream passage solutions have been developed, including physical and behavioral guidance structures, managed spill regimes, less damaging turbines, , and even optimally placed nature-like fishways (Castro-Santos & Haro 2010, Katopodis & Williams 2012, Piper et al. 2018, Seliger & Zeiringer 2018, Nyqvist et al. 2018). Because migrating fish typically follow the main current when approaching a dam, downstream passage solutions should be positioned near dominant flow paths, most often close to turbine intakes or prioritized spill gates to maximize attraction (Fjeldstad et al. 2018). Mechanical guidance devices, such as inclined and angled racks and screens, combined with bypasses have been shown to be effective

passage solutions (Nyqvist et al. 2017, Calles et al. 2021). Behavioral guidance solutions have also been developed, but with varying success in attracting and guiding fish to a bypass (Mussen et al. 2014, Leander et al. 2024, Stoilova et al. 2023, 2025). Spill regimes, periods of controlled, increased discharge through spill gates, are another management strategy used to attract downstream migrating fish using flow cues to an alternate passage route. Studies have shown positive relationships between managed spill and passage success, highlighting its role in improving both efficiency and survival (Ferguson et al. 2005, Scruton et al. 2008). However, the effectiveness of spill gates depends on the proportion of total discharge released; when this fraction is low additional guiding structures are often required to maintain effectiveness. Spill gate opening placement also plays an important role, as both smolts and kelts tend to prefer surface-oriented routes (Arnekleiv et al. 2007, Scruton et al. 2007, Nyqvist et al. 2017a). Managed spill operations timed to coincide with peak downstream migrations of smolts and kelts have shown mixed results, with success varying by site and hydrological conditions (Wertheimer and Evans 2005, Arnekleiv et al. 2007, Scruton et al. 2007, Shry et al. 2021). At large dams with low head and high species diversity, where multiple passage solutions are required to support all fish populations, low-injury turbines can be used to accommodate fish passage. These specially designed turbines are supposed to reduce injury and mortality by minimizing blade strike, pressure changes, and turbulence. This is achieved through modifications such as slower rotational speeds, optimized blade design, and reduced spacing between blades and turbine walls (Čada 2001, Foust et al. 2011). To mimic natural side channel stream conditions, nature-like fishways are constructed, and today they are one of the most widely used multi-species upstream passage solutions in Europe (Katopodis et al. 2012, Tamario et al. 2018). If nature-like fishways are designed to incorporate site-specific hydrodynamics and are placed at optimal locations, they can also function as bi-directional passage routes for both upstream and downstream passage (Calles & Greenberg 2009, Nyqvist et al. 2017). However, like spill gates, these solutions typically require high proportions of river discharge, creating a tradeoff with energy production. While downstream passage solutions can be effective at individual dams, many river systems contain multiple barriers, where

repeated encounters may compound energetic costs, delays, and mortality despite the presence of fish passage solutions.

There can be significant cumulative negative effects within river systems containing multiple barriers, even when passage solutions are implemented (Norrgård et al. 2013, Nyqvist et al. 2016, Keefer et al. 2018). Even when fishways are considered functional, their overall passage efficiency may still be insufficient, particularly in rivers with multiple, cascading barriers (Shuman 1995, Schmutz & Moog 2018). The direct and indirect mortality risks associated with blade strikes, shear force, disorientation, and barotrauma at a single dam can accumulate across multiple barriers, further reducing survival along the migratory route (Östergren and Rivinoja 2008, Nyqvist et al. 2016, Algera et al. 2020, Vikström et al. 2020). Whether the proportion of individuals successfully passing consecutive barriers is sufficient to sustain viable populations and whether these passage solutions actually enhance population sustainability is still poorly understood. Most existing passage solutions have never been comprehensively evaluated for their performance, with little known about their efficiency in improving passage, timeliness, and long-term survival of all native species and life stages (Silva et al. 2018, Birnie-Gauvin et al. 2019). In addition, few studies have evaluated the cumulative effects of downstream passage across multiple hydroelectric power plants (Whitney et al. 1997, Norrgård et al. 2013, Nyqvist et al. 2016). Field-based evaluations are therefore critical for improving the design, implementation, and operation of fish passage solutions, ensuring that they effectively support downstream migration and long-term population resilience.

Objective

The convergence of anadromous salmonids complex life cycle and anthropogenic river modifications has rendered migration increasingly difficult and multifaceted, even when fish passage solutions are integrated to mitigate delays and mortality. The overarching aim of this thesis was to (1) evaluate downstream passage of salmonids of different life stages in rivers with multiple HEPs by comparing passage efficiency and migration speeds across fragmented and unfragmented river

sections, (2) identify key factors influencing passage success, and (3) assess the performance of existing downstream passage solutions. These objectives were addressed using acoustic telemetry to track and analyze individual movement patterns during migration. In chapter **I**, salmon smolt emigration was evaluated at two small-scale HEPs with a spill regime mitigation measure and at the restored river stretch of a former HEP. In chapter **II**, the effect of flow velocity on migration behavior and route selection was evaluated for salmon smolt navigating spill gate passage at two small-scale dams. In chapter **III**, smolt passage at two large-scale dams without fish passage solutions was evaluated over three years. In chapter **IV**, dam passage at three small-scale dams was evaluated for adult, post-spawned (kelt) salmonids. In each instance, downstream passage was evaluated for varying degrees of fish passage solutions available, from no solutions in place (chapter **III**), to spill regimes (chapter **I** & **II**), to multiple solutions (chapter **IV**).

Methods

All studies for this thesis were conducted in the field under real-world conditions. Chapters **I** and **II** were conducted simultaneously in the river Mörrumsån (Figure 2, Figure 3). Chapter **III** was conducted over three years in the river Dalälven (Figure 4). Chapter **IV** was conducted in the river Emån (Figure 5).

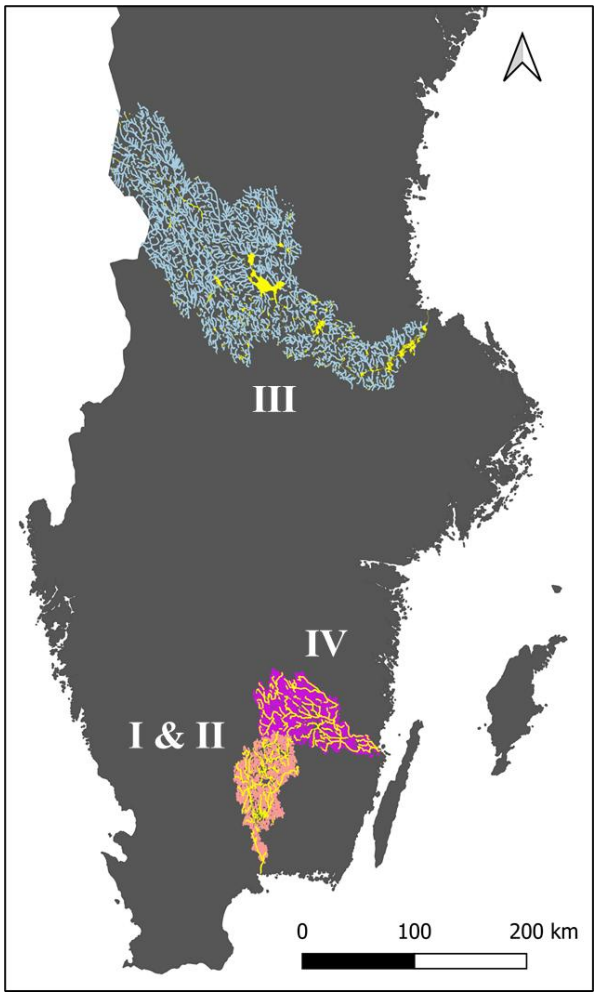


*Figure 2. Overview map of study locations with corresponding chapter roman numerals. Chapter **I** & **II** in the river Mörrumsån (pink), Chapter **III** in the river Dalälven (blue), and Chapter **IV** in the river Emån (purple).*

Study areas

The study for Chapters **I** and **II** was conducted in the lower 25 km section of the river Mörrumsån (56°09'31.1"N 14°44'52.0"E) located in Southern Sweden (Figure 3). The river Mörrumsån is the largest river system in the region, extending approximately 186 km from its headwaters to the Baltic Sea, containing around 34 migration barriers (23 HEPs, only the four lowermost are equipped with passage solutions), and supports one of Sweden's southernmost populations of Atlantic salmon. Migratory fish are able to access the lower 34.5 km of the river with the four HEPs within this section equipped with various types of fish passage solutions designed to accommodate both upstream and

downstream migration. The fifth HEP (Granö HEP) is currently impassable for upstream migrating fish. The study area encompassed the two lowermost hydropower plants in the system, upper Hemsjö HEP and lower Hemsjö HEP, as well as the restored site of the former Marieberg HEP (dam was removed in 2020). Together, these sites represent a key section of the river for assessing passage efficiency and migratory behavior in relation to hydropower operations and fish passage solutions.

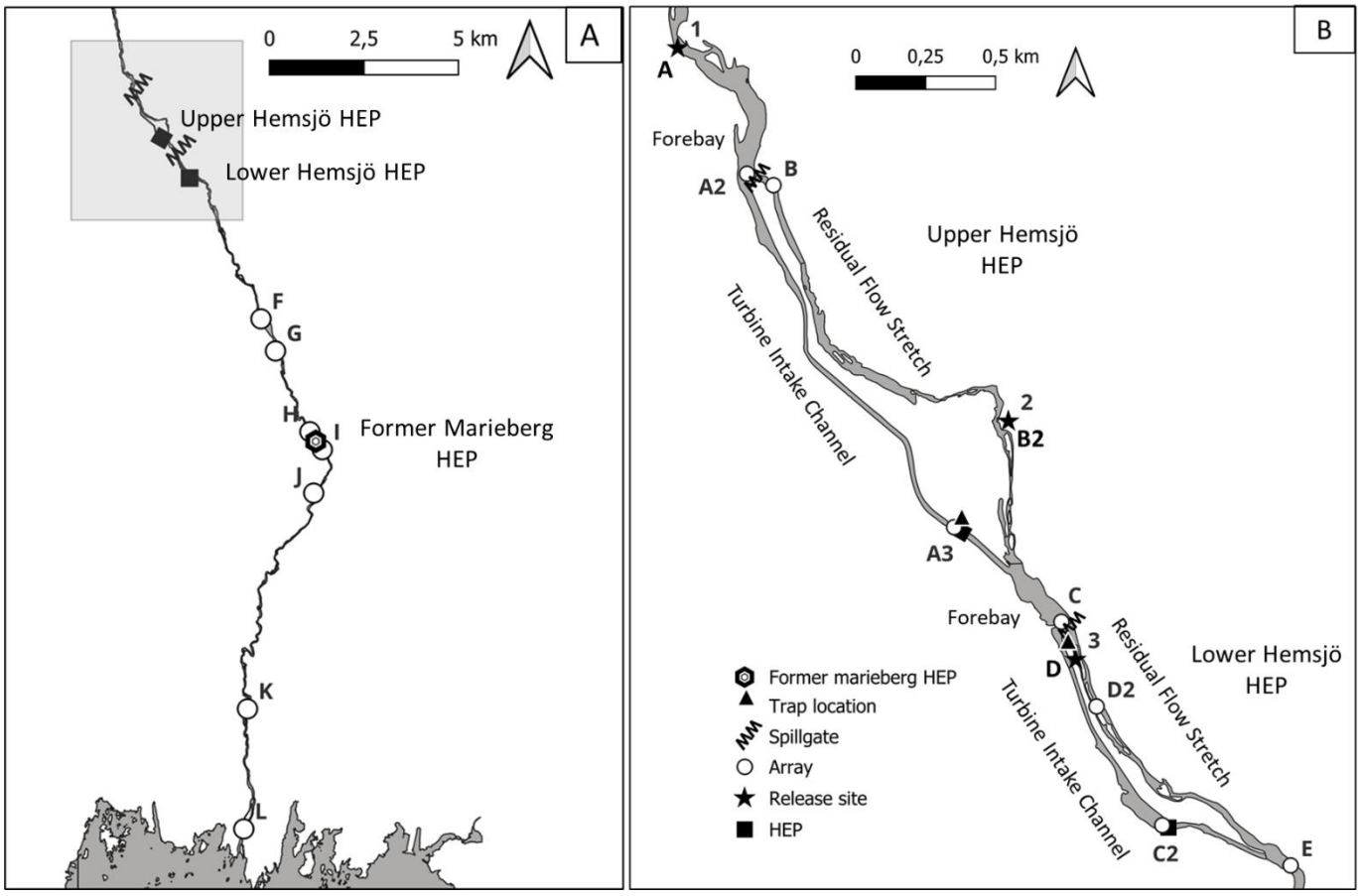


*Figure 3. Overview of study area for chapters **I** & **II** in the river Mörrumsån. A) Overview of the lower 25 km of river, indicating locations of the Hemsjö hydroelectric plants (HEPs), spill gates (zig-zag symbols), the former Marieberg HEP (hexagon), and receiver arrays (F-L). B) The locations of the release sites (stars, 1-3), HEPs (squares), spill gates (zig-zag symbols), residual flow stretches, trap locations (triangles), and receiver arrays (A-E).*

The river Dalälven, located in central Sweden (60.5639276°N, 17.4404065°E), was the study site for Chapter **III**, with the study focusing on the lower 28 km of the river (Figure 4). The river Dalälven is one of Scandinavia's largest river systems (542 km long) and the river historically supported a substantial population of Atlantic salmon. Before the construction of dams for hydropower generation, the river sustained an estimated annual salmon catch exceeding 35 tons in Älvkarleby during the late 19th century (Nordquist et al. 1911). Today, there are around 64 migration barriers (42 HEPs) along the river and a remnant of this once-abundant population persists in the lowermost 10 km of the river, where approximately 1 km of suitable spawning and rearing habitat remains within a residual flow stretch below the lowermost dam. The absence of upstream fish passage solutions at this dam restricts diadromous fish to this section of the river. The study section encompassed the lower 28 km, including the two lowermost hydroelectric power plants in the system, Lanforsen HEP and Älvkarleby HEP, which play critical future roles for determining the extent of accessible habitat and the potential for re-establishing longitudinal connectivity in the system.

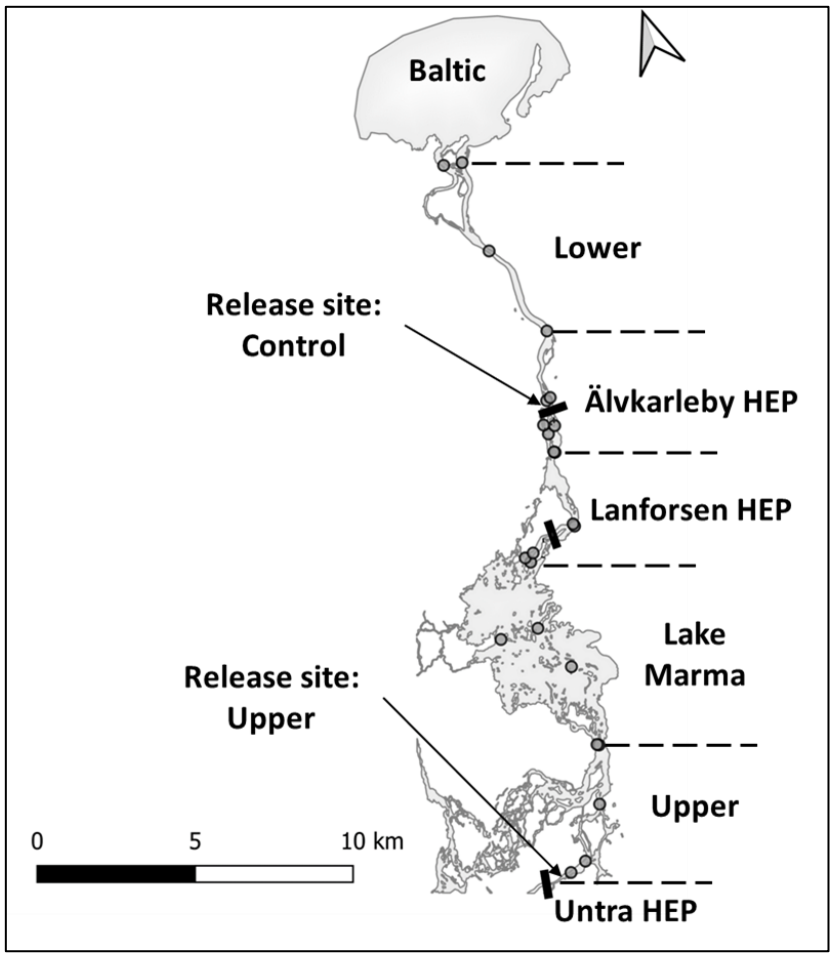


Figure 4. Map of the study reach in the river Dalälven with acoustic receivers (grey circles) deployed to track the downstream migrations of Atlantic salmon smolts past multiple HEPs (black bars). River sections of interest are divided into: Upper, lake Marma, Lanforsen HEP, Älvkarleby HEP, and Lower (dashed lines). Release sites (Upper and Control) are also indicated (arrows). Capture location located at control release site.

The river Emån is situated in southeastern Sweden (57.1429° N, 16.4517° E). The study described in Chapter **IV** was conducted within the lowermost 53 km of the river (Figure 5). The 220 km-long river system comprises of approximately 40 HEPs and about 300 additional barriers that restrict fish migration. Only around 10 percent of these structures are currently equipped with functional fish passage solutions (Halldén 1999, Stenström 2018). By 1952, dam construction had already blocked fish migration about 10 km upstream from the river mouth. In the early 2000s, the lowermost dam at Emsfors was removed, and nature-like fishways were installed at lower and upper Finsjö (2000) and Karlshammar (2020). These restoration efforts

extended the range of accessible habitat for migratory fish by roughly 40 km, up to the Högsby HEP, which now represents the first complete migration barrier. The designated study reach therefore included the three lowermost hydropower plants: upper Finsjö HEP, lower Finsjö HEP, and Karlshammar HEP.

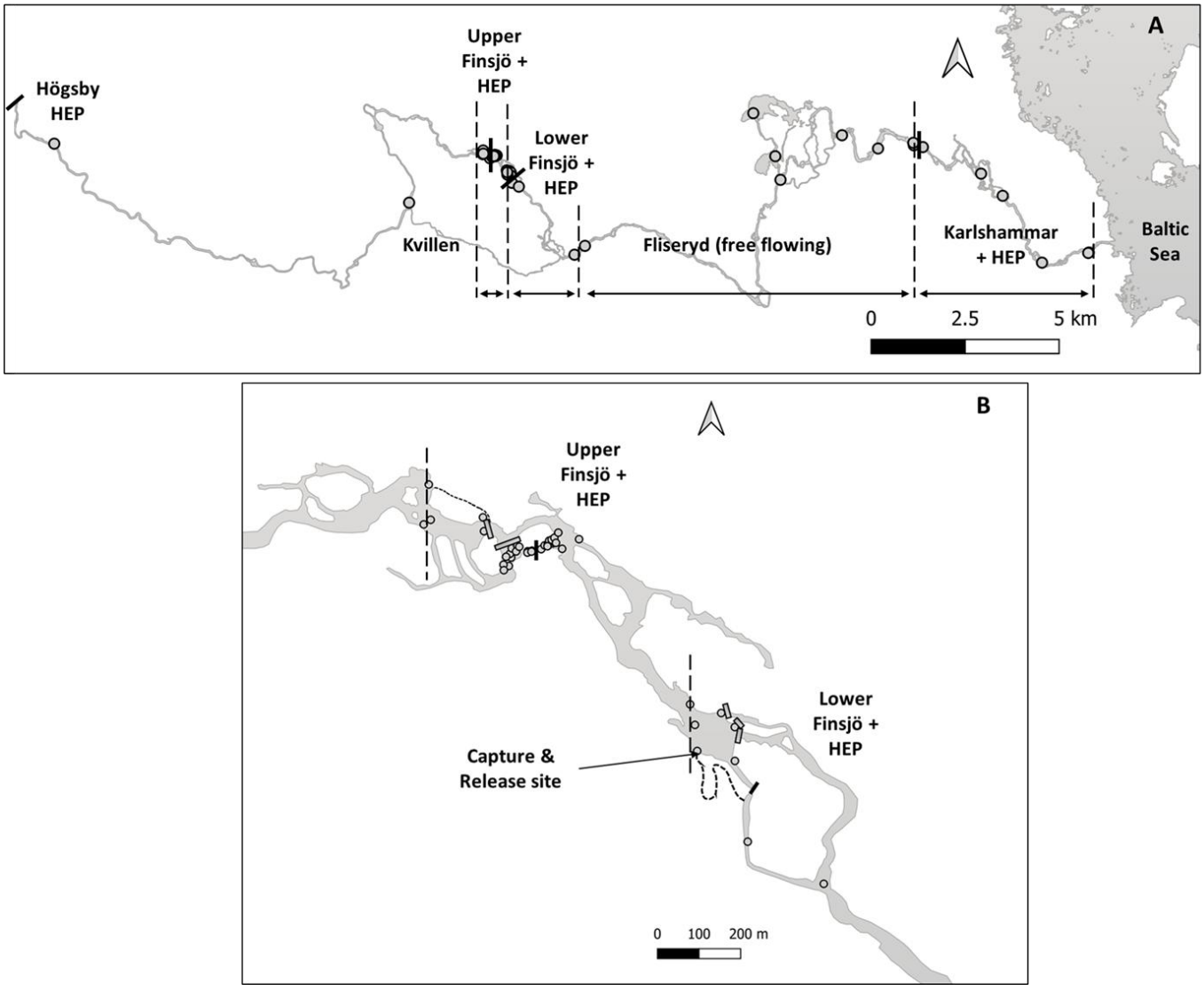


Figure 5. Map of study area (A) in the river Emån with acoustic receivers (gray circles) to track spawning/post-spawning salmonid migrations past multiple HEPs. Additional map of Finsjö HEPs (B) with spill gates (gray bars) and powerhouse (black bars), and nature-like fishways (short dashed lines). Dashed vertical lines divided river sections of interest: upper Finsjö, lower Finsjö, Fliseryd, and Karlshammar (long dashed lines). Capture and release site is also indicated (arrow).

Acoustic telemetry

To investigate passage rates, survival, route selection, and migration speed, spatial and temporal data from tagged individuals were collected in the field using acoustic telemetry. This technique enables passive monitoring of individuals throughout their migration and is widely recognized as one of the most effective tools for studying movement ecology and migratory behavior of fish in natural environments (Crossin et al. 2017, Hellström et al. 2022, Jacoby et al. 2025).

Acoustic transmitters were surgically implanted into a sample of wild-caught salmonids in each study. Fish were captured using traps (wolf traps or funnel traps) or by electrofishing prior to or during their downstream migration. Individuals were anesthetized and surgically implanted with one or more acoustic transmitters into the abdominal cavity through a ventral incision (Table 1). All acoustic transmitters were manufactured by Innovasea (Nova Scotia, Canada). Also, in the river Emån study (Chapter **IV**), passive integrated transponder (PIT) tags (Oregon RFID, Oregon, USA) were surgically inserted into the dorsal muscle tissue. Across all studies, tag burden did not exceed 4.6% of fish body mass and remained within accepted thresholds reported in previous studies (Newton et al. 2016, Lothian et al. 2024). Total length and body mass were recorded for all tagged individuals. Following surgery, fish were given a recovery period before release. Fish were either released at the capture location (Chapter **IV**) or transported to a designated release site, given an acclimatization period, and then released (Chapters **I**–**III**).

Table 1. Summary of tagged individuals by study, including study location, year(s) when study took place, species, life stage, number of individuals used in the study, acoustic or PIT transmitter type, and capture method.

Study	Year(s)	Species	Life stage	N total	Transmitter type	Capture method
River Mörrumsån (Chapters **I** – **II**)	2021	*Salmo salar*	Smolts	120	V5-180kHz	Wolf trap
River Dalälven (Chapter **III**)	2019, 2020, 2021	*Salmo salar*	Smolts	260	V5-180kHz, V5D-180kHz	Electrofishing
River Emån (Chapter **IV**)	2024	*Salmo salar, Salmo trutta*	Adults	64	V9-180-kHz, V13-69-kHz, 12mm HDX PIT	Funnel trap

In Chapters **I**, **III**, and **IV**, arrays of acoustic receivers were deployed across the study reaches in gate-like configurations along the river to record presences/absence data for tagged, migrating fish. Information on when and where individuals passed specific receiver locations was then used to analyze migration dynamics. In Chapter **II**, multiple receivers were positioned in close proximity within the forebays of two HEPs to obtain high-resolution telemetry data. When three or more receivers simultaneously detected the same acoustic transmission, triangulation methods were applied to estimate the relative positions of tagged fish every 2-3 seconds while within detection range (Campbell 2025). These positional data were subsequently used to track individual movements and assess how migratory behavior responded to varying environmental conditions, with a particular focus on river flow velocity.

Analyses

Passage and losses

Detection data from acoustic receiver arrays were retrieved for each study, and detection efficiency was assessed by comparing detections with the known migratory extent of individual smolts. Efficiency was 100% for most arrays (99% in Chapter **IV**) and assumed 100% at river-mouth arrays. Detection probability was assumed to be 1 and survival was estimated directly from observed entry-exit proportions. Passage success was calculated as the number of fish detected at both upstream

and downstream arrays of a river section, and passage efficiency as the proportion exiting relative to those entering. Fish not detected exiting a section were classified as lost, and section-specific instantaneous loss rates were calculated as –ln(survival)/section length to standardize among sections of differing lengths. In multi-channel sections, fish route selection was monitored by recording the number of individuals using each route based on array detections.

Passage speeds

Passage times were calculated as the interval between first upstream and first downstream detections for each river section, including only fish detected at both arrays to avoid bias from incomplete passages. In Chapter **IV**, kelts overwintering within a section (passage >30 days) were excluded. Section distances were used to calculate downstream migration speeds ($km \cdot day^{-1}$) and loss rates ($\% \cdot km^{-1}$). Two complementary speed metrics were computed: mean individual section speed, reflecting individual-level variability, was calculated by dividing section distance by each fish's travel time and averaging across all successful migrants; section-level speed, reflecting population-level movement, was calculated as total section distance divided by total travel time across all fish. These metrics together capture individual behavioral variation and overall section migration dynamics.

Speeds were compared among sections using the Kruskal-Wallis test, with post-hoc pairwise Wilcoxon tests and Benjamini-Hochberg p-value adjustment. Factorial effects of section, sex, and species were tested using aligned rank transform (ART) ANOVA (R package ARTool), and post-hoc section contrasts within species or sex were obtained using estimated marginal means with Bonferroni correction.

Generalized linear models

To assess the influence of biological, environmental, and anthropogenic factors on passage success, binomial logistic regression (GLMs) was applied to each river section, with the response variable indicating whether a fish successfully exited a section. Global models included fish length, condition factor, release day, year, diel period, and release site as additive predictors. Length and condition factor were standardized by global means and standard deviations for Chapters **I-III**; for

Chapter **IV**, condition was standardized within species due to significant interspecific differences. Environmental covariates such as water temperature, total discharge, and diel period at section entry were obtained from the nearest upstream HEP or, when available, from HEPs within the section. To account for predictable seasonal variation and temporal autocorrelation, temperature and discharge were detrended by calculating residuals from seasonal trends, estimated as 7-day (Chapters **I**-**III**) or 14-day (Chapter **IV**) sliding averages of daily values across the study period.

Time-to-event models

Passage timing within each river section was analyzed using time-to-event models to assess how biological, environmental, and anthropogenic factors influenced downstream passage rates, defined here as the proportion of smolts passing per unit time (Castro-Santos & Perry 2012). Cox proportional hazards models were fitted, with the event defined as successful downstream passage and time measured from first upstream to first downstream detection; fish not exiting a section were right-censored at their last detection. A global model including all candidate covariates was fitted, followed by full subset model selection using the MuMIn package (Bartoń 2020), retaining models within ΔAIC < 6 and excluding uninformative parameters (Arnold 2010). Best-fit and most parsimonious models were examined, and proportional hazards assumptions were evaluated with Schoenfeld residuals. Higher hazard rates indicate faster passage. Temporally varying covariates such as total, turbine, and spill discharge, and standardized hourly temperature, were assigned based on each individual's time of entry; in non-hydropower sections, total discharge was obtained from the nearest upstream HEP, and spill rates were calculated per HEP.

Hydraulic modeling

In Chapter **II**, two-dimensional hydraulic models were created using BASEMENT (Vanzo et al. 2021) with technical data on structures and discharge provided by the relevant operators. Bathymetry was obtained from surveys and refined using LiDAR data to improve river boundaries and interpolate missing values. Known elevation points were used to validate and correct the bathymetry. Raster resolution ranged from 0.25 to 0.5 m depending on the model.

Smolts were clustered based on inflow and proportional spill using K-means clustering and the elbow method (Umargono et al. 2020), yielding two cluster groups for analysis. Model runtime was set to allow stabilization, and inflow data were offset to account for travel time from upstream sources and verified against local discharge measurements. Proportional spill was calculated as the fraction of total inflow passing through spill structures, and discharge data from all outflow locations (spillways, turbines, fishways) were used to ensure accurate representation of flow conditions.

Static hydraulic models were developed to represent observed conditions for the two smolt clusters. The computational mesh used finer elements in areas of high interest (e.g., spillways) and coarser elements elsewhere. Hydraulic outputs at each mesh node (GPS coordinates, X, Y, and Z velocities) were extracted and interpolated using natural neighbor interpolation via the WhiteboxTools Python package (Geospatial 2023).

Fish and receiver positioning

High-resolution smolt tracks in spill-gate forebays were produced by combining raw acoustic detections to calculate location estimates per transmission, generating individual tracks using the R package kaltoa (Campbell 2025). Array receiver clocks were synchronized using a mixed model in the R package TMB (Kristensen et al. 2016), treating clock drift as a Gaussian random walk and applying hourly drift corrections, yielding clock accuracy of 2–4 ms.

Positions were estimated using the PMC-TOA model with $\sigma\_det = 2$ ms, $\varphi = 466$ ms, and $\beta = 32$ (Campbell et al. 2025), accounting for direct and reflected detection errors. Position estimates and uncertainties were then smoothed using a continuous-time correlated random walk with a Kalman filter and Rauch–Tung–Striebel smoother (Johnson et al., 2008; Campbell et al., 2025), with horizontal velocity following a Rayleigh distribution (mode = 0.2 $m \cdot s^{-1}$) and velocity correlation dropping below 0.05 after 5 s. Environmental covariates were attached to each position to assess flow effects, including the vector difference between fish velocity and local water surface velocity (delta velocity

magnitude). Additional transformed parameters (e.g., squared, log) were included to improve model fit.

Route selection

Observed smolt route selection through the spill gates and turbine intake channels was determined from individual tracks. Fish were classified as using a route if their final positions were within or within 10 m of that route. Individuals that did not exit the forebay or showed signs of predation (i.e., prolonged movement within the forebay) were excluded. Additional behavioral metrics included array time, calculated as the interval between first and last detections, and entry location, based on the first position in the array relative to the river channel thirds (west, middle, east). Passage route proportions were calculated as the number of fish exiting via each route divided by the total exiting the array downstream.

Animal movement analysis

Step selection functions (SSFs) were used to assess how environmental covariates influenced smolt navigation within spill-gate arrays. SSFs were implemented as conditional logistic regressions using Cox proportional hazards models (survival package; Therneau 2015), treating all tracks as a single fish under the assumption of similar swimming behavior. Random steps were simulated from a continuous-time correlated random walk (CTCRW) fitted to the smoothed tracks. Observed and random positions were compared with associated environmental covariates to evaluate relative preference. Models were assessed using ranked AIC, variable significance, and goodness-of-fit metrics, with the best-fitting and most parsimonious models examined in detail.

Simulation analysis

The best-fitting SSF model was used to simulate smolt tracks within each spill-gate array. For each simulated track, an upstream starting point was selected, and up to 100 steps were simulated. At each step, random available positions were generated using the fitted CTCRW model, and the SSF was applied to select the next position. Tracks ended when a route entrance (within 10 m of a spillway or turbine intake) was reached or the maximum number of steps was completed. The simulation was validated by replicating the observed dataset 200

times: each observed fish's track was simulated from its first detected position, and simulated route choices were compared to observed route selections to assess model performance.

Summary of results

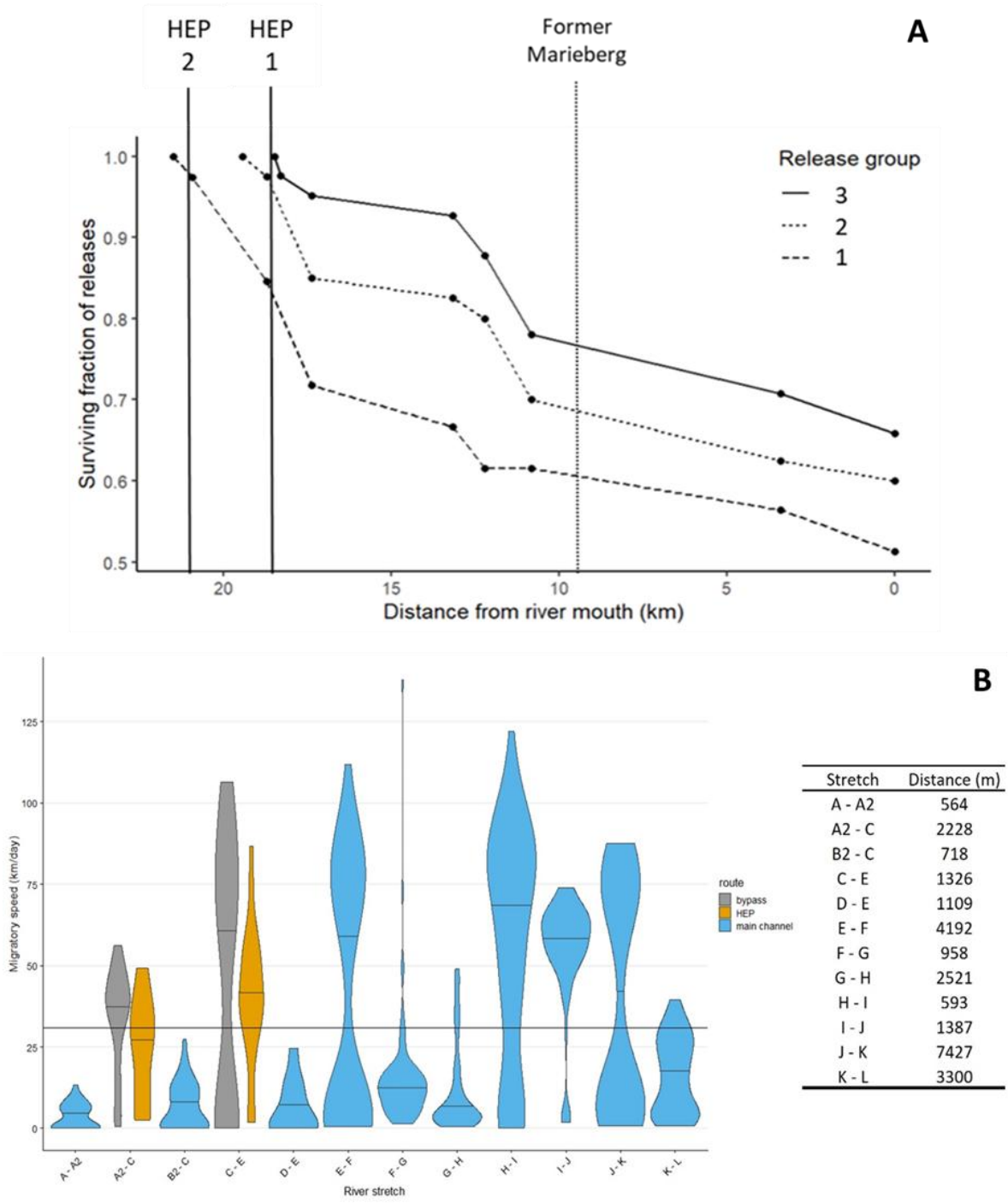
In Chapters **I** - **III**, smolt passage efficiencies at HEPs ranged from 71-95%, compared with efficiencies of 75-100% in free-flowing river sections. The lowest recorded passage efficiency was at Älvkarleby HEP (2019: 71%), in river Dalälven, a large-scale dam lacking downstream passage solutions. Small-scale dams with a spill passage solution (upper and lower Hemsjö HEPs in river Mörrumsån) had relatively high passage efficiencies (87% and 86% respectively), but the proportion of smolts passing via the spill passage solution was only 60%. Smolt movement in HEP spill-gate forebays was influenced by flow velocity and velocity gradients. Smolts preferentially selected areas of higher velocity while avoiding strong gradients affected their route selection. River section loss rates for smolt across the studies ranged between 0 and 13.6% · km^{-1}, and section migration speeds varied from 2.1 – 24.2 km·day^{-1}. The highest lost rates for smolt were observed in river section containing HEPs or lentic habitat, where as some of the highest passage rates and migration speeds for smolt were observed in free-flowing river sections. Dam removal (Marieberg HEP) in river Mörrumsån improved smolt migration speeds, which were approximately twice as fast post-removal. Among the variables analyzed, diel period, body size, and water temperature had the greatest impact on passage rates.

In Chapter **IV**, kelt passage efficiencies at dams and free-flowing river sections ranged from 81-93%, with the lowest passage efficiency observed at an HEP lacking a dedicated downstream passage solution at the turbine intake (lower Finsjö HEP). The highest passage efficiency was at a HEP that incorporated multiple downstream passage solutions (Karlshammar HEP). Downstream migration loss rates across study sections ranged between 1.0 – 13.2% · km^{-1}, with the highest loss rates within an HEP river section (upper Finsjö HEP). Downstream migration speed across study sections ranged from 0.6 - 6.2 km·day-1, with the lowest speeds recorded at the HEP lacking a dedicated downstream

passage solution at the turbine intake (lower Finsjö HEP). Among the variables analyzed, sex, species, diel period, and water temperature had the greatest impact on passage rates. Overwintering was also found to be an important aspect of downstream migration for kelts, with only individuals overwintering in the river successfully migrating to the river mouth in the spring, with no successful outmigration in the fall.

Chapter I

In the river Mörrumsån, passage efficiencies for smolt were 86% and 87% at upper and lower Hemsjö HEPs respectively, with variation observed in route selection, delays, and loss rates between the HEPs. Approximately 60% of individuals passed each HEP via the spill gates. Passage rates were influenced the most by body size, diel period, and water temperature, whereas total river discharge had little effect. Overall cumulative passage success to the river mouth was 61%, with most losses occurring within lentic sections of river, particularly in HEP forebays and naturally slow-flowing river sections (Figure 6A). In the river sections that had been restored following dam removal, migration speeds were significantly faster than all other sections of the river (post-restoration $\bar{x}$= 56.1 km·day^{-1}, Figure 6B) representing a significant increase compared to pre-restoration speeds (pre- $\bar{x}$ =28.0 km·day^{-1}, post-$\bar{x}$= 56.1 km·day^{-1}, Mann Whitney U: $p < 0.001$).



Stretch	Distance (m)
A - A2	564
A2 - C	2228
B2 - C	718
C - E	1326
D - E	1109
E - F	4192
F - G	958
G - H	2521
H - I	593
I - J	1387
J - K	7427
K - L	3300

Figure 6. (A) Cumulative passage success from release to the river mouth for each release group (release group 3: solid line, release group 2: dotted line, release group 1: dashed line). Locations of each HEP are also highlighted in relation to their distance from the river mouth (HEP 2: upper Hemsjö, HEP 1: lower Hemsjö, and the removed Marieberg HEP). (B) Smolt speeds for each river stretch from release to the river mouth. Color indicates river passage type (free flowing main channel, turbine intake and HEP powerhouse, or HEP bypass and residual flow stretch). Median lines indicated for each river section as well as a mean line of overall migration speed Table indicates river stretch distances in meters.

Chapter II

High-residency arrays in the spill gate forebays of upper and lower Hemsjö HEP successfully tracked smolt movement through two passage options: turbine intake channels or spill gates. Observed hydraulic scenarios indicated that smolts passed each forebay under two dominant proportional spill conditions, with increased spill discharge increasing spill gate passage (observed: 11–14%; simulated: 4%). Forebay entry location likely influenced route selection, with the highest spill gate passage when smolts entered the HEP forebay on the same side of the river as the spill gates (64% and 100% for the upper and lower HEPs, respectively). The Cox proportional hazards models showed that flow velocity, velocity magnitude, and change in velocity magnitude were highly influential in determining step selection probabilities. Increased velocity magnitude increased step selection probability (HR = 3.31×10^{3}, 95% CI: 1.80×10^{3}–6.06×10^{3}, $p < 0.001$), whereas greater changes in velocity magnitude reduced it (HR = 1.47×10^{-7}, 95% CI: 7.88×10^{-8}–2.74×10^{-7}, $p < 0.001$). An individual-based model (IBM) parameterized with SSF results produced 16,800 simulated tracks (Figure 7B), which closely approximated observed patterns, though spill gate passage was slightly underestimated (predicted: 44% vs. observed: 56%, Figure 7A).

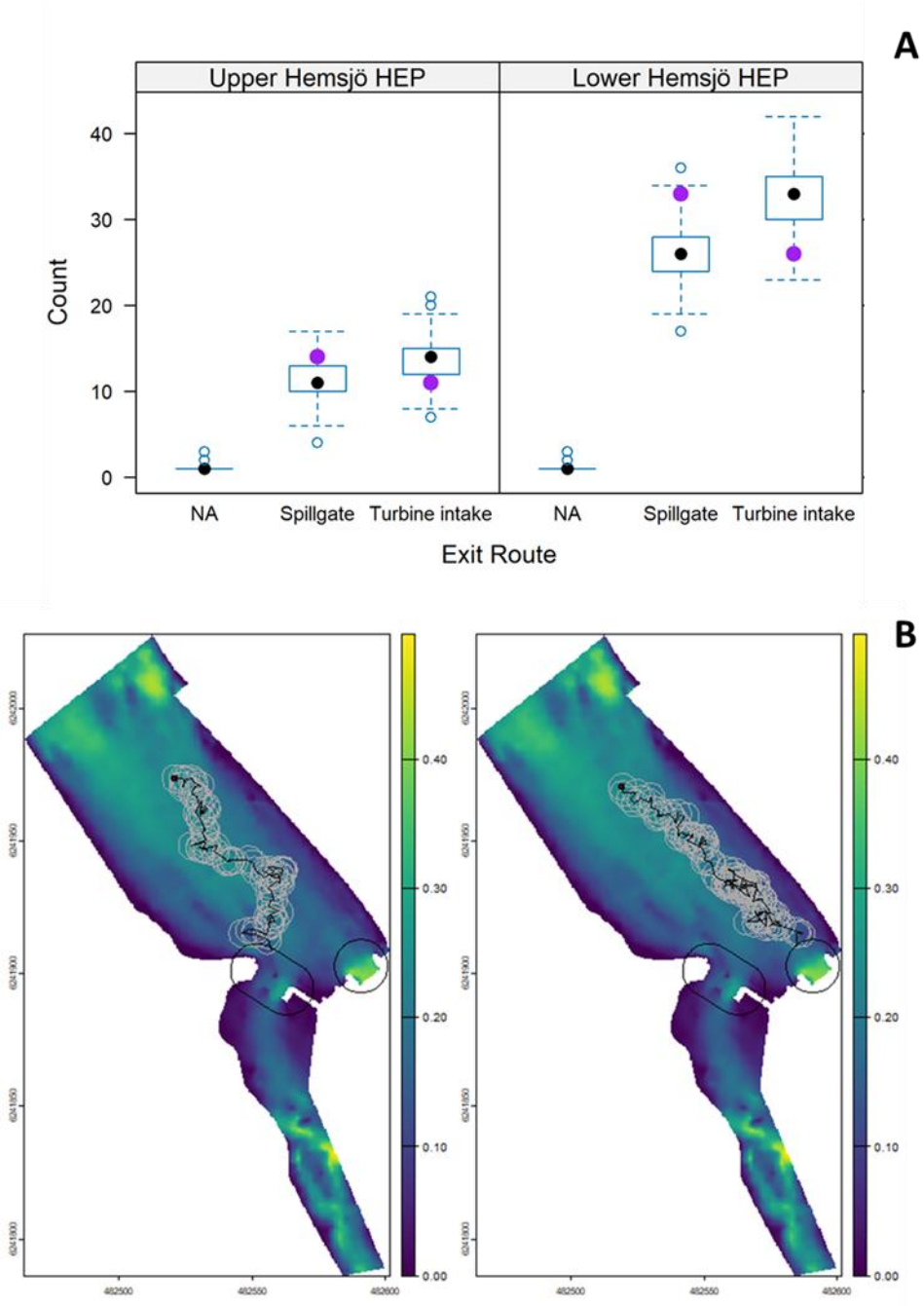


Figure 7. (A) Aggregated simulated passage route counts for smolts at upper and lower HEPs under both flow clusters. Blue boxplots show simulated counts across replicates (IQR and outliers, median as black circle), with observed counts shown as purple circles. (B) Example of simulated tracks for lower HEP, generated from observed entry points using the SSF and CTCRW model. Tracks ended upon reaching a route entrance (10 m radius around spillway or turbine, black ellipses) or after 100 steps; gray error ellipses show positioning uncertainty.

Chapter III

In the river Dalälven, passage success across the 27 km study section, with two large-scale dams lacking fish passage solutions, was similar across the three study years, averaging 57% (2019: 53%, 2020: 61%, 2021: 58%, Figure 8A), corresponding to a mean loss rate of 2 % · km-1. As a comparison, passage success across the 10 km long unfragmented control section, was 94%, corresponding to a mean loss rate of 0.62% · km^{-1}. Mean section migration speeds were also consistent among years, with smolts traveling an average of 2.7 $km \cdot day^{-1}$ and typically requiring around 11 days to reach the Baltic Sea from the upper release site (27 km upstream from river mouth) after passing the two large-scale HEPs. Passage rates and migration speeds were lowest through lentic habitats and HEP sections, suggesting potential migratory bottlenecks. Average section speeds were 4.0 $km \cdot day^{-1}$ through Lanforsen HEP and 0.76 $km \cdot day^{-1}$ through Älvkarleby HEP. The *Älvkarleby* section also exhibited the highest loss rates, averaging 5.5% · km^{-1} across the three study years, with an average passage efficiency of 80% (2019: 71%, 2020: 78%, 2021: 94%). Among the variables analyzed, water temperature, body size, release year, and diel period were the strongest predictors of passage rates. Passage rates in some sections increased during the night, with increasing water temperatures, and with increasing body size. For Älvkarleby HEP, release year was an important variable for passage rates and the operation of the G6 turbine improving passage rates at high discharge levels. Both release groups exhibited similar passage rates through the *Lower* river section, 94% for the control group and 97% for the HEP-passage group; however, section migration speeds in the control group were more than twice those of the HEP-passage group in 2020 (Figure 8B). Section speed in the *Lower* river section were the highest recorded across the study area and were significantly faster than all other sections (pairwise Wilcoxon rank sum test, p-values range = 3.8e-8 to <2e-16).

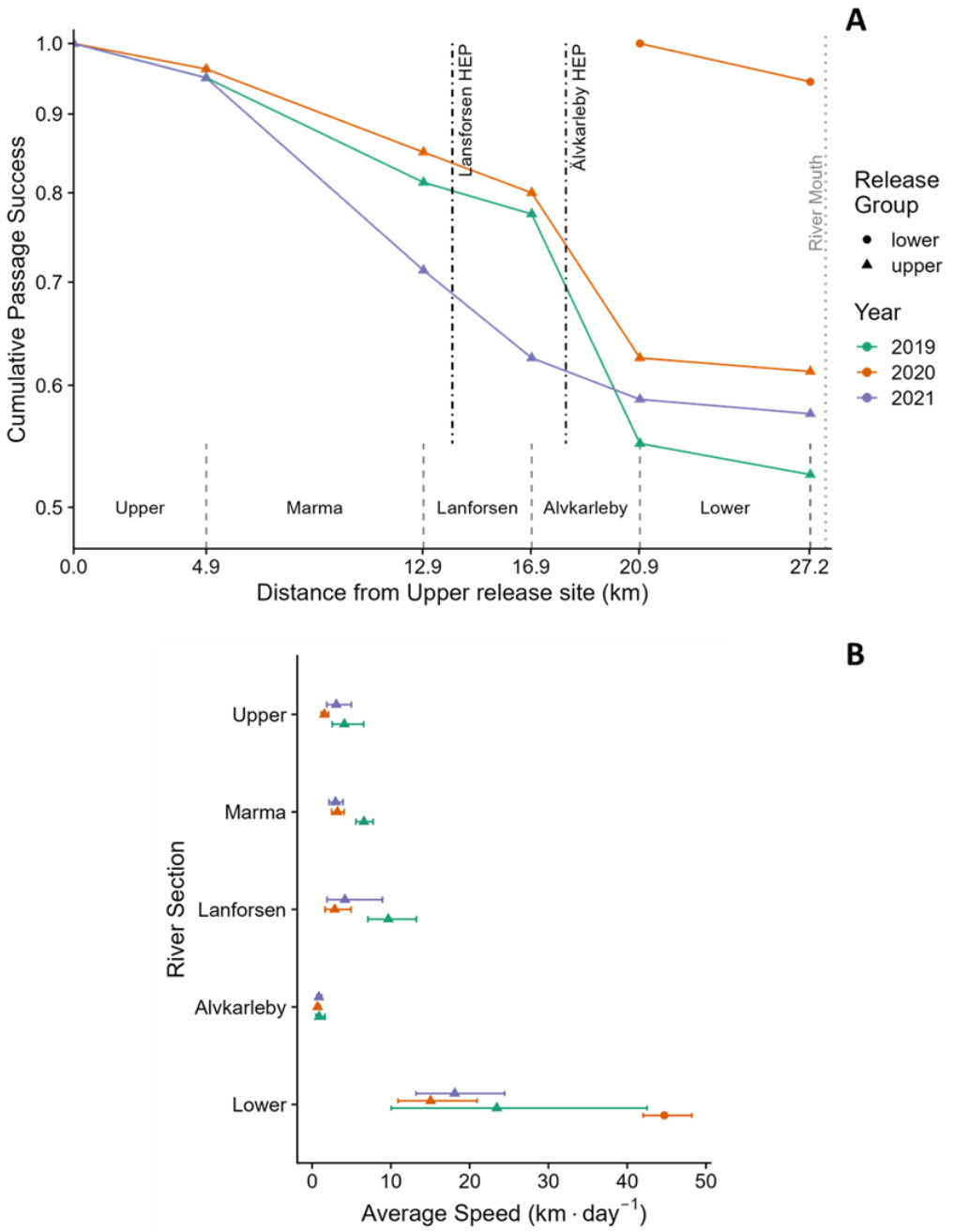


Figure 8. (A) Cumulative passage success (log10 scale) during downstream smolt migration from the respective release sites (upper and control) to the river mouth across study years (2019-2021). Dotted black vertical lines indicate the locations of the two HEPs where turbine passage was required (Lanforsen HEP and Älvkarleby HEP). Dotted grey vertical lines delineate the five river sections used in the analysis and the river mouth. Line color denotes study year (2019: green, 2020: orange, 2021: purple) and point shape indicates release location (upper release site: triangle; lower release site: circle). (B) Mean migratory speeds (km/d) through each river stretch of the study area. Color denotes year (2019-2021) while error bars are bootstrapped 95% confidence intervals for the mean (n = 1000). Symbol denotes release location (triangle = upper, circle = lower).

Chapter IV

In the river Emån, 61 salmon and anadromous brown trout continued migrating upstream after release, and 50 (82%) successfully passed the upper Finsjö HEP using the nature-like fishway; no individuals entered the double rotating screw turbine. A subset of tagged individuals (27%) migrated an additional 24 km upstream to Högsby HEP, the first definitive barrier in the river system. The majority of losses occurred during the fall, with 20 individuals having their last detections during this period. Overwintering occurred in 35 individuals with two-thirds of overwintering upstream of upper Finsjö HEP (>30km upstream from river mouth) throughout winter. Downstream migration was initiated by 44 individuals and occurred primarily during daylight hours and in spring. Passage efficiencies at HEPs ranged between 81-93%, with the lowest efficiency at lower Finsjö HEP (81%), the only HEP in the study area without a dedicated downstream passage solution.

Passage success across all analyzed river sections remained relatively high (81–93%), yet travel efficiency differed markedly, with section-level speeds ranging from 0.6 km·day^{-1} in the lower Finsjö section to 6.2 km·day^{-1} in the *Karlshammar* section. Downstream individual passage speeds differed significantly among river sections (Kruskal–Wallis: $\chi^2 = 29.50$, df = 3, $p < 0.001$; Figure 9) and pairwise comparisons showed that both *upper Finsjö* and *lower Finsjö* sections had significantly lower speeds than the *Fliseryd* and *Karlshammar* sections, while no differences were detected between *upper Finsjö* and *lower Finsjö* or between *Fliseryd* and *Karlshammar* sections. Individual passage speeds also differed by sex, with females migrating faster than males ($\chi^2 = 4.87$, df = 1, $p = 0.027$), whereas no overall difference was detected between species. However, aligned rank transform ANOVA revealed significant effects of river section, species, and their interaction on passage speeds, indicating section-specific species responses. Post-hoc tests showed that salmon migrated at lower speeds in the *lower Finsjö* section compared to the *upper Finsjö* and *Fliseryd* sections. Overall, 25 fish (21 brown trout and 4 salmon) successfully migrated to the river mouth and exited the river in spring, corresponding to an overall survival of 42% for trout and 29% for salmon. Only individuals that overwintered in the river were ultimately detected at the river mouth, with no successful outmigration in the fall.

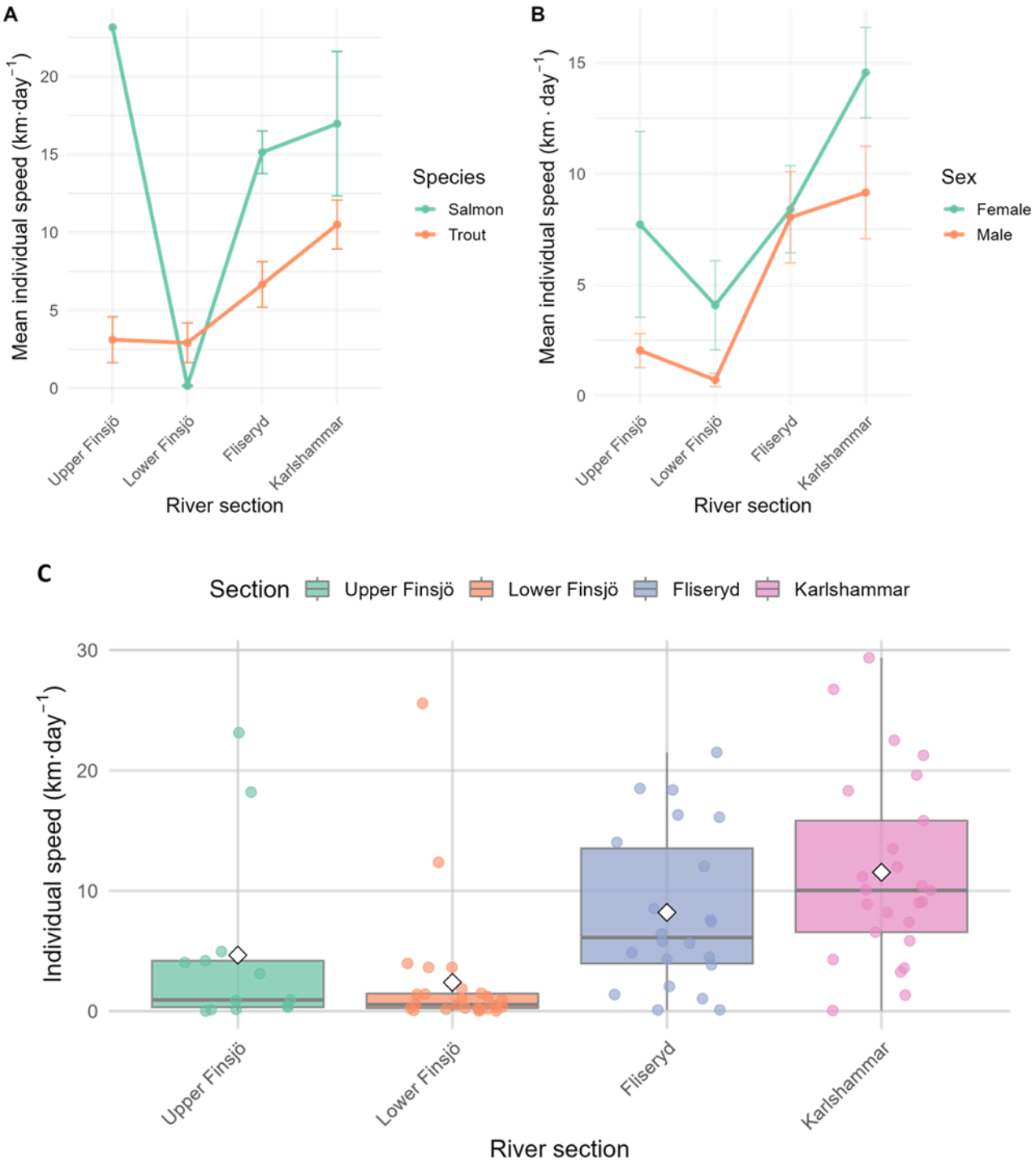


Figure 9. Individual passage speeds for each river section. (A) Species specific with green denoting Salmo salar and orange denoting Salmo trutta. (B) Sex specific with green denoting female and orange denoting male. In both (A) & (B) error bars represent ± standard error of the mean. (C) All individual passage speeds with mean speeds (white diamond) indicated. Boxplots represent the interquartile range (25th-75th percentile) with the median line (gray line) and colors denote river sections.

Discussion

This thesis examined the downstream migrations of Atlantic salmon and anadromous brown trout smolts and kelts in regulated river systems. Across four studies, the research evaluated fish passage rates, migration speed, and the influence of environmental and anthropogenic factors under varying river conditions. Collectively, the results demonstrate that hydropower infrastructure continues to impose significant constraints on downstream migration efficiency. However, targeted restoration measures, such as dam removal and other fish passage solutions, can substantially improve migration outcomes.

Passage efficiencies at individual HEPs ranged between 71% and 95%, with some below the recommended 90% threshold for effective fish passage (Calles et al., 2013, Silva et al., 2018). Although these values indicate moderate success at individual sites, overall smolt passage rates to sea after navigating two large HEPs without FPSs averaged 58%, with kelt passage rates to sea after spawning and navigating three HEPs with a variety of FPSs averaging 39%, reflecting the cumulative effects of multiple barriers and natural mortality. The comparison between HEP- and control-release groups in rivers Mörrumsån (Chapters **I**) and river Dalälven (Chapter **III**) highlighted possible cumulative effects of multiple barrier passages, demonstrating how cumulative losses arise from both HEP passage and natural mortality. These cumulative losses increase with the number of barriers encountered, such that fish originating higher in the system experience greater losses. However, because the fate of lost individuals cannot be directly determined, disentangling the specific causes of mortality remains challenging. Losses associated with HEP sections may result from forebay delays (e.g., navigational difficulties leading to increased predation risk or energetic costs), direct turbine-related injuries (e.g., blade strike, pressure changes, or shear forces), post-passage effects (e.g., sublethal injuries or disorientation increasing vulnerability to predation), or some combination of these factors (Coutant & Whitney 2000, Thorstad et al. 2012, Algera et al. 2020, Mensinger et al. 2023). Even when individual passage efficiencies appear acceptable, sequential exposure to multiple dams can reduce overall migratory success (Whitney et al. 1997, Norrgård et al. 2013, Nyqvist et al. 2016). This cumulative impact

is illustrated by the upper and lower Finsjö HEPs. Passage efficiency at upper Finsjö was relatively ok (88%); however, passage at lower Finsjö was lower (81%). The two Finsjö HEPs are located in close proximity (approximately 850 m apart), likely compounding their negative effects on downstream migration within a very limited river reach. Thus, even though multiple downstream passage solutions were present at upper Finsjö HEP, their positive effects were partially offset by the absence of an adequate downstream passage solution at the turbine intake of lower Finsjö HEP.

Full-river losses accumulated progressively downstream, particularly within impounded sections. Most losses were concentrated to lentic habitats, particularly within hydropower forebays and reservoir reaches, consistent with previous studies reporting increased predation risk for smolts and disorientation in low-flow environments (McCormick 1998, Renardy et al. 2021, Mensinger et al. 2023). This pattern was evident in the *Lake Marma* river section upstream of Lanforsen HEP, in river Dalälven, where passage rates ranged from 75% to 88% across the three study years. This reservoir section, approximately 8 km in length and up to 3 km in width, appeared difficult for smolts to traverse, with a mean section passage speed of only 3.7 km·day^{-1}. Historically, this river section was a naturally lentic environment, which may have posed challenges for smolt migration; however, damming exacerbated these conditions by elevating water levels and further reducing the limited flow velocity cues available to migrating smolts. The observed differences in losses between river sections with and without HEPs suggest that these barriers impose substantial additional costs on downstream migration beyond what fish would experience in unfragmented river. These differences between presences or absence of HEPs is further supported by the observed differences in migration speeds among river sections.

Section migration speeds ranged between 0.6 and 24.2 km day^{-1} across river sections, with speeds typically lowest within HEP sections and highest within free-flowing sections. The slow progression through these areas could indicate increased behavioral hesitation or difficulty locating passage routes, likely associated with HEP factors such as altered hydrodynamics, predation risks, and navigational difficulties

(Hvidsten & Johnsen 1997, Larinier 2008, Serrano et al. 2009). An example of this would be Älvkarleby HEP, where passage speeds were consecutively the slowest across all study river sections in the river Dalälven and across all three study years. In contrast, migration through free-flowing and restored river sections, as well as at HEPs that have incorporated downstream fish passage solutions, demonstrated that improved connectivity and flow conditions can enhance migration speeds, emphasizing the importance of maintaining or restoring free-flowing reaches. Karlshammar HEP, which is equipped with multiple integrated downstream passage solutions, exhibited the fastest river section speeds of all study sections. In contrast, this pattern was not observed at upper Finsjö HEP, where multiple downstream passage solutions are also present but passage speeds remained relatively slow compared to other river sections. One possible explanation for the slower speeds at upper Finsjö HEP relates to its upstream location and the kelt life stage. Upper Finsjö HEP is located approximately 30 km upstream from the Baltic Sea, placing it relatively high in the river system accessible to migratory fish. Across the study system, river section speeds generally increased in a downstream direction (with the exception of *lower Finsjö*), which may reflect increasing migratory readiness or physiological condition, as well as rising spring water temperatures that could be a cue for out-migration (Östergren & Rivinoja 2008). Downstream migration of kelts also differs fundamentally from that of smolts, as it often occurs over longer timescales. Kelts may pause to overwinter or move slowly through certain river sections, especially individuals in our study that were last detected during the fall and were ultimately classified as lost. These slow passage speeds may be more closely linked to physiological condition than to passage performance at the HEP itself (Halttunen et al. 2013, Penney & Moffitt 2015). River restoration through the removal of the Marieberg HEP in the river Mörrumsån also improved migration speeds, with this section speed more than doubling following HEP removal. Reduced delay times relative to pre-removal conditions and to HEPs lacking downstream passage solutions further support the ecological value of such mitigation and restoration measures.

The different types of downstream fish passage solutions assessed provided insight into how passage design influences downstream passage

rates. Dam removal, as discussed above, reduced passage delays and restored a free-flowing river section, improving connectivity and representing, from an ecological perspective, the most beneficial passage solution. For HEPs that remain in place, the presence of multiple downstream passage solutions appeared to be a key factor contributing to higher passage rates and faster passage speeds. Karlshammar HEP exhibited some of the highest passage rates and speeds in this study and incorporates both a wide, nature-like fishway and physical guidance structures (racks) that direct fish toward a bypass at the turbine intake, likely contributing to these positive outcomes. Spill gate passage appeared to facilitate downstream migration at small-scale dams for both smolts and kelts to some extent; however, the primary limitation may be the ability of individuals to locate the spill route. Hydraulic modeling and fish movement tracks from the Hemsjö HEP forebays indicated that flow velocities into spill gates must be sufficiently strong for smolts to detect and follow during downstream migration (Williams et al. 2012, Jebria et al. 2023). Increasing spill discharge may improve spill gate passage proportions, but potential hydropower losses must also be considered. A similar pattern appeared to occur at lower Finsjö HEP, where kelts experienced delays and may have had difficulty locating the spill gate or the entrance to the nature-like fishway. At these HEPs, incorporating a combination of downstream passage solutions, such as physical guidance structures at spill gates and turbine intake channels leading to a bypass, could potentially improve passage rates and speeds (Calles et al. 2012, Nyqvist et al. 2017, Fjeldstad et al. 2018). At upper Finsjö HEP, the majority of kelts passed via the spill gates, although some individuals used the low-injury turbine for downstream passage. With similar passage success observed between spill and low-injury turbine routes, this combination of downstream passage solutions, together with the nature-like fishway, appeared to provide adequate downstream passage conditions. Passage However, most HEPs in Sweden today, including several evaluated in this thesis, are not equipped with downstream passage solutions, leaving turbine passage as the only available route for downstream-migrating fish.

HEPs lacking dedicated passage solutions generally exhibited lower passage rates compared to sites where some form of downstream passage solution was available. This pattern was evident at Älvkarleby

HEP, where no dedicated downstream passage exists and the only available route is through the turbines. The *Älvkarleby* river section exhibited the lowest passage rates of all sections analyzed and some of the slowest section speeds. However, *Lanforsen* had relatively good passage rates, with speeds comparable to other river sections. This was the first HEP encountered by smolt in the river Dalälven, so perhaps the lack of cumulative dam passages improved passage rates and speeds (Elder et al. 2016). The forebay layout of Lanforsen HEP is relatively narrow, funneling the river into a 60m wide turbine intake channel, with strong flow velocities and few low velocity areas, which could have led to increased speeds during HEP passage. Lanforsen HEP is also less than half of the head height of Älvkarleby HEP (10 meters and 23 meters respectively) and Lanforsen HEP has Kaplan turbines, whereas Älvkarleby HEP has primarily Francis turbines. These differences in head height and turbine type could also play a role in passage rates (Algera et al. 2020, Vikström et al. 2020). At lower Finsjö HEP on the river Emån, the turbine intake is equipped with a rack, preventing turbine passage for kelt, which most likely improved kelt passage rates in this river section, but this HEP still induced passage delays as downstream passage solutions seemed difficult to locate, highlighting the importance of passage placement (Williams et al. 2011). Overall, HEPs equipped with downstream passage solutions, particularly when well positioned, tended to exhibit higher passage rates and speeds relative to sites lacking such measures.

Analyses across chapters identified diel period, water temperature, and body size as significant predictors of passage rates and timing, whereas discharge played a more limited role. The findings regarding diel period align with established patterns in salmonid migration, where kelts often migrate more efficiently during daylight hours, while nocturnal movement may function as a predator-avoidance strategy for smolts (Östergren & Rivinoja 2008, Thorstad et al. 2012). At the free-flowing *Fliseryd* river section, kelt passage rates were significantly higher during the day than at night, whereas smolts exhibited significantly higher nocturnal passage rates in both rivers Mörrumsån and Dalälven. Daylight duration might also have been an important factor for the start (shorter day lengths) and end (longer day lengths) of overwintering in kelt. When examining water temperature, smolts increased passage

rates with increasing water temperatures, but this relationship appeared to be less influential for kelts. These temperature effects likely reflect physiological thresholds related to migratory readiness, environmental cueing, and possibly linked to predator avoidance, which may be more critical for smolts than for kelts (McCormick et al. 1998, Hvidsten et al. 2009). For kelts, both the start and end of overwintering holding periods occurred at similar water temperatures, suggesting a possible thermal threshold for overwintering behavior, and may act as a cue for initiating or reinitiating downstream migration during spring (Östergren & Rivinoja 2008, Nyqvist et al. 2017). Migration timing in relation to diel period and water temperature is particularly important in spring, when increasing day length and rising water temperatures coincide. As we find these variables can affect passage rates, their timing represents a key consideration for migratory survival and management (McCormick et al. 1998, Thorstad et al. 2012). Fish length was also positively correlated with passage rates in smolts, with no corresponding effect observed in kelts. In contrast, biotic influences on kelt passage rates were more strongly associated with sex and species. The stronger size dependency observed in smolts may reflect differences in predation risk and swimming performance, as larger smolts are stronger swimmers and less vulnerable to predation (Ibbotson et al. 2011, Jonsson et al. 2016). Kelts likely experience reduced predation-driven selectivity and instead appear to be more influenced by physiological condition, potentially linked to spawning recovery rather than migratory performance (Halttunen et al. 2013). Release date also emerged as an influential variable for smolts in certain sections of the river Dalälven, with later releases having a negative effect on passage rates. This is noteworthy given that the timing of smolt migration is highly predictable, with peak emigration typically occurring within a narrow window of only a few days to a few weeks each year. A similarly synchronized emigration pattern was observed for kelts, with nearly all successful emigrants leaving the river within a brief period in spring. These results suggest that timing is a critical factor for both smolts and kelts, likely reflecting selection for entry into the marine environment at an individual's optimal period that maximizes feeding opportunities, minimizes mortality risks, or a combination of both and other, less well-understood processes (Hvidsten et al. 2009, Thorstad et al. 2012, Simmons et al. 2024). The relatively weak influence of discharge

contrasts with previous studies showing positive associations between increased flow and downstream migration rates. This discrepancy may stem from the regulated flow regime, where operational constraints at HEPs dampen natural discharge variability, thereby reducing its ecological signal as a migratory cue (Renöfält et al. 2010). Nevertheless, flow velocity appeared to strongly influence fine-scale smolt movement behavior within the Hemsjö HEP forebays, suggesting that discharge effects may operate at finer spatial or temporal scales than those captured by our river section scale passage models. Additionally, because our studies focused on passage efficiencies during migration rather than on the precise timing of migration initiation, discharge may have more importance as a migratory cue rather than directly influencing passage rates within individual river sections (Carlsen et al. 2004, Bendall et al. 2005). Together, these studies highlight the importance of environmental variables as key cues guiding migratory salmonids, shaping migration timing and behavior, and ultimately influencing their ability to successfully navigate river systems enroute to the marine environment.

Overall, this thesis demonstrates that while barriers continue to constrain downstream migration of salmonids, meaningful improvements can be achieved through barrier removal and improved passage solutions. Because it is nearly impossible to construct fish passage solutions to be 100% effective, these results highlight the importance of river-wide connectivity planning and prioritization of dam removal where feasible. These findings reinforce that hydropower-induced habitat fragmentation can create both physical and behavioral bottlenecks that increase exposure to predation, stress, and energetic costs, factors known to affect survival (Lawrence et al. 2016, Baktoft et al. 2020, Mensinger et al. 2023). However, the impacts of fragmentation can be mitigated through the development of site-specific passage solutions that are evaluated to ensure they improve passage efficiency and reduce delays. We also found that some passage solutions performed less effectively than expected, while certain HEPs lacking dedicated passage solutions nevertheless exhibited high passage rates. This underscores the importance of thorough passage evaluations, efficiency testing, and long-term monitoring to quantify site-specific conditions and develop a more accurate understanding of river-specific migratory challenges,

thereby supporting more effective management strategies. The use of acoustic telemetry provided a robust empirical foundation for assessing movement dynamics, passage rates, migration speeds, and the effectiveness of restoration actions and fish passage solutions (CEN, 2021). Continued integration of long-term ecological monitoring with adaptive management will be critical for effectively balancing renewable energy production with the conservation of migratory fish populations.

Implications and concluding remarks

The findings presented in this thesis provide an evidence-based picture of the current conditions for downstream passage of salmonids in regulated rivers. We see that passage can be difficult, especially when barriers are present, causing delays and increased losses. But we also see how fish passage solutions can help mitigate the negative effects of dams, and that some dams without passage solutions have an unexpectedly high passage efficiencies, emphasizing the importance of evaluations.

Together, these studies reflect both the challenges and the opportunities inherent in reconciling renewable energy production with the health of aquatic ecosystems. As a biologist, this duality is ever-present: on one hand, the depressing realization that we, as a society, have and still are profoundly disrupting the natural systems on which we depend; on the other, the hopeful recognition that with innovation, cooperation, and adaptive management, we can meaningfully reduce our impact and foster recovery, providing an opportunity for future generations.

Balancing hydropower and fish migration is a complex human-wildlife conflict, or rather, a challenging relationship. It requires clear communication, shared responsibility, and adaptive co-management between policymakers, hydropower companies, engineers, and ecologists. Achieving this balance requires compromise on both sides. We as a society must find ways to retain the societal and climate benefits of

hydropower while conserving the ecological integrity and biodiversity of our rivers.

The broader implication is clear: sustainable hydropower is possible only if ecological considerations are treated as fundamental design and operational principles, not as afterthoughts. Technological innovations of fish passage solutions offer promising pathways forward. However, these solutions must be applied within a river-wide perspective that accounts for all fish species and life stages, not only iconic migratory salmonids. Ongoing national initiatives, such as Sweden's hydropower relicensing program, represent important steps toward this goal. This program provides the opportunity to integrate updated ecological knowledge into policy and practice, ensuring that renewable energy development aligns with environmental sustainability.

Ultimately, I hope that the work presented in this thesis contributes to meaningful action, restoring rivers, improving fish passage, and enabling smolts and kelts to migrate safely and efficiently, without the burden of humans hindering their life cycle. If we are going to make our world a better place, we have to take action and find solutions that sustain both our environment and society.

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Anadromy in Fragmented Rivers

Migration is essential for anadromous salmonids, but hydropower (HEP) development has fragmented rivers and disrupted downstream passage for smolts and kelts. Passage solutions can mitigate these impacts, but their performance remains rarely evaluated, particularly in multi-barrier systems. This thesis assessed downstream passage performance in fragmented rivers and evaluated mitigation effectiveness using acoustic telemetry to quantify movement patterns, speeds, and passage/loss rates across rivers with multiple HEPs, including sites with/without passage solutions and free-flowing sections. Free-flowing sections showed high passage success, and HEP removal more than doubled migration speeds. Passage losses and reduced speeds were greatest in lentic habitats and HEP sections, identifying these areas as bottlenecks. In contrast, HEPs with dedicated downstream passage solutions showed improved performance, with faster speeds and higher passage success. Biotic and abiotic factors influenced passage success, and cumulative barriers possibly influenced passage speeds. Overall, while passage efficiency can be high at individual HEPs, river-scale migration is constrained by interacting natural and anthropogenic factors, highlighting the importance of site-specific mitigation measures.

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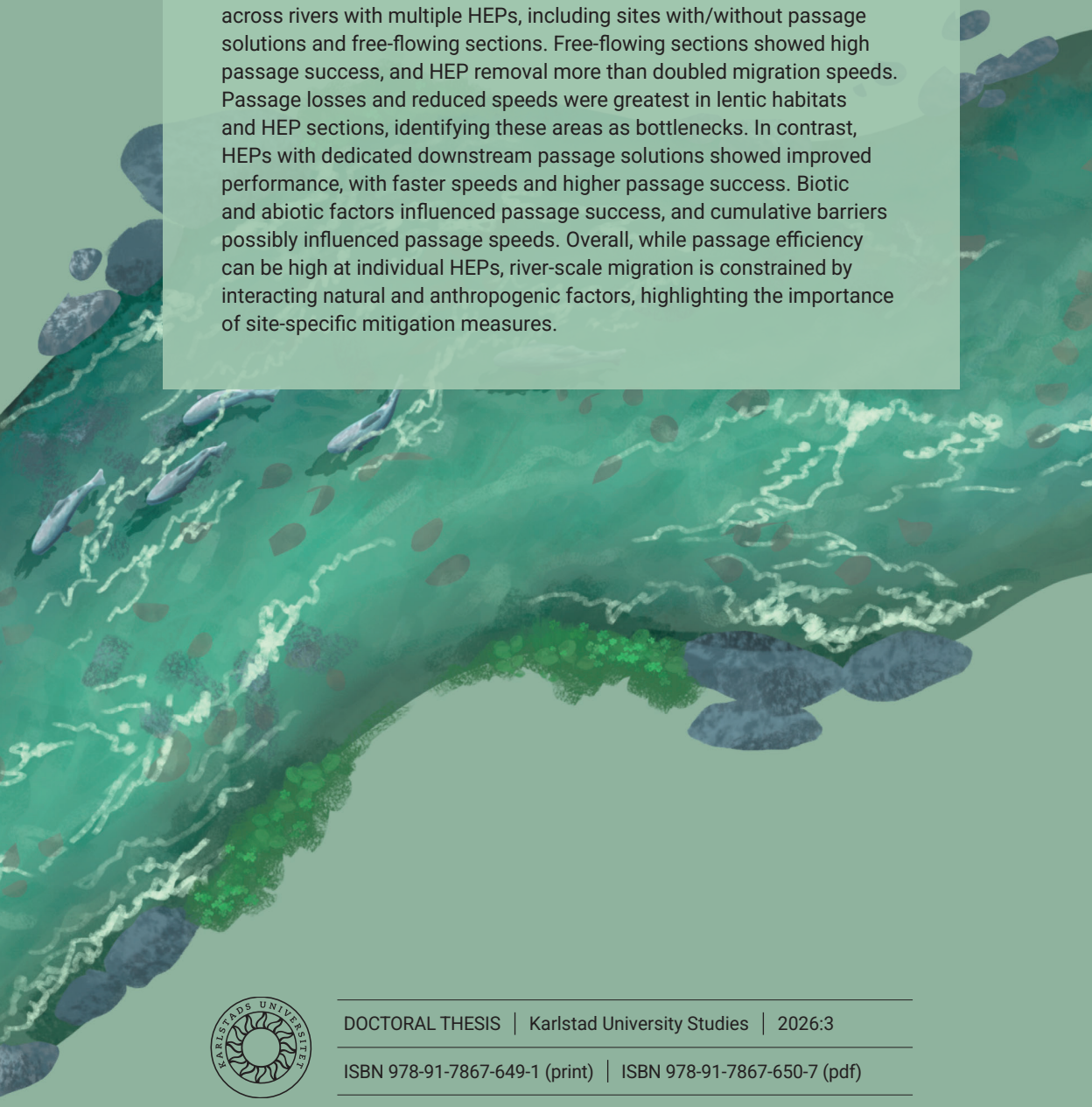

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