Atlantic salmon in regulated rivers
Migration, dam passage, and fish behavior

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Abstract

Hydropower dams block migration routes and disrupt longitudinal connectivity in rivers, thereby posing a threat to migratory fish species. Various fish passage solutions have been implemented to improve connectivity, but with varying success. A well-functioning passage solution must ensure safe and timely passage for a substantial portion of the migrating fish. In this thesis, I report the results from telemetry studies where the behavior and survival of migrating Atlantic salmon spawners, post-spawners and smolts have been evaluated in relation to hydropower dam passage. I evaluated downstream passage performance at dams with no passage solutions in the River Klarälven, and with simple passage solutions in the Winooski River. In the River Ätran, I studied both upstream- and downstream passage performance at a dam with sophisticated passage solutions based on the best available technology. In addition, I have studied the survival and behavior of post-spawners and hatchery-released smolts.

A substantial portion of the spawners survived spawning and initiated downstream migration. Most males migrated downstream in autumn following spawning, whereas females tended to stay in the river until spring. For hatchery-reared smolts, early release was associated with faster initiation of migration and higher survival compared to late release. Multiple dam passage resulted in high mortality for downstream migrating smolts and post-spawners. For smolts, dam passage, even with simple passage solutions, was associated with substantial delay and mortality. High spill levels were linked to high survival and short delay for downstream migrating salmon. The best available passage solution, which consisted of a nature-like fishway and a low sloping intake rack to guide fish to a bypass, resulted in rapid passage of a large portion of the adult migrants, both spawners and post-spawners.
Svensk sammanfattning

Lax i reglerade älvar: migration, dammpassage och fiskbeteende


En relativt hög andel av lekfisken överlevde leken och började vandra åter mot sjön/havet. Den observerade efterleksöverlevnaden i de olika vattendragen varierade mellan 38% och 94%. De flesta hanar vandrade nedströms under hösten efter leken, medan honorna ofta stannade i älven fram till efterföljande vår. Tidigt utsatta odlade smolt vandrade nedströms efter kortare tid och hade högre överlevnad än odlad smolt utsatta senare under våren. Dammpassage innebar ofta lång tidsåtgång och betydande dödlighet för den nedströmsvandrande laxen. Få smolt och kelt överlevde passagen av flera vattenkraftverk. En stor andel vatten som spills förbi dammen, alltså inte passerar turbinerna, förknippades med hög överlevnad och kort tidsåtgång vid kraftverkspassage för både smolt och kelt. De enkla passagelösningarna resulterade inte i effektiv fiskpassage medan bästa tillgängliga teknik, bestående av ett nedställt fingaller och en naturlig fiskväg, resulterade i snabb passage av en hög andel av den vandrande vuxna laxen.
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This doctoral thesis is based on the following papers, which are referred to by their Roman numerals.


Paper I and II are reprinted with permission from John Wiley & Sons.
Contribution

Paper I
DN contributed to study design, data collection, had a leading role in data analysis and conclusions, and wrote the paper. LG, OC and EB contributed to study design, and comments on data analysis, conclusions and text. AH contributed to the field work.

Paper II
In close collaboration with TCS, DN contributed to study design, data collection, data analysis, and wrote the paper. Other coauthors contributed with input on the study design and text. In addition, EG also did fieldwork.

Paper III
In close collaboration with TCS, DN contributed to study design, data collection, data analysis, and wrote the paper. SM, in collaboration with WA, designed and analyzed the physiology section. Other coauthors contributed with input on the study design and text. In addition, EG contributed to the field work.

Paper IV
DN designed and performed the data analysis, led the discussion concerning the results and wrote the paper. OC designed the study and did work in the field. AN provided inputs on analysis and text. Other coauthors contributed with field work and input on the interpretation of the results.

Paper V
DN contributed with telemetry study design, data collection, data analysis and wrote the paper. LG contributed with design of the sonar study and with input on the general study design, the data analysis, and the text.
Indroduction

Fish migration

Fish migrate for feeding, reproduction and refuge, often in response to temporal or ontogenetic changes. The scale of fish migration varies from meters to thousands of kilometers and can occur in the marine environment, in freshwater or between freshwaters and the sea (Lucas et al. 2001; Morais and Daverat 2016). Throughout human history, people have depended on migrating fish for food and income (Lucas et al. 2001). During the last centuries, the construction of dams has hindered fish from migrating between habitats and caused declines and sometimes even local extinctions of migratory species (Jonsson et al. 1999; Lenders et al. 2016; Marmulla 2001). Maintaining open migratory routes is an important aspect of safeguarding ecological connectivity and conserving migratory fish species (McIntyre et al. 2015).

Hydropower and migrating fish

Hydropower constitutes an important renewable energy source, representing about 16% of the global electricity production (Rudberg et al. 2014). In Sweden about half of the electricity produced comes from hydropower (Swedish Energy Agency 2015). Increasing energy demand is causing a global boom in hydropower development, with at least 3700 major dams planned or under construction (Zarfl et al. 2015). Hydropower dams come with high ecological and social costs (Olden 2015), not the least concerning longitudinal connectivity in rivers and fish migration. Fishways and other fish passage solutions, however, have been used to lead migrating fish past hydropower dams (Noonan et al. 2012).

The need for fishways and other passage solutions to facilitate two way passage at migration barriers has been acknowledged for hundreds of years (Montgomery 2004). Despite this, fishways are lacking at many dams (Calles 2013a; Nieminen et al., 2016). Where fish passage solutions exist, they are typically designed for upstream passage of strong salmonid swimmers (Katopodis and Williams 2012). This design has historically resulted in the construction of technical fishways, such as denil, vertical-slot and pool-and-weir fishways (Katopodis and Williams 2012) to pass adult salmonids on their spawning migrations. More recently, so called nature-like fishways have been
widely promoted, principally for upstream migrating fish. Nature-like fishways simulate natural streams by offering a diversity of substrates and spatially variable hydraulic conditions that are supposed to provide both suitable passage conditions and habitat for a wide variety of fish species (Castro-Santos et al. 2009; Katopodis et al. 2001). Also, during the last decades the need for downstream passage solutions has received increasing attention by both researchers and managers, first in the western United States and later elsewhere (Calles et al. 2013c; Whitney and Council 1997). For all types of fishways, their functionality is variable and often not known (Bunt et al. 2012; Noonan et al. 2012).

A functional fish passage solution must ensure safe passage routes that a substantial portion of the migrating fish will use. Even at dams with fishways, migrating fish might experience migratory failure. Upstream migrating fish might fail to locate the fishway, or enter the fishway but fail to pass through it (Bunt et al. 2012). Downstream migrating fish, in addition, might suffer direct or delayed mortality as an effect of passage through the turbines or spill gates (Muir et al., 2001; Ferguson, 2005; Ferguson et al., 2006). Both upstream and downstream migrating fish may also experience costly delays (Marschall et al. 2011; Thorstad et al. 2008; Venditti et al. 2000) associated with increased susceptibility to disease, predation and sport fishery mortality (de Leaniz 2008; Gowans et al. 1999; Gowans et al. 2003). Delay at passage has also been associated with post-passage mortality for both upstream and downstream migrating fish (Caudill et al. 2007; Roscoe et al. 2011; Stich et al. 2015). To improve the performance of fish passage solutions, remedial measures need to be evaluated (Roscoe and Hinch 2010). When evaluating fish passage performance, fish behavior should be studied in relation to the fish passage solution, fish characteristics and local environmental conditions.

Evaluation of the functionality of fish passage solutions is needed to ensure that longitudinal connectivity is restored (Roscoe and Hinch 2010). Simple forms of fishway evaluation can be performed by sampling fish found in the fishway, recording fish passing the fishway or detecting fish present above the migration barrier (eg. Laine et al. 1998; Mallen-Cooper and Brand 2007; Yamanaka and Minamoto 2016). One drawback of these methods is that they do not account for the fish that fail to use the fishway. Common evaluation metrics that account for fish that fail to use fishways are fish guidance/attraction efficiency (i.e. the proportion of fish that are successfully
guided to a particular passageway) and passage efficiency (i.e. the overall or route-specific passage success percentage) (Bunt et al. 2012; Noonan et al. 2012). Delay is another important fish passage performance metric that, if reported at all, has usually been considered separate from passage performance (Calles et al. 2012; Scruton et al. 2007). An emerging method used to study fish passage is time-to-event analysis, where delay and the proportion of fish passed are analyzed simultaneously and in relation to fixed and time-varying covariates (Allison 2010; Castro-Santos and Haro 2003; Zabel et al. 2014). With time-to-event analysis, fish passage is analyzed as the proportion of fish passing over time, describing passage as the time dependent process that it is.

**Atlantic salmon**

Salmon (*Salmo* and *Oncorhynchus*) are iconic migratory fish with great social and economic importance. Salmonids have suffered population declines and local extinction in regulated rivers throughout their distribution (Jonsson and Jonsson 2011; MacCrimmon and Gots 1979; Parrish et al. 1998), but have also been the subject of most of the fish passage solutions implemented up to date. Atlantic salmon (*Salmo salar*) occur naturally on the east coast of North America, from the Connecticut River in the south to Ungava Bay in the north, and on the west coast of Europe, from rivers on the Iberian peninsula to Arctic Russia (Klemetsen et al. 2003). Most Atlantic salmon populations migrate between riverine habitats and the marine environment. Also, landlocked salmon populations exist on both sides of the Atlantic Ocean (Kazakov 1992; Loughlin et al. 2016; Ozerov et al. 2010). Landlocked salmon typically migrate between a river and a large lake but river resident populations also exist (Berg 1985; Verspoor et al. 2008).

Atlantic salmon typically spawn in rivers during autumn and early winter; the eggs are buried in gravel and hatch the following spring when the fry emerge and start feeding. Juvenile fish, called parr, typically stay in the river for a period of 1-5 years before they leave the river and migrate to feeding areas at sea or in lakes. After a few months to several years with high growth rates at sea, or in a lake, the adult salmon return to their river of origin to spawn. After spawning, some salmon – now called kelts - return to feeding areas, recuperate lost energy reserves, grow even larger and come back to the river to spawn again (Jonsson and Jonsson 2011; Klemetsen et al. 2003).
Post-spawning survival of Atlantic salmon may be substantial, but varies from close to zero up to more than 80%. Females typically have higher survival than males, and small fish have higher survival than large fish (Baglinière et al. 1991; Halttunen 2011; Jonsson et al. 1997; Jonsson et al. 1990b). The post-spawners usually return to feeding areas in autumn immediately following spawning or in the subsequent spring (Halttunen et al. 2013; Jonsson et al. 1990b). In some cases almost continuous kelt downstream migration from October to April has been observed (Jonsson et al. 1990a). Mortality during in-river migration is typically low (Halttunen et al. 2009; Hubley et al. 2008), whereas mortality at sea can be considerable (Belding 1934; Halttunen et al. 2009). Post-spawners typically return to spawn again within one or two years (Hedger et al. 2009; Jonsson et al. 1991; Moore et al. 1995).

Not surprisingly, repeat spawning rates are also highly variable between rivers and years. The percentage of repeat spawners ranges from a few percent (Cuinat 1988; Jokikokko et al. 2006; Niemelä et al. 2000; Runnström 1940) to a considerable part of the spawning population (Ducharme 1969; Halttunen 2011; Moore et al. 1995). Most repeat spawners spawn twice (Halttunen 2011; Loughlin et al. 2016), but individual fish spawning four or more times have been reported (Ducharme 1969; Moore et al. 1995; White 1968). Repeat spawners, although often few in numbers, are typically large, highly fecund fish that can contribute considerably to the overall egg production in a population (Halttunen 2011). Further, repeat spawners may increase population stability over time (portfolio effect; Moore et al. 2014; Schindler et al. 2010) and might, especially in small populations, reduce the loss of genetic diversity (Saunders and Schom 1985).

Juvenile salmon, before leaving the river, go through a series of behavioral, physiological and morphological changes, called smoltification, that adapt them to entry into the marine or lake environment. They become silvery, more streamlined, lose positive rheotaxis and territoriality, begin shoaling, change their visual pigments, and increase their salinity tolerance and metabolic rate (McCormick et al. 1998). The transformed, migrating juvenile is called a smolt and typically migrates downstream in spring, with smoltification governed by the combined effects of photoperiod and temperature. The onset of migration is often triggered by temperature, but may in some cases also involve increases of river discharge (Hesthagen and Garnås 1986; Jonsson and Jonsson 2011; McCormick et al. 1998; Whalen et al. 1999). The smolt status of the fish is
temporally constrained and loss of smolt characters, including the migratory urge and salinity tolerance, occurs if the fish are prevented from exiting the river (McCormick et al. 1998).

Captive propagation and subsequent releases of hatchery-reared smolts have been used to mitigate negative effects of dams and habitat loss, to increase harvest, or to increase populations at low abundance (McClure et al. 2008). Although the conservation value of hatchery releases is questioned, hatchery release programs are widespread across the natural range of Atlantic salmon (Brannon et al. 2004; Brown et al. 2013; Kostow 2009; McClure et al. 2008). The hatchery environment is very different from a natural stream’s diversity of hydraulic conditions, structures, predators and prey. As a consequence, hatchery-reared smolts differ from wild smolts in many aspects. Hatchery-reared smolts have, for example, been observed to have inferior swimming performance (Pedersen et al. 2008), weaker anti-predator response (Jackson et al. 2011), lower in-river migration survival (Aarestrup and Koed 2003) and lower migration speed (Hansen et al. 1984) than wild smolts. In many rivers, smolts of both hatchery and wild origin can be expected to migrate downstream and pass hydropower stations, making the migration and dam passage behavior of hatchery-reared fish an important study object.
Objective

Compared to other fish genera, salmonids have been subject to relatively extensive fish passage research (Bunt et al. 2012; Noonan et al. 2012). Even so, upstream passage has historically received most attention both in terms of research and management actions, with less done to facilitate passage for downstream migrating fish (Calles et al. 2013c). Particularly downstream migration and passage of Atlantic salmon kelts has, until recently, been largely ignored (Halttunen 2011). Also, studies of landlocked Atlantic salmon passing hydropower dams (Nettles and Gloss 1987; Norrgård et al. 2012) are few. Evaluations are needed for fish passage solutions in general, but the need might be especially pressing for downstream passage solutions and currently widely promoted nature-like fishways. In this dissertation, I use radio telemetry to address these issues. In Paper I study the post-spawning survival, downstream migration and hydropower dam passage success of landlocked Atlantic salmon kelts in a river without any downstream fish passage solutions. In Paper V I further explore kelt behavior in the same river, focusing on movement to and from the turbine intake zone at a hydropower dam. In Paper II, I study smolt downstream passage performance at a hydropower dam with a simple bypass opening. I evaluate the passage performance in relation to fish characteristics and environmental conditions using time-to-event analysis. Paper III evaluates the effect of multiple dam passages for smolt and the effect of the timing of hatchery smolt releases and the wild smolt run on migration behavior in the same river. In Paper IV, I evaluate both upstream and downstream passage performance for adult Atlantic salmon at a hydropower dam, before and after the construction of a nature-like fishway for upstream and downstream passage and a low sloping intake rack guiding downstream migrating fish to a bypass. In other words, I evaluate passage performance in a system with no fish passage solutions (Paper I, V), simple passage solutions (Paper II, III) and best available passage solutions (Paper IV).
Methods

The behavior, migration, dam passage performance and survival of Atlantic salmon spawners (Paper IV), smolts (Paper II-III) and kelt (Paper I,IV,V) were studied using radio telemetry in three different rivers - the River Klarälven, the Winooski River and the River Ätran. Fish were tagged, released and their movements were tracked manually and with stationary receivers along the rivers and at the hydropower dams.

The rivers and their salmon

The River Klarälven (Paper I,V; Fig. 1) originates in Jämtland, Sweden, flows into Hedmark, Norway, returns to Sweden in northern Värmland and empties into Lake Vänern. It has a mean annual discharge of 162.5 m$^3$ s$^{-1}$ and a mean annual high water discharge of 690 m$^3$ s$^{-1}$.

Figure 1. Map over the lower Swedish part of the River Klarälven (Papers I, V) with hydropower dams marked by bars. Spawning grounds are located between Edsforsen and Höljes dams.
The River Klarälven was historically home to economically important populations of migrating, large-sized, landlocked brown trout (*Salmo trutta*) and Atlantic salmon (Piccolo et al. 2011). During the last centuries the salmonid populations have been affected by industrial activity, timber floating, intensive fishing and the construction of eleven hydropower dams in the main stem of the river. As a consequence, migratory salmonids in the River Klarälven have experienced large scale declines, resulting in today’s population of around 1000 migrating spawners (Qvenlid 1985; Piccolo et al. 2011). The currently available spawning grounds are located in a 140 km free-flowing stretch of the river upstream of Edsforsen, the eighth dam upstream of Lake Vänern. No functional fishways are present in the river. Instead spawners are caught in a fishtrap at the lower most dam, Forshaga, transported past the eight hydropower dams and released so that they can continue their spawning migration (Figure 1; Piccolo et al. 2011).

The Winooski River (Paper II-III, Fig. 2) and other Lake Champlain tributaries historically supported large numbers of landlocked Atlantic salmon (Webster 1982).

**Figure. 2.** The Winooski River (Paper II-III) with hydropower dams denoted as bars. The automatic receiver station at Richmond (Paper III) is designated by an arrow and the release site (Paper II-III) in the tributary Huntington River by a filled circle. Water flow direction is towards Lake Champlain.
Dams and other industry-related activities extirpated the salmon populations in the 19th century (Edmunds, 1874; Watson, 1876; Marsden and Langdon, 2012), and efforts to re-establish landlocked Atlantic salmon have been ongoing since the 1960s. As part of the restoration plan, fry and smolts are stocked in the Winooski River where three hydropower dams, equipped with fish bypasses for downstream migrating fish, separate available nursery areas from the lake (Marsden and Langdon, 2012; Chipman, 2013). A few upstream migrating spawners are caught each year at the lowermost dam and transported upstream, past the three dams, and released so that they may continue their migration to spawning areas in the tributary Huntington River.

The River Ätran (Paper IV) is located in southwestern Sweden and enters the North Sea (Kattegatt subbasin) at the city of Falkenberg. The river has a mean annual discharge of 57m³ s⁻¹ (range 20 – 319 m³ s⁻¹; 1990–2011; Olofsson, 2013) and contains a large number of barriers to migrating fish, with eight hydropower dams in the lowermost 58 km of the main stem (Fig. 3).

Figure. 3. The River Ätran (Paper IV) with tributary River Högvadsån and the Herting dam, the Åtrafors dam (upper barrier to migration in the main stem). HEP = hydroelectric power dam.
Herting is the first hydropower dam in the river, situated about 3 km upstream from the sea, and the only dam in the main stem equipped with fish passage solutions (Fig. 4). Fish that pass Herting have access to 24 km of the River Ätran, up to the second hydropower dam (Ätrafors), and 34 km of the tributary River Högvadsån (Fig. 3; Calles et al., 2010; Calles et al., 2012; Calles et al., 2013a). During the last decade, 2000 to 4000 spawners have returned to the river each year.

Figure 4. Herting hydropower dam (Paper IV) with the two power plants (H1 and H2) and release sites (X) before (A) and after (B) improved fish passage conditions. Dotted arrows indicate flow direction.
**Studied fish**

In the River Klarälven (Papers I,V) upstream migrating Atlantic salmons were radio-tagged (external tags) after being captured in the fish trap at Forshaga (Fig. 1) during three separate years. The tagged fish were then transported by truck 88 km, past the eight hydropower dams, and released into the river. Their spawning migration and fallback behavior were studied in parallel studies (Hagelin et al. 2016; Hagelin et al. 2015). After spawning, post-spawning survival, the timing of downstream migration, behavior and passage route selection at the first dam the fish encounter on their downstream migration (Fig. 5), and survival through multiple dam passages were studied.

![Figure 5. Edsforsen hydropower dam, the first dam the fish encounter on their downstream migration in the River Klarälven, with powerhouse, turbine intake zone (Paper V) and spill gates. The Yagi antennas (small arrows) and the unidirectional antenna (small circle) were present during the bulk of the study period, and sometimes complemented with additional antennas. (Paper I,V).](image)

In the Winooski River (Paper II-III) hatchery-reared and wild caught smolts were tagged (internal tags) and released in the Huntington River and followed on their downstream migration and passage past three hydropower dams. Wild smolts were caught in a rotary screw-trap in the tributary (Huntington River) and tagged and released as they were caught, whereas the hatchery-released fish were tagged and released in three distinct batches. Initiation of
migration and migration speed were analyzed for the wild and hatchery smolts (Paper III). Detailed movements to, from and within the forebay of Essex 19 (Fig. 6), the upper most dam, were analyzed in relation to fish characteristics and environmental conditions (Paper II). In addition, passage route specific survival at the same dam, and differences in passage rate and post-passage delay between the three dams were also analyzed (Paper III).

![Figure 6. Map of the hydropower plant area at Essex 19 in the Winooski River, showing the turbine intake, bypass entrances and spill gates. The forebay consists of the entry zone (downstream of the dotted line) and the approach zone (upstream of the dotted line). Yagi-antennas are shown as small arrows and dropper antennas as black dots. Flow direction is indicated by the large thick black arrow. (Paper II-III).](image)

In the River Ätran (Paper IV) wild migrating Atlantic salmon spawners were caught in the river, and brought to facilities at Herting where they were tagged (internal tags) and released downstream and upstream of the hydropower dam (Fig. 4) during late summer and autumn in 2009 and 2014. The fish released downstream of the dam had to locate and pass through the fishway to be able to continue their upstream migration to the spawning grounds. Fish were released upstream of the dam to evaluate the effect of confounding factors such as handling and tagging effects. In 2009, upstream migrating fish could pass via a denil fishway; in 2014 they passed through a nature-like fishway. The fish were tracked over spawning, and post-spawning survival was quantified. Fish that survived spawning and migrated downstream were then used to study downstream passage performance at the dam. Downstream migrating fish passed via a surface trash-gate or via spill water in 2009-10 and were guided
by a low-sloping rack to a fish bypass or passed through the nature-like fishway in 2014-15. I studied fish behavior for both upstream- and downstream migrating fish and compared passage performance between the two years.

In all three rivers, the tagged fish’s movements were tracked using arrays of stationary automatic receivers and complementary manual tracking.

**Fish passage performance**

Typically fish passage performance is analyzed in terms of passage proportions (efficiencies; Bunt et al. 2012; Noonan et al. 2012; Paper I-IV) and, occasionally, the time it takes to pass (delay; Calles et al. 2012; Scruton et al. 2007; Papers I-V). Successful passage and delay are however interlinked; passage success increases over time (as more fish pass) and so does the accumulated risk of failure (predation, exhaustion, loss of migratory urge). Time-to-event analysis is a method used to study the occurrence and timing of events and is increasingly used to study covariate effects on events in a wide variety of scientific disciplines (Allison 2010; Hosmer et al. 2008). Fish passage science is one field where time-to-event analysis can be a useful tool (Castro-Santos and Haro 2003; Castro-Santos and Perry 2012;Paper II-IV). In time-to-event analysis the passage event and the time it takes to pass are analyzed together as passage rate, that is, proportion fish passing over time. An additional advantage of time-to-event analysis is that all fish present and intent on migrating (e.g. downstream migrating fish in the forebay or upstream migrating fish downstream of the dam) are used in the analysis of covariate effects on passage rate. Fish not passing are censored, i.e., removed from the passage rate analysis, first when they die or leave the area. Cox-regression (Papers II,IV,V) is a type of time-to-event-analysis that also allows for both fixed and time varying covariates and is suitable for fish passage events where temperature, discharge, spill, hydropower generation and daylight can vary substantially over time. In this thesis, I use time-to-event analyses to study covariate effects on transitions between zones and dam passage in the forebay of a dam (Paper II,V), difference in passage rate among dams (Paper III) and differences in passage rates and covariate effects before and after remedial measures for upstream and downstream passing fish at a dam (Paper IV).

Fish passage can be seen as a series of events. Following arrival to the forebay, the fish should ideally approach the entry zone of the fishway, enter and pass...
through the fishway (Castro-Santos et al. 2009). This notion is used when analyzing attraction efficiency and passage efficiency (Noonan et al. 2012; Paper IV) as the proportion of fish approaching and then passing the fishway. Modelling the rates of this series of events may help us better understand the behavior and passage performance of the fish (Castro-Santos and Perry 2012). In Paper II I study the effects of covariates on events leading to passage or failed passage for downstream migrating smolts. I analyze rejection rates (retention) of fish in the forebay and the entry zone, approach rate to the entry zone and overall passage rate as well as route specific passage rates (Fig. 7). In Paper V, I study kelt approach to a turbine intake zone and their turbine passage or upstream movement away from the intake zone.

![Figure 7](image.png)

*Figure 7. A schematic diagram showing modelled events (arrows.) Dotted arrows are events censored but not modelled. Approach zone and entry zone are both nested within forebay (Paper II).*
Results

Dam passage was associated with substantial mortality (Paper I,III,V) and delay (Paper II,IV) for migrating Atlantic salmon. Higher spill levels were associated with higher survival and shorter delay for downstream migrating kelts (Paper I) and smolts (Paper III). Fish passage solutions did not always provide effective fish passage (Paper II-III) but the implementation of state-of-the-art remedial measures substantially improved passage performance (Paper IV). Post-spawning survival was substantial for both landlocked (Paper I,V) and anadromous (Paper IV) Atlantic salmon. Also, time of release of hatchery-reared smolts affected their migration behavior and success in the free-flowing parts of the river (Paper III).

Paper I

Forty-nine percent of the salmon survived spawning and initiated downstream migration. Females and small fish had higher post-spawning survival than males and large fish. Females tended to migrate downstream in spring while most males migrated downstream in autumn; the fish remained relatively inactive in the river during winter. Downstream migration speed in the free-flowing part of the river was highly variable with a median of 9.30 km day\(^{-1}\). Seventy percent passed the first hydropower station via upward-opening spill gates, 16% passed via the turbines and 16% died in the forebay. All fish survived spill passage whereas two of the three fish that passed via the turbines died in the process. Median residence time in the forebay was 25 min. No tagged fish survived passage of all eight hydropower dams to reach Lake Vänern (Fig. 8).

Paper II

Only 65% of the tagged smolts present in the forebay passed the dam. More fish passed via the bypass (33%) than via spill (18%) and the turbines (15%). Even though individual fish visited the forebay and the entry zone on multiple occasions, most fish passed during the first exposures to these zones. The time-to-event analyses revealed positive relationships between discharge and approach, passage, and retention rates. It also indicated reduced effects of discharge or hydropower generation on fish attraction over time in the area adjacent to the turbine intakes. We did not detect any differences in behavior between wild and hatchery fish.
Figure 8 Accumulated survival through multiple hydropower dam passage in the River Klarälven, from upstream river reaches to Lake Vänern, for 2011-13 (Paper I; solid line, n = 31) and 2013-14 (Paper V; dashed line, n = 17). The y-axis corresponds to river kilometer and hydropower dams are denoted with names. Survival assumed from radio detections.
Paper III

Hatchery reared smolts released early were more likely to initiate downstream migration compared to those released late. These early-released hatchery-reared fish also initiated downstream movement after a shorter delay than hatchery-reared fish released late. The hatchery fish released late, however, traveled faster once they started to migrate. Throughout the river system, hatchery-released fish performed similarly to wild fish. At the first dam the fish encountered, passage through the bypass was not preferable to passage via the turbines or spill gates. Median post-passage delay varied between 27 min and 2.9 h. Dam passage rate varied between the three dams and was highest at the dam with unusually high levels of spill (Fig. 9). Only 10% of the fish initiating downstream migration managed to reach the lake, swimming 30 km in the river and passing all three hydropower dams.

Figure 9. Kaplan-Meier curves for time to passage at Essex dam (solid line), Gorge dam (short dashed line), and Winooski dam (long dashed line). Fish that failed to pass/return upstream are included as censored observations (X). During large parts of the study period the hydropower plant at Gorge was not producing electricity and all water passed via overflow spill gates. Both Gorge and Essex have continuous surface spill for aesthetic reasons (Paper III).
Paper IV

A technical fishway for upstream migrating salmonids and a simple bypass entrance/trash gate for downstream migrating fish were replaced by a nature-like fishway for upstream and downstream migrating fish and a low sloping rack guiding downstream migrating fish to a bypass entrance. These remedial measures improved passage performance for both upstream and downstream migrating fish (Fig. 10). Passage rate increased for fish migrating in both directions, and passage success percentage increased and overall delay decreased for upstream migrating fish. After the improved passage solutions were implemented, almost all fish passed after little delay.

![Diagram](image-url)

Figure 10. Delay before and after the construction of the nature-like fishway and installation of the low-sloping intake rack at Herting hydropower dam for A) upstream migrating Atlantic salmon spawners from release after tagging to passage and continued upstream migration and B) downstream migrating Atlantic salmon kelts from arrival to the forebay to hydropower passage. For downstream migrating fish, fish overwintering in the forebay are excluded from the delay analysis. Passage success proportions are indicated above the box whiskers.
For upstream migrating fish, passage performance through the Denil fishway (before the nature-like fishway was implemented) was higher during the day than at night, for males compared to females and was positively related to water temperature. After passage conditions were improved by construction of the nature-like fishway, none of these effects on passage rate could be observed. Downstream migrating fish passed via the bypass and spill-gates the first year and via the bypass and the nature-like fishway the last year, discharge positively affected passage rate before but not after the fishway modifications.

**Paper V**

Dam passage success for Atlantic salmon kelts at Edsforsen dam was low, with 41% of the fish passing the dam. Mortality was largely associated with turbine passage (38% survival), whereas the two fish passing via the spill gates survived and continued their downstream migration. At the dam, all but one radio-tagged kelt approached the intake zone shortly (median = 15 min) after arrival to the forebay. For fish present in the intake zone, passage rate was higher at night than during the day and increased with increased hydropower generation.
Discussion

Hydropower dams block migratory routes, disrupting longitudinal connectivity in rivers and threatening migratory fish species (McIntyre et al. 2015). In this thesis, I show low migration survival associated with multiple hydropower dam passage (Papers I,III,V), but I also highlight the possibility of re-establishing longitudinal connectivity in a river with hydropower production (Paper IV). The low migratory success in a system with fish passage solutions (Papers II-III) also demonstrates the need for properly designed fishways, and the evaluation of their functionality.

Post-spawning survival has been reported to vary substantially between rivers and years (Baglinière et al. 1990; Halttunen 2011; Nyqvist 2013), and the studied fish in this thesis are no exception. In the River Klarälven 38% to 59% (Papers I,V) of the spawners survived spawning and initiated downstream migration during the three years of the study, whereas the corresponding percentages in the River Ätran were 38% to 94% (Paper IV). In free flowing rivers, downstream migration mortality is typically low (Halttunen et al. 2009; Hubley et al. 2008). Conversely, hydropower dam passage is associated with high mortality for migrating kelts (Calles and Greenberg 2009; Östergren and Rivinoja 2008; Paper I). The potentially high reproductive, genetic and stabilizing value of repeat spawners (Halttunen 2011; Moore et al. 2014; Saunders and Schom 1985), in combination with relatively high post-spawning survival and low dam passage survival in the River Klarälven, underscores the need for functional fish passage solutions for migrating kelts (Paper I). High downstream passage rates and passage efficiencies achieved through the bypass solution and nature-like fishway in the River Ätran show its feasibility (Paper IV).

In Europe, only a few extant populations of landlocked salmon remain, with Lakes Ladoga, Onega and Vänern supporting the largest populations (Berg 1985; Ozerov et al. 2010; Verspoor et al. 2008). The landlocked populations have been assigned high conservation values (Ozerov et al. 2010) at the same time as hydropower dams have blocked rivers and contributed to the population declines of landlocked salmon (Kazakov 1992; Piccolo et al. 2011). Despite this, there are few studies on landlocked Atlantic salmon. Their relatively high post-spawning survival (Paper I,V) is within the range of reported post-spawning survival from anadromous populations (Baglinière et
al. 1990; Halttunen 2011). Also, the timing of migration (spring for smolts; autumn and spring for kelts) and dam passage survival (Paper I, V) are in line with data reported for ocean-migrating salmonids (Halttunen 2011; Jonsson and Jonsson 2011; Östergren and Rivinoja 2008). Migrating landlocked salmon have evolved from anadromous salmon and still need to make the transition from a riverine environment to pelagic life in the lake (Norrgård et al. 2014; Piccolo et al. 2011). At least some landlocked salmon populations even retain the physiological transformation to saltwater tolerance (Lemmetyinen et al. 2013; Norrgård et al. 2014; Piironen et al. 2013). Behavioral similarity between anadromous and landlocked salmon during their river migration was therefore expected.

The hydraulic environment that the migrating fish experience at a hydropower dam affects the fish’s behavior and passage performance. Typically, downstream migrating salmonids are surface-oriented, follow the bulk flow of water (Coutant and Whitney 2000) and avoid abrupt accelerations of flow (Enders et al. 2012; Haro et al. 1998; Vowles and Kemp 2012). High spill was associated with high downstream passage performance in the comparisons between dams in both the Winooski River (Paper II) and in the River Klarälven (Paper I). In the River Ätran, increased discharge – with accompanying increased spill – was associated with increased downstream passage rate before, but not after, the improved remedial measures (Paper IV). Discharge and spill were also seen to influence bypass entry zone approach, passage, and retention rates in the forebay of a dam (Paper II). Positive relationships between spill and passage performance have been seen in other rivers (Čada et al. 1997; Stich et al. 2014) and increased spill is used by management to pass fish past dams (Adams et al. 2014; Colotelo et al. 2012). One might be able to time increased spill levels with fish migration to safely pass migrating fish with short delays (Calles et al. 2013c). The trade-off is, of course, that this would come at a cost in form of reduced hydroelectric generation.

At the hydropower dam in the River Ätran (Paper IV), no effect of discharge was seen on downstream passage rate after the passage conditions were improved, indicating that the facilities provided passage independent of variation in discharge and spill. Continuous surface spill into the nature-like fishway likely contributed to this result (see also Paper III on surface spill). Also, the construction of the low sloping intake rack successfully guided fish to the bypass with very high efficiency and with short delays. In fact, all fish
analyzed passed through the bypass on their first visit to the intake channel, after a very limited delay, following the installation of the low-sloping rack. Bypasses typically pass fish using a limited volume of water but might not always attract enough of the downstream migrating fish (Paper II; Johnson and Dauble 2006). Low-sloping intake racks guide downstream migrating fish towards the bypass entrance, and high passage performance has also been reported for eels and Atlantic salmon smolts (Calles et al. 2013b; Nettles and Gloss 1987). The potential of high passage rates and passage efficiencies with limited volumes of water should be of interest to fisheries management and the hydropower industry.

When downstream migrating fish experienced multiple dam passages, accumulated mortality was very high. Between 0% and 6% of the tagged kelt survived passing the eight hydropower dams to reach the lake in the River Klarälven (Paper I,V), whereas only 10% of migrating smolts successfully passed three dams to reach the lake in the Winooski River (Paper III). Low accumulated survival has also been reported from multiple dam passages in other regulated river systems, but reasonably high survival is achievable (Calles and Greenberg 2009; Norrgård et al. 2012; Williams et al. 2001). In the Winooski River, fish bypass solutions were present but failed to provide effective fish passage (Paper II-III). The higher passage rates associated with surface spill in the Winooski River (Paper III) suggests that spill water might be a short term solution for passing downstream migrating fish. Dam removal, passage solutions at multiple dams or trapping downstream migrants at the first dam they encounter on their downstream migration are other possible solutions discussed for the River Klarälven (Gustafsson et al. 2015).

Nature-like fishways are typically promoted to provide suitable passage conditions for a variety of fish species, especially weak swimmers (Castro-Santos et al. 2009; Katopodis et al. 2001) and, in addition, they can serve as habitat for fish and invertebrates (Gustafsson et al. 2013). In this study we show how the construction of a nature-like fishway can substantially improve passage performance also for strong swimming adult Atlantic salmon. Passage rates were substantially improved, delays were reduced and nearly every fish (96%) approaching the dam successfully passed it to continue their upstream migration after the construction of the nature-like fishway. The relatively large volume of water allocated to the nature-like fishway likely attracted fish to the fishway, contributing to the high passage performance (Larinier 1998;
Thorstad et al. 2008). In addition, passage was likely also less demanding compared to passage through the Denil fishway. Higher passage performance for males than for females (Kennedy et al. 2013; Lundqvist et al. 2008; Paper IV), at higher temperatures compared to lower temperatures (Gowans et al. 1999; Kennedy et al. 2013; Paper IV), and during daytime compared to night (Gowans et al. 2003; Naughton et al. 2005; Paper IV) through the denil fishway constituted potentially important barrier effects that were not observed in passage through the nature-like fishway.

Safeguarding longitudinal river connectivity is one of several important aspects of conserving global freshwater fish biodiversity and production (Closs et al. 2015). My dissertation, like many other fish passage studies (Noonan et al. 2012; Roscoe and Hinch 2010), focus entirely on Atlantic salmon. Nevertheless, my work may potentially be of use in a wider context. Time-to-event analysis (Paper II-V) and the analysis of the progressive transition between zones before passage (Paper II,V) should be useful for other fish species and fish passage systems. The nature-like fishway and low-sloping rack (Paper IV) already show promising results also for other species (Calles et al. 2015; Calles et al. 2013b). Moreover, documentation of ecologically harmful effects of dams (Paper I-III) serves as an impetus for the implementation of different measures to improve river connectivity. Further impetus comes in the knowledge that highly functional fish passage solutions are feasible, allowing for coexistence between hydropower and longitudinal river connectivity (Paper IV).

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Atlantic salmon in regulated rivers

Hydropower dams block migration routes, thereby posing a threat to migratory fish species. Fishways and other fish passage solutions may aid fish to pass hydropower dams. A functional fish passage solution, however, must ensure safe and timely passage for a substantial portion of the migrating fish. In this thesis, I focus on downstream passage and evaluate the behavior and survival of migrating Atlantic salmon in relation to dams in systems with (1) no fish passage solutions (2) simple passage solutions (3) best available passage solutions. In addition, I studied the survival and behavior of post-spawners and hatchery-released smolts.

A large portion of the spawners survived spawning and initiated downstream migration. For hatchery-reared smolts, early release was associated with faster initiation of migration and higher survival compared to late release. Multiple dam passage resulted in high mortality, and high spill levels were linked to high survival and short delay for downstream migrating salmon. For smolts, dam passage, even with simple passage solutions, was associated with substantial delay and mortality. Rapid passage of a large portion of the migrating adult salmon was achieved using best available passage solutions.