Faculty of Social and Life Sciences
Biology

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Landlocked Atlantic salmon *Salmo salar* L. and trout *Salmo trutta* L. in the regulated River Klarälven, Sweden

Implications for conservation and management

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ABSTRACT

Conservation and management of migratory salmonids requires an understanding of their ecology at multiple scales, and a holistic view, including assessment of historical and present anthropogenic impacts. In the regulated River Klarälven, with 11 hydropower dams, populations of landlocked Atlantic salmon *Salmo salar* and migratory brown trout *Salmo trutta* have declined due to human activities. Maintaining viable populations of salmon in the River Klarälven has high priority, given there are fewer than 10 native stocks of landlocked salmon in Europe. To date, natural smolt production has been maintained by collecting and transporting spawners past eight hydroelectric plants in the river, where they are released to spawn. No functioning fish passage facilities are available that allow the fish to return to the lake. To evaluate the situation for landlocked salmon and migratory trout in Lake Vänern and the River Klarälven, an analysis of catch and river return data, based on data sets covering time periods from 15 to 200 years, was performed. In addition, the loss rates and behavior of downstream-migrating wild salmon smolts as they swam past eight power stations in the regulated River Klarälven was quantified.

For the migration study, wild salmon smolts were tagged with acoustic transmitters, and the smolts were monitored as they swam along a 180 km long river segment, including eight dams, with regulated and unregulated stretches. Kaplan-Meier estimations showed that only 16% of the smolts passed all eight dams. The loss due to HEP passages was estimated to be 76%, which contrasts with the 8% loss along unregulated control stretches. Migration speed was 83% lower along regulated stretches than along unregulated stretches, and migration speed at regulated stretches was dependent on fish size, with large fish moving slower than small fish.

The analysis of historical data showed that annual returns of wild salmon are less than 3% of what they were at the beginning of the 19th century. Returns of wild trout are even lower, with just some 30 fish caught annually. Lack of basic ecological information, as river return and fisheries catch rates, estimates of wild smolt production and survival, and releases of hatchery-reared fish, complicate an effective management of these unique populations. There is need for coordination of present and future research, monitoring and restoration strategies. In this thesis I identify some measures to improve the status of the River Klarälven salmon and trout that should be of broad interest to resource and fishery managers.

CONTENTS

PUBLICATIONS

The thesis is based on the two following papers, which are referred to by their Roman numerals.

I. Piccolo JJ, Norrgård JR, Greenberg LA, Schmitz M, Bergman E. 2011. Conservation of endemic migratory salmonids in regulated rivers: A case study from Lake Vänern, Sweden. *In press for Fish and Fisheries*

II. Norrgård JR, Greenberg LA, Piccolo JJ, Schmitz M, Bergman E. 2011. Multiplicative loss of landlocked salmon *Salmo salar* L. smolts during downstream migration through multiple dams. *Submitted*

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INTRODUCTION

Atlantic salmon *Salmo salar* L. and sea-migratory brown trout *Salmo trutta* L. show a complex and diverse array of life history patterns. Typically, their life starts with a freshwater phase, followed by smoltification and migration to the sea for feeding and growth, and a return to their native river for spawning (Elliott 1994; Thorstad et al 2011). After the last glacial period some Atlantic salmon and brown trout stocks were isolated from the sea in both North America and Europe. These landlocked populations complete their entire life cycle in freshwater, mainly spending their adult growth period in large lakes instead of the sea. Although both Atlantic salmon and brown trout are well studied species, relatively little is known about these landlocked lake-migrating stocks (Klemetsen et al 2003). Declines in native anadromous salmonid populations worldwide are well-documented (Mills 1991; Parrish et al 1998; Lichatowich 1999; Behnke 2002; IUCN 2011), and the landlocked stocks of salmon have also declined throughout their whole distribution range (Kazakov 1992). At present, landlocked European populations of salmonids are found in Norway, Sweden, Finland and Russian Karelia (Berg 1985; Kazakov 1992; Pursianen et al 1998; Kirchhofer and Hefti 1996; King et al 2007; Ozerov et al 2010). The rivers have generally been negatively affected due to human activities such as exploitation for hydropower projects, log driving (cleaning riffles from stones and boulders), boating and industrial pollution. To mitigate for loss of wild salmonid populations, stocking of hatchery-reared smolts has long been used in river ecosystems affected by man (Einum and Fleming 2001; Fjellheim and Johnsen 2001; Jonsson and Jonsson 2011). In some cases supplemental stocking may be a useful way of recovering populations (Pearsons 2008), but it may also result in further large-scale unwanted effects on the behavior, ecology, and genetics of native fish stocks (Utter 2004; Fraser 2008; Hansen et al 2009; McGinnity et al 2009; Jonsson and Jonsson 2011). In many large river systems, indiscriminate mixing of hatchery stocks with wild stocks has resulted in the loss of locally-adapted populations (e.g. Williamson and May 2005; but see also Behnke 2002; Waples et al 2008). Thus, there are relatively few large river systems in exploited regions that have maintained strong endemic stocks of large-bodied salmonids.

Hydroelectric projects as migration barriers

Migration is a synchronized movement over a distance that is large relative to the average home range for the species, and it occurs at specific and predictable stages of the life cycle, involving a large portion of the population (Lucas and Baras 2001). The movements of landlocked Atlantic salmon and migratory brown trout between their natal streams and adult feeding grounds, fulfill all of these criteria (Elliott 1994; Thorstad el al 2011). To complete their life cycle, these populations require free pathways, including both upstream and downstream migration routes that enable the fish to move between feeding, spawning and winter habitats (Lucas and Baras 2001; Klemetsen et al 2003). Flow regulation and hydroelectric plants (HEPs) interrupt the longitudinal connectivity necessary for fish migration (Ward and Stanford 1995; Calles et al 2007). As a consequence, river regulation has often led to declines in fish populations (Northcote 1998; Parrish 1998; Svensson 2000; Rivinoja 2005; Johnsen et al 2011).

To maintain longitudinal connectivity in regulated rivers, fishways have been built at some HEPs and other obstacles (Saltveit 1993; Calles and Greenberg 2005; Calles and Greenberg 2009). The functionality of these fishways has been studied to some extent (e.g. Gowans et al 1999; Rivinoja et al 2001; Aarestrup et al 2003; Gowans et al 2003; Thorstad et al 2003, Roscoe and Hinch 2010). However, those studies have historically focused on the passage success of upstream migrating spawners, and little is still known about downstream migrating salmonids passing HEPs (Arnekleiv et al 2007; Östergren and Rivinoja 2008; Kraabol et al 2008; Calles and Greenberg 2009; Calles et al 2011; Muir and Williams 2011). Downstream migrating juvenile salmonids generally experience decreased survival caused by direct turbine or spillway mortality, and indirect mortality due to predation when delayed in reservoirs (Montén 1985; Coutant and Whitney 2000; Ward and Hvidsten 2011). Dam passages may also indirectly influence mortality as fish often become wounded and disoriented as a result of dam passage, and are therefore expected to be vulnerable to subsequent predation and other mortality risks (Budy et al 2002; Ferguson et al 2006; Whitney et al 2006). Furthermore, delays at dams and changes in water regimes could increase mortality due to enhanced exposure to potential predators, and result in a suboptimal time for leaving the river or reaching the spawning grounds (McCormick et al 1998; Johnsen et al 2011).

The multiplicative losses of migrating juvenile salmonids passing a large number of dams could be high (Whitney et al 2006; Muir and Williams 2011). In the River Emån, a Swedish lowland river with multiple HEPs, Calles and Greenberg (2009) found only a 15 % migration success for seaward migrating smolts. Other studies have also shown high losses associated with downstream passages, and yet implementation of remedial measures for downstream migrating fish occurs far less often than for upstream migrants. The lower Snake River and Columbia River differ in this regard, where a lot of effort has been taken to re-establish connectivity, and where measures for both upstream and downstream migrants have been implemented and tested (Williams et al 2001; Whitney et al 2006; Muir and Williams 2011). Yet, despite guiding devices and alternative routes for downstream migrating fish, the loss of downstream migrating juveniles can still be high during years with low water discharge (Williams et al 2001). According to Muir and Williams (2011) there is still no satisfactory holistic solution ensuring free migration routes which enable fish to fulfill their full life cycle in the Columbia River. Even if most of the past attempts at re-establishing longitudinal connectivity in rivers have addressed the issue of upstream passage (Calles and Greenberg 2009), and the importance of efficient fishways and limited delays for upstream migrating spawners has been emphasized by e.g. Ferguson et al (1998) and Gowans et al (2003), efficiencies of remedial measures for upstream passages are generally not measured (Calles and Greenberg 2005). Not surprisingly, holistic evaluations of remedial measures in regulated rivers, where one tests efficiency of different measures designed to facilitate both upstream and downstream passages, have rarely been preformed in the same system.

River Klarälven

The River Klarälven (59° 23′ 0″ N, 13° 32′ 0″E) is Lake Vänern's largest tributary. It originates in Härjedalen, Sweden, passes through Hedmark, Norway (the Norwegian parts are named Trysilelva or Femundselva) and Värmland, Sweden to finally empty into Lake Vänern. The mean annual outlet discharge to Lake Vänern is 162.5 m^3/s, and mean annual high water discharge is 690 m^3/s (www.smhi.se). The large sized salmon and trout of the River Klarälven historically migrated as far as 400 km upstream to spawn in the Norwegian parts of the river (Nordberg 1977; Ros 1981). At present, only small populations of wild migratory salmon and trout remain in River Klarälven.

The River Klarälven has played a large role in the region's historical development, not the least of which in terms of fishing and as a transport route. Legal documents regulating the rights of the fishery existed already in the 1200s (Nordberg 1977). In the beginning of the 1700s, timber floating in the River Klarälven was regulated with regard to time and extent to minimize the negative effect on fish migration and on the fishery ("Fiskeavgiftsmålet, AM 9/1925, p.8" cited in Nordberg 1977). However, these regulations were later removed. By the mid-1800s the Swedish part of the river was being exploited on a large scale; small hydropower projects were used for saw mills and metal industries, riffles were cleaned of boulders to facilitate log driving, canals were built for log driving and boating in the lower river, and industrial pollution increased (Nordberg 1977). Nordberg (1977) estimated that only 30% of the historic spawning and rearing habitat for salmon remained in the Swedish part of the river by the mid-1800s. Large-scale hydropower development began in the early 1900's, and the last of eleven dams in the main stem was completed in 1964, blocking all spawning fish from reaching the main historic spawning grounds. At present, only the lower 25 km of the river are available to migratory fish. Since the 1930s natural smolt production has been sustained via active transport of spawners, which are collected in a fish trap at the lowermost dam in Forshaga, transported by truck some 100 km upstream past 8 HEPs, and then released to spawn (Runnström 1940; Törnquist 1940). The fish are released downstream of the only remaining known spawning grounds in the Swedish part of the river, situated downstream of the ninth HEP, the Höljes dam (Anonymous 1998). Hatchery brood stock is also collected at the fish trap in Forshaga, and stocking of hatchery-reared smolts in the lower part of the river and direct to the lake has been carried out since the 1960s.

To date, there is no specific management program for the wild and hatchery salmon and trout of Lake Vänern and River Klarälven. Moreover, the current status of Lake Vänern's endemic salmon and trout, based on scientific evidence, is unknown, and there is no clear plan for future key research, or monitoring requirements. There is, however, an overall management plan for the fish and fishery in Lake Vänern under development (pers com Frida Laursen), and an international project between Norway and Sweden has been initiated to investigate the possibilities for establishing free migration routes for the salmon in River Klarälven (Anonymous 2011). Together with this thesis, these new initiatives could be the start of a new era for managing these unique landlocked populations of lake-migrating salmon and trout.

OBJECTIVES

The overall objective of this thesis was to compile historical data and thereby bring new light and better understanding of the present situation for salmon and trout in Lake Vänern and the River Klarälven. There is a need to identify the conflicts between hydropower development and conserving the lake-migrating populations of salmon and trout in the River Klarälven. Furthermore, as the historical development, and present situation in Klarälven, is by no means unique, this thesis could serve as a case study representing the situation for many other salmonid rivers in northern Europe.

More specifically, the aim of this thesis was to i) present historical information about catches of lake-migrating salmon and trout of River Klarälven (**Paper I**), ii) assess the current status and trends for the remaining wild lake-migrating salmon and trout populations in the River Klarälven (**Paper I**), and iii) estimate the multiplicative loss of migrating wild smolts caused by multiple HEP passages (**Paper II**). In addition, I identify some immediate implications that can improve the management and the population status of the River Klarälven salmon and trout.

MATERIAL AND METHODS

As a source of hydropower, the River Klarälven has been of major historical importance for the people living in the region. At present, there are nine HEP's in the Swedish section of the main stem, from HEP-1 at Forshaga, near Vänern, to the largest power plant, HEP-9, situated at the Swedish-Norwegian border, some 280 km upstream of Lake Vänern (Figure 1). There is an approximately 150 km long free-flowing stretch of river between HEP 9 and Edsforsen, HEP 8. The next 100 km long stretch of river has eight HEPs (1-8). Water storage is possible only at one of the smaller plants, the Krakerud reservoir (HEP-6). The lower 25-km of the river, downstream of HEP-1 at Forshaga, is free-flowing. At present, none of the lower nine dams in the Swedish part of the river have functioning upstream or downstream fishways.

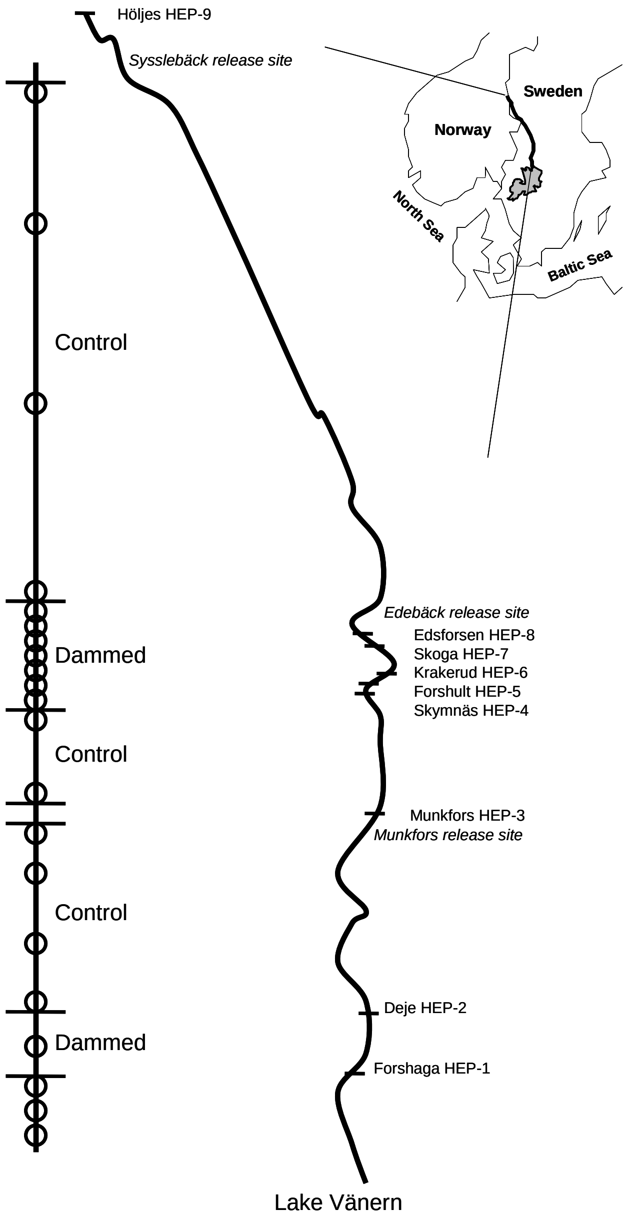


Figure 1. Schematic overview of Klarälven, showing HEP names and locations. In addition, the free-flowing control and dammed stretches, placement of receivers and *release sites* are shown (**Paper II**). Fish were caught at Edebäck (RST) and upstream of of Munkfors (fly-fishing).

This thesis is based on historical material, published as well as unpublished, and on a smolt migration study using acoustic telemetry. In **Paper I**, historical data was provided by the Swedish Board of Fisheries (Fiskeriverket), Fortum (the hydroelectric operating company), the Värmland County Administration Board (Länsstyrelsen Värmland), and Statistics Sweden (SCB). The data include reports earlier not made public, published reports, digital data and handwritten records of river return rates, fisheries catch and records of re-catches of Carlin-tagged fish from both the fisheries in Lake Vänern and the River Klarälven, and counts of fish collected in fish traps at Forshaga and Deje. Prior to dam and fish trap constructions, records of catch reported to local authorities for river fisheries operated along the length of the River Klarälven were used. The latter data largely come from an unpublished report (Nordberg 1977). To estimate the total combined catch of salmon and trout, fishery data from commercial (logbooks), subsistence (annually catch reports), and sport (questioner surveys) fishermen were used. Since the River Klarälven has been used as stocking site for hatchery-reared Gullspång stocks since the 1960s, returns to Deje and Forshaga fish traps include hatchery stocks from both the River Klarälven and the River Gullspångsälven. Beginning in 1980, records of catches at the fish traps are separated by species and stock, identifiable by fin clips administered in the hatcheries before release. Due to the implementation in 1993 of the no-catch regulation for wild salmon and trout (FIFS 1993:32), the origin of the fish (wild vs. hatchery) collected in the fish traps are recorded, starting in 1996. Return rates of Carlin-tagged fish were analyzed for release years 1982-2003, separate correlations were used to assess trends for lake and river returns. Statistical analyses in **Paper I** were performed using XLSTAT Version 2011.2.05 (Addinsoft 2011). All time series were tested for autocorrelation, and Mann-Kendall tests were used to assess trends in corrected data.

In **Paper II**, wild salmon smolts were monitored as they migrated downstream in the River Klarälven from May-July 2009. Smolts were caught using a rotary screw trap (Thedinga et al 1994) and by fly-fishing. Totally, 97 smolts were tagged with uniquely identified acoustic transmitters (VEMCO Ltd, Canada, V7–1L and V7–2L). Because we expected large losses of smolts, we used three separate releasing sites to ensure sufficient migration data from the entire river reach. To monitor the migration of the tagged smolts, 37 acoustic receivers (VEMCO Inc., VR-2W) were submerged near the bottom at 21 stations along the migratory route, starting approximately 200 km upstream of Lake Vänern and ending approximately 15 km upstream of river delta, 10 km below Forshaga, HEP-1 (Figure 1). The main objective was to compare the losses and migration speed of smolts in an 80 km free-flowing stretch upstream of HEP 8 to the 100 km long dammed stretch between HEPs 1 and 8. In addition, by placing receivers both upstream and downstream of all HEPs, passages at single HEPs were also monitored. Since receivers at the HEPs were often placed a couple hundred meters upstream and 1-2 km downstream of the dams, the observed losses include both direct and indirect mortality associated with passing the HEPs (reservoir and dam) (Montén 1985; Coutant and Whitney 2000; Whitney et al 2006). Data analyses in **Paper II** were performed using the statistical package SPSS for Windows v. 18.0. Observed losses and migration speed were analyzed, as was the migration success by using the staggered-entry Kaplan–Meier formula (Pollock et al 1989, but also see Castro-Santos and Haro 2003; Serrano et al 2009).

SUMMARY OF RESULTS

Records of catches from the 1600s of up to 50 000 wild salmon and trout (species combined) from the River Klarälven are known (**Paper I**). Later, in the early 1800s, annually catches were approximately 30 000 fish, and according to official reports catches declined to 5 000 by the end of the 1800s. This negative trend has continued, and for the period 1961-70 the mean annual catch of wild River Klarälven stocks was only approximately 140 salmon and trout combined (Figure 2). However, during the period 1996-2009 the return rates of wild salmon to the River Klarälven changed from approximately 220 to up to 780, even if this increase was not significant (Mann–Kendall test, $p=0.09$, $t=0.35$) (Figure 3a). Return rates for wild trout increased significantly (Mann–Kendall test, $p<0.05$, $t=0.45$) during the same period (Figure 3b), but despite this, numbers of wild trout remains very low (< 50 per year). Large scale hatchery production began in the 1970s, and reached current levels by 1990 (Figure 2). During the period 1996–2007, return rates of hatchery-reared Klarälven salmon and trout have remained relatively constant. In total, mean returns of both wild and hatchery-reared salmon and trout have increased from the critical low levels in the 1970s, to an average of 2 300 during the period 1990-2007. There is a large annual variation in trap catches, which probably is a result of variable trap efficiency, as the trap at Forshaga are not run at low flows, and does not work well at high flows.

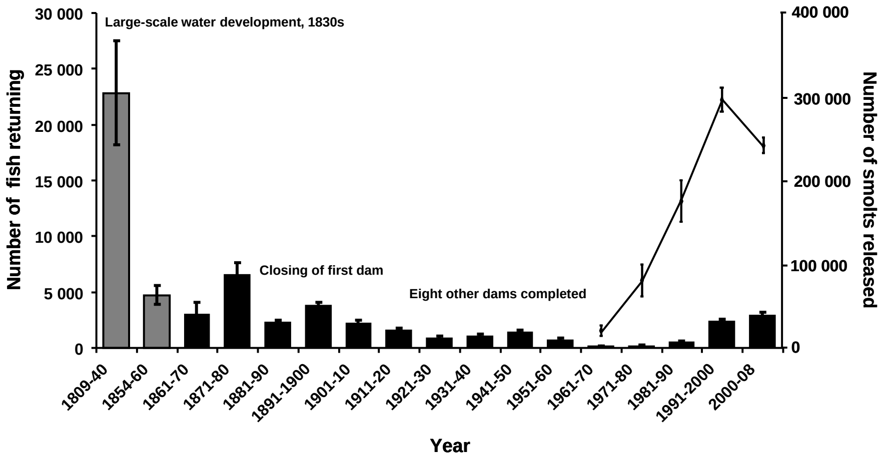


Figure 2. The mean number of salmon and trout, combined (bars, ±1 SE), returning to Klarälven, 1809–2008, and the number of hatchery smolt released (line, ±1 SE). Note that each bar is the mean and standard error for a 10-year period, except the first two grey bars. Catch methods, locations and effort vary over this period (see **Paper I** for full explanation). Prior to 1960, the catch is wild Klarälven salmon and trout. After 1960, wild fish, and Klarälven and Gullspångsälven hatchery stocks are all included.

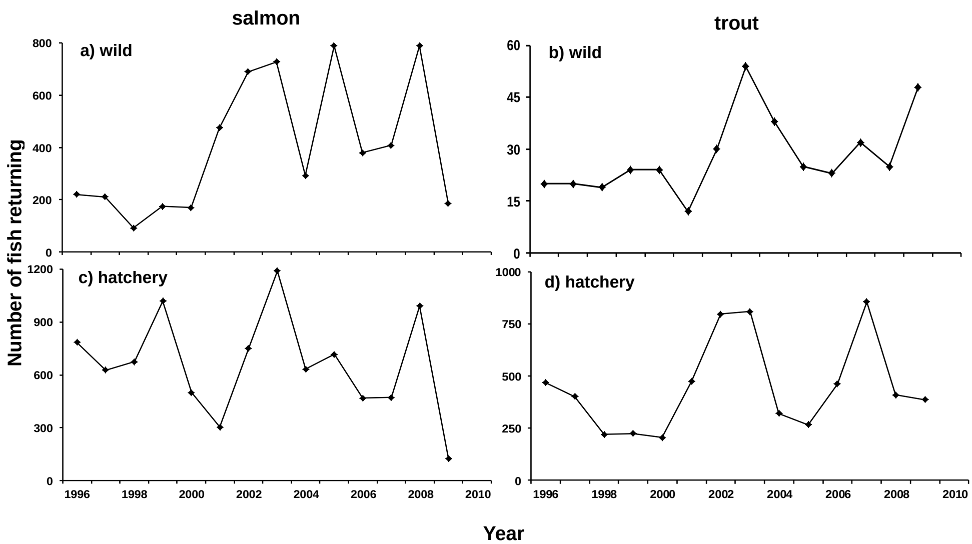


Figure 3. Annual number of salmon and trout of Klarälven origin returning to the fish trap at Forshaga, 1996-2009: a) unclipped (wild) salmon, b) unclipped (wild) trout, c) fin-clipped (hatchery) salmon, and d) fin-clipped (hatchery) trout. Note that the y-axes differ on each panel.

Return rates of hatchery-reared Carlin-tagged salmon and trout smolts to the River Klarälven have remained relatively constant during the period 1982–2003, averaging about 1%. Also, total return rates of hatchery-reared fish to the trap in Forshaga appear stable at roughly 1%. And yet, return rates of Carlin-tags from the lake fishery have declined steady since the 1980s.

Early records of the commercial catch of salmon and trout in Lake Vänern suggested that catch rates generally follow the same trend as the river. In **Paper I**, the total estimated annual catch of hatchery-reared salmon and trout is at least 75 metric tons. Catches in the commercial fishery have fluctuated between 30-50 metric tons since 1996, with an apparent decline to around 25 metric tons since 2000. Due to declined effort, the reported subsistence catch went from 20 metric tons to <5 metric tons during the period 1984–2006. On the other hand, the estimated sport fishery catch has increased from 30 to 80 metric tons during the same period, mainly due to an increase in effort. Our estimate of sport fishery catch (**Paper I)** is well below official estimates (Anonymous 2008), as we have accounted for later decreases in CPUE for trolling data (unpublished data Erik Degerman and Mikael Johansson).

In **Paper II**, there was a 100 % migration success of actively migrating smolts along the 80 km long free-flowing control stretch, i.e. no losses. In contrast, along the 100 km long dammed stretch (HEP-8 to HEP-1), 43 of the 65 of actively-migrating smolts were lost. Of these 43 lost smolts, 40 were lost at HEP passages, and the losses were fairly evenly distributed between HEPs, ranging between 6-23% (Figure 4). Based on the Kaplan-Meier model, the smolts had a 16% migrating success along the studied 180 km long river reach (Figure 5), i.e. 84% were lost. In total, 76% of the smolts were estimated to be lost due to HEP passages on their migration route from the rearing areas to the lower part of the river

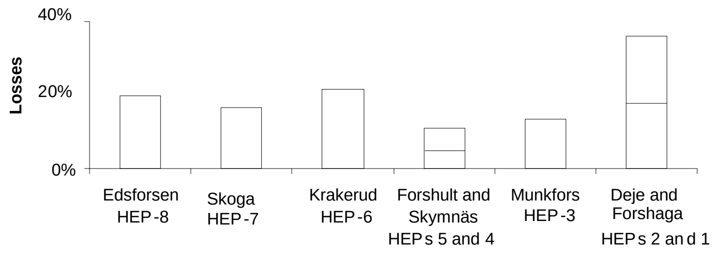


Figure 4. Actual losses of actively migrating fish at HEP passages. The horizontal lines for the histobars showing losses at HEPs 4 and 5 and HEPs 1 and 2 depict the average loss per HEP as individual HEP loss was not possible to calculate (see **Paper II** for explanation).

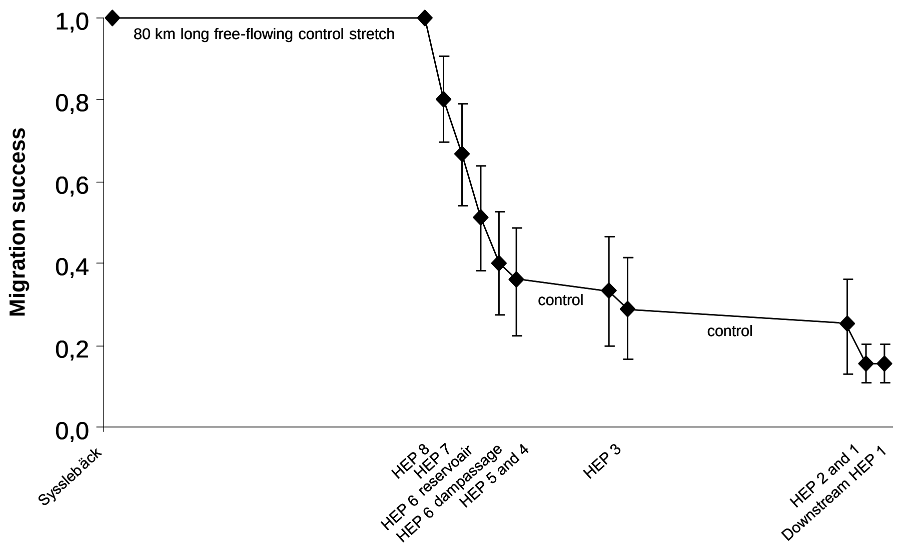


Figure 5. The estimated migration success (%), based on a Kaplan–Meier model, along the 180 km long studied stretch of the river. Lines represent the 95 % confidence interval.

In **Paper II**, smolts migrated 83 % faster along free-flowing control stretches than along dammed stretches, and there was a positive correlation between migration speed and discharge along both free-flowing (Spearman's rho: r=0.496, n=37, p=0.002) and dammed (Spearman's rho: r=0.628, n=46 p=<0.0001) stretches. Furthermore, there was a negative correlation between migration speed and fish size at dammed stretches (Spearman's rho: r=-0.351, n=37, p=0.033), but no relationship between migration speed and fish size was found for free-flowing control stretches (Spearman's rho: r=0.138, n=46 p=0.360).

DISCUSSION

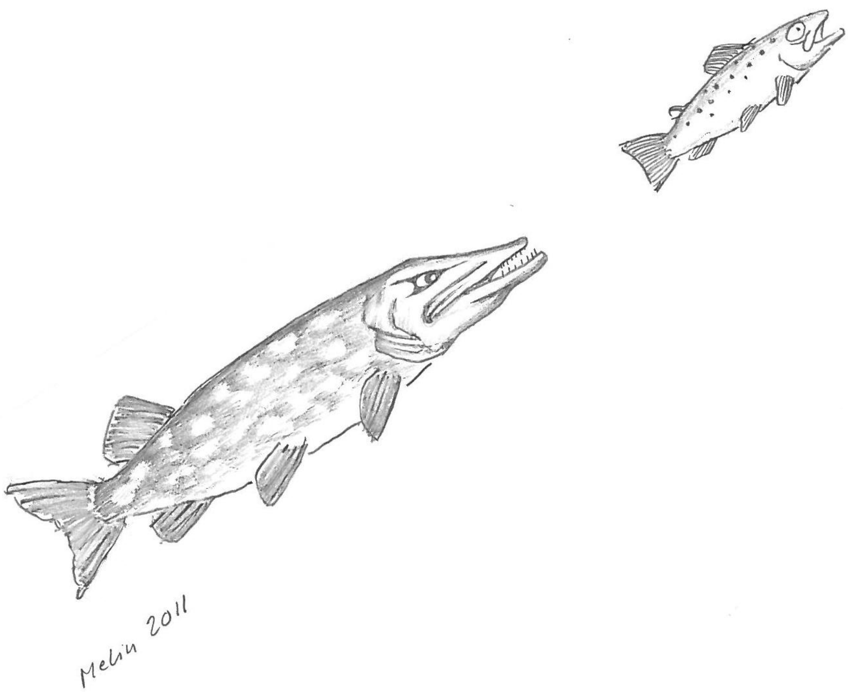
In this thesis, I highlight the importance of using a holistic approach in the conservation and management of migratory fish in regulated rivers. The historical exploitation of the River Klarälven, the development of the fishery and catch rates, and the present lack of management of the fishery in Lake Vänern is presented in **Paper I**. In the past, focus has been set on transporting spawners upstream to the spawning grounds, and maintaining the fishery by stockings of hatchery-reared fish. The management authorities have for some time assumed that the downstream losses in this river system are negligible (Anonymous 1998), whereas data presented in **Paper II** indicate that this is not the case. The data and the research needs presented in this thesis should be of great interest to resource managers dealing with the conservation of the wild stocks of salmon and trout in River Klarälven, as well as to management authorities in charge of managing the fishery in Lake Vänern. Lessons learned from the River Klarälven and Lake Vänern should also be applicable to other water systems facing similar challenges.

The salmon and trout of the River Klarälven has been of major historical importance for the people and for the development of the region; the river is often described as one of the most important sources of fish in Sweden (Nordberg 1977). Historical catch reports of more than 30 000 salmon and trout annually are well documented, and there are no reasons to doubt older reports of 50 000 fish. However, due to human activities, the populations of salmon and trout have declined during a period of at least 300 years. Concerns were raised, particularly to the impact of hydropower on the fishery, already in the 1700s (Fernow 1773). Habitat degradation, mainly as a consequence of timber floating activities (Palm 2007), surely has lowered the potential maximum production of salmon and trout in River Klarälven (Nordberg 1977). The increased effort in the lake fishery in the late 1800s may also have contributed to a reduction of the salmonid populations (Nordberg 1977). However, it was not until the completion of the ninth hydroelectric dam in the 1960s that the return rates of salmon and trout declined to critically low levels. Despite the recovery seen during the last 15 years, the annual returns of wild salmon are less than three percent of what they were at the beginning of the 19th century. Returns of wild trout are still critically low, with just some 30 fish caught annually. Thus, the current status of wild lake-migrating salmon and trout populations in the River Klarälven has to be considered as extremely vulnerable. These results mirror the worldwide decline in the abundance of wild lake and sea running salmonid populations, and the local declines of wild salmon in Sweden (Ranke et al 1999).

By assembling both historical and new data available for the lake-migrating salmon and trout of Lake Vänern, trends in catches and stock status have been identified. However, lack of basic ecological information, as river return and fisheries catch rates, estimates of wild smolt production and survival, and releases of hatchery-reared fish, complicate an effective management of these unique populations. As wild stocks recover, it will become increasingly important that both the ecological and genetic perspectives of the interactions between wild and hatchery-reared fish are considered and studied. According to the data available, the hatchery program seems to support an annual commercial, sport, and subsistence fishery of at least 75 metric tons of salmon and trout in Lake Vänern. River return rates of hatchery-reared Carlin-tagged fish to the fish trap in Forshaga have been fairly stable, with return rates of about one percent since 1982. However, return rates of Carlin-tagged fish have declined steeply in the lake fishery, even if there has not been a decrease in total fishery catches during the same period. The most likely explanation for the discrepancy between river and lake tag-recovery rates is a reduced reporting of tagged fish by the fishermen, which has earlier been identified as a common problem for fish tagging programmes (Brendan et al 2010). To maintain this fishery at current levels, and simultaneously let wild stocks recover, new initiatives that coordinate present and future research, monitoring programs, and restoration strategies are urgently needed. The life history-based research and management efforts presented in **Paper I** should be implemented in the future management of the salmon and trout in Lake Vänern.

The most important finding from **Paper II** is the extensive loss of migrating smolts in the regulated part of the river, which highlights the problems with multiplicative losses in regulated rivers with several HEPs (Muir and Williams 2011). During the smolt migration period, discharge in Klarälven is normally below the maximum capacity of the turbines at the HEPs. This is largely due to water regulation at Höljes, HEP-9. Thus, in most years, downstream migrating smolts are forced to swim through turbines on their way to Lake Vänern. Here we show that even low losses at a single HEP, as low as 6%, the multiplicative losses of many HEPs can have a substantial effect on the total survival of migrating fish, resulting in a major loss of the smolt production in a river system. We estimated the loss of smolts caused by fish passing all eight HEPs to 76%, although this is likely to be a minimum loss rate. This is because fish passing multiple turbines may also suffer from sublethal impacts, making them more susceptible to predation and other mortality risks as compared to non-affected fish (Budy et al 2002; Ferguson et al 2006). Thus, the low number of smolts lost at free-flowing stretches indicates that loss of migrating smolts was probably not a major problem in the past. A long-term restoration of the wild stocks of trout and salmon in River Klarälven will require well-functioning up- and downstream migration facilities (e.g. Calles and Greenberg 2009).

Further, in **Paper II**, migration of the fish was delayed along the dammed sections of the river, and there was a negative relationship between migration speed and fish size along dammed stretches, indicating greater delays for large-sized smolts. As there are stretches along the dammed parts of the River Klarälven that are known for their high abundance of piscivores, fish delayed in these areas might experience an increased predation risk (Johnsen et al 2011). In **Paper II** the focus was on exploring the total loss of smolts and the average migration speed. Future studies could be designed to separate the sources of losses and explore detailed migration patterns, as well as examine the effects of a delayed lake entrance on subsequent river return rates.



Immediate implications

In summary, the lake migrating salmon and trout of the River Klarälven were historically among the world's longest-migrating, and most productive landlocked salmon stocks. Extensive exploitation of the river almost drove the populations to extinction, but due to management efforts the wild populations have been maintained, albeit at numbers far below historic values. Due to hatchery stockings, the landlocked salmon and trout of the River Klarälven remain of considerable value for commercial, subsistence, and sport fisheries. The results presented in this thesis can be used to suggest management implications which should be of great interest to the managing authorities. I stress that if the aim is to conserve these unique wild populations, a holistic approach in the conservation and management should be implemented. This might be prioritized as follows: First, one should strive for improved estimates of fisheries catches of both hatchery-reared and wild salmon and trout, adult river returns, and smolt production. Second, more information is needed about the ecology of wild and hatchery-reared fish, how to identify genetic stocks, and how to manage locally-adapted stocks. This holistic approach is in line with reports from ICES (2011).

Nordberg (1977) suggested that there was a minimum smolt production of 120 000 smolts annually in the 1800s. Currently, there are no reliable estimates of wild smolt production in Klarälven. Yet, considering the relatively low number of spawners transported to the spawning area, recent smolt production can be assumed to be small compared to historical levels. However, the number of wild salmon returning to the fish trap in Forshaga has increased during last years, as well as the proportion of wild salmon compared to salmon of hatchery origin. Assuming that i) the total catch of salmon in the fishery is relatively stable, despite the shift in capture method, from commercial fishery to trolling, and ii) the return rates of fish of hatchery origin is stable, as the return of tagged fish to the fish trap has not shown any temporal trend, the increased proportion of wild fish might indicate that there has been an increase in wild smolt production. This is likely, since the number of transported spawners has increased, juvenile salmon have been found in recently restored areas (Palm et al 2010), and fishing mortality probably has declined due to reduced use of gillnets by the commercial fishery and the no-catch regulation for wild salmon and trout. To improve conditions for wild salmonids, trapping at Forshaga should be made more effective, and remedial measures should be implemented to enhance migration success of downstream-migrating fish. Therefore, I propose the following measures to be implemented immediately:

1. The fish trap at Forshaga should be rebuilt to ensure effective trapping at all water flows. Focus should be set on creating attraction flows and minimizing handling of the fish. Further, the trap should be operated during the entire spawning season, and transport of spawners should be done using state-of-the-art methods. Until the trap is rebuilt, one should consider alternative methods of trapping spawners i. e. special designed trap nets or gillnets used for catching spawners of landlocked salmon and trout in the Rivers Lieksanjoki and Pielisjoki (Anonymous 2005).

2. Adopt a strategy to foster downstream migration of kelts and smolts past dams. One possibility is the use of spill water during the relatively brief downstream migration period for kelts and smolts (Thorstad et al 2011). There is no universal solution to guide downstream migrating fish past HEPs, but it is generally assumed that spillways provide a benign route for passage at most projects (Whitney et al 2006). In Klarälven, an ecologically-friendly operation of the HEPs could significantly increase the migration success of both kelts and smolts. This modification in operation could involve spilling water during a 2-4 week long period, allowing fish to pass during the main migration period. Surface spill should be prioritized, as this has been showed to be preferred by both kelts and smolts (Coutant and Whitney 2000; Johnson et al 2006. Whitney et al 2006; Arnekleiv et al 2007; Kraabol et al 2008). Use of spill water gates has earlier been proven successful in the Columbia River system (Whitney et al 2006; Muir and Williams 2011).

3. An alternative method of enhancing survival of downstream migrating smolts and kelts, is to construct fish collectors at Edsforsen HEP-8 and Skoga HEP-7, where fish could be collected and then transported to Lake Vänern. This could either be viewed as a temporary measure until downstream bypasses and/or fish guidance facilities have been constructed at each dam, or as a permanent solution if guidance facilities could not be built at all HEPs. Transportation of juvenile salmonids past dams has been successfully used in the management of salmonids in the Columbia River (Whitney et al 2006; Muir and Williams 2011).

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Landlocked Atlantic salmon *Salmo salar* L. and trout *Salmo trutta* L. in the regulated River Klarälven, Sweden

Conservation and management of migratory salmonids requires an understanding of their ecology at multiple scales, and a holistic view, including assessment of historical and present anthropogenic impacts. In the regulated River Klarälven, with 11 hydropower dams, populations of landlocked Atlantic salmon *Salmo salar* and migratory brown trout *Salmo trutta* have declined due to human activities. Maintaining viable populations of salmon in the River Klarälven has high priority, given there are fewer than 10 native stocks of landlocked salmon in Europe. To date, natural smolt production has been maintained by collecting and transporting spawners past eight hydroelectric plants in the river, where they are released to spawn. No functioning fish passage facilities are available that allow the fish to return to the lake. To evaluate the situation for landlocked salmon and migratory trout in Lake Vänern and the River Klarälven, an analysis of catch and river return data, based on data sets covering time periods from 15 to 200 years, was performed. In addition, the loss rates and behavior of downstream-migrating wild salmon smolts as they swam past eight power stations in the regulated River Klarälven was quantified.

For the migration study, wild salmon smolts were tagged with acoustic transmitters, and the smolts were monitored as they swam along a 180 km long river segment, including eight dams, with regulated and unregulated stretches. Kaplan-Meier estimations showed that only 16% of the smolts passed all eight dams. The loss due to HEP passages was estimated to be 76%, which contrasts with the 8% loss along unregulated control stretches. Migration speed was 83% lower along regulated stretches than along unregulated stretches, and migration speed at regulated stretches was dependent on fish size, with large fish moving slower than small fish.

The analysis of historical data showed that annual returns of wild salmon are less than 3% of what they were at the beginning of the 19th century. Returns of wild trout are even lower, with just some 30 fish caught annually. Lack of basic ecological information, as river return and fisheries catch rates, estimates of wild smolt production and survival, and releases of hatchery-reared fish, complicate an effective management of these unique populations. There is need for coordination of present and future research, monitoring, and restoration strategies. In this thesis I identify some measures to improve the status of the River Klarälven salmon and trout that should be of broad interest to resource and fishery managers.

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