Migration and quality of landlocked Atlantic salmon smolt

Implications for conservation and management

Johnny R Norrgård

Faculty of Health, Science and Technology

Biology

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Faculty of Health, Science and Technology
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Doctoral Thesis

Johnny R Norrgård

Abstract

Atlantic salmon *Salmo salar* has a complex life cycle, including long migrations and habitat shifts for both juveniles and adults. As such, salmon populations are vulnerable to habitat degradation and fragmentation along their migratory routes. This makes management and conservation a complex task requiring knowledge of salmon ecology at different temporal and spatial scales. In this thesis I highlight the use of a holistic life-history based approach in the conservation and management of wild and hatchery-reared salmon in regulated rivers and lakes.

Small populations of wild-reproducing landlocked salmon and trout *Salmo trutta* exist in the regulated River Klarälven, Sweden. Since the 1930s, transportation of adult spawners upstream of eight dams has given the fish access to spawning grounds. The number of returning wild spawners became critically low in the 1960s, but stocking of hatchery smolts resulted in an increase in spawners that continues today. My data show that wild smolt may suffer high mortality due to multiple dam passages. To ensure viable populations of wild populations, future management should include both up- and downstream solutions that ensure connectivity in the system.

The recreational and commercial salmonid fishery are maintained by compensatory stockings, yielding annual catches of about 75 tons, and a river return rate of hatchery fish of about 1%. As a large portion of the stocked smolts does not survive downstream migration to the lake, there has been discussion about the quality of the stocked smolt and about stocking strategies. Based on my studies, producing hatchery smolts more closely resembling wild-born conspecifics should result in reduced loss rates. I suggest changes in the hatchery and stocking procedures to increase the survival of stocked smolts. The results of my research should be applicable to other regulated systems, particularly those with mixed stocks of wild and hatchery salmonid populations.

Contents

List of papers

The thesis is based on the following papers, which are referred to by their Roman numerals. Papers I and II are reprinted with the permission from John Wiley and Sons.

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. Fish and Fisheries, 13: 418–433.

II. Norrgård JR, Greenberg LA, Piccolo JJ, Schmitz M, Bergman E. 2011. Multiplicative loss of landlocked Atlantic salmon *Salmo salar* L. smolts during downstream migration through multiple dams. River Research and Applications 29(10): 1306-1317.

III. Norrgård JR, Bergman E, Greenberg LA, Schmitz M. 2014. Effects of feed quality and quantity on growth, early maturation and smolt development in hatchery-reared landlocked Atlantic salmon *Salmo salar*. *Manuscript.*

IV. Norrgård JR, Bergman E, Schmitz M, Greenberg LA. 2014. Effects of feeding regimes and early maturation on migratory behavior of landlocked hatchery-reared Atlantic salmon *Salmo salar* smolts. *Manuscript.*

V. Norrgård JR, Ludvigsson A, Bergman E. 2014. Predation by northern pike *Esox lucius* on migrating hatchery-reared salmonid smolts. *Manuscript.*

The idea for Papers I-IV was given by Larry A Greenberg, Eva Bergman, and Monika Schmitz. John J Piccolo and I co-authored Paper I, I mainly contributed with compiling and analyzing data, and by transcribing historical sources. The planning of Paper II was done by me, Larry A Greenberg, and Eva Bergman. I organized and carried out field work, did the statistical analyses and wrote the manuscript. The planning of Paper III and IV was done by me, Larry A Greenberg, Eva Bergman, and Monika Schmitz. I did sampling, part of the statistical analyses and mainly wrote the manuscript for Paper III. In Paper IV, I organized and carried out the field work, mainly did the statistical analyses and wrote the manuscript. The idea and planning for Paper V were given by me and Adam Ludvigsson, I contributed in field sampling, did the data analyses and wrote the manuscript.

Introduction

Management and conservation

Management and conservation of migratory salmonid populations is a biologically, socially, and politically complex task (Bottom et al 2009; Hilborn 2009; Irvine 2009). It requires an understanding of their ecology at multiple scales, both temporal and spatial, so that their life history needs can be met (Knudsen and Michael 2009). This needs to be done in conjunction with assessments of anthropogenic impacts such as fishing, hydroelectric production and resource extraction. Managers usually do not have complete information of specific populations and rivers, and conservation measures will therefore in many cases be based on general knowledge. In rivers subjected to large-scale habitat degradation and disrupted connectivity, with small vulnerable salmonid populations, considerable knowledge is needed to ensure sustainability of fish populations (Aas et al 2011).

Some species show complex and diverse life history patterns, involving movements between different habitats. One such species, the Atlantic salmon *Salmo salar*, has a complex life history, including long migrations and habitat shifts for both juveniles and adults. As such, populations of Atlantic salmon are vulnerable to habitat degradations as well as to fragmentation along their migratory route (Saltveit 1993; Calles and Greenberg 2005, 2009). Successful management of populations with such complex life cycles is a great challenge for managers, the well-documented declines in native anadromous salmonid populations worldwide can serve as an example (Mills 1991; Parrish et al 1998; Lichatowich 1999; Behnke 2002; IUCN 2013). Thus, there are few large river systems in exploited areas that have maintained strong endemic stocks of large-bodied salmonids.

Dams and hydroelectric plants are one sort of anthropogenic activity that has great impact on migrating salmonid populations, hindering both upstream migrating spawners and downstream migrating juveniles. At some hydropower projects remedial measures, such as fishways for upstream migrating spawners and guiding devices for downstream migrating juveniles, have been implemented to reestablish longitudinal connectivity (Saltveit, 1993; Calles and Greenberg, 2005). However, in many rivers the fish have to pass multiple hydropower projects along their journey between different habitats, and efficiencies of remedial measures are generally not measured (Calles and

Greenberg 2005). Most of the measurements done to re-establish longitudinal connectivity in rivers have focused on upstream passage (Calles and Greenberg 2009), but it is well known that the losses of downstream migrating juvenile salmonids passing a large number of dams can be high (Whitney et al 2006; Muir and Williams 2012). Downstream migrating salmonid juveniles generally experience decreased survival caused by direct turbine or spillway mortality, and indirect mortality due to increased predation as a result of wounds and disorientation after dam passage (Montén 1985; Coutant and Whitney 2000; Budy et al 2002; Ferguson et al 2006; Whitney et al 2006; Ward and Hvidsten 2011). Furthermore, even if guiding devices and fishways exists, delays at dams 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).

Supplementary stocking of smolts is the main method used to compensate for lost salmonid production in rivers where spawning and juvenile rearing habitats are degraded, or connectivity is fragmented by human activities (Einum and Fleming 2001; Jonsson and Jonsson 2011). The survival of hatchery-reared smolts is generally considerably lower than the survival of their wild conspecifics (Jonsson and Jonsson 2011), but in some cases supplemental stocking may be a useful way of recovering populations (Pearsons 2008). However, supplemental stockings may also result in 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), and in many large river systems mixing of hatchery stocks with wild stocks has resulted in loss of locally-adapted populations (eg Williamson and May 2005; Behnke 2002; Waples et al 2008).

Smolt quality and survival of hatchery-reared fish

Smolting involves morphological, biochemical, physiological and behavioral changes that allow the fish to adapt to their new environment (McCormick et al 1998). While smolting and migration of anadromous Atlantic salmon are well studied, less is known about them in landlocked stocks (Klemetsen et al 2003). Smolt from landlocked populations do not generally show a clear smolt-related increase in gill N+/K+-ATPase (NKA) activity or an ability to hypo-osmoregulate when subjected to saltwater tests (Nilsen et al 2003; Stefansson et al 2008). In contrast, Schmitz (1995) reported that landlocked Atlantic salmon from the River Gullspångsälven, a tributary of Lake Vänern, have retained some hypo-osmoregulatory ability. The morphological changes associated with smolting for anadromous populations include a pointed head, slim body form, and silvery body flanks. These morphological changes seem to have been retained to some degree by landlocked populations of Atlantic salmon (Stefansson et al 2008). In fact, the degree of silvering and condition factor has been shown to influence survival and migration success of released hatchery-reared Atlantic salmon smolts in the River Klarälven (Lans et al 2011).

In hatcheries salmonids are generally fed large rations of lipid-rich feed (Eriksson et al 2008). Consequently, the size, condition factor and body lipid content of hatchery-reared smolts are considerably higher than for their wild conspecifics (eg Higgs et al 1995; Shearer et al 1997; Eriksson et al 2008; Serrano et al 2009; Lans et al 2011). It has been assumed that smolt size is positively correlated with survival for both wild and hatchery fish (eg Henderson and Cass, 1991; Lundqvist et al 1994; Saloniemi et al 2004). Recently, this assumption has been questioned in the Baltic region as the declining return rates in terms of both absolute numbers of fish and the Carlin-tag recovery rates since the 1990s are negatively correlated with body size, condition factor and lipid levels of the stocked hatchery fish (Salminen and Kuikka 1995; Sers et al 2007; Eriksson et al 2008; Vainikkia et al 2010, Larsson et al 2012). Further, the lipid-rich feed affects both maturation and smolting (Thorpe 1986; Berglund 1995; Silverstein et al 1997; Shearer and Swanson, 2000; Maugars 2007). Early maturation as parr is fairly common in the wild for Atlantic salmon males (Hindar and Nordland 1989; Flemming and Einum 2011), and in Swedish hatcheries up to 80% of the 1+ year old males may be sexually mature (Eriksson et al 2008). However, early maturation among male parr reduces the probability of smolting (Berglund et al 1991; Fängstam et al 1993), and neither early mature males nor fish with poorly developed smolt characteristics are desirable in stocking programs because these fish tend not to migrate when stocked into rivers (Eriksson et al 1987). If a high proportion of fish show a resident behavior and an unwillingness to migrate the result will be lower catches in the fishery and lower adult return rates (Lundqvist et al 1994; McKinnell and Lundqvist 1998). Thus, one possible mechanism behind observed negative correlation between smolt size and return rates might be related to low migration success among large, early mature males and low development of smolt characteristics. However, studies have also showed that migratory behavior of hatchery-reared salmonids can be enhanced by manipulating feed availability and the fish's energetic status (Nordeng 1983; Tipping and Byrne 1996; Lans et al 2011; Larsson et al 2012; Vainikka et al 2012), where reduced feed rations during the last months in the hatchery before release generally promote migratory behavior for hatchery-reared salmonid smolts stocked in rivers. Interestingly, the decision of Atlantic salmon to smolt in the spring is based on their energetic status during the previous summer and autumn (Metcalfe et al 1988; Thorpe et al 1998). This suggests that feed manipulations probably should be initiated earlier to get the full effect of the manipulation.

Poor survival of smolts may not only be related to smolt quality of hatchery-reared salmonids, but also to predation (eg Larsson 1985; Hvidsten and Lund 1988; Jepsen et al 2000, 2006; Dieperink et al 2001, 2002; Kekäläinen et al 2008; Ward and Hvidsten 2011). Studies have highlighted that hatchery fish have poorly developed anti-predator behaviour (Fleming et al 1997; Einum and Fleming 2001). In addition, predators will move to areas of high prey abundance, for example to areas where hatchery fish are released (Collis et al 1995; Shively et al 1996; Major et al 2005), and these predators will probably prey upon species occurring at high abundance. Thus, stocked smolts that lack a strong motivation to migrate will expose themselves to potential predators during a longer period than fish that initiate migration immediately upon release (Salminen et al 2007). Several freshwater fishes, such as northern pike *Esox lucius*, zander *Sander lucioperca* and burbot *Lota lota* may prey heavily on smolt (Larsson 1985; Jepsen et al 1998, 2000; Koed et al 2002, Kekäläinen et al 2008).

Objectives

To develop a sustainable management plan for a species with a complex life history, knowledge about the ecological requirements for each life stage is needed. In the River Klarälven, Sweden successful management of the salmonid populations requires consideration of the ecological requirements both in Lake Vänern and the river, different aspects of the stocking program, and remedial measures to assist passage of the hydropower dams. The current status, future prospects and management of the wild Atlantic salmon and lake migrating trout in the River Klarälven and Lake Vänern were unclear when I started my doctoral studies, and the overall goal with this thesis was to shed light over the situation and to make some suggestions for future actions and monitoring. One has to keep in mind that it is a challenge to change existing management and juridical regulations, and such changes should be made over an extended period of time. With this thesis I wanted to identify different features of the system that have the potential to 1) improve fisheries management and procedures regarding rearing and stocking of hatchery fish, and 2) improve the status of the wild populations of salmon and trout in the River Klarälven. The historical development and present situation in the River Klarälven and Lake Vänern is by no means unique, and this thesis could serve as a case study representing the situation for many other salmonid populations.

Specifically, the objectives of this thesis are: 1) to gain a better understanding of the historical decrease of the salmonid populations in Lake Vänern and the River Klarälven, 2) to estimate the effects of hydropower dams on downstream migration by wild smolts, 3) to examine the possibilities to produce hatchery-reared smolts with increased migration success when stocked into the river, as well as (4) to examine losses of stocked hatchery smolts as they migrate in the lower part of the river. These objectives are addressed in five papers. In the first paper, I compiled available historical data to identify trends and better understand the present status of wild salmon and trout populations as well as the results of many years of stocking hatchery salmon and trout. In Paper II, I estimated losses, migration speed and delays of migrating wild smolts caused by the multiple hydroelectric plant passages in the River Klarälven. The third paper tested the effects of feed quantity (ration) and quality (lipid content of the feed) on growth and smolting of hatchery-reared salmon. In the fourth paper, I explored smolt migratory behavior of the hatchery-reared Atlantic salmon described in Paper III. Finally, in Paper V I investigate predation on hatchery-reared smolts when stocked in the lower part of the River Klarälven.

Methods

Study area

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 and Värmland, Sweden to finally empty into Lake Vänern. The mean annual outlet discharge to Lake Vänern is 163 m^3/s, and mean annual high water discharge is 690 m^3/s (www.smhi.se). Historically, the river supported Lake Vänern with substantial numbers of non-anadromous Atlantic salmon and lake migrating trout. The major pristine spawning and rearing grounds were most likely situated in the upper Norwegian part of the river. However, it remains unclear how productive, in terms of smolt production and catches of returning spawners, these remote areas were compared to better documented reaches in the lower river. At present, eleven hydroelectric plants are found in the main stem, nine in the Swedish part and two in the Norwegian part of the river. There are no fish passages at the lower nine hydroelectric plants, and only the lower 25 km of the river are available to migratory fish. The first hydroelectric plants that blocked the main stem were equipped with technical fishways for upstream migrating salmonids, but due to assumed low efficiency these were removed, and since the 1930s natural smolt production has been sustained via active transport of spawners. Returning spawners are collected in a fish trap at the lowermost dam and transported by truck some 100 km upstream the lower eight dams (Runnström 1940; Törnquist 1940). The fish are released downstream of the only remaining known river stretch with potential spawning and rearing grounds in the Swedish part of the river, situated downstream of the ninth hydroelectric plant (Anonymous 1998). Hatchery brood stock is also collected at the fish trap, and the Lake Vänern salmon and trout fishery has been maintained by stockings of hatchery-reared fish since the 1960s. During the last years, the Klarälven salmon and trout have received increased attention from authorities and managers, and recently the first fisheries management plan for Lake Vänern was produced (Nilsson 2014). However, there are still no specific management programs for wild or hatchery-reared salmon and trout.

In Paper I, I have compiled historical and monitoring data provided by the former Swedish Board of Fisheries (now Swedish Agency for Marine and Water Management), Fortum Generation AB (the current operating power company), the Värmland County Administrative Board, Statistics Sweden (SCB), and a summary report initiated by the former power company Uddeholms Kraft AB (Nordberg 1977). The data include reports and records earlier not made public. Catch data prior to 1960s largely come from Nordberg (1977), later estimations of fishery catches of salmon and trout are based on data from commercial (logbooks), subsistence (annual catch reports), and recreational (questionnaires) fishermen. Fortum Generation AB has provided catch data from the fish traps, historically operated by several power companies. A no-catch regulation for wild salmon and trout was implemented in 1993 (FIFS 1993:32), and since then all hatchery-reared smolts have had their adipose fin clipped before release to distinguish them from wild fish. Thus, catch records from the fisheries includes only hatchery-reared fish after 1993, and by-catches of wild fish are not recorded in the fishery. The origin of the fish (wild vs. hatchery) collected in the fish trap has been recorded from 1996 onwards. The fish are considered as wild if they have an intact adipose fin, but as hatchery-reared spawners that return to the fish trap are also transported to the spawning grounds, these fish could be offspring of hatchery-reared parental fish. The lower part of the River Klarälven has been used as a stocking site for hatchery-reared stocks from both River Gullspångsälven and Klarälven since the 1960s; therefore returns to fish traps include hatchery stocks from both

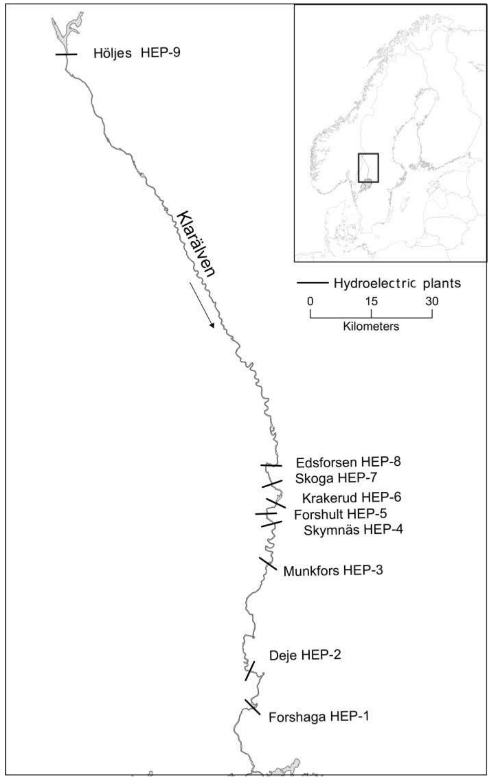


Figure 1. Overview of the River Klarälven showing names and locations of the lower nine hydroelectric plants (HEP).

rivers. Since 1980, hatchery fish records of catches at the fish traps have been separated by species and stock, identifiable by unique fin clips administered in the hatcheries before release.

Since 1961, approximately 3–4000 hatchery smolts have been marked with Carlin tags annually before being released. Reporting of Carlin tagged fish by fishermen is voluntary, information about the tagged fish that are caught at the lowermost dam in the River Klarälven are collected and reported by the hydropower company staff operating the fish trap. Return rates of Carlin tagged fish, released during the period 1982–2003, from both the fish trap and the fishery are analysed in Paper I.

Telemetry techniques

Acoustic telemetry techniques were used in Papers II, IV and V. Atlantic salmon were marked with surgically implanted id-specific acoustic transmitters (model LP-7.3; Thelma Biotel AS, Trondheim, Norway, and models V7–1L and V7–2L VEMCO Inc. Halifax, Nova Scotia, Canada) before released into the river. The fish were monitored by automatic listening stations (model VR-2W; VEMCO Inc., Halifax, Nova Scotia, Canada) situated along the river. The acoustic receivers were range tested by letting submerged transmitters float at known distances from them. In these tests the detection ranges varied between 30-150 m, and at areas with low detection range, up to four receivers per station were used. The fish were also manually tracked (model VR100 receiver; VEMCO Inc. Halifax, Nova Scotia, Canada) to determine the final endpoint of those that did not reach the lake.

Smolt classification

Smolt status was determined visually (Paper II-IV) using a silvering index based on a four-graded scale; (0) fish with clear parr marks and no silvering, (1) some silvering but still clear parr marks, (2) silvery with dark fin edges but some fuzzy parr marks, and (3) silvery with black fin edges and no visible parr marks (Birt and Green 1986; Sigholt et al 1995).

In the rearing experiment (Paper III), smolt status was also evaluated by measuring Na^+/K^+-ATPase (NKA) activity as described in McCormick (1993), as well as using a modified seawater challenge test (Blackburn and

Clarke 1987). In the seawater challenge test, fish were challenged for 48 hour in artificial seawater at 28 salinity (Instant Ocean, Blacksburg, Virginia, USA) at 10°C water temperature. Blood samples were taken when the fish were removed from saltwater, and the sampled blood was immediately centrifuged. Plasma sodium concentration was measured using an ISL IL 943 Flame Photometer (GMI, Minnesota, USA).

Wild smolt migration

In Paper II, wild salmon smolts were caught using a rotary screw trap (Thedinga et al 1994) and by fly-fishing during May-July 2009. Totally, 97 smolts were marked with uniquely identified acoustic transmitters, and monitored by 37 acoustic receivers at 21 stations, as they migrated downstream the River Klarälven. The fish were released at three separate release sites along the river to ensure sufficient migration data from the entire river reach. Losses and migration speed along the 80 km free-flowing stretch upstream of the eight hydroelectric plants were compared with the 100 km long dammed stretch between hydroelectric plants 1-8. Since receivers at the hydroelectric plants generally were placed a couple hundred meters upstream and 1-2 km downstream of the dams, the observed losses at hydroelectric plants include both direct and indirect mortality associated with passing the hydroelectric plants (reservoir and dam) (Montén 1985; Coutant and Whitney 2000; Whitney et al 2006).

Rearing fish - Feeding experiment with hatchery-reared fish

In Paper III, salmon fry were hatched at Yngen hatchery (59° 40’ N, 14° 19’ E). After emergence the fry were fed a commercial salmon start feed (Aller Futura EX, Aller Aqua, Christiansfeld, Denmark) for c. one month. In July 2008, approximately 16 000 fry were moved to Fortum Generation’s fish rearing facility in Brattfors (59° 40’ N, 14° 01’ E) and put on two different diets in high lipid feed (HL) Aller Performa, and low lipid (LL) feed Aller Performa without postextrusion of fish oil. Both groups were fed ad libitum at rations recommended by the manufacturer, and feed was delivered at dusk and dawn using automatic feeders (SB1500M2, Torp Aquateknik ApS, Holstebro, Denmark). In October 2008 fish were randomly assigned to 16 tanks according to one of the following four different feeding regimes: 1) high lipid – high ration (HL/HR), 2) high lipid – low ration (HL/LR), 3) low lipid – high ration

(LL/HR) or 4) low lipid – low ration (LL/LR). Thus, each treatment was replicated four times until the end of the experiment in May 2010 (Fig. 2). High rations were equal to the ration recommended by the manufacturer (approximately 0.2 – 3% of their body mass per day, depending on water temperature and fish size), whereas the reduced ration was approximately 50 % of the high ration. The only difference between high and low lipid feed was the lipid content (15% versus 9%). The fish were monitored every day, filter screens at the water outlet were cleaned, and dead fish removed from the tanks. Feeders were regularly checked and calibrated when needed during the entire study period. As the fish grew, space became limited and the number of fish was reduced to 500 per tank in October 2009. Water temperature was measured with temperature loggers (Onset, HOBO, Bourne, Mass., USA), and ranged from just above 0°C in January–February to approximately 25°C in summer 2009. Windows in the facility allowed the fish to experience natural photoperiods with slightly reduced intensity.

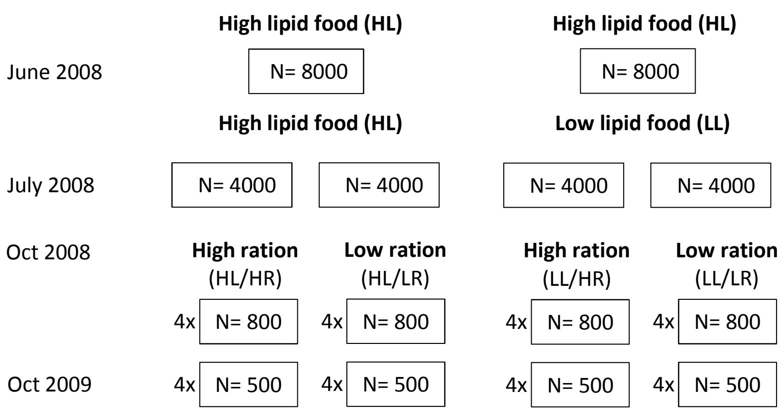


Figure 2. Experimental set up (N = number of fish). Abbreviations indicate different feeding treatments; HL/HR = high lipid/high ration, HL/LR = high lipid/low ration, LL/HR = low lipid/high ration, LL/LR = low lipid/low ration.

Fish were sampled for weight and fin damage approximately monthly during the whole study period. On ten sampling occasions subsamples of fish were sacrificed, and on these occasions individual measures were recorded for length, weight, gender, maturity status (among males), smolt status and whole-body lipid content. Body lipid content was measured using infrared transmission (MIT) spectroscopy technique (Elvingson and Saunja 1992), as previously described by Trombley et al (2012). During the second autumn, non-lethal assessment of early sexually mature males in all tanks was done by gently squeezing along the ventral side of the fish to check for running milt. An assumed sex ratio 1:1 was applied. A subsample of 60 early mature males from the HL/HR treatment was individually tagged with streamer tags (Hallprint Pty Ltd, Hindmarsh) in late autumn 2008 to be able to identify early mature males the following spring.

Hatchery fish migration

In Paper IV, migratory behavior of the fish described in Paper III was studied. Only three of the treatments were used as most of the fish from the low lipid – low ration (LL/LR) treatment did not smolt. Forty fish from each of the three remaining treatments were tagged with uniquely identified acoustic transmitters. In addition, 30 early mature males from the high lipid-high rations (HL/HR) treatment, were tagged with acoustic transmitters. The tagged fish were released on five occasions together with unmarked conspecifics downstream of the lowermost hydroelectric plant in the River Klarälven. The fish were monitored by 18 acoustic receivers at 10 localities from the release site as they migrated to the lake.

Predation on released hatchery-reared smolts

In Paper V, I investigated losses of stocked hatchery reared salmon and trout tagged with radio and acoustic transmitters in the River Klarälven during the period 2006-2010. Smolt losses were compared across three habitat types in the river between the lowermost hydroelectric plant and the delta. The three habitats are; (i) 0-3 m deep vegetated areas, (ii) more than 6 m deep pool areas with accumulated timber logs in sloughs and backwaters, and (iii) 2-4 m deep reaches with sandy, uniform bottom substrate without vegetation. Smolts were defined as dead if they were repeatedly found in same location with no indications of movements when manually tracked. Smolts were associated with one of these three habitats if located in the habitat or within 100 m of these habitats. The three habitat types were also sampled for northern pike during three periods in March to May in 2010. Total pike density was not measured, but number of fish caught by standardized fishing with rod and line was used as a proxy for pike density. Gut contents of all landed pike were analysed.

Results

History of salmon and trout in the River Klarälven

Catch reports dating back to the 1600s were found when data was compiled for Paper I, but as there were large time gaps data from the 1600s and 1700s were not included in the analysis. In the early 1800s, annually catches of spawners in the River Klarälven reached 30 000 salmon and trout in some years. However, by the end of the 1800s catches declined to approximately 5 000 salmon and trout annually. In the early 1900s, connectivity was interrupted by the first hydroelectric dams blocking the whole river width, and the annual catches declined to 2-3000 fish at this time. For the period 1961–70, the mean annual catch of Klarälven stocks was only 139 salmon and trout combined (Fig. 3). Hatchery production and stocking of smolts started in the 1960s, and by the end of the 1980s hatchery production reached its current levels of >200 000 smolts (compensatory stockings mainly to the river by the power company, and stockings to the lake by the regional recreational fisheries stakeholders). For the time period 1996-2008 the mean annual number of Klarälven salmon and trout stocked in the River Klarälven was 129 000.

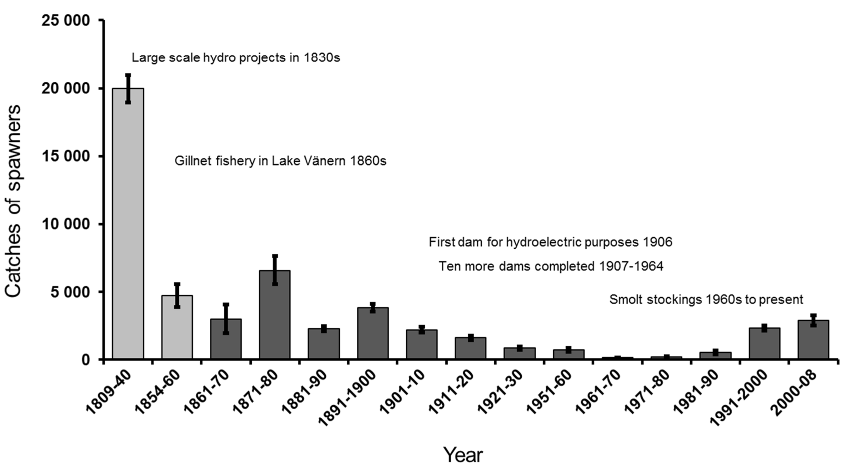


Figure 3. The mean number of spawners (salmon and trout combined) caught in the River Klarälven, 1809-2008. Each bar is the mean for a ten-year period, except the first two light grey bars. Catch methods, locations and effort vary over this period. After 1960, wild fish, and both Klarälven and Gullspångsälven hatchery stocks are all included in the catch numbers. Modified from Fig 2. in Paper I.

As hatchery fish can be distinguished from wild conspecifics by the lack of an adipose fin, a special analysis for the period after 1996 was done. The number of wild trout returning to the fish trap has remained very low (< 50 per year), even if the return rates increased significantly during the period 1996-2009. The return rates of wild salmon are larger, and have increased from approximately 220 to up to 780 during the same time period, even if this increase was not significant.

The tag-recovery rates from Carlin-tagged fish in the lake fishery decreased during the period 1982–2003, from around 8% to <2% (Fig. 4). However, return rates of hatchery reared salmon and trout to the fish trap have remained relatively constant during the period 1982–2003, averaging about 1%. The estimated return rate of unmarked hatchery-reared salmon and trout to the fish trap for the period 1996–2007, based on number of released smolts and absolute number of fish caught in the fish trap, was 0.9% (Fig. 4).

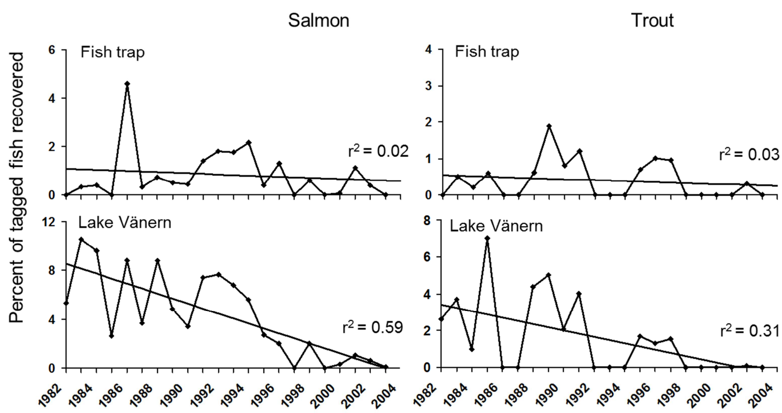


Figure 4. Percent returns of Carlin-tagged (Klarälven stock) salmon and trout to the fish trap at Forshaga (upper panels) and from the Lake Vänern fishery (lower panels) from 1982-2002. Note differences in the y-axes for each panel. Modified from Fig 7. in Paper I.

The compiled catch data, based on commercial and subsistence fisheries records and recreational fisheries surveys, indicates annual catches of at least 75 metric tons of salmon and trout in Lake Vänern starting from the 1990s. This estimation incorporates only 50 metric tons of catch allocated to the sport fishery, a figure well below official estimates but more in line with more conservative unpublished trolling catch data produced by the Swedish University of Agricultural Sciences, SLU (pers com M. Johansson). With an assumed average catch weight of 4 kg (based on mean weight in trolling tournaments during recent years), this yields a conservative estimation of 7.5% of the smolts stocked being recruited to the fishery.

Migration of wild smolts

The estimated migrating success of wild Atlantic salmon smolts along the studied 180 km long river reach was 16% (Paper II). Most (76%) smolts were lost due to power plant passages, whereas no smolts were lost at the 80 km long free-flowing control stretch. Only 8% (3 smolts) were lost at the two free-flowing control stretches between the second and third, and third and fourth hydroelectric plant (Fig. 5). The smolts migrated faster along free-flowing control stretches than along dammed stretches, and there was a negative correlation between migration speed and fish size at dammed stretches, this was not seen at free-flowing control stretches. The total delay due to hydroelectric plant passages, based on observed migration speed, was estimated to eight days.

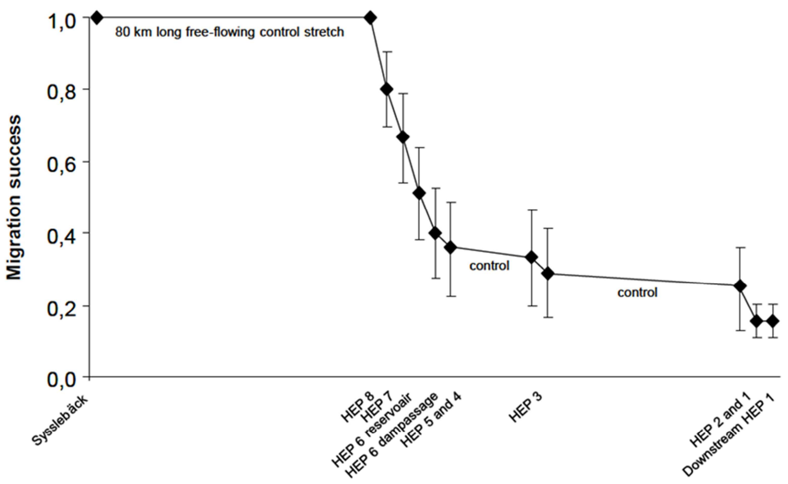


Figure 5. Estimated migration success (%), based on the Kaplan–Meier model, along the 180 km long studied stretch of the river, including eight hydroelectric plants (HEP). Error bars represent 95 % confidence intervals.

Hatchery-reared fish

Fish body mass was significantly affected by feed ration, and nearly so by feed lipid content, but there were no significant interactions (Paper III). Fish in high feed ration treatments had a significant higher body mass than fish in low feed ration treatments (Fig. 6a). In addition, fish fed low lipid feed had lower body lipid levels than fish fed high lipid feed (Fig. 6b).

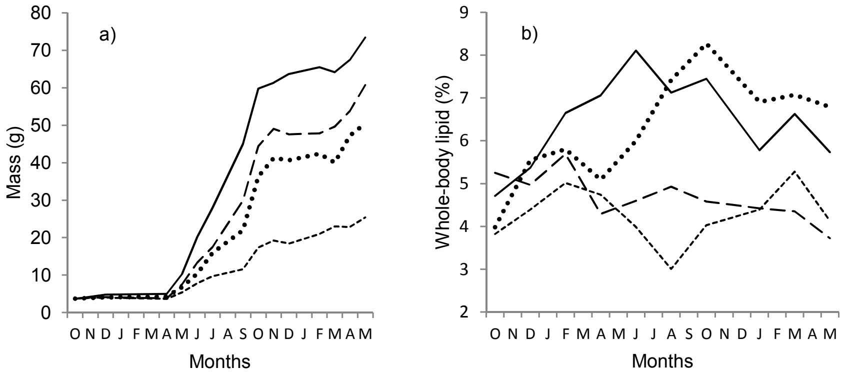
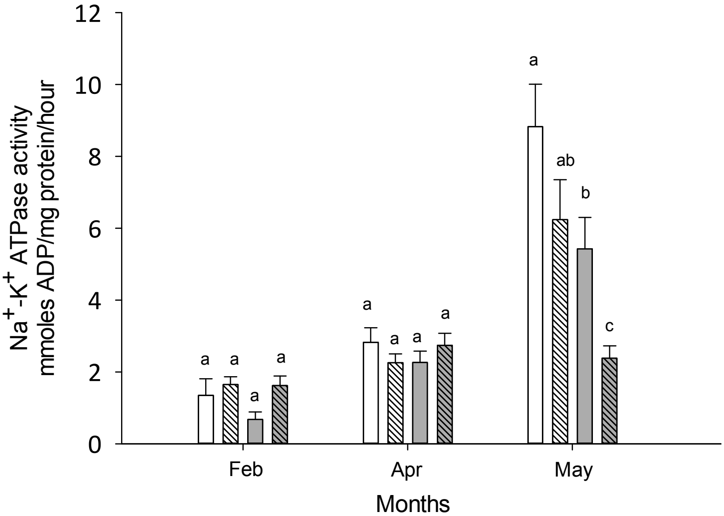


Figure 6. Body mass (a) and whole-body lipid levels (b) of juvenile Atlantic salmon fed various fed (— high lipid/high ration, — — low lipid/high ration, ••• high lipid/low ration, and - - - low lipid/low ration). Each line is the mean of four replicate tanks.

A majority of the fish displayed morphological smolt characteristics during their second spring. In all treatments, except for the fish fed low rations of low lipid feed, 69% or more of the two year old fish were classified as mainly silvery (smolt class 2 or 3) in early May. Fish from all treatments, except the fish fed a low ration of low lipid feed, also showed an increased freshwater gill Na+/K+-ATPase activity in May during their second year (Fig. 7a). Similar results were observed when fish were challenged in saltwater (Fig. 7b). The individually tagged male parr that matured early in their second autumn also exhibited silvering during the subsequent spring (72% were classified as smolt class 2 or 3), but their plasma sodium levels were significantly higher than freshwater controls when exposed to saltwater, indicating poor hypo-osmoregulatory ability (Fig. 7b).



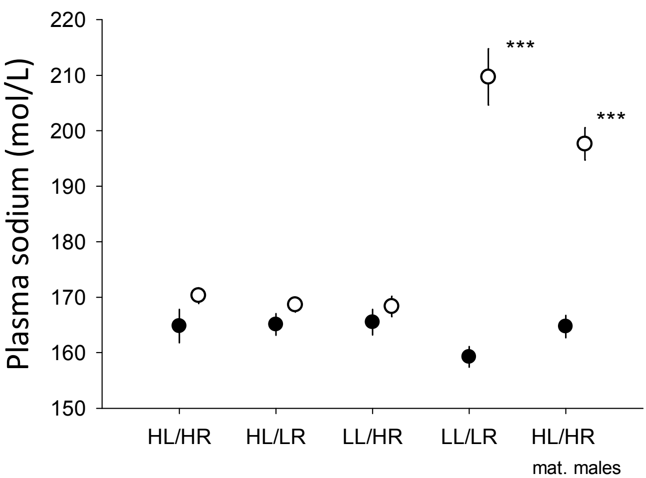


Figure 7. Upper figure (a); Gill Na+/K+-ATPase activity (mean ± S.E., n=16-20 per group) in February, April and May for two year old hatchery-reared Klarälven salmon smolt raised on the four feeding regimes (□ high lipid/high ration, ▧ high lipid/low ration, ▩ low lipid/high ration, and ▨ low lipid/low ration) . Different letters indicate significant differences between treatments. Lower figure (b); Plasma sodium levels (mean ± S.E.) in May for two year old hatchery-reared Klarälven smolt raised on the four feeding regimes (HL /HR = high lipid / high ration, HL/LR= high lipid / low ration, LL/HR= low lipid / high ration, LL/LR= low lipid / low ration). Open symbols represent plasma levels after exposure for 48 h to 28 salinity seawater (n=10-20), solid symbols show the levels of freshwater controls (n=5-8). *** indicate significant difference between freshwater controls and after seawater exposure.

Fish fed low lipid feed initiated migration to a greater extent and had a higher migration success than fish fed standard feed, regardless of ration size, when they were released into the wild (Paper IV) (Fig. 8). Moreover, fully silvered smolts migrated faster and had a higher migration success than fish displaying weaker smolt characteristics. Almost half (46.7%) of the fish from the early mature male group did not move beyond the receiver station 2.5 river kilometers downstream of the release site, which was significantly lower percent than for fish from the three treatment groups. Also, fewer migrators from the early mature male group than from the three treatments groups reached the lake-

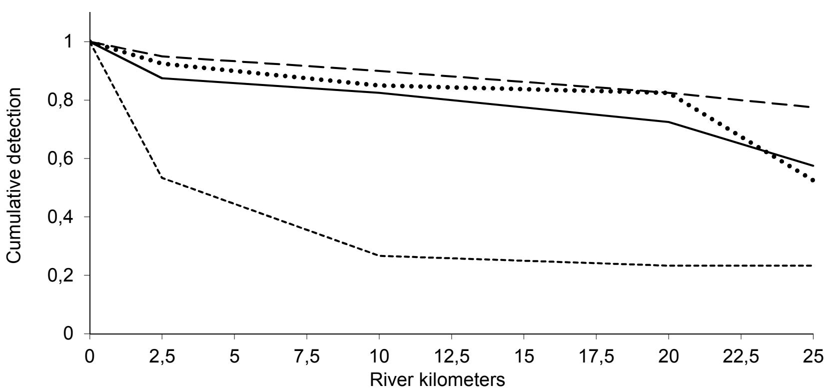


Figure 8. Cumulative detection curves for the three treatment groups of smolts; — high lipid/high ration, — — low lipid/high ration, ••• high lipid/low ration, and in addition --- early mature males from the high lipid/high ration treatment.

In total, 182 (50.6%) of the 360 tagged Atlantic salmon and trout smolts that were released during 2006-2010 were detected at outlets to Lake Vänern, 66 fish (18.3%) did not leave the release site (< 1km downstream movement during the study period), 80 fish (22.2%) were found by manually tracking along the river, 20 fish (5.6%) were found by manually tracking in the delta area, and the fate of 12 fish (3.3%) is unknown. The loss rate of hatchery reared smolts was higher in habitats with a high CPUE of northern pike (Fig. 9).

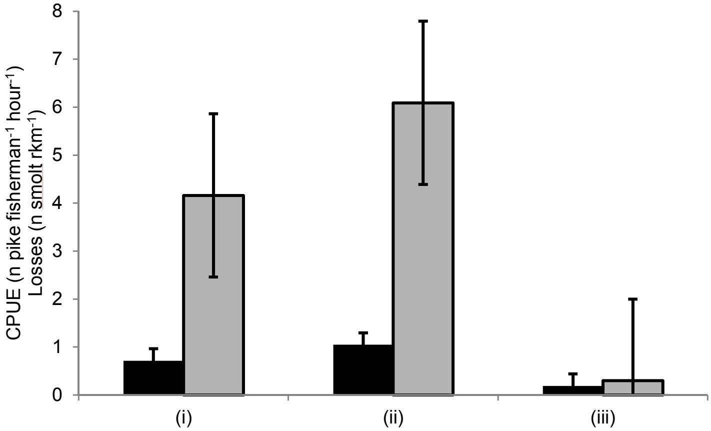
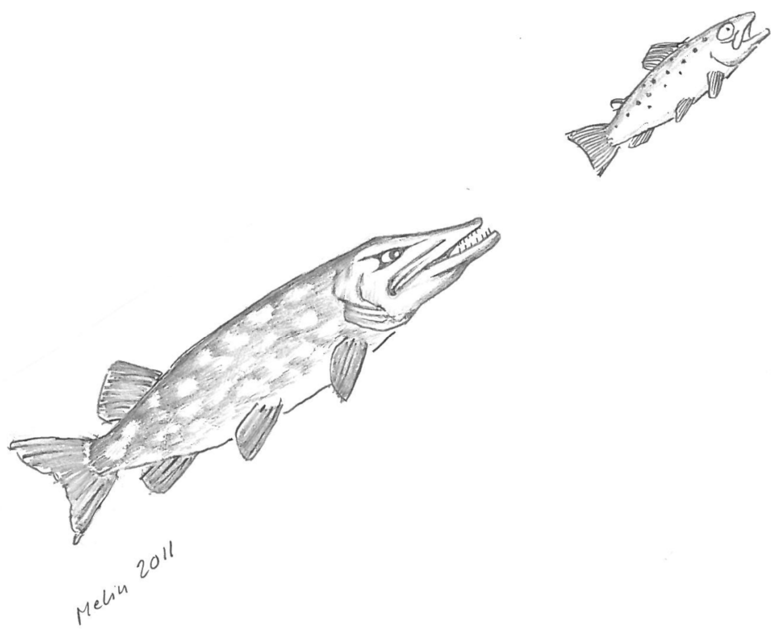


Figure 9. CPUE of pike (number of pike fisherman^{-1} hour^{-1}) and loss rate of released hatchery-reared Atlantic salmon and brown trout smolts (number of smolts rkm^{-1}) in (i) vegetated stretches with 0-3 meters depth, (ii) stretches with areas deeper than 6 meters, and (iii) stretches with sandy, uniform bottom substrate with 2-4 meters depth in the lower River Klarälven. Values are mean ± S.E. for CPUE (2010) and smolt losses (2006-2010).



Pike diet changed over time (Fig. 10). The most frequently captured prey during the first sampling period (late April) was European smelt (87%), during the second period (mid-May) smolts of Atlantic salmon and brown trout (78%), and during the third sampling period (early June) European river lamprey (79%). Thus, different prey species dominated the gut content during the three sampling periods.

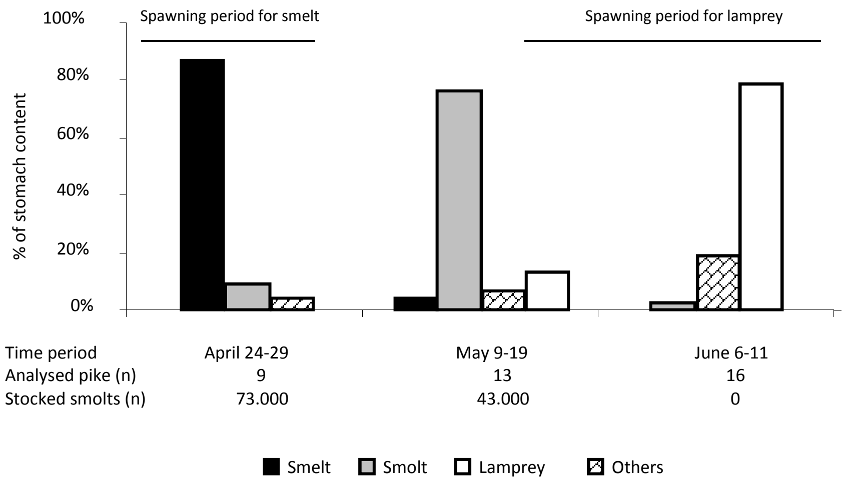


Figure 10. Distribution (%, by numbers) of food items eaten by 38 pike in the lower River Klarälven during April 24-29, May 9-19, and June 6-11 2010. Number of analysed guts containing food items and number of stocked smolts during the three time periods (including five days prior to each period) are shown under the histobars. Horizontal lines indicate the approximate spawning periods of smelt and lamprey.

Discussion

Human exploitation of the River Klarälven has played a dominant role in the region's historical development, and anthropogenic activities in the tributaries of Lake Vänern were already having negative effects on salmonid populations several hundred years ago (Nordberg 1977). The River Klarälven was first exploited for large-scale hydropower in the early 1800s. In addition, riffles were cleared from boulders, and the lower river was channelized to facilitate log-driving and boating. Only an estimated 30% of the historic salmon spawning and rearing habitat in the Swedish part of the river remained by the mid-1800s. In addition, river fishing techniques were improved continuously, and by the 1860s a large-scale gillnet fishery was initiated in Lake Vänern (Nordberg 1977; Nilsson 1980).

In this thesis, I highlight the importance of using a holistic approach in the conservation and management of wild and hatchery reared salmon and trout in regulated rivers and lakes. Wild populations of Klarälven salmon and trout have been conserved through the early management decision to transport returning adults upstream multiple dams to the remaining spawning grounds, and by the supplementary stocking of endemic Klarälven hatchery smolts, which has maintained an attractive recreational and commercial fishery in the River Klarälven and in Lake Vänern. For a long time it was assumed that the losses of downstream-migrating salmonids were negligible in this river system (Anonymous 1998), whereas data presented in Paper II indicate that this is not the case for salmon smolts. This should be of great concern for conservation managers. Also, the possibilities to produce hatchery-reared salmon smolts more similar to wild conspecifics than smolts reared under standard rearing procedures, both in physiological terms and migration success when released (Paper III and IV), as well as the potential use of ecological windows when releasing smolts suggested in Paper V, should be of great interest to stakeholders and fisheries managers. The situation and questions raised in the River Klarälven and Lake Vänern are common for regulated river systems with wild and hatchery salmonid populations, and the lessons learned from this thesis should be applicable to other water systems facing similar challenges.

The populations of salmon and lake migrating trout in the River Klarälven have been conserved and recovered by supplementary stockings of hatchery smolts and upstream transport of both wild and hatchery-born adult spawners returning to the river. The number of returning spawners was critically low in the 1960s and 1970s, but the increased number of stocked hatchery smolt during the 1980s started a positive overall trend that still continues. Further, the implementation in 1993 of adipose fin clipping of hatchery-reared fish and the no-catch regulation for wild-born salmon and trout (FIFS 1993:32) have most likely been key factors in the continued increasing numbers of wild spawners. Currently, the numbers of returning wild-born salmon exceed a thousand fish (2013; 1118 spawners), and the trend is also positive for wild-born trout (2013; 145 spawners) at the fish trap (pers com K. Jarmuzewski). Thus, a variety of different conservation and management measures have been implemented during the last 80 years, and despite the loss of connectivity, these joint efforts have preserved these unique populations of landlocked salmonids.

The use of endemic stocks has probably been a key factor in the management success in the River Klarälven, as endemic stocks generally have greater survival than non-native stocks when stocked to rivers (eg Behnke 2002; Bosch et al 2007). These findings support the perception that hatchery fish may have a positive effect on populations that are below their carrying capacity (Lister 2014). However, supplemental stockings may result in unwanted behavioral, ecological, and genetic effects on native fish stocks (Jonsson and Jonsson 2011), and mixing of hatchery stocks with wild stocks can result in loss of locally-adapted populations (eg Williamson and May 2005; Behnke 2002; Waples et al 2008). Due to assumed low spawning success of hatchery fish (Anonymous 2014a), and the risk of unwanted genetic effects (Palm et al 2012), the regional authorities has recently decided that Klarälven salmon spawners of hatchery origin (ie released hatchery-reared salmon returning to the fish trap) should not be transported to the spawning ground. Klarälven trout spawners of hatchery origin are still transported as the number of returning wild-born trout is lower than for salmon. The effect of this decision on the number of return spawners cannot be predicted with current knowledge about the wild salmon population.

According to the available data, the hatchery program seems to support an annual commercial and recreational fishery of at least 75 metric tons of salmon and trout in Lake Vänern, translating to a recruitment rate of roughly 7.5% of the hatchery smolts to the fishery. Carlin-tag recovery rates from the lake fishery have declined steeply since the 1990s, ICES (2011) has reported similar declines in recapture of Carlin tagged hatchery reared smolts in the Baltic area, which is assumed to be the result of decreased post-smolt survival. The general declines in catch rates of hatchery reared salmon and trout in Sweden have raised concerns about the 'quality' of the smolts being released (Eriksson et al 2008). Such a decrease is not seen in the fishery catches during this period in Lake Vänern, although there has been a shift from a commercially-based to a recreationally-based fishery. Further, river return rates of hatchery-reared Carlin-tagged fish to the fish trap in Forshaga have been fairly stable over time, with return rates of about one percent since 1982. The most likely explanation for the discrepancy between river and lake tag-recovery rates is the shift in the fishery and a reduced reporting of tagged fish by the fishermen, which has previously been identified as a common problem for other fish tagging programs (Brendan et al 2010).

Basic ecological knowledge and monitoring, such as productivity of the system, the fishing effort and efficiency, catches and natural mortality, are necessary for good management. For the River Klarälven and Lake Vänern there is much uncertainty about different measures used to evaluate the status of the populations. Records of spawners captured in the fish trap at the lowermost dam in the River Klarälven serve as the only continuous monitoring of wild-born fish. Electrofishing monitoring programs exist in some tributaries, and during recent years electrofishing from a boat at presumed rearing areas has been conducted, but the monitoring technique and data are not yet good enough for reliable production estimations. Analyses of the Lake Vänern salmon and trout fishery have mainly been based on catch reports from the commercial fishery, but gear and effort based data useful for trend analysis are still lacking. Also, during the last twenty years the recreational salmon and trout fishery (mainly the trolling fishery) has had higher estimated catches than the commercial and subsistence fisheries. Catch estimations of the trolling fishery are based on occasionally questionnaires, characterized by high uncertainty. Thus, managers do not have access to basic effort and catch data needed (Hillborn 1992) for successful fisheries management.

A Carlin-tagging program of 3000-4000 hatchery-reared fish per year began in the 1960s to assess different stocking strategies. The program has not followed a long-term plan, and the data are difficult to evaluate as the number of Carlin-tagged fish returning to the fish trap is low, and the reporting of tagged fish from the fishery has declined. Similar, low tag recovery rates in several tributaries of the Baltic Sea have led some authorities to discontinue tagging fish with Carlin-tags. As long-term conservation and management should be based on comprehensive life history-based research, it is crucial that monitoring programs and management plans with a holistic approach are developed (eg Stanford et al 1996; Knudsen and Michael 2009; ICES 2013) and implemented as soon as possible. Fortunately, several critical questions concerning the River Klarälven and Lake Vänern have been addressed recently. Currently a new pit-tag monitoring program is being considered for the River Klarälven and Lake Vänern, and there are several ongoing research projects that focus on downstream migration of smolts and kelts, trap efficiency, migration and spawning success of wild and hatchery fish as well as fishing effort and catches in the recreational fishery (www.nrrv.se). Also, a fisheries co-management group for Lake Vänern, with representatives from stakeholders, scientists, and regional and local authorities has recently been created (Anonymous 2014b). Findings from these ongoing studies and actions may fill some of the important knowledge gaps in the life history-based management needed to conserve wild stocks and maintain the salmon and trout fishery at current levels.

Traditionally one has focused more on upstream migration than downstream migration. In my study of downstream migrating wild smolt I found an extensive loss of smolts in the regulated part of the River Klarälven (Paper II), which highlights the problems with regulated rivers with multiple hydroelectric plants (Muir and Williams 2012). Even if losses at a single hydroelectric plant were less than 10% in some cases, the cumulative losses of passing eight dams had a substantial effect on the total survival of the wild migrating fish. The discharge was close to the annual average for the studied time period, which means that there is rarely any spillwater at the hydroelectric plants, and all fish had to pass dams through turbines. In this study (Paper II) it is not possible to distinguish direct turbine mortality from indirect mortality due to increased predation as a result of delays, wounds and disorientation (Montén 1985; Coutant and Whitney 2000; Budy et al 2002; Ferguson et al 2006; Whitney et al 2006; Johnsen et al 2011; Ward and Hvidsten 2011), but most smolts were lost in areas approximately one kilometer upstream or downstream the hydroelectric dams. The average delay of eight days due to the hydroelectric plant passages may have led to an increased exposure to potential predators in the forbays upstream of the dams. 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. From a conservation perspective, the observed loss rate could be of great importance for the recovery of the wild-born salmon and trout populations.

Potential positive result of attempts to increase the number of juveniles produced at the rearing grounds may be hard to detect in terms of numbers of returning adults due to the substantial losses during the smolt downstream migration.

Raising juvenile salmon on different feeding regimes from fry stage until two-years of age (Paper III) affected growth, lipid levels, and smolting. Fish fed high rations of low lipid feed most closely resembled their wild conspecifics in terms of size and lipid levels as smolts. Also, fish fed higher rations displayed the strongest morphological and physiological characteristics associated with smolting. When the fish were released to the wild, fish fed high rations of low lipid feed initiated migration to a greater extent and also had a higher detection rate at the outlets to Lake Vänern than fish fed standard feed, regardless of ration size. This is somewhat contradictory to earlier studies finding that reduced feeding rations enhance smolting and migratory behavior (ie Lans et al 2011; Larsson et al 2012). However, in this study (Paper III) the hatchery-reared smolts were smaller as feed quantity and quality were manipulated during their entire hatchery phase, rather than subjecting fish to reduced rations of standard feed during their last period in captivity. It is possible that the reduced feeding in these earlier experiments started after the decision to smolt was already taken (Thorpe et al., 1998), and that food deprivation during the following spring may not affect the overall decision to migrate, only the timing of the smolting (Lans et al., 2011). As in previous studies of hatchery-reared Klarälven salmon (Lans et al 2011), migration success and speed were positively related to morphological smolt characteristics. We also found an agreement between morphological and physiological smolt characters. Interestingly, the changes in physiological variables associated with smolting indicates that the Klarälven salmon to a certain degree have retained the same physiological changes associated with smolting as found in anadromous Atlantic salmon (Paper III). Thus, by relatively simple changes in feeding regimes I showed that it is possible to produce hatchery-reared smolts with characteristics and migration success similar to wild conspecifics (Paper III and IV; unpublished data). The relationship between smolt status and migration success highlights the importance of timing the physiological smolt window (McCormick et al 1998) when attempting to maximize migration success of stocked smolts. However, an enhanced migratory behavior and increase survival of hatchery fish might result in an increased competition for wild-born smolt, and therefore effects on the wild-born fish due to changes in the hatchery protocols should be carefully monitored.

Fish kept at high feed rations, regardless of lipid content of the feed, had a higher frequency of sexually mature age-one male parr, and most of these early mature male parr became silvery during the subsequent spring (Paper III). However, the saltwater challenge test indicated poor hypo-osmoregulatory ability for the early mature males, and thus they did not fulfill the physiological smolt criteria. These results are in line with earlier studies by Lundqvist et al (1989) and Berglund (1995). When released into the wild (Paper IV), many of the early mature males did not initiate downstream migration. The weak migratory behavior of the early mature males is consistent with results reported by eg Hansen et al (1989), Fängstam (1993) and Vainikka et al (2012). Since early mature males tend not to migrate when they are released into rivers (Eriksson et al 1987), having a large proportion of early mature males in the stocked batches will result in lower catches in the fishery and lower adult return rates (Lundqvist et al 1994; McKinnell and Lundqvist 1998). Thus, to reduce the proportion of early mature males and increase the number of spawners produced by stocking, feeding regimes in hatcheries should be manipulated during critical periods as proposed by Vainikka et al (2012).

In many cases the low survival rate of hatchery reared smolts has been ascribed to predation (eg Larsson 1985, Jepsen et al 2000, 2006; Dieperink et al 2001, 2002; Kekäläinen et al 2008), and as a result of a poorly-developed anti-predator behavior (Einum and Fleming 2001). During the period 2006-2010 only half of the stocked hatchery-reared smolts tagged with telemetry transmitters reached Lake Vänern (Paper V). The loss rate of smolts was higher in areas with a high occurrence of northern pike. The changes in pike diet indicated that there may be ecological windows of opportunity to increase the migration success for the smolts when the predation pressure is low, as might occur when alternative energy-rich prey such as European smelt and river lamprey are available. I suggest that, just as wild fish can benefit when migrating at the same time as hatchery-raised fish are stocked (Peterman and Gatto 1978; Wood 1987), stocked fish can benefit from being released at the same time as there is high abundances of alternative prey. The potential of matching the physiological smolt window (McCormick et al 1998) with ecological windows of opportunity should be of great interest and a possible future research topic. To obtain this match, the rearing and release must be based on good ecological knowledge about both the fish and the system into which they are released. In the River Klarälven the water is relatively cold in April and the majority of the wild-born smolts migrate in June, which suggest that June should be the most suitable time for release of hatchery-reared smolts.

In summary, the lake migrating salmon and trout of the River Klarälven were historically among the most productive landlocked large-bodied salmon stocks in the world. Extensive exploitation of the river almost drove the populations to extinction, but due to management efforts the wild populations were saved. Through hatchery stockings, the landlocked salmon and trout of the River Klarälven remain of considerable value for both commercial and recreational fisheries. In this thesis, I stress the need for a holistic life-history based approach in the conservation and management of the salmonid populations. To ensure viable populations of wild populations, future management should include both up- and downstream solutions that ensure connectivity in the system. Also, the suggested changes in the hatchery and stocking procedures have the potential to increase the survival of stocked smolts, and thereby generate increased catches in the fishery. The results of my research should be applicable to other regulated systems, particularly those with mixed stocks of wild and hatchery salmonid populations.

Swedish summary - Sammanfattning

Atlantlax *Salmo salar* har en komplex livscykel som omfattar långa vandringar och nyttjande av flera olika typer av livsmiljöer, vilket gör dem extra sårbara för fragmentering av vattendrag (t.ex. dammar och vattenkraftverk) och degradering av vattenmiljöer (t.ex. rensning av sten och block i vattendrag för att underlätta timmerflottning). Förvaltningen och bevarandet av en art som denna är komplex, och man behöver kunskap om deras ekologi både på en tidsmässig och på en rumslig skala för att kunna förstå alla olika skeden i dess livscykel. I den här avhandlingen lyfter jag fram behovet av en helhetssyn inom bevarande och förvaltning av vild och odlad lax i utbyggda och påverkade vattendrag och sjöar.

I Klarälven finns bestånd av sötvattenslevande lax och öring *Salmo trutta*. Sent om hösten leker de i älven, ynglen som kläcks under våren tillbringar 2-3 år i älven innan de vandrar ut till Vänern för att växa sig stora och i sin tur återvända till älven för lek. Människorna i Klarälvsdalen har i flera hundra år nyttjat älven för fiske, vattenkraft, transporter och flottning av timmer. För att underlätta flottningen och båttrafik rensades älven på sten och block, samtidigt som sidofåror blockerades och strandkanterna skoddes med sten och stock. Man uppskattar att 70% av laxens ursprungliga lek- och uppväxtområdena i älvens svenska del hade förstörts redan under 1800-talet. I början av 1900-talet byggdes Klarälven ut med kraftverk för elproduktionsändamål. Kraftverksdammarna hindrar fiskens vandring, och för att bevara bestånden fångar man in lekmogen lax och öring vid den nedersta kraftverksdammen och transporterar upp dem till de kvarvarande lekområdena som finns mellan den åttonde och nionde kraftverksdammen. Man antog länge att kraftverken i Klarälven inte utgjorde någon större fara för de små laxar och öringar som vandrar ut ur älven, men mina studier tyder på att den samlade dödligheten vid kraftverkspassagerna kan vara mycket hög, upp till 84%, då fisken passerar kraftverken. De vilda bestånden var mycket svaga under en period på 1960–70-talet, men stödutsättningar av odlad lax- och öringungar vände trenden. Idag fångas drygt 1000 vilda laxar och 100 vilda öringar årligen för upptransport förbi dammarna.

Utsättningarna av odlade lax- och öringungar möjliggör ett attraktivt fiske både i Klarälven och i Vänern. Cirka 7,5% av de utsatta fiskarna landas av fiskare (medelvikt på drygt 4 kg, årsfångst på ca 75 ton), och ca 1% av de odlade fiskarna återfångas som lekmogen fisk i fällan vid den nedersta dammen. Dödligheten hos fisken som sätts ut i älven är stor under deras första tid i frihet, många hinner inte ens påbörja sin vandring ut till Vänern. Den odlade fiskens tilltagna storlek och höga fetthalt har lyfts fram som troliga orsaker till den i vissa fall låga vandringsviljan och överlevnaden. Mina studier tyder på att odlade laxungar som är mindre, dvs. av liknande storlek och fetthalt som vilda artfränder har en hög vandringsvilja och -framgång då de sätts ut i älven vid lämplig tidpunkt. I avhandlingen föreslår jag förändringar i odlings- och utsättningsrutinerna för att ge den odlade fisken större överlevnadschanser vid utsättning i det vilda.

För att möjliggöra en långsiktig hållbar förvaltning av lax- och öring bestånden i Klarälven och Vänern behöver man en ökad kunskap om den naturliga produktionen av fisk, fisketrycket och effektiviteten både i det yrkesmässiga och fritidsbaserade fisket, fångsterna, samt beståndsstrukturen och den naturliga dödligheten hos både vild och odlad fisk. Dessutom behöver man inkludera problematiken med vandringshinder och de negativt påverkade lek- och uppväxtområden. En långsiktig förvaltning bör innefatta lösningar för såväl uppströmsvandrande lekfiskar som nedströmsvandrande utlekt fisk och juvenil fisk på väg ut till Vänern. Begränsningar av nuvarande lek- och uppväxtområden, i form av yta och kvalité, som utgör eventuella flaskhalsar och hinder för fortsatt ökning av de vilda bestånden bör noggrant och skyndsamt utredas. Vid ett scenario som omfattar fortsatt ökande bestånd av vild lax och öring, i kombination med ökad migrationsöverlevnad för den odlade fisken som sätts ut, bör man ytterligare studera interaktionen mellan vild och odlad fisk. Detta arbete bör beakta lokala delbestånd i älven och biflöden, samt alternativa utsättningsstrategier för odlad fisk. Lämpligen inkluderas genetisk övervakning för att med större säkerhet kunna följa bestånden.

Mina forskningsresultat och den erhållna kunskapen är inte enbart specifikt knuten till Klarälven och Vänern, utan har ett generellt värde och torde kunna tillämpas även i andra påverkade vattendrag och sjöar som hyser bestånd av så väl vild som odlad lax och öring.

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Migration and quality of landlocked Atlantic salmon smolt

Atlantic salmon *Salmo salar* has a complex life cycle, including long migrations and habitat shifts for both juveniles and adults. As such, salmon populations are vulnerable to habitat degradation and fragmentation along their migratory routes, which make management and conservation a complex task requiring knowledge of salmon ecology at different temporal and spatial scales. In this thesis, I highlight the use of a holistic approach in the conservation and management of wild and hatchery-reared salmon in regulated rivers and lakes.

Small populations of wild-reproducing landlocked salmon and trout *Salmo trutta* exist in the regulated River Klarälven, Sweden. Since 1930, transportation of adult spawners upstream of eight dams has been done to give the fish access to the spawning grounds. My data indicate that a large proportion of the wild smolts are lost due to multiple dam passages, and future management should include both up- and downstream solutions, ensuring connectivity in the system. The fishery in Klarälven and Lake Vänern is maintained by compensatory stockings, yielding catches of about 75 metric tons and a river return rate of stocked fish of about 1%. I suggest changes in the hatchery and stocking procedures to increase the survival of stocked smolts.

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