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Migration Problems of Atlantic Salmon (*Salmo salar* L.) in Flow Regulated Rivers

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Academic Dissertation for Doctor of Philosophy in Biology (Ph.D.), speciality in Fish Biology

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Cover picture:
Calle Bredberg
Two salmon jumping at Laxhoppet in River Umeälven in the summer of 2004.

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Abstract

Rivinoja, P. 2005. Migration Problems of Atlantic Salmon (*Salmo salar* L.) in Flow Regulated Rivers. Doctor's dissertation. ISSS: 1652-6880. ISBN: 91-576-6913-9.

Migration patterns of adult Atlantic salmon (*Salmo salar*) and smolts of salmon and brown trout (*Salmo trutta*) were studied in the flow controlled areas of two northern Swedish rivers. Fish behaviour and migration success at passages of various hydropower facilities were evaluated in different flow regimes. In addition, the impacts of the power-stations on the salmon populations were modelled.

On average, 30% (annual mean 0-47%) of the upstream migrating salmon that were captured at the mouth of Umeälven and marked with radio-, PIT- or Carlin-tags in 1995-2005 (n = 2651), reached the fish-ladder 32 km upstream. The migration took, on average, 44 days from the river mouth to the fish-ladder. Salmon were hindered or delayed at the power-station outlet, waterfalls and the fish-ladder area. At the turbine outlet area, salmon generally responded to increased bypass flows by upstream migration. In total, a 70 % average loss of potential spawners to the catchment area was estimated. Predictions based on population modelling showed that if 75 % of the females passed the regulated section successfully and reached spawning areas in the tributary Vindelälven, the population could increase by about 500 % over a ten-year period.

Radio-tagged smolts (n = 206) of Atlantic salmon and brown trout released upstream of the power-stations at Umeälven and Piteälven in 2002-2004 migrated downstream in the main flows at a speed of about 2 body length s^{-1}, eventually leading them to the turbine intakes. Migrating smolts were observed surface oriented at depths of 1-3 m. Flow modelling estimated relatively low fish guidance efficiencies for the spillways at natural flows. About 13 % of the smolts at Piteälven were hindered as they approached the power-station, and mortality of smolts at turbine passage was positively related to body size. By using the data for radio-tagged smolts and data from Carlin-tagged smolts (n = 7450) in 1998-1999, the overall average mortality for smolts at the power-station was estimated to 17%. Population modelling predicted a potential increase in the escapement return from 5-30 % to 70-120 % in ten years if the smolts had no losses as they passed the power-station.

Keywords: spawning migration, smolt, power-station, turbine outlet, bypass channel, fish-ladder, passage success, population model, radio tag.

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Till Nemo

Contents

Appendix

Papers I-VI

This thesis is based on the following papers, which will be refereed to by their Roman numerals:

I. Rivinoja, P., McKinnell, S. & Lundqvist, H. 2001. Hindrances to upstream migration of Atlantic salmon (*Salmo salar*) in a northern Swedish river caused by a hydroelectric power-station. *Regulated rivers: Research & Management* 17:101-115.

II. Lundqvist, H., Rivinoja, P., Leonardsson, K. & McKinnell, S. Upstream passage problems for wild Atlantic salmon (*Salmo salar*) in a flow controlled river and its effect on the population. *Manuscript.*

III. Leonardsson, K., Belyaev, Y., Rivinoja, P. & Lundqvist, H. Modelling upstream migration of Atlantic salmon as a function of environmental variables. *Manuscript.*

IV. Rivinoja, P., Leonardsson, K. & Lundqvist, H. Migration success and migration time of gastrically radio-tagged versus PIT-tagged adult Atlantic salmon. *Journal of Fish Biology (Accepted).*

V. Rivinoja, P., Kiviloog, J., Östergren, J., Brydsten, L., Leonardsson, K. & Lundqvist, H. Migration of Atlantic salmon (*Salmo Salar*) and Brown trout (*Salmo trutta*) smolt at flow regulated areas in two northern Swedish rivers. *Submitted manuscript.*

VI. Rivinoja, P., Leonardsson, K. & Lundqvist, H. Size dependent power-station induced mortality of smolts (*Salmo sp.*) and the potential effects on the spawning stock. *Submitted manuscript.*

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Introduction

To maintain natural anadromous salmonid populations both the adult upstream and the juvenile downstream migrations are essential. However, in many regulated rivers the natural migrations have been harmed (Eriksson & Eriksson, 1993; Karlsson & Karlström, 1994), which together with declining worldwide salmonid populations (NRC, 1996; Parrish *et al.*, 1998; Lackey, 2003) have raised great concern about their future existence. River regulations generally cause problems when adults aim for their spawning grounds (Bjornn & Peery, 1992; Thorstad *et al.*, 2003) and when smolts migrate seawards (Coutant & Whitney, 2000; Mathers *et al.*, 2002). Diverse bypasses are built to preserve or renew migration possibilities for fish (Clay, 1995; Calles & Greenberg, 2005), nevertheless the function of these structures are not always fully understood or adequately evaluated. The main research on fish migrations at power-station bypasses originate from North America and focuses on Pacific salmonids, *Oncorhynchus spp.* (Clay, 1995; Williams, 1998). However, since species have different migratory patterns and biological preferences these results should not be directly applied to include all fishes. Conversely, even if fish bypasses for Atlantic salmon (*Salmo salar* L.) and anadromous brown trout (*Salmo trutta* L.) have been developed, these constructions are occasionally ineffective and lack appropriate assessment (Sandell *et al.*, 1994). Thus, the knowledge of these species migration behaviour in regulated rivers and bypasses seems rather limited.

In this thesis upstream spawning migrating adult Atlantic salmon were studied together with downstream migrating smolts of both salmon and anadromous brown trout at power-station passages. Additionally, based on the observed passage problems for the fish, the population dynamics were modelled under assumption that these problems could be reduced. The lifecycle of the species and general migration problems in regulated rivers are briefly reviewed, additionally the results from the appended studies are compared to international studies on anadromous fish in regulated rivers.

The life cycle of the anadromous salmon and brown trout

The anadromous Atlantic salmon and brown trout have resembling life-histories with their juvenile phase in freshwater and adult phase at sea (Figure 1). Even though the phenotypic characters and migratory behaviour vary even within the species (Fleming, 1996; Klemetsen *et al.*, 2003), the upstream spawning migration of adult fish generally starts in summer (McKinnell, 1998). These migrations normally have a seasonal pattern and range in length from days to months (Klemetsen *et al.*, 2003). The timing of the migration as well as the individual migration patterns is related to sex and size of fish, river discharge and water temperature. The general pattern for wild salmon in the Bothnian bay area is that large females arrive to the rivers earliest, followed by large males and finally by small males, grilse (McKinnell, 1998). The riverine migration can consist of different phases, where ascending fish show limited migrations initially and thereafter migrate rapidly upstream to spawning sites (Hawkins & Smith, 1986; Laughton, 1991). Although the spawning is energetically demanding and adult

Atlantic salmon cease feeding in the rivers, both salmon and trout can survive post spawning (Klemetsen *et al.*, 2003). After the spawning in late autumn, the survivors, named kelts, migrate downstream and might return for repeated spawning (Niemelä *et al.*, 2000). After the eggs are hatched the offspring spend one to several years in freshwater (Klemetsen *et al.*, 2003). Subsequently the juveniles undergo smoltification that prepares the fish for seawater and initiate downstream migration (Hoar, 1976; Thorpe, 1994). These smolt-runs generally start in spring to early summer, depending on external cues, (Bilton *et al.*, 1982; Lundqvist *et al.*, 1988) and the fish form shoals and seasonally synchronize seaward migration (Österdahl, 1969; Eriksson & Lundqvist, 1982). After entering the feeding grounds at sea the salmon mature after one to five years dependent on environment and population character (Klemetsen *et al.*, 2003). At the following spawning migration most fish home to their natal stream (Buck & Hay, 1984).

Salmon migration in regulated rivers

In hydroelectrically regulated rivers water is generally diverted away from the natural river via a dam or a channel to one or several turbines at a power-station. Consequently various power-station obstacles together with flow regulations affect the migration possibilities for fish. Mathers *et al.* (2002) summarized the primary effects that damming of running waters had on migrating fish in three ways; 1) losses of natural habitats, 2) impaired upstream migration, and 3) increased mortality for downstream migrants. To maintain migrations of fish in regulated rivers bypasses have been applied. These constructions can be complex and require understanding of the relationships between fish behaviour and environmental factors (Clay, 1995). The effectiveness of bypasses depends on attraction and rapid and safe passage of fish (Katopodis, 1990), and discharge is generally considered as one of the most important factors to secure passages (Larinier, 1998; Williams, 1998).

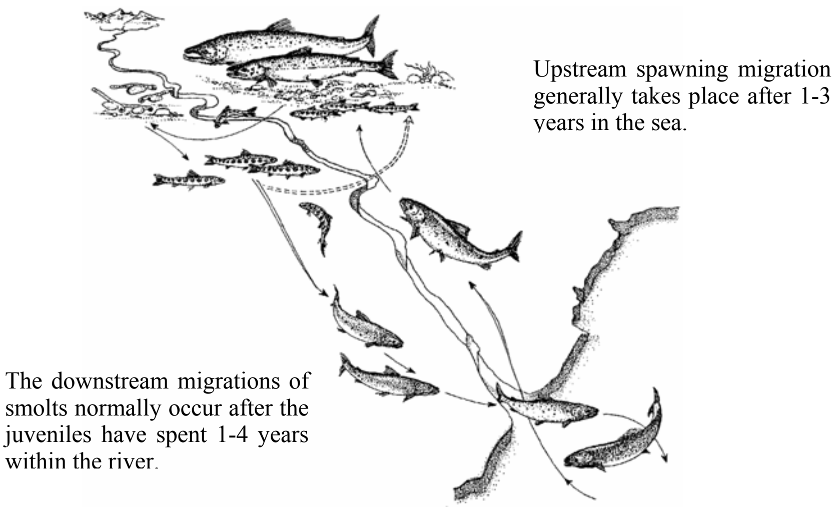

Fig. 1. The lifecycle of the anadromous Atlantic salmon (modified from Lundqvist, 1983).

Problems for upstream migrating adults

Upstream migrating fish encounter diverse obstacles in regulated rivers due to unnatural flows and obscure migration routes. Spawning migrating adult salmon generally search for the highest flows (Williams, 1998; Thorstad *et al.*, 2003). As a result passage problem can arise due to low attraction flows in bypasses which might hinder fish if they are attracted towards impassable routes from turbine outlets or dams rather than to bypasses (Arnekleiv & Kraabøl, 1996; Karppinen *et al.*, 2002; Thorstad *et al.*, 2003).

Common bypasses for upstream migrating salmonids consist of fish-ladders (Figure 2) that are normally designed in three varieties (Clay, 1995; Kamula, 2001): 1) Pool and weir, 2) Denil slot, and 3) Vertical slot. These should be adapted to the weakest swimmers in the run (Laine, 2001), and to be effective pass more than 95% of the adult upstream migrants in a safe and rapid manner (Ferguson *et al.*, 2002).

Problems for downstream migrating smolts

The main impact of power-stations on downstream migrating fish is mortality associated to turbine or spillway passage (Montén, 1985; Coutant & Whitney, 2000). In addition, dammed reservoirs often favour predators and slower migration of smolts which can cause high mortality rates (Mills, 1965; Olsson *et al.*, 2001). A delayed migration can also stress fish due to unnatural migration periods and extended exposure to diseases and pollutants (Mathers *et al.*, 2002).

Depending on power-station construction fish can descend through turbines, spillways or bypasses (Skalski *et al.*, 2002; Scruton *et al.*, 2003). Generally turbines cause the highest mortality, related to power-station design, fish size and behaviour. Both direct mortality by mechanical damage or pressure changes, and indirect mortality by stress, injuries and disorientation can occur (Čada, 2001). A variety of structures exists to bypass downstream migrating fish to minimize mortality and delayed migration (Muir *et al.*, 2001). Although power-stations have different potential to direct descending fish, the fish guidance efficiency (FGE) generally increases by releasing more water in the desired direction (Coutant & Whitney, 2000) or by adapting guidance devices (Muir *et al.,* 2001; Scruton *et al.*, 2003).

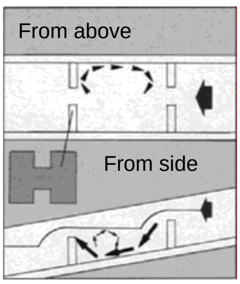

Fig. 2. Pool and weir ladders are created by step like pools where fish move either through the weirs in the surface or the orifices at the bottom. The arrows show flow patterns. The ladders in Umeälven and Piteälven are of this type. (Modified from Sandell *et al.,* 1994; Kamula, 2001).

Thesis objectives

This thesis aimed to increase the understanding of the Atlantic salmon and anadromous brown trout behaviour at power-station passages. Special focus was given to evaluate fish migration patterns to various flow regimes. The overall ambition was to identify if any problem areas exist for the species migrations and to evaluate consequences that the possible passage problems could have on the populations. The work covers relatively new study methods with telemetry, echo-sounding and flow assessments in cooperation between biologists and engineers. The model rivers were Umeälven, with its largest tributary Vindelälven, and Piteälven, regulated by the power-stations Stornorrfors and Sikfors, respectively. The focus was to examine the following subgoals:

1. Migration behaviour of adult salmon in flow controlled areas (Papers I-IV).

2. Migration of salmon and brown trout smolts approaching power-stations (Paper V).

3. Mortality of salmon and brown trout smolts passing a hydropower complex (Paper VI).

4. Salmon population responses to improved passage success of power-stations (Papers II, VI).

5. Effects of gastric radio-tags on adult salmon migration performance (Paper IV).

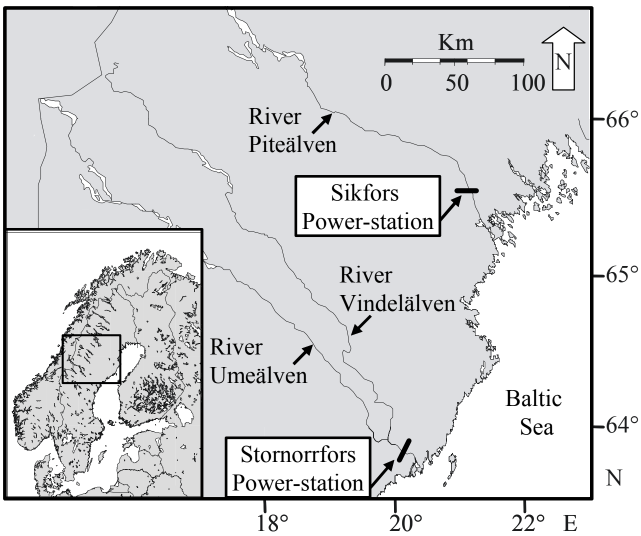

Fig. 3. Map over the studied rivers in northern Sweden with location of the two power-stations.

Materials and Methods

Study areas

River Umeälven and River Piteälven in northern Sweden originate from mountains c. 450 km from the coast and enter the Bothnian Bay at about 64-65°N 20-21°E (Figure 3). The rivers are regulated for hydropower in their lower parts. Upstream the power-stations vital salmonid spawning areas exist and fish-ladders of pool and weir type at the dams allow fish upstream migration. Anadromous salmon and trout normally start ascending the ladders in June and continue to pass to October when the ladders are closed. At present, data on the natural smolt migration timing and sizes in these two rivers are lacking, yet wild smolts are assumed to migrate seaward in May-June. Since no bypasses for descending fish exist at the hydropower facilities, two main passage routes emerge: a) pass via the turbines, or b) pass through the spillways or the fish-ladders at the dams.

River Umeälven

Umeälven is totally exploited for hydropower. Migrations of anadromous fish are blocked in the main branch 12 km upstream the power-station Stornorrfors and a hatchery below the dam compensates for the losses of wild fish. Yearly c. 80 000 salmon smolts and 20 000 sea-trout smolts, with their adipose fin removed, are released downstream the dam. In addition a 240 m long fish-ladder at the base of the dam, 32 km from the estuary, allows fish to migrate upstream to the largest tributary River Vindelälven. At the top of the ladder fish are trapped and manually netted and separated into wild or hatchery origin. The annual catches of wild salmon from 1974 to 2005 have varied from 250-6065 (Figure 4). The average yearly flow downstream Stornorrfors, where four Francis-turbines with a total capacity of c. 1000 m^3s^{-1}operate, is c. 430 m^3s^{-1}. Minimum dam spills are 10 m^3s^{-1} from 10thMay-15thJune, 20-50 m^3s^{-1} from 15thJune-1stSeptember, and 15 m^3s^{-1} from 1stSeptember-1stOctober, after which no water is released from the dam. The area close upstream the dam is represented by the reservoir and rapids 3-4 km further up (VI, Figure 1). Water from the forebay created by the dam is directed towards the turbines, and afterwards flows through a submerged 4 km long tunnel via an outlet channel back to the river (Figure 8 and I, Figure 1). At the confluence, from the point of the outlet channel the 8 km long old river bed, the residual river stretch, acts as a bypass route for upstream migrating fish to the ladder. Flow regimes during the salmon migration period (20thMay-1stOctober) in the studied years have varied from relatively low bypass spills with an average of 23 m^3s^{-1} in 2003 (max flow 85 m^3s^{-1}, Figure 5) to a maximum of 2022 m^3s^{-1} in 1995 (average 182 m^3s^{-1}). Turbine flows the same periods averaged 569 m^3s^{-1} and were lowest in 1996 (297 m^3s^{-1}) and highest in 2001 (806 m^3s^{-1}). During the study the bypass flows were artificially altered from the normal in 2001-2005 (II; III; V). The river temperatures increased in spring and summer, except in 2003 when it dropped under the smolt migration period (Figure 5). At all years the temperatures decreased in the autumns (I-III; V-VI).

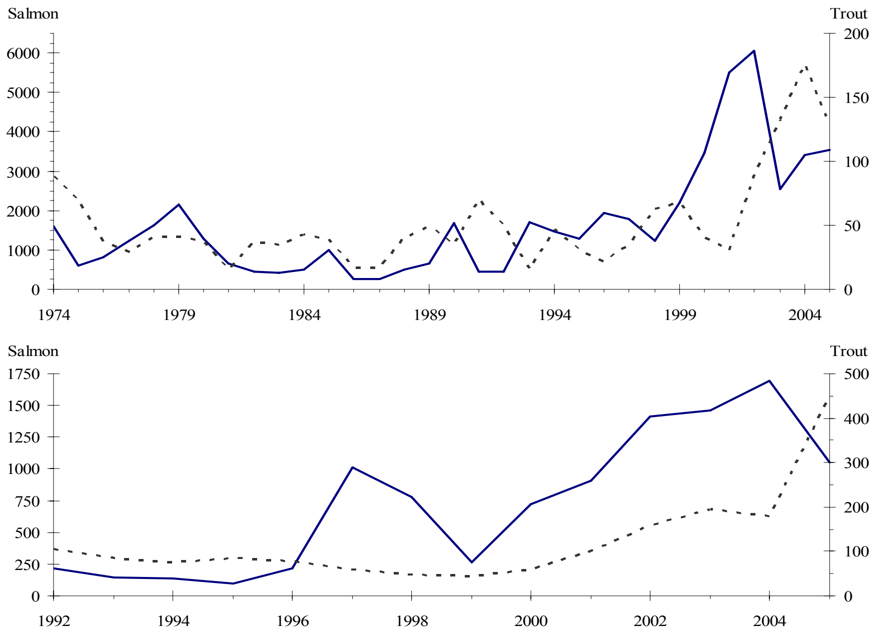

Fig. 4. Annual upstream migration of wild salmon (solid lines) and brown trout (broken lines) at the ladders in Umeälven (above) and Piteälven (below).

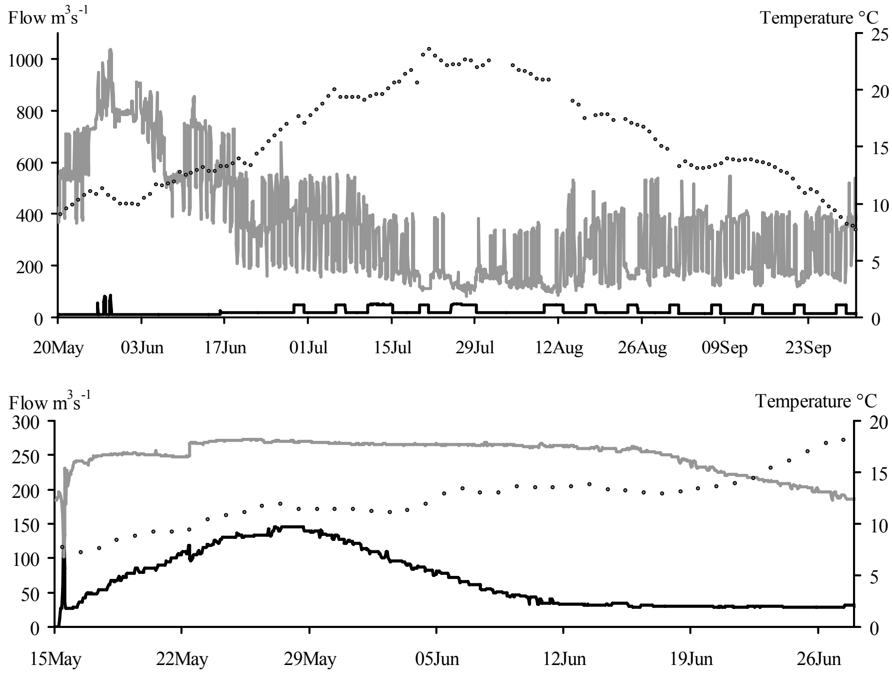

Fig 5. Daily river temperature (circles), hourly turbine (grey line) and spill flows (black line) in Umeälven (above) and Piteälven (below) during the study periods in 2003. Data from Vattenfall AB and Skellefteå Kraft AB.

River Piteälven

Piteälven with an annual mean flow of c. 150 m^3s^{-1} is regulated 40 km from the sea with the single power-station Sikfors. The water in the reservoir upstream the power-station is mainly slow flowing with rapids 1-2 km upriver (V, Figure 1). The power-station has two Kaplan-turbines and a capacity of c. 270 m^3s^{-1}, while excess of water is spilled over the dam, with a minimum of 10 m^3s^{-1} from 15thMay-15thOctober. The water from the turbines pass a tunnel that confluence with the river 0.6 km downstream the power-station. As in Umeälven the residual river stretch, with a 115 m long fish-ladder at the base of the dam, acts as a bypass channel for upstream migrating fish. A total of around 900 salmon and trout per year (Figure 4) have been registered to pass upstream the fish-counter system at the top of the ladder since it was rebuild in 1992. The total river flows at the study periods in the early summers of 1998-1999 and 2003-2004 have varied from 220 to 540 m^3s^{-1} while maximum discharges through the power-station varied from 200 to 270 m^3s^{-1}. During these periods the temperatures in the river increased from about 11 °C to 13 °C (IV). The environmental data in 2003 is shown by Figure 5.

Depth, water velocity measurements and CFD-modelling

The water depths and flows upstream Stornorrfors and Sikfors power-stations were measured as explained in V. Flows were then modelled using three dimensionally computational fluid dynamics (CFD) and together with particle-tracking (Kiviloog, 2005) smolt migration routes and the FGE's (Fish Guidance Efficiency) for the power-stations spillways were estimated (V). Flow data from the last decade during the seasons for natural smolt migration (20thMay-20thJune) together with the predicted FGE's were used to calculate the average odds for smolt to descend over the spillways.

Tagging of fish

Active radio-transmitters that emit a unique combination of frequency and pulse were used on fish together with passive taggings (Figure 6). The streamlined and flat external radio-tags, with a mass of 16 g, were attached to adult salmon with wires under the dorsal fin. Cylindrical transmitters, with a mass of 8 g for adults and 1 g for smolts, were gastrically or surgically implanted into the fish. For mark-recapture studies, individually coded Carlin-tags, i.e. small plastic discs attached externally via wires on the fish, were used (Carlin, 1955) together with PIT-tags (Passive Integrated Transponder) inserted into the fish. The PIT-tag consist of a small glass capsule (12 mm in length x 2 mm in diameter) with a microchip and a coil that emits specific codes when activated (Prentice *et al.*, 1990).

Adult spawning migrating salmon were captured and tagged at their arrival to the mouth of River Umeälven (I-IV). External radio-tagging followed Økland *et al.* (2001) while gastric tagging is described in IV. All fish were release immediately after being individually tagged, measured in length, and a piece of the adipose fin were taken. The adipose fin cut were used as an external flag for tagged fish as well as used for genetic sampling (I, IV). The weight of the transmitters never exceeded general recommendations of 2-6 % of the total fish mass (e.g. Winter, 1983; Adams *et al.*, 1998). In total 503 radio-tags, 1967 PIT-tags and 574 Carlin- tags were used on adult fish and from 1999 and onwards all radio-tagged fish were also tagged with a PIT-tag (II; Table 1).

Atlantic salmon and anadromous brown trout smolts of hatchery origin were tagged with gastrically and surgically implanted radio-transmitters ATS-F1410 (n = 206) at the studied rivers (V; VI; Table 2), according to Adams *et al.* (1998) and Økland *et al.* (2004), respectively (Figure 7). Transmitter mass was under the upper limit of c. 5-6 % of the fish expressed by Adams *et al.* (1998). Additionally, Carlin-tags were used in Piteälven 1998 and 1999 (VI). In the studies a total of 7656 tagged smolts have been released upstream the power-stations during periods that correspond to the natural time for smolt migration in the rivers.

Radio-tracking

Telemetry presupposes that active radio-signals can be registered and tracked with radio units (Winter, 1996). In the present studies the movements of radio-tagged fish were followed with manual tracking receivers and automatic archival loggers (Cooke *et al.*, 2004). Manual tracking from boat and shore frequently covered the regulated areas of the rivers as described in I-VI. All archival loggers were calibrated and tested for precise transmitter registrations to be able to specify the migration routes for individual fish as exactly as possible. In studies on adult fish (I-IV) several loggers were located in areas downstream the power-station facilities (Figure 8) and in the studies on downstream migration of smolts (V-VI) the loggers were mainly placed close upstream the power-stations and dams

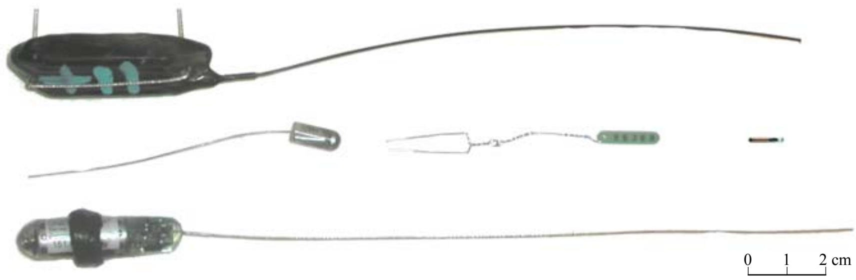

Fig. 6. The different tags that were used, with an external radio-tag for adult fish at the top (ATS-F2120), an internal tag for smolt at left middle (ATS-F1410) and a gastric tags for adults at the bottom (ATS-F1825). A Carlin-tag and a PIT-tag (right) is in the middle.

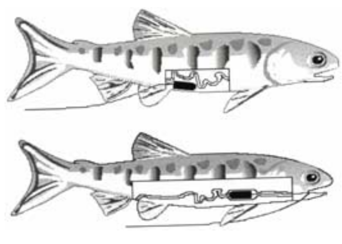

Fig. 7. The standard placements of surgically and gastrically implanted radio-transmitters (redrawn from Hockersmith *et al*., 2000).

Table 1. *Yearly data over adult Atlantic salmon tagged with various techniques at the mouth of River Umeälven. For explanations on legends see Paper II.*

	1995	1996	1997	1999	2001	2002	2003	2004	2005	Tot.
Tag date	30/6-17/8	3/6-29/8	24/6-3/7	16/6-13/7	25/6-4/7	6/6-26/7	23/6-8/8	16/6-30/7	13/6-25/7	
Size (cm)	63 (49-92)	86 (48-112)	89 (69-109)	84 (63-105)	86 (71-105)	66 (39-116)	77 (46-106)	80 (47-112)	87 (55-116)	
Wild:Hatchery	30:0	485:89	55:25	60:0	70:0	493:0	391:0	503:0	450:0	
Female:Male	20:10	387:187	74:6	34:26	60:10	126:367	226:165	263:240	235:215	
External radio	30		80	60	70	14	6			260
Gastric radio						69	58	60	56	243
PIT-tag						410	327	443	394	1574
Carlin-tag		574								574
Total	30	574	80	60	70	493	391	503	450	2651

Table 2. *Amount and size of tagged Atlantic salmon and anadromous brown trout smolts at the two studied rivers.*

	Salmon		Trout	
	No.	Length, mm (min-max)	No.	Length, mm (min-max)
Umeälven 2002-2003; Radio	30	189 (165-220)	36	237 (205-286)
Piteälven 1998-1999; Carlin	7450	165 (130-200)		
Piteälven 2003-2004; Radio	120	207 (166-262)	20	238 (215-270)
Total	7600	207 (166-262)	56	238 (215-270)

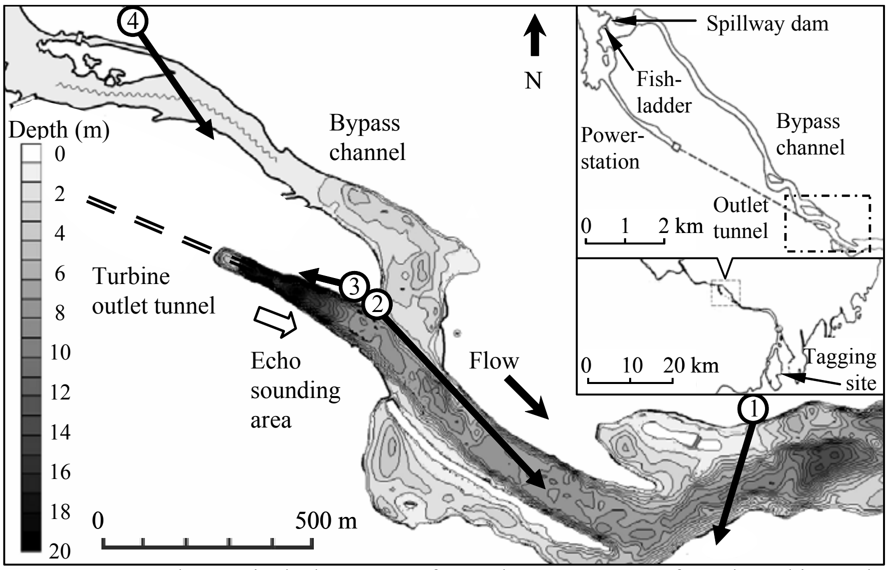

Fig. 8. Map over the area in the lower part of Umeälven where water from the turbine outlet tunnel confluence with the bypass channel for upstream migrating fish. The location and main transect of archival loggers for registration of tagged upstream migrating adult salmon are shown by numbered circles. The echo-sounding area is indicated by the white arrow.

Echo-sounding

Echo-sounding is valuable for exactly locating fish in three dimensions (e.g. Steig & Iverson, 1998; Lilja, 2004) and in the present work a hydro-acoustic split-beam echo-sounder (Simrad EY60, GPT 200 kHz, Split Beam) was used. In Umeälven adult salmon behaviour downstream the power-station outlet was studied (II) and in Piteälven migration of smolts approaching the power-station was followed (V). Recorded data was analysed with Sonar 5 (Balk & Lindem, 2004) to gain information on the positions of fish and to reveal fish migration patterns.

Results - Summary of papers

Upstream migration problems for adult Atlantic salmon

Paper I

Installation of a fourth turbine at Stornorrfors in 1986 did not appear to have affected the timing or the seasonal distribution of wild Atlantic salmon migration to the fish-ladder. Consequently, the run time of upstream migrating adults remained unchanged for the periods 1974-1985 and 1986-1995, with no significant effects on the duration of the middle 50 % of the run in any weight-class for wild salmon. Additionally, daily counts of wild salmon at the fish-ladder were not related to daily turbine discharges or water temperature. Telemetry in 1997 (n = 80) showed that only 26 % of the wild salmon and no hatchery salmon passed the ladder. In the confluence area between the power-station outlet and the bypass channel salmon generally followed the main water discharge to the turbine outlet, and were thus directed away from the bypass channel leading to the fish-ladder. Salmon responded to changes in flow regimes with up- or downstream migration depending on flows. In the bypass channel partial hinders at waterfalls and the fish-ladder area were observed, which, together with prolonged migration time at the confluence area, might explain the long average travel time of 52 days for salmon from the river mouth to passage of the fish-ladder.

Paper II

The overall results from 1995 to 2005 for a total of 2651 adult salmon tagged with radio-tags (n = 503), PIT-tags (n = 1574) or Carlin tags (n = 574) in the mouth of River Umeälven showed a low upstream migration success to the fish-ladder and varied from 0-47 % over the years, with an average of 30 % for all years. Salmon also had a slow migration speed, and the migration time to the ladder showed large variation within years and was independent of study year, fish size or sex. It took on average 44 days to swim the 32 km upstream to the fish-ladder, while fish migrated 10-15 days to reach spawning areas 230 km upriver in Vindelälven after passage of the fish-ladder. Genetic analyses indicated that radio-tagged salmon most likely belonged to the River Ume/Vindelälven salmon stock and were thus not strayers from other rivers. The amount of radio-tagged fish that entered the river varied between 73-93 % between years, with an average of 83 %. Generally fish were registered 17-23 km upriver 3-4 days post-tagging. The migration time of salmon and number of fish registered at the first logger in the river did not differ between years, fish sex or size. Salmon responded strongly to changes in flow regimes and a majority of the fish showed up- and/or downstream swimming directions depending on flow regimes. Echo-sounding showed that salmon in the turbine outlet area were mainly located 1-4 meter deep yet fish were also observed close to bottom at 40 m depth. Increased spill flows generally attracted salmon to the entrance of the bypass channel while high discharges from the turbine outlet seemed to attract salmon away from the bypass area. An average loss of 70 % potential salmon spawners was estimated, and the population was predicted to be able to increase about 500 % if the proportion of successful migrants could be increased to 75 %.

Paper III

The influence of environmental factors on upstream migrating wild adult Atlantic salmon in the flow-regulated section of Umeälven was modelled. Five years telemetry data on daily migration responses for a total of 234 radio-tagged salmon were used to analyse the influence of the variables; daily river discharge, turbine flow, bypass flow, water temperature, day of salmon river entry and time of the season. Logistic regression was used to parameterise the Markov model containing the least number of variables with the best fit. The most influential variable on salmon migration behaviour was discharge while combinations of bypass- and turbine flows explained most of the variation in the individual migration response in the confluence area. The volume of bypass flow was positively correlated with the probability for salmon to ascend the bypass channel. Conversely, for salmon in the bypass channel the chance to also pass the first waterfall, acting as a partial hindrance, was higher at lower bypass flows. There was also a higher probability that fish in this area returned downstream to the confluence area at increasing temperature. The modelled trade off between optimal bypass attraction flow and passage flow of the waterfall predicted that the overall upstream migration success for salmon could improve with c. 30 % if c. 70 m^3s^{-1} more than normal was released in the bypass channel. However, a threshold of c. 150 m^3s^{-1} was observed and at flows exceeding this amount only few salmon passed upstream the waterfall. Finally, the observed variation in migration success between years could not be fully described by the available model variables.

Paper IV

Migration success from the mouth of River Umeälven to the fish-ladder, 32 km upstream, was similar for adult salmon with gastric radio-transmitters and PIT-tags (n = 127) as for salmon with only PIT-tags (n = 318). The upstream migration success, that averaged 38 %, was higher in 2002 (43 %) than 2003 (32 %). Data pooled over the years showed that successful migrants were tagged earlier in the season than fish that did not pass the ladder. Individual migration time for salmon to the ladder varied between 9-91 days, but was independent of fish tagging day, sex and size. Moreover, the migration time was similar between the years, 42 days in 2002 and 48 days in 2003, respectively. However, for pooled data over the years, faster migration was found for salmon with gastric radio-tags (average 39 days) compared to only PIT-tagged fish (average 47 days). Regurgitation of radio-transmitters, that averaged 9 %, mainly took place at rapids in the bypass channel and originated from all sizes of salmon and was equally divided between sexes.

Downstream passages of Atlantic salmon and brown trout smolts

Paper V

Upstream power-station releases of radio-tagged Atlantic salmon and anadromous brown trout smolts (n = 206; 150 salmon, 56 trout) in the springs 2002-2004 at Umeälven and Piteälven demonstrated that smolts followed the main flows while migrating downstream. The fish were repeatedly positioned to areas of c. 5 m radius, and in Piteälven smolts were located at 1-3 m depths via echo-sounding. Measurements of water velocities and depths used for the three-dimensional CFD-modelling, combined with particle tracking modelling, were used to simulate fish migration paths. These models agreed with data on positions of radio-tagged fish and demonstrated that fish generally migrated downstream in the highest water velocities with same speed as water. Average speed of migration for smolts ranged from 0.3-0.5 m s^{-1}, i.e. c. 2 body lengths s^{-1} (BL s^{-1}). Since most water was diverted to the turbine intakes at the power-stations a majority of the descending tagged smolts also entered the turbines. However, a group of larger fish stopped their migration close above the turbine intakes in Piteälven and was observed holding surface positions against the water current. No other size or species dependent differences in the migration behaviour were observed. The estimated FGE’s for the spillways were relatively low at both power-stations but increased with flows. Using data on river flows during the smolt migration periods over the last ten years the average odds for downstream migrating smolts to descend over the spillways in Piteälven and Umeälven was predicted to be 15 % and 20 %, respectively.

Paper VI

A majority of the 90 radio-tagged smolts in Piteälven that approached the power-station Sikfors entered the turbines, which resulted in a passage mortality of 19 %. No fish passed downstream via the spill. Both direct and indirect mortality was observed and the mortality was positively size-dependent so larger smolts had higher mortalities. In addition, 13 % of the radio-tagged smolts remained close upstream the power-station during the study. Carlin-tagged salmon smolts showed decreased recaptures in relation to upstream distance of release site, showing largest mortality for fish released high upriver. The loss at the power-station was estimated to 16 %, resulting in combined passage loss of 17 % from both studies. The size-dependent power-station passage losses of smolts were used to model the effects on the escapement returns. First only the actual observed losses were used in the model, and second the radio-tagged smolts that remained upstream the power-station was added into total losses. The first scenario showed that for a hypothetical smolt population with an average length of 155 mm the escapement returns could increase by 5-30 % in ten years if no mortality for smolts took place at power-station passage. For larger smolts at a size of 210 mm the corresponding increase in the future spawning stock would be 30-70 %. When the additional losses caused by the ceased migration were considered the related population increase could be up to 30-70 % and 70-120 %, respectively, that is if all negative effects on migrating smolts at the power-station were eliminated.

Discussion

Upstream migration problems for adult Atlantic salmon

The most important finding in this study is the observation of an average loss of c. 70 % potential salmon spawners during their migration from the Umeälven estuary upstream to the fish-ladder (II). Even though the cumulative negative effect on fish migration in rivers with numerous obstacles can be large and reduce the amount of upstream migrants to spawning areas (Gowans *et al.,* 2003), the amount of unsuccessful spawning migrating salmon in Umeälven was surprisingly high. The migratory problems at different sections of the flow controlled river below the dam and the hydropower-station caused the high overall losses (II). Based on various international studies on this topic it is well known that upstream migrating fish in hydropower regulated rivers generally have migration problems. I, II and III identified areas where turbine water confluences with the natural river flow as the major hindrance and similar results have been shown by Karppinen *et al.* (2002) and Thorstad *et al.* (2003). In these areas complex flow patterns that are very different from natural flows can be created, and therefore do not guide salmon correctly on their upstream migration. Biological and hydrological preferences for fish at upstream migration differ between species and size-classes (Katopodis, 1990; 1999) and cause various migratory behaviours (Johlander, 1999). Still, water discharge is considered as the most important guiding factors for migrating fish (Larinier, 1998; Williams, 1998). Upstream migrating adult fish generally search for the highest flows (Thorstad *et al*., 2003) and direction cues from the water current (Arnold, 1974). Ferguson *et al*., (2002) explained this as an evolved mechanism providing high spawning success since fish attracted to the highest discharges generally track the main branches of rivers on their way to the spawning grounds. In regulated rivers this behaviour can conversely hinder migration if fish are attracted to high turbine flows, and thereby blocked routes, rather than to entrances of bypasses leading upstream (I; II; III; Thorstad *et al.*, 2003). Problems for fish to bypass flow-regulated areas downstream power-stations can also prolong the time for upstream migration since fish might spend long time to find the proper route. At extreme situations when low spills occur fish could also completely loose the attraction cues and fail to pass upstream (Power & McCleave, 1980; Ferguson *et al.*, 2002). In Umeälven the major disturbance, causing the highest losses of salmon spawners on their upstream migration, was related to problems for fish to find the bypass channel at the confluence area and to pass the first waterfall in the bypass channel (II). The conclusion was that the ability for salmon to find the upstream route was associated to bypass flows (I; II; III). Similarly, studies by Linløkken (1993), Arnekleiv & Kraabøl (1996) and Arnekleiv & Rønning (2004) on brown trout support these conclusions, and upstream migrations were positively related to discharges in the bypasses, while fish entered turbine outlets at low spill flows. By echo-sounding adult salmon were also registered at the turbine tunnel outlet in Umeälven (II). Salmon generally entered the turbine outlet oriented at 1-4 meter depth before they dived deeper and approached the turbine outlet tunnel at 40 m depths (II). Most likely the combined amount of turbine and spill flows attracted a majority of fish to enter the turbine outlet tunnel, and Mills (1989) showed that enhanced directional cues could strongly affect the fish migration positively. This was demonstrated in I, II, III and by Arnekleiv & Kraabøl (1996), thus the rate of upstream migration could increase by higher spills outside the turbine outlets, or as found by Calles & Greenberg (2005), via constructing a bypass close to the power-station outlet.

Another important finding in this thesis is that salmon positioned in the confluence area and bypass channel responded differently to flow changes. Increased spills in the bypass channel in combination with low turbine flows generally guided salmon to the bypass channel, yet occasionally without passing the closest rapid c. 1 km upstream the confluence (I; II; III). These findings show the complex nature of salmon upstream migration since the actual position of fish at a certain time probably influence the swimming response on increased- or decreased flows. Likewise, salmon in natural flows also express upstream migration both at decreasing (Trépanier *et al.*, 1996) and increasing flows (Jensen *et al.*, 1986; Erkinaro *et al.*, 1999). Locally adapted behaviour may create a large individual variation in migration behaviour in relation to river-specific conditions so salmon await falling flows before passing further upstream. In addition, Trépanier *et al.* (1996) showed that salmon migration at river entrance was positively correlated to increased flows while passage of rapids and waterfalls could be enhanced by both decreased and increased flows. Hence, the observed different behaviour patterns for salmon in the bypass channel, where fish mainly entered at high spill flows and passed the waterfall at lower flows (I; II; III) can be expected. By the modelling also a low probability for fish to pass the waterfall in the bypass channel at flows exceeding c. 150 m^3s^{-1} was predicted (III). Nevertheless, the disparity in salmon migratory response is not completely understood and variation might also be caused by a weak imprinting process for the bypass channel if the wild salmon leave the river through the turbines as smolts (I). How important the path for downstream migration as juveniles is on the imprinting process and how this affect the adult return migration in regulated rivers has to be tested in controlled experiments.

Other environmental factors besides flow can affect salmon migration (Banks, 1969; Northcote, 1998) and temperature is well known to play a central role for fish behaviour. McKinnell *et al.* (1994) was unable to show any effect of ambient river temperatures on upstream migration of salmon in Umeälven, while III predicted that upstream migration had an optimal temperature range and upstream movements decreased at low and high temperatures. Additionally, the relatively small temperatures differences of c. 0.2-0.3 °C between the turbine water and the bypass spill were probably too small to cause any behavioural effects on salmon migration response, thus not causing fish to be affected by directional temperature cues (II). Trépanier *et al.* (1996) and studies therein also showed limited effects of temperature on salmon upstream migration while Jensen *et al.*, (1986) observed Atlantic salmon to pass upstream rapids in a Norwegian river on increasing water temperature. Gowans *et al.* (1999) also pointed out that salmon ascent of a fish-ladder in Scotland was positively correlated with temperature. However, water temperature in the above listed studies never exceeded 20°C and high temperature effects on Atlantic salmon migration is not well studied. Still, various upper and lower thermal limits for upstream migration of Atlantic salmon have been reported (Mills, 1989; Trépanier *et al.*, 1996). Most likely the optimal temperature intervals vary among populations due to local adaptations.

In total, c. 50 % of all salmon failed pass upstream the confluence area and the first waterfall in the bypass channel on their migration (II). Additional losses of c. 20 % were found at waterfalls further upriver and at the fish-ladder area. At this river section fish were partially hindered and the fish-ladder seemed somewhat ineffective to attract fish and secure passages (II). Ferguson *et al.*, (2002) stressed that a successful upstream passage facility should pass more than 95 % of the migrating adult fish. Quinn *et al.* (1997) reported delayed migration of sockeye salmon (*Oncorhynchus nerka*) past fishways at dams during periods of high spillway discharges. A resembling pattern was observed in Umeälven and ladder entry of radio-tagged salmon was highest at relatively low spill flows, while none of the fish ascended at spills over 105 m^3s^{-1} (II). These findings are supported by Bjornn & Peery (1992) who stated that high spill flows can hinder fish to discover fish-ladder entrances and delay migration. Similar reports have also been described by Gowans *et al.*, (1999) and Karppinen *et al.* (2002). After fish successfully moved into the ladder in Umeälven, the upstream passage time of the ladder could be relatively long and individual time varied from 3-133 hour (II). Others have also indicated that passage time for salmon at ladders can vary considerably (Bjornn & Peery, 1992; Sandell *et al.,* 1994).

Another interesting finding is that salmon positioned in the relatively deep outlet area usually showed downstream migrations of several kilometres, especially when turbine discharge was lowered (I; II). Such behavioural patterns were observed in all years at about the same rates and are most likely caused by the high activity that fish showed in the confluence area during their search for an upstream route (II). Similar observations was done by Arnekleiv & Kraabøl (1996) who noted up- and downstream swimming of brown trout in a turbine outlet and that fish swam several kilometres downstream if they did not find the correct way upstream. As noted in II some fish migrated back and forth more than 60 km before they advanced upriver. This up- and downstream migration under relatively short time periods in the flow controlled area was defined as "yo-yo swimming". Since fish move back and forth, also swimming through high velocity water in the turbine outlet this ultimately leads to a delay in the migration and increased energy consumption (II). These statements is supported by Katopodis (1999) who showed that fish occasionally burst with maximum swimming speed to overcome high velocity water, and according to Beach (1984) this swimming behaviour is highly energy demanding. Consequently this "yo-yo swimming" most likely lowers the reproductive fitness of the fish, and furthermore fish that did not find the upstream migration route probably stopped their migration and returned back to the sea. The "yo-yo swimming" took place at all times of the day, with a peak when turbine flows decreased at evenings. Even if Webb (1990) and Laughton (1991) found that upstream migration of adult salmon was mainly nocturnal, Erkinaro *et al.* (1999) and Lilja & Romakkaniemi (2003) found no such pattern in two northern rivers with continuous light during nights. Similarly, the salmon entry of the ladder in Umeälven took place at all times of day (II), and therefore the downstream migrating fish most likely responded to decreased turbine flows rather than to the hour of day. Furthermore, Lilja & Romakkaniemi (2003) found that salmon river entry took place all times of the day and among different environmental factors tested, e.g. flow, temperature, air pressure, wind conditions, periods of sunshine, only seawater level affected the upstream migration.

Whether or not the "yo-yo swimming" behaviour has increased after a fourth turbine was added at the Stornorrfors power-station in 1986 can not be assessed. Yet, even after the installations of the fourth turbine the migration patterns of wild salmon past the fish-ladder seemed unaffected (I). This is most likely due to that flow regimes in the turbine outlet and the bypass channel have been similar to discharges before and after the turbine installations during the salmon upstream migration season. Consequently, salmon have had similar problems to migrate in the confluence area from the period of time since the hydro-power station was built, e.g. high flow regimes in the turbine outlet and low flow regimes in the bypass channel.

The demonstrated high cumulative losses of migrating salmon in the regulated part of Umeälven, caused by the passage problems at the confluence area, the waterfalls in the bypass channel and the ladder area, together had major negative effect on the escapement returns of wild adults. The overall upstream migration success of wild salmon from the estuary upstream to the fish-ladder over all years seemed independent on tagging day, sex or size of fish (II). However, hatchery fish showed lower migration quantity to the ladder (I; II) and was left out from the analyses in II. Genetic analyses from wild radio-tagged salmon indicated that these fish belonged to the River Ume/Vindelälven salmon stock (Vasemägi *et al*., 2005) and once the salmon were released upstream the fish-ladder they migrated relatively quickly during 10-15 days to spawning areas about 230 km upstream in Vindelälven (Lundqvist *et al.,* unpublished). The fact that potential spawners were lost at passage of the regulated section every year depresses the growth of the natural salmon population in Vindelälven, and as predicted the population could grow substantially in the future if the upstream migration success could be improved. Even if the population estimations might be uncertain at high population levels an increase of about 500 % was predicted if the passage success could be improved from 30 % to 75 %.

Downstream passages of Atlantic salmon and brown trout smolts

The descent of smolt in natural rivers is considered to be a period of high risk for juveniles since passage of obstacles, delayed migration and predation can lead to high mortalities in the smolt-run (Hvidsten & Johnsen, 1997). In the present studies downstream migration of smolts generally took place in the main flows and fish were surface oriented (V). Ruggles (1980) suggested that this migration behaviour of selecting high water velocities is a way to minimize predator pressure. Reports have demonstrated that smolts generally migrate in high flow areas in the river and close to the surface (e.g. Hvidsten & Johnsen, 1997; Moore *et al.*, 1998b; Scruton *et al.*, 2003b), but few studies have actually followed and positioned smolts in three dimensions during migration. However, Steig & Iverson (1998) highlighted the advantages of locating downstream migrating fish with echo-sounder techniques and observed smolts of Pacific salmonids to be surface oriented at close distances upstream a power-station. They also noted delayed migrations among smolts and changed migration behaviour depending on flows. The study in Piteälven (V) supported the findings by Steig & Iverson (1998) since delayed migrations and altered behaviour by active swimming in opposite to flows was observed for larger radio-tagged smolts in the vicinity above the power-station. Kemp *et al.* (2004) also confirmed active migration of fish upstream bypass structures designed to pass downstream migrating smolts, and that larger smolts could retain positions upstream the bypasses.

Further upstream of the power-stations smolts usually followed the water flows at downstream migration even if active migration at low velocity areas was indicated. Atlantic salmon smolts have been shown to migrate actively at lentic areas (Moore *et al.*, 1998a; 1998b) and data by Peake & McKinley (1998) demonstrated that the smolt have high swimming capacity and can burst up to c. 10 BL s^{-1} (1.95 m s^{-1}). The average migration speed of c. 0.3-0.5 m s^{-1} for smolts at both Umeälven and Piteälven corresponded well with measured and CFD-modelled water velocities (V). Even though no difference in speed was noted between salmon and trout in these studies, Aarestrup *et al.* (1999) and Aarestrup *et al.* (2002) showed that the migration speeds of smolts of the two species, and also among different populations of salmon smolts can differ. The observed migration speeds of smolts in V were higher than reported by Dempson & Stansbury (1991) and Fängstam *et al.* (1993) on Atlantic salmon smolts. This difference in speed of smolts is not readily explained but could be due to population specific differences or simply by the relatively high and homogenous water velocities above the power-stations compared to the test situation for smolts in the two cited papers above. No effects of smolt size on migration speed, other than the reverse swimming direction of large smolts, as mentioned above, was observed (V). The effects of temperature on smolt swimming speeds could not be fully judged due to limited data. Still, the lowest recorded downstream migration speed for smolts was associated to a temperature drop in 2003 (V) and ambient water temperature is widely accepted to affect the speed of fish migration so maximum swimming speeds generally can increase with temperature (Beach, 1984).

A majority of the downstream migrating smolts above the power-stations were diverted to the turbines (V). Albeit spills were altered at both power-stations they were both ineffective to guide smolts to the spillways. The CFD-modelling and particle tracking showed that the probability for smolts to descend in the spillways increased at higher spill and at surface spill, yet both power-stations showed low FGE's (V). Coutant &Whitney (2000) also mentioned that various power-stations have different FGE's for spillways and show diverse guidance patterns. The differences in FGE's at Stornorrfors and Sikfors were explained by the spillway locations in relation to flow patterns above the dams and in these studies the theoretically assessed fish downstream migration routes varied depending of different flow conditions. Even if fish and the modelled neutral particles may behave in different ways, as discussed in V, the low FGE's together with the modelled flow scenarios pointed out low average odds for smolt to pass over the spillways in the studied rivers over the last ten years. Thus, the conclusions were that downstream migrating smolts are normally guided towards the turbines at seaward migration.

Smolts passing power-station via turbines generally express increased mortality (Montén, 1985; Coutant & Whitney 2000). By using groups of Carlin-tagged and radio-tagged smolts released upstream the power-station the mortality of smolt passing the power-station in Piteälven was estimated to c. 17 % (VI). Even if these studies were done different years the smolts most likely had comparable passage routes due to the low FGE predicted for the spillway (V). The estimated average mortality of smolt at turbine and tunnel passage was higher than generally reported from power-stations with Kaplan turbines. References in Coutant & Whitney (2000) indicate smolt mortalities of 4-7 %, while Bickford & Skalski (2000) revised several studies and estimated a mortality rate of c. 13 %. The relatively high mortality found at Sikfors can be explained by the 0.6 km long submerged outlet tunnel that smolts have to pass after the turbines. Montén (1985) also observed increased mortalities of c. 12-13 % for smolts passing the comparable submerged tunnel at Umeälven. Anon. (2002) reported similar observation after smolt passage of an underground tunnel at a Russian power-station. The direct mortality of fish involves physical damage at passage, e.g., mechanical strike and pressure, while indirect mortality is caused by stress, injuries, disorientation and predators after passage (Coutant & Whitney, 2000; Čada *et al.*, 2001).

By using telemetry techniques direct and indirect losses of smolts after passage of the power-station were assessed (VI), even if studies rarely explicit these two. The direct mortality (11.5 %) of radio-tagged smolts at the power-station passage in Sikfors was higher than the indirect (7.7 %), and the passage losses were size-dependent (VI). Similar findings, that larger fish were subjected to higher mortality than small fish, were also shown by CEATI (1982), Montén (1985) and

Coutant & Whitney (2000). Hence, the relatively high losses of smolts observed at Sikfors compared to other studies, could also be due to the relatively large size of fish used in the study. Additionally the telemetry study demonstrated that 13 % of the radio-tagged smolt remained upstream the power-station during the study, and these fish could also have been lost to the smolt run (VI).

Data from the Carlin-taggings indicated constantly rising mortality of smolts per unit river distance (VI), which can be expected since losses normally take place at downstream migration (Hvidsten & Johnsen, 1997; Lundqvist *et al.*, 2006). Conversely, the size-dependent mortality demonstrated for radio-tagged fish only predicted c. 4 % losses for the size that represented Carlin-tagged smolts. Since higher mortality was observed (16 %) this could be explained by that ceased migration, as noted for radio-tagged fish close above the power-station, most likely added to the overall losses of smolts. Hvidsten & Johnsen (1997) and Mathers *et al.*, (2002) also reported a general increase in mortality of smolts in dammed and lentic areas due to delayed or stopped migrations.

The population modelling of the passage mortalities of smolts at Piteälven predicted different scenarios depending on smolt size and whether or not the additional losses of smolts caused by ceased migration was considered (VI). Even so, this demonstrated that the population of returning adult salmon could increase from 5-30 % up to 70-120 % in ten years if all power-station losses were reduced to zero. As stated, the predictions were tentative for high population densities, and close to carrying capacity a passage mortality of 17 % causes same decrease in amount of adults. These estimations could not be compared to other published studies since resembling approaches have not been found.

Both the studies in V and VI were performed at periods when the natural smolt migrations in the rivers take place, and predicted a similar fate for natural smolts as for fish in the studies. However, the studied smolts were of large size and hatchery origin, which might lead to that they do not have the same migration routes as natural smolts in the rivers, and different behaviour between wild and hatchery smolts have been reported (Aarestrup *et al.*, 2002). Nevertheless, migrating wild smolts were believed to most likely be guided to the power-station turbines at most natural flow regimes (V). This will cause passage mortality (VI), and there is no reason to believe that these mortality rates would differ between similar sized hatchery and wild smolts. At present there is no reliable information on the size distribution and exact timing of the wild smolt migration in either Vindelälven or Piteälven. As pointed out, the hatchery fish could however have showed a lower migration instinct than wild smolts, which could have caused an overestimation of the total passage losses. Still, the mortality of smolts at passage of Sikfors power-station is predicted to be an important aspect for mortality of fish in the river stock.

Evaluation of tagging methods

During recent decades numerous tagging techniques have been developed for studying fish behaviour (Guy *et al.*, 1996). The tags can be divided into external and internal, and be either passive or active. Depending on research aim several methods can be applied to receive reliable information. Passive tagging in the field normally generates a limited amount of data and relies on relatively large tagging groups while active transmitters provide more comprehensive information on individual fish behaviour. In this thesis the following tagging methods were used; 1) Hole-punching or clipping of adipose fin, 2) PIT-tags, 3) Carlin-tags, 4) Surgical implanted radio-tags, 5) External radio-tags, and finally 6) Gastric radio-tags.

The punching of a hole or clipping of the adipose on adult fish (II; III; IV) was not expected to affect fish performance. Furthermore, the regeneration of the fin was regarded as slow which lead to the conclusion that these fish could be easily recognized at the ladder (II). The PIT-tags used on adult fish were small and inserted in such a way that tag losses would be eliminated (IV), therefore no effects on fish and high retention was expected. Carlin-tags are widely used for tagging salmonids (Larsson, 1984; Lundqvist *et al*., 1994). These tags have a long retention time (Guy *et al.*, 1996) and are usually considered to have only minor effects on swimming performance and survival of smolts and larger fish, although they may affect smaller fish negatively (Strand *et al.*, 2002). The loss rates and behavioural effects of Carlin-tags on the adult fish were considered negligible (II). The use of Carlin-tags on smolts (V) could potentially affect fish (even if no changes in behaviour or swimming performance was expected), yet it would not cause irregularities between the groups of fish released at Piteälven which supported the study design and thus the results. Neither the gastric nor the surgical implanted relatively small sized radio-transmitters used on smolts (VI) are likely to affect the swimming behaviour (Adams *et al*., 1998; Connors *et al.,* 2002). No surgically implanted tags were lost during the study period, yet gastric radio-tags suffered 12 % losses at release of fish, hence these fish was excluded from the further analyses (V). External radio-transmitters were used on adult salmon and are likely not to affect the swimming behaviour (Thorstad *et al.*, 2000). Since these tags are attached via wires, fish might however suffer from wounds at the insertion points due to mechanical disturbance from the wires (Bridger & Booth, 2003; II). In addition, irregular tag-losses can take place (Bridger & Booth, 2003), and in II losses of external radio-tags (a total of 22 %) were mostly reported in waterfalls and at the fish-ladder, which was explained by high swimming activity of fish and the surrounding environment. Due to the high losses of external radio-tags these were replaced by gastrically implanted ones to reduce the risk of losses. As a result of that the effects of gastric radio-transmitters on adult Atlantic salmon in the field had not been adequately evaluated previously, this was assessed in IV. The results demonstrated no negative effects on the swimming performance, and radio-tagged fish actually migrated slightly faster to the ladder than did only PIT-tagged fish. Besides this the tag-losses were fairly low (9 %), which was also verified by the low loss rate of 7 % that was noted in the four years of gastric taggings evaluated in II.

Conclusions

1. Migration behaviour of adult salmon in flow controlled areas.
   At Umeälven, salmon showed low upstream migration success and an average of 70 % of the salmon did not find the correct upstream migration route. Fish were hindered and delayed, and responded with up- or downstream movements depending on flow. At high turbine flows salmon entered the power-station outlet, and at low spill flows fish had problems to find the entrance of the bypass. In the bypass channel fish were partially hindered at rapids, and passages of the first waterfall improved when flow decreased. At the ladder area salmon showed search behaviour resulting in prolonged migrations. No effects in migration timing to the fish-ladder could be observed after installations of a fourth turbine. The overall migration patterns were independent of tagging day, sex and size of salmon.

2. Migration of salmon and brown trout smolts approaching power-stations.
   Similar patterns, where fish mainly migrated downstream in the highest flows with similar speed as water, were demonstrated in Umeälven and Piteälven. No difference was observed between salmon and trout. In Piteälven smolts were observed in the surface water and migration could cease close to the power-station. Most fish entered the turbines and no fish descended via spills. Flow-modelling indicated low fish guidance efficiencies for the spillways, increasing with spill, still predicting low odds for wild smolts to pass via the spillways.

3. Mortality of salmon and brown trout smolts passing a hydropower complex.
   Smolts passing the power-station at Piteälven showed passage losses related to fish-size. The overall average losses of 17 % indicated both direct and indirect mortality. Smolts also had a constantly increasing mortality per unit river distance and indicated that additional losses caused by ceased migration at the power-station might take place.

4. Salmon population responses to improved passage success of power-stations.
   Predictions on how the escapement returns could be enhanced by improved adult upstream migration at Umeälven (e.g. by increased spill flows), and eliminated power-station losses of smolt at Piteälven (e.g. by an effective smolt bypass device), demonstrated a potential population growth of up of to c. 500 % and 5-120 %, respectively.

5. Effects of gastric radio-tags on adult salmon migration performance.
   Adult Atlantic salmon with gastric radio-tags in Umeälven had similar upstream migration success to the fish-ladder as the control group and showed slightly faster migration. Since no negative effects on migration performance was observed the short handling time at tagging and the moderate tag losses indicated the benefits of using gastric radio-tags in regulated rivers.

Management implications

As demonstrated in this thesis flow regulations due to hydropower can have major negative effects on anadromous fish migrations and also on the population level. Changes of river hydraulics caused by hydropower constructions during the past hundred years have hindered or eliminated fish migrations in many watersheds.

With only about twelve rivers with natural salmon populations remaining in the Baltic region the situation is alarming. At the same time the conditions for anadromous salmon and trout at regulated rivers that still support natural populations above dammed areas could be improved by increasing passage success for the fish. This could be achieved by constructing bypasses that secure high migration success and cause minimum delay, or by releasing more water in the bypass routes.

Most efforts to solve passage problems have been carried out in the USA and Canada and, conversely, in northern Europe, e.g. Scandinavia, there seems to be limited knowledge on how to efficiently bypass fish. Additionally the information about fundamental biological traits of the salmonid lifecycle and migration behaviour is scarce in some aspects (e.g. the natural smolt migration), making it difficult to improve bypass success. Basic biological research on smolts is needed in northern areas. Moreover, since hydraulic patterns initiate different migration responses, e.g. adult upstream swimming in bypasses and fish-ladders and smolt downstream movements, interdisciplinary studies between biologists, engineers and technicians should be encouraged.

Even though a number of unsolved questions remain regarding fish passage problems at regulated rivers new techniques as improved radio-transmitters, receivers, hydro acoustic sonar’s and hydraulic meters will aid future research to become more accurate and maintainable. Presumably most of the passage problems that fish are subjected to at power-stations can be reduced by recovering the fish migratory routes, which would aid to maintain the threatened wild salmon and trout populations.

Swedish summary - Sammanfattning

Rivinoja, P. 2005. Vandringsproblem för lax (*Salmo salar*) i flödesreglerade älvar. Doktorsavhandling. ISSS: 1652-6880. ISBN: 91-576-6913-9.
Originaltitel: Migration Problems of Atlantic Salmon (*Salmo salar* L.) in Flow Regulated Rivers.

Uppströmsvandring av vuxen lax (*Salmo salar*) på väg mot lekområden samt nedströmsvandring mot havet av lax- och havsöringsmolt (*Salmo trutta*) studerades i två flödesreglerade älvar i norra Sverige. Fiskarnas vandringsmönster vid passage av kraftverken och dammarna relaterades till olika vattenflöden. Populationsmodeller nyttjades för att bedöma den framtida effekten på laxpopulationerna om påverkan från kraftverken minimeras.

Individuellt lekvandrande laxar från Umeälvens mynning märktes med Radio-, PIT- och Carlin-märken under åren 1995-2005 (*n* = 2651). Resultaten visade att 0-47 % (medel 30 %) av fisken årligen vandrade till laxtrappan 32 km uppströms i älven. Vandringen från kusten till trappan tog i snitt 44 dagar och fiskens vandring fördröjdes eller hindrades vid kraftverkets turbinutlopp, olika forsar samt i fisktrappans område. Lax i kraftverkets utloppskanal observerades genom ekolodning, vanligtvis på 1-4 meters djup. Här reagerade fisken starkt på flödesförändringar genom att vandra upp- och/eller nedströms. Lax i kraftverkets turbinutlopp reagerade generellt positivt på ett ökat spillflöde när turbinflödet minskade genom att vandra uppströms till den gamla naturliga älvfåran som också fungerade som vandringsled uppströms. Vid höga spill (ca 150 m^3s^{-1}) minskade framgången i vandringen uppströms det första vattenfallet. Förlusten av lax till lekområden uppströms beräknades till 70 %. Genom populationsmodellering förutsades en ökning på 500 % inom en tio års period, om 75 % av uppströmsvandrande laxhonor kunde nå Vindelälven, genom att fiskvandrings-problemen i den reglerade älvsträckan minimierades.

Radiomärkta lax- (*n* = 150) och havsöringsmolt (*n* = 56) som frisläppts uppströms kraftverken i Umeälven och Piteälven år 2002-2004 vandrade normalt nedströms i huvudfåran och anlände till kraftverkens turbinintag. Smoltens hastighet under vandringen sammanföll generellt med vattnets hastighet och var i snitt ca 2 fisklängder per sekund (BL s^{-1}). Ekolodning i Piteälven visade att merparten av smolten vandrade ytnära på 1-3 meters djup. Flödesmodellering (CFD, Computational fluid dynamics) visade att de spilluckor som vanligen nyttjas vid respektive kraftverksdamm inte effektivt vägleder nedströmsvandrande smolt i spillets riktning (Fish Guidance Efficiency, FGE). I Piteälven stannade 13 % av den radiomärkta smolten närmast uppströms kraftverket. Inga smolt passerade nedströms över spillet och smolt som passerade genom turbinerna uppvisade storleksberoende förluster så att stora individer hade högre dödlighet än små. Tillsammans med data från utsättningar av Carlin-märkt smolt (*n* = 7 450) under 1998-1999 skattades den genomsnittliga förlusten av smolt vid kraftverket till 17 %. Med populationsmodellering bedömdes andelen lekvandrande lax öka från 5-30 % till 70-120 % inom en tioårsperiod om kraftverket inte orsakade några smoltförluster. Mina arbeten diskuterar olika förslag till hur vandringsproblemen för fisk kan minimeras så att det långsiktigt går att etablera uthålliga vandringsfiskbestånd.

Finnish summary - Tiivistelmä

Rivinoja, P. 2005. Atlantin lohen (*Salmo salar* L.) vaellukseen liittyvät ongelmat säännöstellyissä joissa. Tohtorinväitös. ISSS: 1652-6880. ISBN: 91-576-6913-9.
Englanninkielinen alkuperäisotsikko: Migration Problems of Atlantic Salmon (*Salmo salar* L.) in Flow Regulated Rivers.

Aikuisen lohen (*Salmo salar*) sekä lohen ja taimenen (*Salmo trutta*) vaelluspoikasten vaelluskäyttäytymistä tutkittiin kahden pohjoisruotsalaisen joen säännöstellyillä osuuksilla. Voimalaitosten ja niihin liittyvien rakenteiden vaikutusta kalojen käyttäytymiseen ja vaelluksen onnistumiseen tarkasteltiin erilaisissa virtausolosuhteissa. Voimalaitosten vaikutusta lohipopulaatioihin arvioitiin mallinnuksen avulla.

Uumajajoen suulla vuosina 1995-2005 yksilöllisesti radio-, PIT- ja Carlin-merkityistä nousuvaelluksella olleista aikuisista lohista (n = 2651) vain 0–47 % (keskiarvo 30 %) nousi vuosittain kalaportaalle 32 kilometrin päässä jokisuulta. Vaellus rannikolta kalaportaalle kesti keskimäärin 44 päivää. Lohen vaellus hidastui tai pysähtyi voimalaitoksen turbiinivirrassa, vesiputouksissa ja kalaportaalla. Voimalaitoksen alta lohet nousivat ylävirtaan paremmin ohijuoksutusvirtaamien kasvaessa. Menetettyjen potentiaalisten kutukalojen määräksi arvioitiin 70 %. Populaatiomallinnuksen perusteella nousuvaelluksen parempi onnistuminen säännöstellyn osuuden ohitse saattaisi johtaa 500 % populaatiokoon kasvuun kymmenen vuoden kuluessa, jos 75 % naaraslohista saavuttaisi sivujoen eli Vindeljoen kutualueet.

Radiolähettimillä vuosina 2002–2004 merkityt Uumaja- ja Piitimenjoen voimalaitosten yläpuolelle vapautetut lohen (n = 150) ja taimenen (n = 56) vaelluspoikaset vaelsivat alavirtaan keskimäärin nopeudella kaksi kalanmittaa sekunnissa (2 body lenght s^{-1}), jolloin ne päätyivät voimalaitoksen turbiinien imuvirtaan. Vaelluspoikaset liikkuivat pääosin lähellä pintaa 1-3 metrin syvyydessä. Virtaamamallinnuksen perusteella ohijuoksutuskanavien ohjaavuus (Fish Guidance Efficiency, FGE) oli verrattain alhainen luonnollisten virtaamien vallitessa. Piitimenjoen vaelluspoikasista noin 13 prosentilla vaellus pysähtyi voimalaitokselle tultaessa. Turbiineista läpi menneiden kalojen koon ja kuolleisuuden välillä oli positiivinen riippuvuus. Vuosina 1998-1999 tehdyt Carlin-merkinnät (n = 7450) osoittivat voimalaitoksen läpi menneiden vaelluspoikasten kuolleisuudeksi keskimäärin 17 % (radiolähettimillä merkityt kalat mukaan laskettuna). Populaatiomallinnuksen perusteella odotettavissa oleva kudulle palaavien yksilöiden määrän kasvu olisi 5-30 prosentista jopa 70-120 prosenttiin kymmenen vuoden aikana, mikäli voimalaitoksen läpi menevät vaelluspoikaset säilyisivät kaikki hengissä.

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This thesis demonstrates migration problems for adult and juvenile Atlantic salmon (*Salmo salar*) passing up- or downstream in flow regulated areas at hydropower-stations. Unnatural migration behaviour and low upstream passage success of adult salmon in relation to altered flow regimes was observed. Juveniles followed the main flows into the turbine intakes with increased mortality. Population modelling showed future increases in the salmon stocks if problems associated with changing flow regimes and obstacles in the river could be minimized.

Peter Rivinoja received his graduate education at Department of Aquaculture at SLU in Umeå. His undergraduate degree is from Umeå University.

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