Division for Environmental Sciences
Department of Biology

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Re-establishment of connectivity for fish populations in regulated rivers

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List of papers / publications

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

I. Calles, E.O. & Greenberg, L.A. (2005). Evaluation of nature-like fishways for re-establishing connectivity in fragmented salmonid populations in the River Emån. *River research and applications*. **21**: 951-960.

II. Calles, E.O. & Greenberg, L.A. (2005). The pre- and postspawning movements of anadromous brown trout in relation to two low-head power plants. *Manuscript*.

III. Calles, E.O. & Greenberg, L.A. (2005). Survival and movement of wild brown trout smolts past two power plants. *Manuscript*.

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VI. Nyberg, L., Calles, E.O. & Greenberg, L.A. (2005). Impact of short-term regulation on hyporheic water quality in a boreal river. *Manuscript*.

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Introduction

Today, hydropower constitutes the only large-scale renewable source of electricity. The greatest benefits of hydropower are the limited emissions of green-house gases, compared to fossil fuels, and that it constitutes an instantaneous energy reserve, i.e. power can be stored, as opposed to other non-polluting energy sources such as wind energy (Svensson, 2000; Truffer *et al.*, 2003). Hydropower does, however, often have large-scale detrimental effects on the local environment, which has been known for a long time (Clay, 1995). When hydropower was introduced in the early 1900's, little attention was paid to its negative impact on the environment, due to poor knowledge and conflicting economical interests. The environmental issues of hydropower are receiving increased attention, however, as general environmental awareness is increasing and as the drawbacks of hydropower are being identified (Bratrich *et al.*, 2004).

Flow regulation has been shown to interrupt the ecological connectivity in riverine landscapes, ecological connectivity being defined as "exchange pathways of matter, energy and organisms" (Ward and Stanford, 1995). In a hydrologically intact river these exchange pathways are active in four dimensions (Fig. 1), longitudinally (upstream-downstream), vertically (river-groundwater), laterally (river-floodplain) and temporally (Ward, 1989).

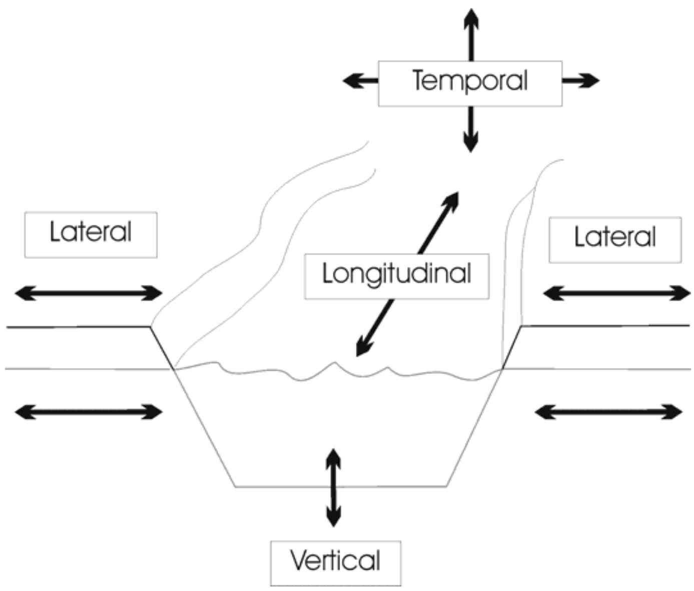

Figure 1. The 4-dimensional nature of lotic ecosystems modified from Ward (1989).

Intact connectivity is of crucial importance for the biology of many aquatic species, and for fish longitudinal connectivity is probably the most well-known dimension, which involves upstream and downstream migration along river corridors so that fish can move between feeding, spawning and winter habitats. Vertical connectivity involves interactions between surface water and ground water in the surrounding aquifer, the hyporheic zone, which primarily affects organisms in the interstitial spaces in the substrate, but can also affect the nutrient budgets of rivers. There is often a lateral extension to the hyporheic zone, and in addition to subsurface lateral exchange, the lateral dimension involves exchange between the river channel and the surrounding riparian zone. Lateral connectivity also involves the river channel and its floodplain where inundation of the floodplain renews connectivity (Ward and Stanford, 1995). The fourth dimension, time, scales the processes and mechanisms occurring along the other dimensions and highlights the importance of frequency and periodicity of hydrological events such as storm floods and snow-melt runoff.

Hydropower and upstream migration

Anadromous fishes in temperate zones spend most of their adult life feeding at sea, since the marine environment offers better conditions for growth than freshwater (Fig. 2) (Myers, 1949; Gross *et al.*, 1988). When the adults leave the sea and migrate into rivers to spawn, the migration is generally initiated and stimulated by changes in discharge and/or water temperature (Jonsson, 1991; Olofsson *et al.*, 1998). When spawners enter the regulated river, the migratory fish come in contact with dams and other obstacles that hinder them from reaching spawning grounds, which are often situated far upstream (Backiel and Bontemps, 1996; Cowx and Welcomme, 1998; Eklöv *et al.*, 1999). To solve the problem of disrupted longitudinal connectivity in a river, measures are often taken to either artificially compensate for the missing reproduction or to re-establish longitudinal connectivity, allowing the fish to reproduce naturally (Saltveit, 1993). Compensatory stocking is generally achieved by catching spawners, stripping them of their eggs and milt and then keeping the fertilised eggs at a rearing facility until release (Ackefors *et al.*, 1991; Eriksson and Eriksson, 1993). Negative effects of such compensatory stocking, which include loss of genetic diversity, lowered fitness, decreasing return rates and diseases,

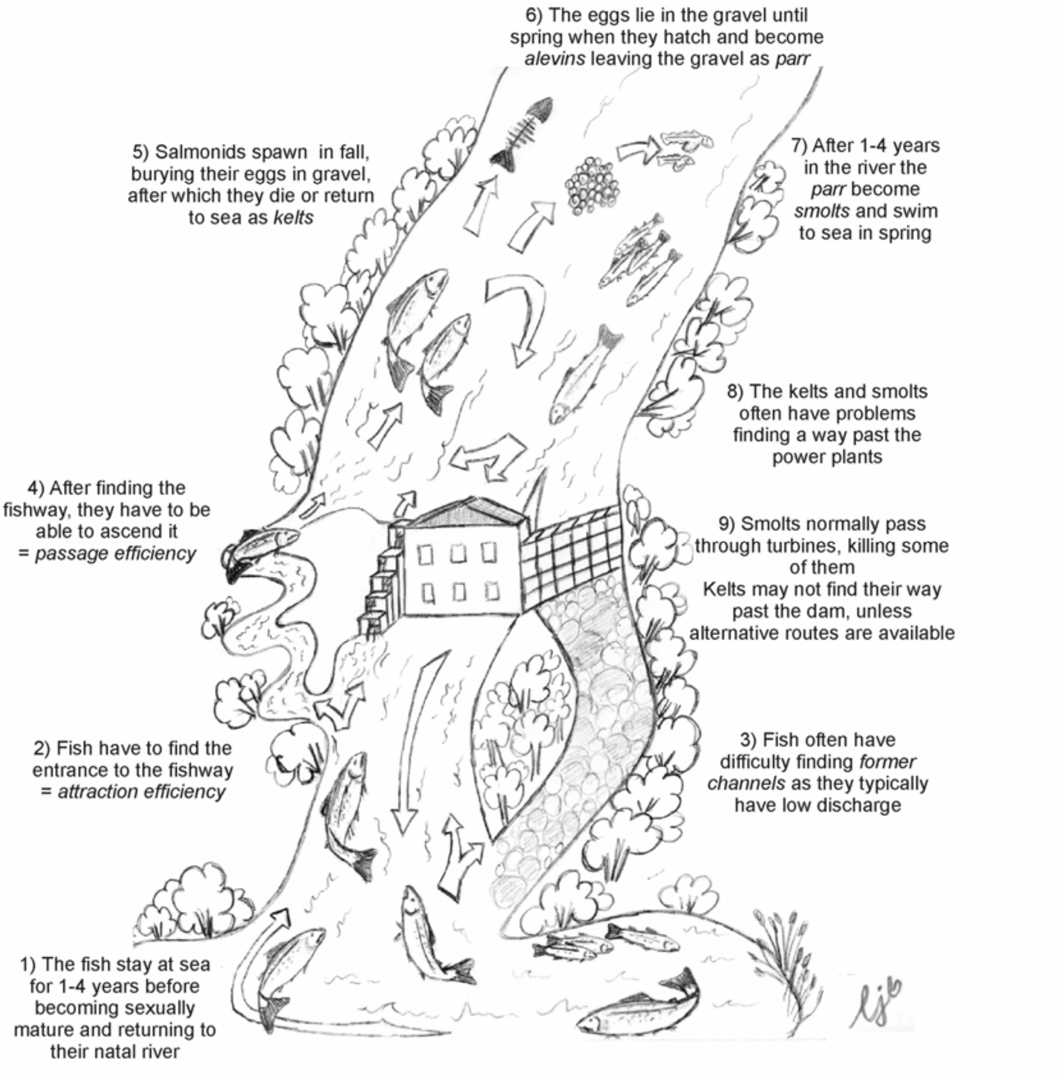

Figure 2. A schematic overview of the life-cycle of anadromous salmonids in a regulated river and problems they encounter during different life-stages (1-9).

have led to the use of alternative measures that allow the fish to reach their spawning grounds and reproduce naturally (Saltveit, 1993; Petersson *et al.*, 1996; Petersson and Järvi, 1997; Laine *et al.*, 1998; Bryant *et al.*, 1999; Rivinoja *et al.*, 2001; Hedenskog *et al.*, 2002). The re-establishment of longitudinal connectivity can be achieved either by catching and transporting the fish past the obstacle or by constructing an alternative route that enables them to proceed upstream (Denil, 1909; Clay, 1995; Larinier, 2001). Catching and transporting fish upstream is generally performed when a fishway is malfunctioning or absent (Backiel and Bontemps, 1996) or when the cumulative loss of fish at a series of fishways is estimated to be too great (Anonymous, 1998). In most cases, however, the transfer of the spawners upstream is achieved by constructing some kind of fish pass, and today there exists many different types of fishways (Bryant *et al.*, 1999; Gowans *et al.*, 1999; Larinier, 2001).

For fishways to function properly not only must the fish be able to find the fishway (attraction efficiency) but they must also be able to successfully ascend it (passage efficiency) (Larinier, 2001; Aarestrup *et al.*, 2003). To guide fish towards fishways is often complicated, especially when fish have to leave the main stem of the river and proceed into a side channel, often the former channel (Arnekleiv and Kraabøl, 1996; Chanseau *et al.*, 1999; Rivinoja *et al.*, 2001). In many cases, former channels are associated with low residual flow conditions and may have partial obstacles, which can cause the fish to move slowly or even stop and return downstream (Thorstad *et al.*, 2005). When the fishway is situated in the main stem, close to the power plant, the design of the fishway entrance and its position in relation to the tail-race influence whether or not the fish locate the fishway (Clay, 1995; Bunt, 2001; Laine *et al.*, 2002). Most fishways in temperate areas were built targeting commercially important salmonids that also have strong swimming and leaping capabilities (Larinier, 1998). In many cases the design is inappropriate for other species such as cyprinids, esocids and percids (Baras *et al.*, 1994; Schmutz *et al.*, 1998; Lucas *et al.*, 1999; Larinier, 2001). During the last decade efforts have been directed towards constructing fishways that are passable for all kinds of aquatic organisms (Eberstaller *et al.*, 1998; Fievet *et al.*, 2001). One example of such a multi-purpose fishway is the nature-like fishway that is built to resemble a natural side channel with suitable substrate, water movements, morphology and gradient (Jungwirth, 1996). The structural heterogeneity of a nature-like fishway creates a hydraulic mosaic that allows most species and life-stages to find a passable route through the fishway.

Hydropower and reproduction

Re-establishment of connectivity is not only dependent on fish finding and swimming through fishways, but also the availability of spawning and rearing habitat upstream of the fishway. At spawning, the fertilised eggs can be attached to the bottom, e.g. chub (*Leuciscus cephalus* L.) (Cowx and Welcomme, 1998; Fredrich *et al.*, 2003), injected deeply into the interstices, e.g. Baltic vimba

(*Vimba vimba* L.) (Ziliukas, 1989; Cowx and Welcomme, 1998; Bless, 2001), or buried in the substrate, e.g. brown trout (*Salmo trutta* L.) and Atlantic salmon (*Salmo salar* L.)(Elliott, 1994; Fleming, 1996; Klemetsen *et al.*, 2003). The incubation time for the eggs depends on water temperature (expressed as degree days), which means that the eggs of spring-spawning cyprinids will hatch within a few days or weeks, whereas the eggs of the autumn-spawning salmonids will remain in the gravel for several months before hatching (Malcolm *et al.*, 2003a). During incubation, the eggs are exposed to fluctuations in water quality, resulting from the mixing of surface water and groundwater into what is termed hyporheic water, and the zone where this occurs is hence termed the hyporheic zone (Jones and Mulholland, 2000). The hyporheic zone is not only a zone of mixing between the two sources of water, as microbiological activity in combination with physical and chemical reactions on particle surfaces alter the water quality along flow paths, sometimes described as a filtering effect (Fig. 3) (Hancock, 2002).

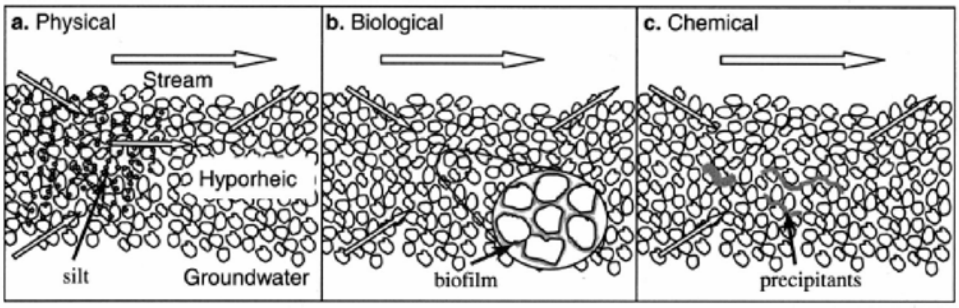

Figure 3. Three different processes occurring along hyporheic pathways. From Hancock (2002).

The characteristics of the water that finally reach buried eggs can be highly variable, but from the point of view of the eggs, the hyporheic water must be able to supply them with sufficient oxygen to allow development and growth as well as remove rest products such as ammonia (Crisp, 1996). For example, the minimum oxygen levels required for survival and growth of the salmonid embryos increase during development, from approximately 0.5 to 7 mg dm^{-3}, and to meet the requirements of all life-stages of a trout population, the oxygen content ought to be >5 mg dm^{-3} (Elliott, 1994; Crisp, 1996; Eklöv *et al.*, 1998). Most studies of how water quality is affected by regulation are based on surface water conditions (Gibert *et al.*, 1990; Boulton *et al.*, 1998; Ashby *et al.*, 1999).

Relatively little is known about how hyporheic water quality is affected by flow regulation and how this varies on a seasonal basis, and consequently how this effects the eggs (Dent *et al.*, 2000; Malcolm *et al.*, 2003a).

Hydropower and downstream migration

In most cases the construction of a fishway is the only measure taken to re-establish longitudinal connectivity in a river, thereby focusing on upstream movements and largely ignoring downstream movements (Lucas and Baras, 2001). Brown trout and Atlantic salmon, as opposed to some North-American salmonids, are iteroparous which means that they spawn repeatedly, returning to sea to recondition themselves before the next spawning event (Klemetsen *et al.*, 2003). The postspawning adults (kelts) return to sea in the fall in small rivers and in spring in large rivers, reflecting the greater availability of suitable winter habitat in large rivers (Degerman *et al.*, 2001). In addition, juvenile salmonids (smolts) migrate to sea in spring, after spending 1-4 years in the river (Olsson *et al.*, 2001). At the same time many species of cyprinids, percids and esocids spawn, which means that many of these species are highly mobile (Cowx and Welcomme, 1998). There is hence a need for a maintained longitudinal connectivity during most of the year, with peaks at fall and in the spring.

The creation of reservoirs in association with building hydroelectric dams produces lentic habitats that are suitable for piscivorous species such as pike (*Esox lucius* L.) and zander (*Stizostedion lucioperca* L.) (Olsson *et al.*, 2001; Koed *et al.*, 2002). Furthermore, reservoirs interrupt flow patterns in rivers, producing weak currents that may disorient migrating fish, and thereby prolong their exposure to predators (Coutant and Whitney, 2000; Olsson *et al.*, 2001; Aarestrup and Koed, 2003). In addition, fish incur problems or even die as they approach dams and enter turbines, bypass devices, spill gates, trash gates or trash racks (Montén, 1985; Matousek *et al.*, 1994; Amiro and Jansen, 2000). Even if fish manage to pass hydropower facilities, they have often been delayed, which can result in increased mortality (Aarestrup and Jepsen, 1998; McCormick *et al.*, 1998). At most power plants there are racks or screens that hinder objects above a certain size and lead them towards a nearby trash gate. The main objective of such devices is to protect the turbines, but when modified they may function as an alternative downstream route past the power plant for fish and other aquatic organisms. The downstream passage of fish is an issue of growing interest and recent work has tested different types of fish guiding and bypass devices (Scruton *et al.*, 2002; Welton *et al.*, 2002; Scruton *et al.*, 2003).

Re-establishing connectivity involves more than just building a fishway. One needs evaluate both upstream passage, in which the fishway is hopefully being used by the fish, and downstream migration, where it is important that fish are guided away from the turbines. When it concerns fishways, few studies have ever evaluated their attraction and passage efficiencies, and only a handful have looked at the overall effect of re-establishing connectivity, e.g. if targeted populations are strengthened by the increased habitat availability (Saltveit, 1993; Bryant *et al.*, 1999).

Ideally, one should conduct a study before constructing the fishway to identify the type of fishway to be constructed and where it should be placed, so that passage and attraction efficiency will be maximised (Cambray, 1990; Bunt, 2001; Gehrke *et al.*, 2002). Furthermore, just facilitating longitudinal connectivity will not have any long-term effects, unless all essential requirements for the different life-stages are taken into account, e.g. appropriate habitats for spawning, rearing, and foraging (Dynesius and Nilsson, 1994; Poff *et al.*, 1997; Fievet *et al.*, 2001; Ward and Wiens, 2001; Bond and Lake, 2003)

Objectives

The overall objective of this thesis was to study longitudinal and vertical connectivity in regulated rivers. The study of longitudinal connectivity involved an evaluation of function of two recently built nature-like fishways, whereas vertical connectivity was studied by examining how hyporheic water chemistry varied temporally and spatially in relation to regulation. The main objective is divided into several questions that focused on different life-stages of migratory fish, particularly brown trout:

- Would anadromous salmonids migrate to non-natal areas made available by the fishways (Papers I & II)?
- Would the trout find the fishways and what were the most important factors affecting their success, i.e. the attraction efficiency (Papers I & II)?
- Would the trout manage to successfully ascend the fishways after locating them (i.e. passage efficiency) (Papers I & II)?
- Would the fishways function for passage by non-salmonid species (Paper IV)?
- Do the fishways function as rearing habitat for fish? (Paper IV)?
- Would fish use upstream spawning grounds made available by the fishways and would this increase the densities of juveniles upstream of the fishways, eventually producing smolts (Papers I & III)?
- Do fish successfully pass the power plants on their way downstream and to what extent are they killed or delayed en route (Papers I, II & III)?
- Does seasonal variation in hyporheic conditions differ between regulated and unregulated rivers and what are the consequences for salmonid embryos (Paper V)?
- How are the hyporheic conditions affected by short-term flow regulation (Paper VI)?

General methods

Study areas

Studies were conducted in one river in the county of Småland in southeastern Sweden and three rivers in the county of Värmland in central western Sweden (Fig. 4).

Rehabilitation of longitudinal connectivity (papers I-IV) was studied from 2000-2005 in the River Emån (57° 07' 59" N; 16° 30' 00 E). The River Emån is a medium-sized river with a mean annual discharge of 30 $m^3 s^{-1}$. The catchment area is 4472 km^2 and is dominated by forest and agricultural land. For fish to use all 54 km downstream of the first definite obstacles for spawning they have to ascend two old vertical slot-type fishways at the power plants Emsfors and Karlshammar, and two recently built nature-like fishways at the two power plants in Finsjö.

The issue of vertical connectivity and flow regulation (papers V-VI) was studied in three small rivers in central-western Sweden. The River Tobyälven is unregulated, the River Järperudsälven is regulated without any minimum discharge requirement, and the River Mangälven is regulated with a minimum discharge requirement of 0.2 $m^3 s^{-1}$.

Methods for studying migration and reproductive success

Fish migration was studied by catching, tagging and releasing fish. A wide selection of traps was used to catch fish: a modified vertical-slot fishway, traps installed in a nature-like fishway, fyke-nets with side-arms, wolf-traps, rod and line and electrofishing. Fish were tracked using PIT- and radio telemetry. Only individuals without visible injuries were tagged and all tagged individuals were held in a cage for 1-6 h to check for post-tagging injuries, before releasing them.

Fish were PIT-tagged to be able determine how many fish that used the fishways (2001-2005). This was done by installing antennae at the entrance and exit of each fishway. The behaviour of the fish as they migrated was studied by radio-telemetry (2003-2004). The radio transmitters were active and could be

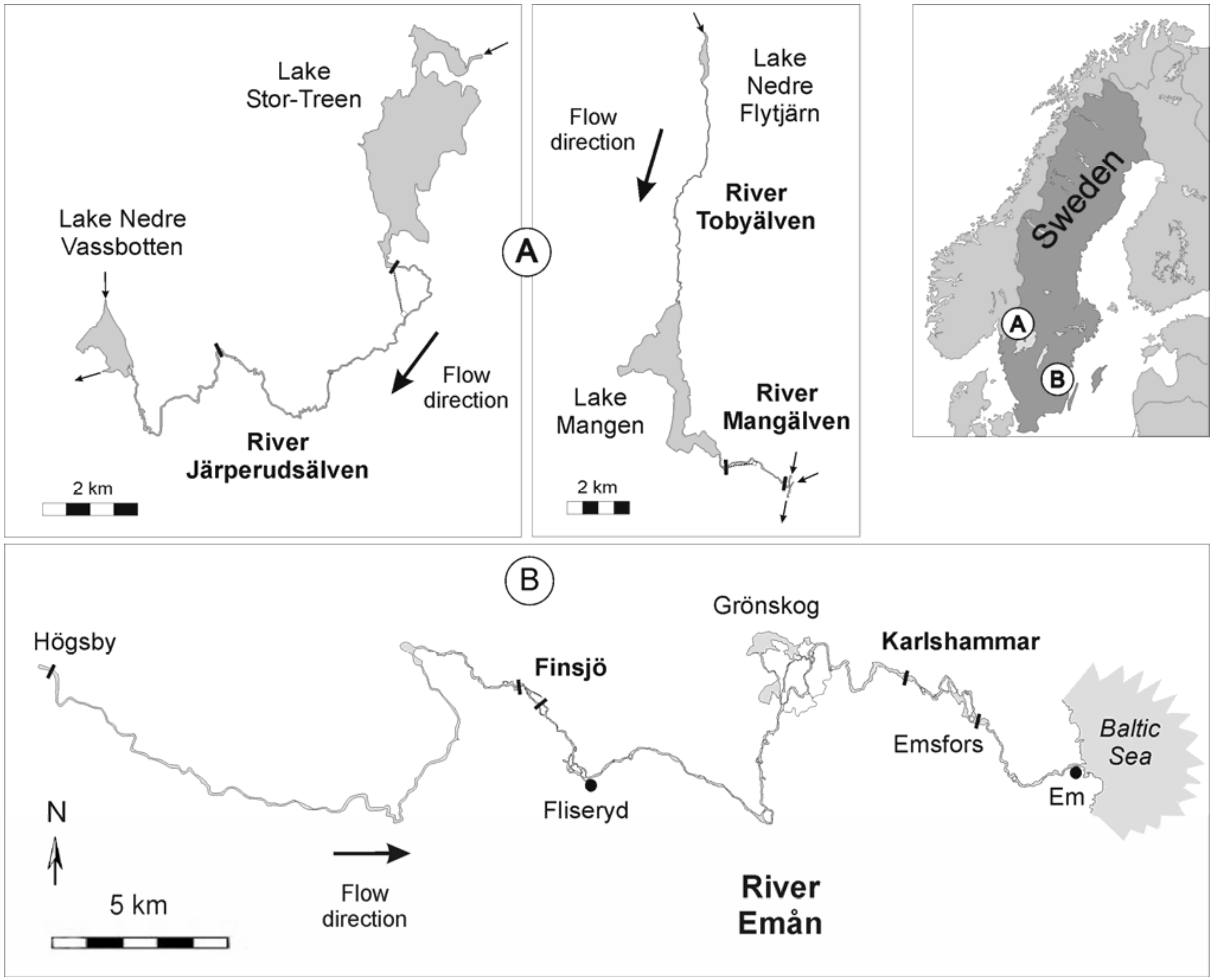

Figure 4. The study rivers in Värmland (A) and Småland (B). Black rectangles show location of power plants.

detected by manual and automatic receivers from 100-1500 m distance, depending on transmitter size, water depth and topography.

The downstream migration was studied primarily by tracking radio-tagged smolts in 2004 and 2005, but all other species and life-stages that were caught in traps and recorded by PIT-antennae were also used in this analysis. Electrofishing was used to estimate densities of juvenile salmonids before and after the fishways were opened. Three river stretches were chosen for electrofishing surveys: River mouth - Karlshammar, Karlshammar - Finsjö and Finsjö - Högsby (Fig. 4). Data from the sites in the lower parts of the River Emån were supplied by the National Fisheries Board.

Methods for studying hyporheic water quality

The sampling of hyporheic water was initiated by establishing a total of 11 transects in the three rivers at sites that were identified as possible spawning grounds for trout. The transects were laid out perpendicular to the direction of flow, covering both the floodplain and the streambed. A total of 146 piezometers or groundwater pipes were hammered into the substrate in pairs (one shallow and one deep) along the transects. The piezometers were then sampled monthly for one year and the following parameters were measured: water level, oxygen content, pH, electric conductivity, [NH_4^+], [NO_3^-], [PO_4^{3-}], hydraulic head difference and total discharge in the rivers. In addition, substrate composition and permeability were measured once. In late fall the rivers were surveyed for trout spawning activity, and redds that were found were instrumented with one shallow piezometer each. The redd piezometers were sampled during a 5 month period, corresponding to the approximate incubation time for trout embryos.

Summary of results

The discharge in the River Emån during the study was highly variable both within and between years (Fig. 5). In all years there were peaks in discharge in spring, but this occurred already in February in 2002 and not until in May 2003. Normally flow averages 10.2 $m^3 s^{-1}$ during summer and early fall (June-August 1986-1997), but in 2003 and 2004 there were extremely high flow conditions in July (peaking at 105.3 $m^3 s^{-1}$ in 2003 and 60.0 $m^3 s^{-1}$ in 2004). The discharge during the main spawning migration (i.e. September-October) was stable and decreasing in 2002 and 2003, and increasing in 2001 and 2004.

The total precipitation in the study area in Värmland during the hydrological year 2001-2002 was 845 mm and the mean air temperature during the same period was 6.7°C. As a comparison, the mean air temperature during the period 1961-1990 was 4.7°C, the mean annual precipitation was 707 mm and the mean annual runoff was 400 mm.

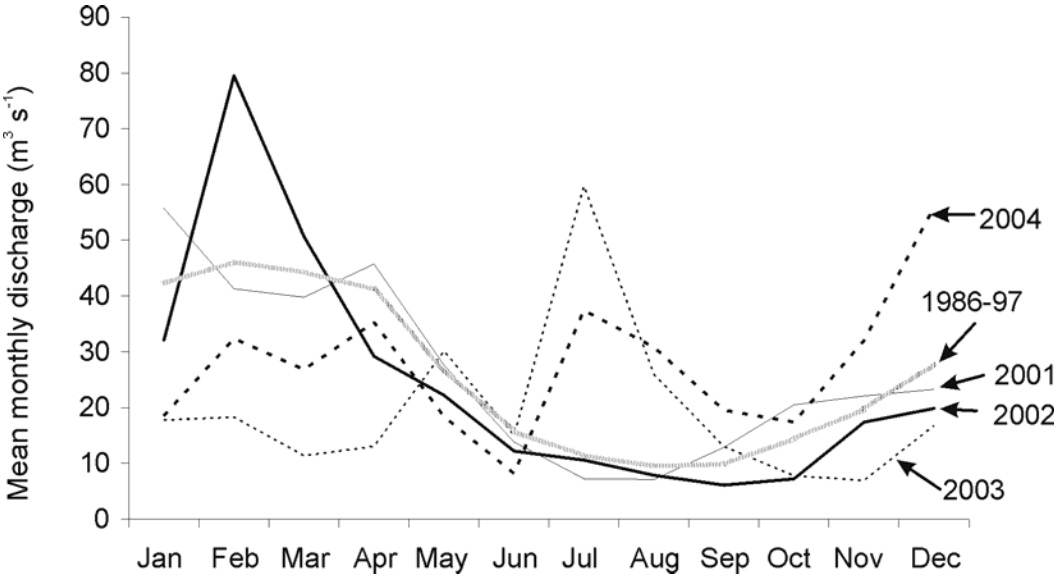

Figure 5. The mean monthly discharge in the River Emån 1986-97 and 2001-2004.

Hydropower and upstream migration

Migration up to the lower fishway (Papers I-II)

Our trap data in combination with data from a photo-cell counter in the fishway at Karlshammar showed that about 66% of all salmonids passing Karlshammar 2001-2004 were caught and PIT-tagged. Of the 844 fish that were PIT-tagged at Karlshammar 2001-2004 (Table I), 121 individuals or 14% were recorded at lower Finsjö fishway (Fig. 4). The majority of these were trout (N=112 or 15% of all trout), followed by salmon (N=6 or 11% of all salmon), Baltic vimba (N=2 or 6% of all vimba), and chub (N=2 or 25% of all chub). The percentage of fish that migrated from Karlshammar to the new fishways was higher for trout that had been to Finsjö in a previous year (44%) than those that had never been there (13%). The proportion of tagged trout that migrated from Karlshammar to Finsjö varied from 11-20% between years, and was directly proportional to the mean discharge during the spawning migration (Fig. 6). Thus, most fish tagged at Karlshammar were never recorded entering the fishways at Finsjö some 20 km upstream. In 2003 (Paper II) spawners were radio-tracked as they swam between Karlshammar and Finsjö, and we found that 88% of the trout stopped at sites downstream of Finsjö identified as possible spawning grounds, e.g. 65% stopped at spawning habitats located in the Grönskog area (Fig. 3). As potential spawning habitat only comprised 2.5% of the total stream area, the fish were showing positive selection for these sites.

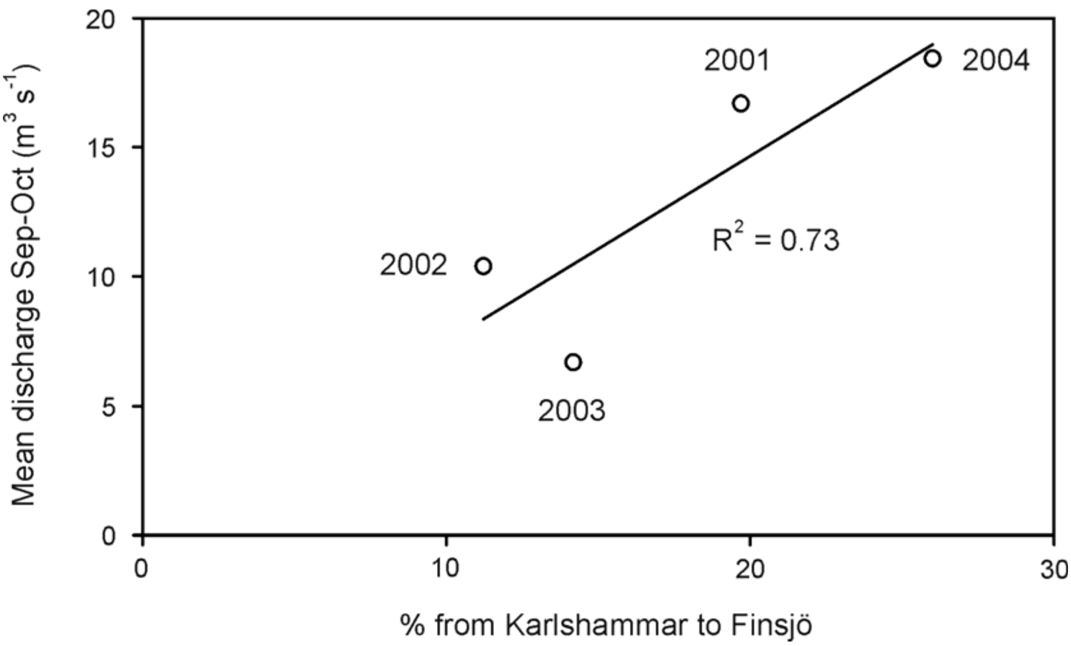

Figure 6. The mean annual discharge in the River Emån vs. the % of trout PIT-tagged at Karlshammar that later ascended the fishway at lower Finsjö power plant.

Upon arrival to Finsjö the fish had to choose between swimming up the former channel or the outlet channel (Figs. 7). In 2003, the two radio-tagged fish that made it to Finsjö selected the former channel, which had the highest discharge (Fig. 7, A). In 2004, all radio-tagged fish (N = 36) also swam into the channel with the highest discharge, but in this case, it was the outlet channel (Fig. 7, B), i.e. 100% attraction efficiency of the outlet channel. The median migration time from Karlshammar to Finsjö in 2001-2004 was 13 days (1.5 km day^{-1}), and the range was 1-311 days (60 m -19.6 km day^{-1}).

Table I. Number, weight and length of fish caught and PIT-tagged (P) or radio-tagged (R) at Karlshammar power plant, from 2001-04 in the River Emån.

Family	**Species**	**Number caught**				**Length (mm)**		**Weight (kg)**		**Tagged**
		2001	**2002**	**2003**	**2004**	**Mean**	**Range**	**Mean**	**Range**	**P/R**
Cyprinidae	Baltic vimba (*Vimba vimba*)	11	10	-	11	341	300 - 400	0.5	0.3-0.7	32 / -
	Chub (*Leuciscus cephalus*)	1	7	-	4	404	280 - 435	0.9	0.3 - 1.2	12 / -
	Ide (*Leuciscus idus*)	-	2	-	-	330	300 - 360	0.4	0.3 - 0.6	2 / -
	Roach (*Rutilus rutilus*)	-	2	-	-	280	260 - 300	0.3	0.2 - 0.3	2 / -
	Rudd (*Scardinius erythrophthalmus*)	-	1	-	-	320	-	0.6	-	1 / -
Percidae	Perch (*Perca fluviatilis*)	-	2	-	1	288	270 - 305	0.3	0.2 - 0.4	3 / -
Petromyzontidae	River lamprey (*Lampetra fluviatilis*)	-	-	2	-	350	-	-	-	- / -
Salmonidae	Atlantic salmon (*Salmo salar*)	8	18	16	16	727	510 - 1090	4.3	1.4-11.2	58 / 4
	Brown trout (*Salmo trutta*)	132	254 [B]	214[C]	134[D]	683	390 - 970	4.0	0.7-11.6	734 / 56[A]
	Rainbow trout (*Oncorhnchus mykiss*)	0	2	1	2	543	530-540	1.8	1.5 - 2.1	0 / -
Siluridae	European catfish (*Silurus glanis*)	0	0	3	6	767	510 - 880	3.3	1.2 - 4.9	- / -
5 families	**11 species**	**152**	**298**	**236**	**174**					**844 / 60**

[A] The 36 radio-tagged trout in 2004 were transported up to Finsjö by car.

[B] 7 of these individuals were recaptures from previous year (3 %).

[C] 37 of these were recaptures from previous years (17 %).

[D] 31 of these were recaptures from previous years (23 %).

At the tail-race (Fig. 7, C & D), the fish took a median of 3.2 h (12 min to 25 days) to ascend the lower fishway. There was considerable variation in the number and duration of attempts made to enter the fishway (1-46 attempts), but most fish entered the fishway during their first visit to the area (73%). The attraction efficiency of the fishway at lower Finsjö was 83%. All 35 radio-tagged individuals swam into or just next to the entrance of the fishway at some time and six of them spent 2-29 days below the power plant before moving back downstream, regurgitating the transmitter, or staying within the detection range of the fixed stations until the end of the study.

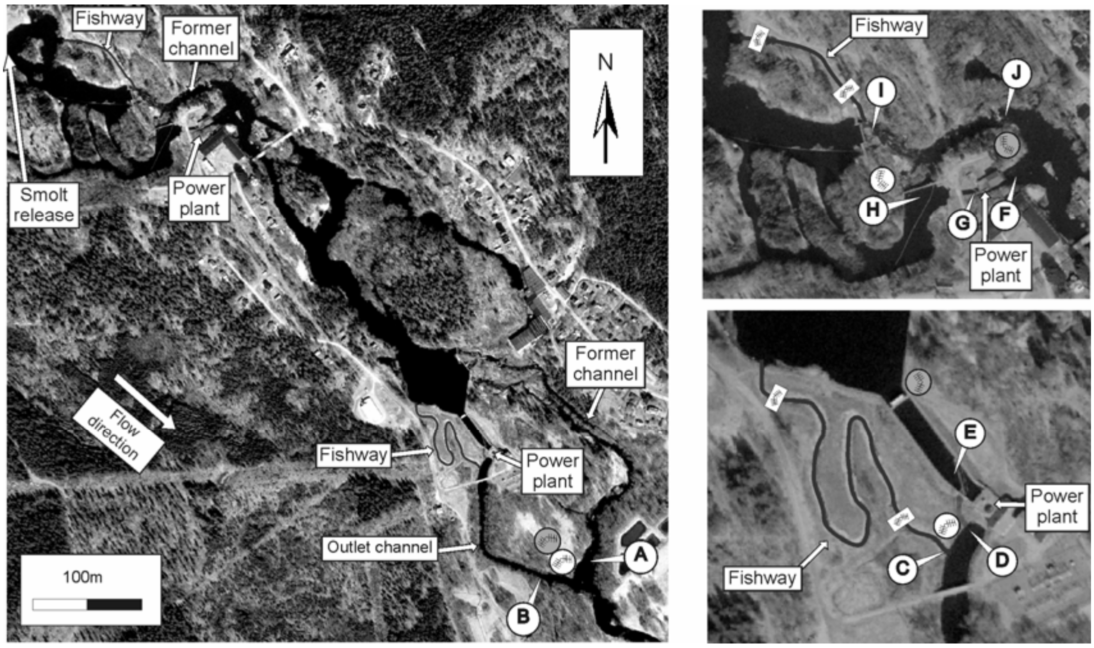

Figure 7. Map showing the Finsjö hydropower plants and the fishways with two PIT-antennae each (), location of the former channels and the three different fixed telemetry stations at fall () and in spring (). To the right are close-ups of the upper and lower power plant, respectively.

Ascending the lower fishway (Papers I-II)

Tagged trout ascended the fishways from May to December when temperatures ranged from 1.6 to 22.3°C. In 2001-2004, a total of 112 PIT-tagged and 29 radio-tagged trout ascended the fishway at lower Finsjö for a total passage efficiency of 94% (range 89-97%). In most cases a successful passage was achieved on the first attempt, i.e. they continued upstream after having passed the first PIT-antenna. The median time required for the fish to move the 300 m between the two antennae was 1.9 h (155 m h^{-1}) and ranged from 34 min to 21.4 h (14 to 529 m h^{-1}).

Migration to the upper fishway (Paper II)

Of the radio-tagged trout that passed the lower power plant, 27 of 28 individuals reached the upper power plant in a median time of 9.5 h (79 m h^{-1}, range 1.4 h to 4 d). The majority of the fish appeared to have problems finding their way into the former channel past the small waterfall, as seen by the larger number of entrance attempts at the tail-race than in the former channel. The attraction problems at the upper power plant were further highlighted by the higher average number of visits to the tail-race area at the upper power plant (median 3 visits) than at the lower power plant (median 1 visit), and the longer time between arriving and entering the former channel at the upper power plant as compared to the fishway at the lower power plant (median delay 3.2 h at the lower plant and 80.4 h at the upper plant). The individuals that made repeat visits to the upper power plant (75% compared to 22% of the same group of individuals at the lower plant) were observed to swim back and forth between the upper and lower power plants.

Tests using artificial freshets to attract fish into the former channel had no direct effect on attraction efficiency of the former channel at the upper power plant, as only two individuals entered the former channel during the control periods and two during the freshets. The fish spent relatively more time at the entrance of the former channel than at the tail-race during freshets as compared to control periods for two of four trials. Many individuals remained inside the reservoir between the two power plants until a natural freshet occurred in the river exceeding the total capacity of the power plant, which generated an increased spill discharge into the former channel. This initiated increased activity among the trout and within six days all individuals, who up to this point had spent six to 30 days in the reservoir, left the area. As a result of the natural freshet, the final attraction efficiency for the former channel at upper Finsjö in 2004 was 89%.

Ascending the upper fishway (Papers I-II)

In total, 25 radio-tagged trout passed the waterfall at upper Finsjö in 2004 and all of them proceeded upstream and entered the fishway after a median time of 1.3 h (range 0.5-21.3 h). Of the PIT-tagged trout that passed the lower fishway in 2001-2004 (for which the movement patterns in the reservoir were unknown) 50-86% made it to the fishway at upper Finsjö 2001-2004. The median time required to move between the fishways was 1.8 d (range 1.5 h to 78.5 d). The passage efficiency at the upper fishway was 99% (94-100%) and the passage time ranged from 18 min to 1.0 h, which is equivalent to 79 to 267 m h^{-1} (median 28 min = 163 m h^{-1}).

A total of 60.5% of the radio- and PIT-tagged trout that visited Finsjö in 2001-2004 successfully passed both power plants, but some individuals seemed to get lost in the reservoir between the two power plants (11.6%) and some returned downstream after entering or after passing the lower fishway (27.9%). More males than females successfully passed both power plants (51 males vs. 37 females), but the proportion of successful individuals was similar for both sexes (61% males vs. 66% females) and reflected the lower proportion of females caught at Karlshammar (46% females).

The radio-tagged trout that passed both power plants continued upstream and were observed at spawning grounds along the recolonised 24 km stretch of river, but with decreasing numbers with distance upstream.

Use and passage of the fishways by other species (Paper IV)

Eight species of varying sizes were caught by electrofishing in the fishways (Table II). At Finsjö a total of 187 individuals of 11 species were PIT-tagged (Table III) and released at the entrances of the fishways 2002-2005. The species most frequently observed ascending the fishways ($N \geq 5$) were burbot (83%),

Table II. Fish species observed ascending (Asc.)/descending (Desc.) and/or caught inside the nature-like fishways (Hab.)(number of individuals 100 m^{-2}) at Finsjö, and the minimum/maximum weight and length of these individuals, from 2002-05 in the River Emån. The observed use of the fishways is indicated as ● = ≥ 5 successful observations, ○ = < 5 successful observations, and **x** = < 5 observations that all failed.

Family	**Species**	**Use of fishway**			**Length (mm)**		**Weight (g)**		**N**
		Asc.	**Desc.**	**Hab.**	**Min**	**Max**	**Min**	**Max**	
Anguillidae	European eel (*Anguilla anguilla*)	-	○	**0.3**	340	800	58	-	2
Cottidae	Bullhead (*Cottus gobio*)	-	●	**1.7**	43	98	1	15	8
Cyprinidae	Baltic vimba (*Vimba vimba*)	○	○	**0**	295	340	267	400	3
	Bleak (*Alburnus alburnus*)	○[B]	●	**0**	36	132	1	15	15
	Chub (*Leuciscus cephalus*)	●	●	**2.8**	32	435	1	1102	26
	Common bream (*Abramis brama*)	○	-	**0**	460	-	1040	-	1
	Roach (*Rutilus rutilus*)	●	●	**3.2**	71	227	2	117	49
	Rudd (*Scardinius erythrophthalmus*)	**x**	-	**0**	151	-	37	-	1
	Tench (*Tinca tinca*)	●	-	**0**	270	410	366	1220	7
Esocidae	Pike (*Esox lucius*)	**x**	●	**0**	150	870	19	3660	4
Lotidae	Burbot (*Lota lota*)	●	●	**0.8**	163	320	28	216	9
Percidae	Perch (*Perca fluviatilis*)	●	●	**0**	100	305	32	354	38
	Ruffe (*Gymnocephalus cernua*)	-	●	**0**	60	110	-	-	27
Salmonidae	Atlantic salmon (*Salmo salar*)	-	●	**1.7**	80	200	5	79	8
	Brown trout (*Salmo trutta*)	●	●	**14.7**	63	290	4	228	42
7 families	**15 species**			**26.5**	**32**	**870**	**1**	**3660**	**240**

[A] Four individuals were caught at Karlshammar, tagged and transported to Finsjö and released.

[B] Individuals only observed entering fishway, fate unknown.

Table III. Number, weight and length of fish caught and tagged at Finsjö power plant, from 2002-05 in the River Emån.

		Year				**Length (mm)**		**Weight (g)**		**PIT-tagged (N)**	
Family	**Species**	**2002**	**2003**	**2004**	**2005**	**Mean**	**Range**	**Mean**	**Range**	**Total**	**To fishway**
Cyprinidae	Baltic vimba (*Vimba vimba*)	-	-	1	3	327	295-340	364	267-440	4	2 (50%)
	Chub (*Leuciscus cephalus*)	2	1	29[A]	2	275	128-480	343	19-1380	34	**13 (38%)**
	Common bream (*Abramis brama*)	5	5	-	-	466	410-510	1112	860-1480	10	1 (10%)
	Roach (*Rutilus rutilus*)	-	-	30	14	168	116-284	52	8-251	44	**10 (23%)**
	Rudd (*Scardinius erythrophthalmus*)	1	3	27	-	179	142-320	93	29-600	31	1 (3%)
	Tench (*Tinca tinca*)	9	4	1	-	394	270-500	1063	366-1660	14	**7 (50%)**
Esocidae	Pike (*Esox lucius*)	4	2	3	-	492	160-870	1150	19-3660	8	1 (13%)
Lotidae	Burbot (*Lota lota*)	-	-	6	-	192	95-265	69	30-123	6	**5 (83%)**
Percidae	Perch (*Perca fluviatilis*)	-	-	22	3	188	117-305	87	18-354	25	**8 (32%)**
	Zander (*Stizostedion lucioperca*)	-	-	4	-	188	150-220	40	21-58	4	0
Salmonidae	Brown trout (juvenile) (*Salmo trutta*)	-	-	7	-	221	124-530	276	19-1540	7	**4 (57%)**
5 families	**11 species (10 to fishway)**	**21**	**15**	**101**	**22**	**-**	**95 - 870**	**-**	**8 - 3660**	**187**	**52 (28%)**

[A] Four individuals were caught at Karlshammar, tagged and transported to upper Finsjö and released.

tench (50%), chub (38%), perch (32%) and roach (23%)(Table III). For both fishways, 74% of the individuals (all species combined) that ascended the fishway did so successfully, i.e. 74% passage efficiency. The individuals that did not successfully ascend the fishway either stopped inside the fishway (21% at lower and 17% at upper) or turned back downstream and left the fishway (5% at lower and 9% at upper). The individuals that stopped inside the fishways were typically burbot and juvenile brown trout. Individuals failing to pass were small cyprinids. Of the 14 individuals that successfully ascended the lower fishway, only one bream also successfully ascended the upper fishway. The data from the traps inside the fishways in combination with recordings of PIT-tagged fish showed that eight of the species that ascended the fishways and another four species used them for downstream passage.

Hydropower and reproduction

Water quality and the flow regime (Papers V-VI)

The results from the study on hyporheic water quality showed a difference in vertical water exchange between the surface water and the hyporheic water for the three rivers with different flow regimes. Hyporheic water quality was best in the unregulated River Tobyälven, followed by the regulated River Mangälven (with minimum flow requirements), which in turn was better than the regulated River Järperudsälven (without any minimum flow requirements).

Mean annual dissolved oxygen content (DO), [NO_3^-] and pH decreased and conductivity and [NH_4^+] increased from surface water to shallow hyporheic water to deep hyporheic water in the three rivers (Fig. 8). This spatial variation in mean annual DO content was partly explained by substrate composition and hydraulic head gradient (Fig. 9). In terms of temporal variation, there were numerous correlations between hyporheic water chemistry and either discharge or surface water chemistry for the unregulated River Tobyälven. In contrast, hyporheic water chemistry was not correlated to discharge and there were few correlations to surface water chemistry in the regulated rivers, the River Järperudsälven and the River Mangälven.

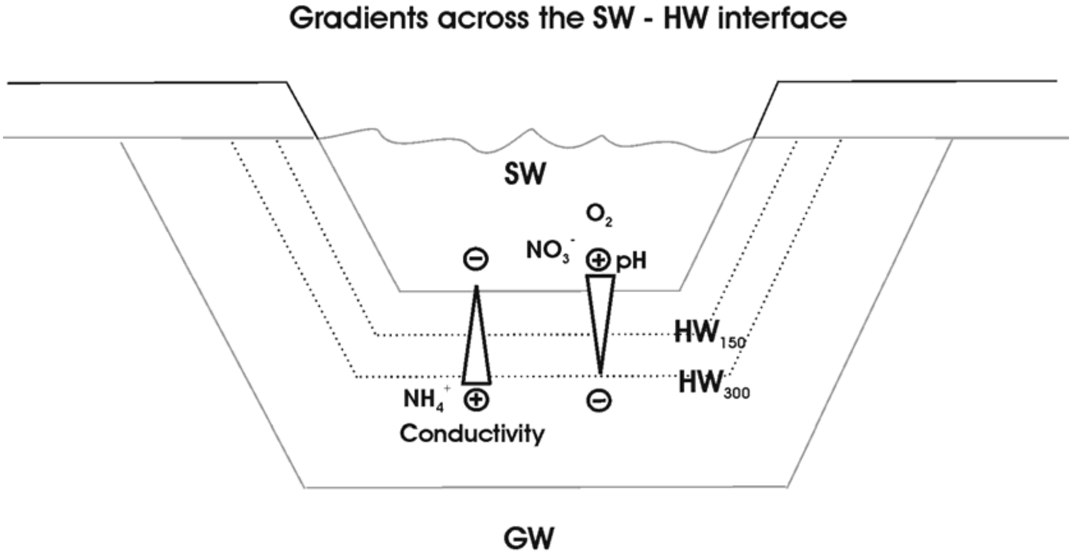

Figure 8. Some general trends in the water chemistry from the surface water (SW) to the shallow (HW_{150}) and finally deep hyporheic water (HW_{300}). Arrows with "+" and "-" signs show the direction of the gradient. GW is groundwater.

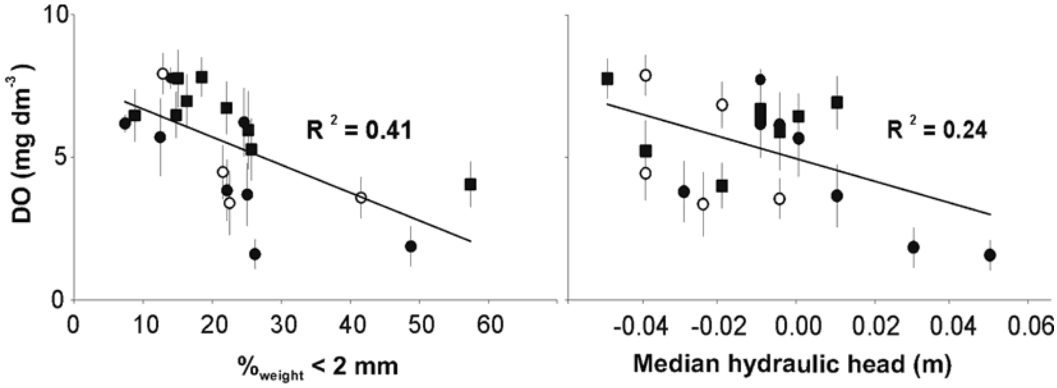

Figure 9. The mean annual levels (+/- S.E.) of: A) oxygen content at 150 mm in the hyporheic zone (HW_{150}) vs. substrate composition (% weight < 2mm particle size), B) oxygen content at HW_{150} vs. median hydraulic head (difference within pairs in m). Samples are from the unregulated River Tobyälven (black boxes, N = 9 $month^{-1}$), the regulated River Järperudsälven (black circles, N = 8 $month^{-1}$) and the regulated River Mangälven (white circles, N = 4 $month^{-1}$) from October 2001 to October 2002, Sweden.

The incubation time for brown trout eggs in the three rivers was set to December-May, since the mean hatching date for brown trout in the River Göta älv is 18 April and the mean date for time of yolk-sac resorption is 13

May (Clevestam, 1993). The most favourable conditions for incubation were found in the unregulated River Tobyälven, where the mean concentration of hyporheic oxygen from all piezometers at 150 mm depth, both with and without redds, generally increased over time and the overall mean was 8.6 ± 0.5 mg dm^{-3} (Fig. 10), with only one measurement (2.5%) below the minimum oxygen requirement level (MOR) for incubation (Crisp, 1996). The seasonal trend in the River Mangälven resembled that of the River Tobyälven, but the levels were less variable, with an overall mean of 7.1 ± 0.7 mg dm^{-3}. Nevertheless, the oxygen levels in the two redds in the River Mangälven (9.3 ± 1.0 mg dm^{-3}) were similar to or higher than levels in the River Tobyälven. In total 15% of all measurements in the River Mangälven were below the MOR.

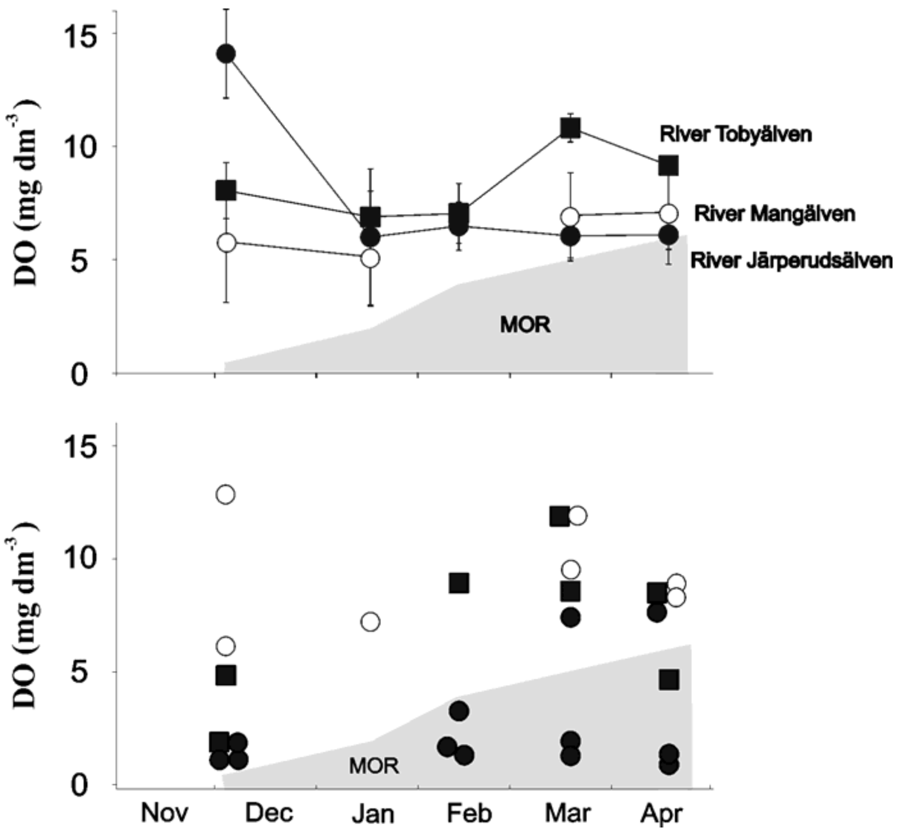

Figure 10. A) The monthly mean oxygen levels (± S.E.) in the hyporheic water at 150 mm depth in the river bed (excluding redds), B) the oxygen content in single redd piezometers at 150 mm. Samples were taken during the incubation period from November 2001 to April 2002 in the unregulated River Tobyälven (black boxes) and the flow regulated rivers, the River Järperudsälven (black circles) and the River Mangälven (white circles). The shaded area represents the minimum oxygen requirements (MOR) of the incubated salmonid offspring at different life-stages, modified from Crisp (1996).

In the River Järperudsälven, the oxygen levels decreased steadily throughout winter, and the mean oxygen level during the incubation period was 6.3 ± 0.7 mg dm^{-3}. There were six piezometers with low oxygen content (of 11 in total), and these included the three redds. All these piezometers were located at transects J5 and J6, which were associated with high contents of fines (< 2 mm). During the incubation period, 37% of the samples fell below the MOR.

With regards to $[NH_4^+]/[NO_3^-]$ in shallow hyporheic water, the highest $[NH_4^+]/[NO_3^-]$ recorded was 459/192 μg dm^{-3} for the River Tobyälven, 1035/252 μg dm^{-3} for the River Järperudsälven, and 191/205 μg dm^{-3} for the River Mangälven. The lowest pH recorded was 6.03 for the River Tobyälven (mean 6.35), 5.81 for the River Järperudsälven (mean 6.27), and 6.02 for the River Mangälven (mean 6.50).

Reproductive success (Paper I)

The densities of 0+ brown trout at the sites upstream of the new fishways in Finsjö showed a marked increase in 2002 and 2005, whereas no such increase was observed downstream of Finsjö (Fig. 11). In 2003 and 2004, when summer

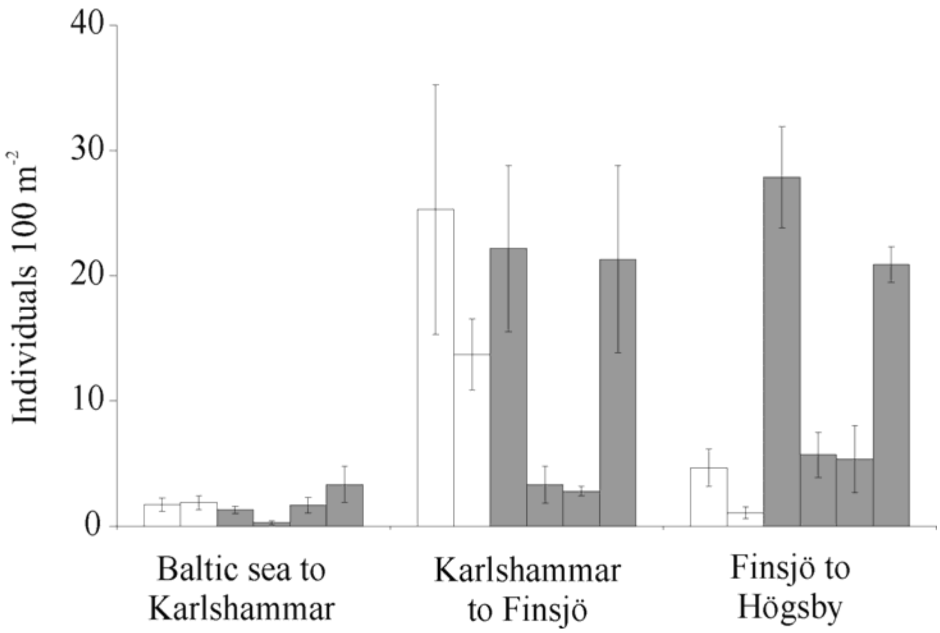

Figure 11. The mean densities (± S.E.) of 0+ brown trout found at sites along three stretches of the River Emån. Data are shown for the pre-fishway years (2000-2001, white bars) and the years after the fishways at Finsjö were built (2002-2005, grey bars). The location of the river stretches can be seen in Fig. 4.

spates occurred, the densities of 0+ trout were low at all sites in the River Emån. The highest densities of 0+ Atlantic salmon were found downstream of the lowermost power plant in the River Emån (> 70 salmon 0+ 100 m^{-2}), with lower densities between Karlshammar and Finsjö (2.1 ± 3.9 S.D.) and very few individuals upstream of Finsjö. Additional species frequently caught during these electrofishing surveys were signal crayfish (*Pacifastacus leniusculus*) and bleak (*Alburnus alburnus* L.).

Hydropower and downstream migration

Downstream migration of kelts and return spawners (Paper II)

Approximately 57% of the kelts were observed moving downstream in the fall (N = 15, 25%) or in the spring the year after spawning (N = 45, 75%). The downstream movement occurred at similar water temperatures in fall and spring, about 10.0 °C, but the mean discharge was lower in the fall than in the spring. The median date for downstream spring migration was 29 April, ranging from 1 April to 26 May. In spring 2002-2004 all migration took place via the fishways, whereas in spring 2005 the kelts used the fishways (30%) and the trash gates at the power plant intakes (70%).

The number of return spawners at Karlshammar constituted 20 % of the total catch in 2003-2004 and the recaptured group was dominated by females, 81% in 2003 and 58% in 2004. This figure contrasts with an even sex ratio (46% females) among all trout captured at Karlshammar in 2001-2004 (N_{tot}=659). The return spawners had gained 0.78 ± 0.07 kg $year^{-1}$ (S.E.) and 52 ± 4 mm $year^{-1}$, equivalent to 25 ± 4% annual increase in body mass and an 8 ± 1% increase in length. Most of the recaptured individuals returned one time (caught twice, N=52), but some individuals were caught for a third time (N=10) and one female was caught four years in a row. The majority of return spawners were recaptured during two consecutive years. Only four individuals stayed one winter at sea and one individual two winters at sea before returning. Return spawners came earlier to Karlshammar the second time, the median date being day 263 the first time (20 September) and day 254 the second time (11 September). The individuals that returned three times (N=10) arrived earlier to Karlshammar for each time, the first time at median day 269 (26 September), the second time at day 256 (13 September) and the third time at day 238 (26 August).

Downstream migration of smolt (Paper III)

The smolt study was performed during April and May 2004 (Paper III) and 2005 (unpublished data). In total 42 smolts in 2004 and 40 smolts in 2005 were caught, tagged and released (Fig. 7, shows site of "Smolt release"). When approaching the upper power plant the smolts were delayed for up to 10 days, with individuals passing through the power plant (Fig. 7, G; median delay 21.4 h) being more delayed than individuals swimming into the former channel (Fig 7, H & I; median delay 1.1 h). The turbine induced mortality in the four Francis runners at upper Finsjö was 40% in both 2004 and 2005. Predation occurred during the passage of upper Finsjö, corresponding to a 8-10% loss in 2004 and 2005.

The individuals that proceeded towards lower Finsjö swam rapidly through the reservoir between the two power plants (median 51 min). In 2004, most individuals swam directly to the power intake and stayed for less than one day before going through the turbines (88%, Fig. 7, E). The turbine induced mortality in the single Kaplan runner at lower Finsjö was 10-13%.

Attempts in 2005 to guide fish away from the turbine intake by using trash diverters leading to adjacent trash gates resulted in 44% guidance efficiency at the upper power plant and 16% at the lower power plant. The total passage success for smolts at the two power plants in Finsjö 2004-2005 was 51%. The loss due to predators was 12%, to the turbines 16% and the remaining 18% ceased migrating, either residing in a lotic habitat or were accidentally killed in traps (Fig. 12). The greatest difference between years was a larger number of individuals stopped in 2004 than 2005 and a larger number of individuals were eaten by predators in 2005 than in 2004. Of the smolts that successfully passed both power plants at Finsjö in 2005, 17% disappeared, 28% ceased migrating, 22% were eaten by predators and 33% reached the sea. When applied to the total number of smolts tagged in 2005, the survival rate from release to the sea was 15%.

Figure 12. The final fate of smolts approaching the two power plants at Finsjö in the River Emån, 2004 (N=39) and 2005 (N=40). The smolts either stopped (Stop), got killed by a predator (Predation), died in the turbines (Turbine) or successfully passed both power plants (OK).

Discussion

This thesis gives an insight to the multitude of aspects that need to be addressed when trying to re-establish longitudinal and vertical connectivity in regulated rivers. To accomplish a functional lotic system I argue that there is a need of a holistic approach. For example, it is not enough just to focus on one component or one species, such as restoring the physical habitat for juvenile brown trout, since restoration is complex and there are many other aspects that need to be taken into account (Bond and Lake, 2003).

Hydropower and upstream migration

The data on upstream migrating spawners in the River Emån 2001-2004 illustrates the impact of interannual variation in the timing and magnitude of discharge and temperature for successful spawning migration. The importance of high and increasing discharge for migration was illustrated by the higher % of individuals migrating from Karlshammar to Finsjö during the wet years 2001 and 2004 than during the dry years 2002 and 2003. A similar effect of low flow on distance moved was also observed by Jensen and Aass (1995). The migration speed of brown trout from Karlshammar to Finsjö (median 1.5 km day^{-1}) is consistent with data from other studies, e.g. landlocked brown trout in the River Klarälven with top speeds of about 30 km day^{-1} (Degerman *et al.*, 2001), anadromous brown trout in the nearby River Mörrumsån with <1 km day^{-1} (Westerberg, 1977), and Atlantic salmon in the River Umeälven with 0.6 km day^{-1} (Rivinoja *et al.*, 2001), but not for anadromous brown trout in the River Vistula with speeds as high as 65–95 km day^{-1} (Bartel, 1988).

The number of spawners that pass Karlshammar (about 50 kg females ha^{-1} spawning ground) is considerably lower than the proposed optimum of 300 kg ha^{-1} (Degerman *et al.*, 2001). If the tendency to stray is density dependent, then the low number of spawners between Karlshammar and Finsjö should result in few spawners reaching Finsjö (Heggberget *et al.*, 1986; Heggberget *et al.*, 1988; Elliott, 1994). Furthermore, density dependence is probably causing the distribution of spawners upstream of Finsjö, with densities decreasing with distance upstream, in addition to the few good spawning- and rearing habitats between Finsjö and Högsby.

Although the majority of migrants stopped downstream of Finsjö to spawn, all individuals that made it to Finsjö did not manage to pass both fishways. The location of fishways differ in such a way that fish have to be attracted away from the former channel at the lower power plant and towards the former channel at the upper power plant. Thus, optimal fishway function at the Finsjö power plants requires a total discharge in the river that is low enough to allow most water to pass through the power plant at lower Finsjö and at the same time high enough to allow enough spill water to be released into the former channel at upper Finsjö. The discharge during the main spawning migration in 2001-2004 favoured fishway function at the lower plant but not at the upper plant. In 2004 when the total discharge in the former channel at lower Finsjö was kept at residual flow levels throughout the spawning migration period, no fish ascended the former channel and the median delay of 2.1 h at the confluence was more or less negligible in comparison with other studies (Jensen and Aass, 1995; Gowans *et al.*, 1999; Gowans *et al.*, 2003; Thorstad *et al.*, 2003; Thorstad *et al.*, 2005). At the upper power plant, however, the delays were substantial as fish preferred the tail-race to the former channel, spending up to 30 days between the plants before ascending the former channel or returning downstream. Such movements between the waterfall and the tail-race at the upper power plant have previously been described as route-seeking behaviour (Karppinen *et al.*, 2002).

The effects of delay can be diffuse, but may include arriving at spawning grounds too late, missing the window of physiological readiness, reduced spawning success and elevated risks of pre- and postspawning mortality (Shikhshabekov, 1971; Baras *et al.*, 1994; Jonsson and Jonsson, 1997; Cowx and Welcomme, 1998; Chanseau *et al.*, 1999; Geist *et al.*, 2000). Studies show that increased energy expenditures as small as 10% can have a detrimental effect on postspawner survival (Jonsson and Jonsson, 1997), which emphasises the need to incorporate the effects of delay into evaluations of fishway function.

The passage efficiency of the fishways at Finsjö was high for several fish species, e.g. anadromous brown trout (89–100%), chub (86%), perch (100%), tench (100%) and lower for others such as roach (50%), which were small in size compared to the other species, and burbot (60%). The overall efficiency of the fishways at Finsjö is higher than that reported for nature-like fishways used by pikeperch (*Stizostedion lucioperca* L.), Danube salmon (*Hucho hucho* L.) and other brown trout populations. The low passage efficiency of other fishways was attributed to their limited dimensions and to low flow (Jungwirth, 1996; Schmutz *et al.*, 1998; Aarestrup *et al.*, 2003). The high passage efficiency we observed indicates that the fishways at Finsjö are not particularly physically demanding for most fish species ascending them, especially when considering that fish successfully ascended the fishways at water temperatures down to <2 °C. Many fishways are physically demanding, and fish, being poikilothermic, generally do not attempt to pass fishways at temperatures below 5–6 °C (Linlokken, 1993; Jensen and Aass, 1995; Laine *et al.*, 1998; Gowans *et al.*, 1999; Thorstad *et al.*, 2003). Furthermore, the mean rate of ascent for brown trout in the Finsjö fishways (c. 160 m h^{-1}) is higher than reported from other studies (Gowans *et al.*, 1999; Aarestrup *et al.*, 2003).

Hydropower and reproduction

Fluctuations of water chemistry in surface waters are generally being mirrored in hyporheic waters, but with an attenuation with depth (Brunke and Gonser, 1997). The observed patterns of hyporheic water chemistry at different depths in the hyporheic zone reflect differential mixing of surface and hyporheic water as well as different retention times of the hyporheic water (Claret *et al.*, 1998; Fraser and Williams, 1998; Fernald *et al.*, 2000; Franken *et al.*, 2001; Malcolm *et* *al.*, 2003a). The decreasing DO content along a hyporheic flow path is mainly caused by community respiration (Brunke and Gonser, 1997; Boulton *et al.*, 1998). The change in DO availability affects many other processes, such as the nitrogen cycle, and along a gradient of decreasing DO there is a shift from aerobic nitrification towards anaerobic ammonification and denitrification (Duff and Triska, 2000; Hill, 2000; Franken *et al.*, 2001).

The observed decrease in pH with depth may be an effect of increased concentration of CO_2 from respiration by the microbial community, which has been previously reported (Brunke and Gonser, 1997; Franken *et al.*, 2001). However, the decrease in pH is generally restricted to the uppermost hyporheic zone where the bulk of microbial activity takes place, and below this zone pH increases again due to increasing impact of the normally high alkaline hyporheic water with long residence time (Malcolm *et al.*, 2003a). The reason we could not find an increase in pH in the deep hyporheic water may be because the microbially active zone extends deeper than the 300 mm we sampled or because shallow groundwater is acidified due to low buffering capacity. We found that pH decreases with distance from the channel in the River Järperudsälven, and since acidification of shallow groundwater is a recognised problem in central western Sweden (Lundstrom *et al.*, 1998), acidification could explain the observed decrease in pH with depth. One important factor behind acidification in this area is the naturally low buffer capacity, which in itself gives a fairly low pH.

The exchange flows between surface water and hyporheic water appeared to be very limited in the River Järperudsälven and moderate in the River Mangälven. The situation in these two rivers contrast with that in the River Tobyälven, where both discharge and surface water chemistry correlated to hyporheic water chemistry, particularly in the shallow piezometers but even in the deep ones. My interpretation of these results is that the vertical connectivity in the two regulated rivers is poor relative to the River Tobyälven, which could be due to more extensive substrate colmation in the regulated rivers. Previous studies have shown that regulated rivers typically have lack of spates that flush out fine sediments from the substrate, which leads to substrate colmation (Tockner *et al.*, 1998; Ward and Wiens, 2001). The combined effect of relatively large peaks in discharge and a more permeable surface water/hyporheic water -interface in the River Tobyälven will lead to more surface water entering the hyporheic zone, both vertically and laterally.

Previous studies suggest that female salmonids choose redd sites based on substrate composition, water depth and water velocity, but that they are also able to sense and avoid interstitial water with low DO (Hansen, 1975; Witzel and MacCrimmon, 1983; Geist, 2000). The redds instrumented in this study, however, were not limited to sites with high DO. In the regulated River Järperudsälven for example, the redds had low DO conditions but still > MOR at spawning, but < MOR during most of the incubation period. The DO in the transect piezometers in the River Järperudsälven decreased during the incubation period and eventually some of them ended up being < MOR. In contrast the DO in shallow hyporheic water was high and quite stable in the River Tobyälven and the River Mangälven and remained at levels that would promote high embryo survival (Crisp, 1996; Malcolm *et al.*, 2003b).

One reason for the low DO levels in redds in the River Järperudsälven was the high content of fines in the substrate. Brown trout have been observed to spawn at sites with large impact of fine sediment in spite of the associated poor water quality (Olofsson *et al.*, 1998), which could be an effect of size restricting the females to spawn in sites with small particle size (Shirvell and Dungey, 1983; Rubin and Glimsater, 1996). Other possible explanations could be that the females could not sense the poor DO conditions (Peterson and Quinn, 1996) or difficulties in identifying redds in sites with coarse substrate.

None of the other water chemistry parameters measured in the piezometers were expected to have any serious effect on embryo development. The critical limit for pH effects on incubated embryos has been set to < 5.5 (Hesthagen *et al.*, 2001; Tammi *et al.*, 2003), which is well below the lowest pH recorded in any of the three rivers in the present study. Both the [NH_4^+] and the [NO_3^-] were highly variable, but the concentrations should not have any negative effects on embryo survival (Malcolm *et al.*, 2003b).

Other organisms that depend on good hyporheic quality for survival are the threatened freshwater pearl mussel (*Margaritifera margaritifera* L.) and the thick shelled river mussel (*Unio crassus* P.), both threatened. Hyporheic water quality is relevant for these juvenile life-stages of these mussels as they bury 10-35 cm into the substrate and remian there for several years (Buddensiek, 1995).

Hyporheic conditions in the River Tobyälven and the River Mangälven were suitable for juvenile mussels, but not the in the River Järperudsälven, where DO was lower than the estimated critical limit of 2.5 mg dm^{-3} at several occasions (Buddensiek *et al.*, 1993).

In the River Emån, about 130 adults, of which 42% were females, moved upstream of Finsjö during 2001-2004, which corresponded to increased densities of 0+ brown trout in 2002 and 2005. In 2003 and 2004, when summer spates occurred, the densities of 0+ trout were low at all sites in the river indicating that the value of existing nursery habitats for trout are dependent on relatively low summer discharge, probably enhanced by low habitat complexity. The negative impact of high discharge on density of early life-stages of trout has been previously found for swim-up fry (Cattaneo *et al.*, 2002) and 0+ trout (Ottaway and Forrest, 1983; McRae and Diana, 2005). Nevertheless, the densities of 0+ brown trout upstream of Finsjö in 2002-2005 were about 50% higher than the densities at sites between Karlshammar and Finsjö and more than ten times as high as the densities downstream of the first power plant in the River Emån. In a similar study on anadromous brown trout recolonising an area upstream of a new fishway in a Lithuanian river, the recolonised habitat upstream of the new fishway had about twice the densities of the habitat downstream of the fishway (Ziliukas and Ziliukiene, 2002).

Hydropower and downstream migration

My results on the timing of spring kelt descent in relation to water temperature resemble those reported by other studies from similar latitudes (Jonsson and Jonsson, 2002). In my study, most postspawners descended the river in spring (75%) rather than fall, which contrasts with the results of Jonsson and Jonsson (2002) for a small Norwegian river (2/3 at fall and 1/3 in spring). One explanation for this may be that the availability of winter habitat increases with river size (Degerman *et al.*, 2001). Given the limited dimensions of the trash gate leading to the smolt trap and the fact that it was submerged (0.2×3.5 m at 0.3 m depth), makes the observed kelt preference for this gate instead of the fishway surprising. The fish appear to move with the main current to the power plant and then try to find an outlet downstream. The fishway may serve as a last way out when no other options are available. In spite of the observed downstream passage problems and delays, the increasing proportion of tagged repeat spawners and their growth indicate that many fish do get out to sea. The high proportion of females among repeat spawners has been previously documented for Atlantic salmon and may relate to a high energy expenditure during spawning by males, which consequently suffer high postspawning mortality (Niemelä *et al.*, 2000). Jonsson and Jonsson (1997) however, attributed the difference in survival to males getting more injuries during spawning. Similar information on anadromous brown trout is scarce, but in a population of potamodromous brown trout, the postspawning mortality among females was higher than for males, which was related to the higher amount of energy expended at spawning (Berg *et al.*, 1998).

Although relatively few smolts were caught, our study confirmed that smolts are now being produced upstream of Finsjö. The results show that > 50% of the smolts that approach the power plants successfully pass both of them, and that survival was lower at the upper power plant than at the lower power plant. In general, survival of smolts passing through Francis turbines is low (Montén, 1985). Matousek *et. al* (1994) reported survival rates of 71 to 100% and 61 to 89% for juvenile and adult rainbow trout (*Oncorhynchus mykiss* W.), respectively, as they passed through Francis turbines at low head dams. Our survival rate of 60% at the upper power plant is consistent with this result. One might have expected survival to be lower due to the large number of blades per runner, a common feature of all Francis runners, which increases the probability of fish being hit when passing through the turbine. Furthermore, the four Francis runners are small and operate at high velocities, both features previously found to have negative impacts on survival (Montén, 1985; Matousek *et al.*, 1994). Still, the low head at upper Finsjö probably limited mortality, as survival at high head power plants is generally quite low e.g. 27% survival at a power plant with two Francis runners and a 99 m head (Hvidsten and Johnsen, 1997).

In contrast to Francis runners, Kaplan runners have few blades and thus a fish has a low probability of being hit. This is supported by our results as survival was 87-90% at lower Finsjö. In addition, the large size of the runner and the relatively low head at lower Finsjö could be factors further contributing to the high survival (Hadderingh and Bakker, 1998; Skalski *et al.*, 2002). Nevertheless, a lower survival rate might have been expected, given the high revolution rate of the runner (333 rpm). Survival rates as high as ours have previously been found for Kaplan runners with 75-90 rpm (Mathur *et al.*, 1996; Skalski *et al.*, 2002).

Predation is often a major cause of mortality for smolts, especially when passing through reservoirs (Jepsen *et al.*, 2000; Olsson *et al.*, 2001), but only 12 % of the tagged smolts in our study were likely to have been killed by predators at the power plants. When the relatively short study distance is taken into account, however, the predation rate is approximately 6.7 % km^{-1}, which is high relative to the predation rate from lower Finsjö to the Baltic (0.8 % km^{-1}). Moreover, this can be compared to the estimated predation rate of 2.2 % km^{-1} previously reported for salmon in the lowermost 23 km of the River Emån (Larsson, 1985). Similar mortality patterns attributed to predation were found in the Danish River Gudenå where smolt loss was 7.5 % km^{-1} in a large reservoir and 2.1 % km^{-1} in a downstream lotic section (Jepsen *et al.*, 1998; Koed *et al.*, 2002) Furthermore, the observed delays at the power plants prolonged the periods of predator exposure (Jepsen *et al.*, 2000).

In spring 2004-2005, excess water was released through several spill gates, especially at upper Finsjö, providing the smolts with alternative routes that allowed them to avoid the turbines. A lower survival would be expected in dry years when a larger proportion of the discharge is led through the turbines (Hvidsten and Johnsen, 1997). One possible measure to increase smolt passage success at Finsjö would be to simultaneously decrease discharge through the turbines and increase discharge in the spillways during the migration period, thereby encouraging passage through the spillways (Coutant and Whitney, 2000).

Conclusions and implications for management

The nature-like fishways at Finsjö have re-established longitudinal connectivity for many fish species in the River Emån. In the future this will help to maintain both biodiversity and gene flow between conspecific populations (Prignon *et al.*, 1998; Knaepkens *et al.*, 2005), which will be of great conservational importance for all species in the River Emån in general and the threatened species in particular (Gärdenfors *et al.*, 2005). Future research on restoration and conservation has to be broadened into incorporating all species and life-stages and not only those that are economically important.

The fishways at Finsjö were most efficient in passing fish when the total flow was intermediate (about 20-28 $m^3 s^{-1}$), favouring attraction towards both fishways. The need for specific flow condition limits the usefulness of the fishways as flow conditions are highly variable within and between years. This means that special attention needs to be paid to when and where spill water is released. A common recommendation when constructing nature-like fishways is to oversize them. If this is done, then large amounts of spill water can be released into the fishways when intake capacity is exceeded, instead of releasing spill water into channels that attract fish away from fishways (Jungwirth, 1996).

Today anadromous fish species are able to swim some 54 km upstream of the Baltic Sea. If longitudinal connectivity is to be established along the entire course of the River Emån, then the total efficiencies of the fishways (i.e. the combined effect of attraction and passage efficiencies) have to be increased. If this is done, the fish will be able to swim 153 km upstream the River Emån by passing nine fishways, compared to today's four fishways. The overall efficiency of both fishways at Finsjö combined indicates that recolonisation of the River Emån upstream of Finsjö will likely take many years (Bryant *et al.*, 1999), especially when taking the large variation between years into account. That fewer females than males ascended the fishways at Finsjö might retard recolonisation, as observed for Atlantic salmon colonising an area made available by a new fishway (Saltveit, 1993). The rate at which recolonisation of the areas upstream of Finsjö occurs could probably be accelerated by transplanting spawners upstream, since my study and other studies indicate that relocated salmonids show a low degree of backtracking (Heggberget *et al.*, 1988). Moving fish upstream should only be a temporary way of helping recolonisation, however, and cannot solve the problem of low cumulative efficiencies of a series of fishways (Chanseau *et al.*, 1999; Gowans *et al.*, 2003). If the mean total efficiency for the Finsjö fishways from 2001-2004 (78% per fishway) is assumed for all nine fishways, the number of spawning migrants successfully passing all nine fishways in the River Emån would be approximately 60 individuals or 11%, which is an overestimate as it assumes that all individuals would try to get as far upstream as possible and does not include the tendency of salmonids to return to their natal sites for spawning (Heggberget *et al.*, 1986; Heggberget *et al.*, 1988; Degerman *et al.*, 2001). On the other hand, the total number of spawners in the River Emån would be expected to increase with time, as the areas upstream of Finsjö are recolonised, and thereby the total area of rearing habitat in the river is increased. The recolonisation rate is expected to be further accelerated when individuals born upstream of Finsjö, and spawners with previous experience from the area, return to spawn.

The issue of increasing the total number of spawners should also be addressed by trying to let more kelts and smolts pass safely downstream past the obstacles. Return spawners are a valuable resource since they are often dominated by large females that are generally highly fecund and successful spawners (Wootton, 1998; Jonsson and Jonsson, 1999; Niemelä *et al.*, 2000). For their reproduction to be successful, however, smolts will have to be allowed to reach the sea and recruit to the spawning population. As the trout population in the River Emån relies on natural spawning alone, measures that facilitate iteroparity and smolt survival are of crucial importance for the future success of the population (Boggs *et al.*, 2004; Evans *et al.*, 2004). Therefore, the most urgent measure is to improve the existing guiding- and bypass systems for downstream moving fish, so that they may function for as many species and life-stages as possible (Scruton *et al.*, 2002, 2003).

It will probably take many years before longitudinal connectivity is fully re-established in the River Emån. This is because it will take time before the carrying capacity of the rearing sites upstream of Finsjö is reached, since the number of spawners is low and increasing. The re-establishment of longitudinal connectivity must be seen as the first necessary step towards restoring population dynamics in the River Emån. For the re-established longitudinal connectivity to create sustainable fish populations, however, I argue that additional measures such as rehabilitation of degraded spawning and rearing habitats will have to be performed (Bond and Lake, 2003). If habitat heterogeneity is increased in the River Emån, this would probably speed up the recolonisation process (Bryant *et al.*, 1999). When rehabilitating the spawning and rearing conditions in the River Emån, issues of vertical connectivity should also be addressed.

The vertical exchange between surface water and hyporheic water was most extensive in the River Tobyälven, followed by the River Mangälven and lastly by the River Järperudsälven. This is interpreted as a decrease in vertical connectivity from the River Tobyälven to the River Järperudsälven. An exchange between the surface water and hyporheic water in the River Järperudsälven is probably still occurring, but at a lower rate than in the other two rivers. One effect of this reduced vertical connectivity is the poor environment for trout embryos (Malcolm *et al.*, 2003b).

To improve hyporheic conditions in the River Järperudsälven, and other rivers with similar flow regulation, minimum flow requirements probably need to be implemented. Additional management practises could include increasing the frequency and magnitude of floods to restore the natural disturbance regime (Ward and Wiens, 2001). Even measures such as narrowing the river channel and removing levées may be needed to increase the effect of floods in flushing out fine sediment from the riverbed and restoring natural channel forming processes (Tockner *et al.*, 1998).

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