RIVER RESEARCH AND APPLICATIONS

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CONNECTIVITY IS A TWO-WAY STREET—THE NEED FOR A HOLISTIC APPROACH TO FISH PASSAGE PROBLEMS IN REGULATED RIVERS

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ABSTRACT

We evaluated the effects of a rehabilitation project, whose goal was to re-establish longitudinal connectivity for anadromous trout in the regulated river Emån. We used a holistic approach, by tagging and following both upstream-migrating spawners ($N = 348$) and downstream-migrating smolts ($N = 80$) and kelts as they passed two hydroelectric plants (HEP 2-3) with nature-like fishways.

When migrating upstream, 84–88% of the spawners stopped, primarily at spawning grounds, before reaching HEP2. The proportion of stoppers was lower (56%) for fish that had been to the fishways in previous years, indicating that the recolonization rate is likely to increase over time. Of the spawners that approached the fishway at HEP2, 77% rapidly located the fishway situated next to the tail-race, resulting in an attraction efficiency of 81% and a passage efficiency of 95%. The time required to locate the fishway inside the former channel at HEP3 was substantial, but the attraction efficiency (89%) and passage efficiency (97%) were nevertheless high.

The kelts swam downstream mainly in spring, using spill gates and the fishways, to swim past HEP2 and 3 and continue downstream to the Baltic Sea. Iteroparity was confirmed by the fact that 20% of the spawners were tagged in previous years. Smolt loss was about 30% for both HEPs, with a higher turbine-induced loss 30% for fish passing through Francis runners than a Kaplan runner. Fifteen per cent of the tagged smolt reached the sea and none of these fish had swum through the Francis runners.

It will probably take many years before longitudinal connectivity is fully re-established in the river Emån, due to substantial losses of both upstream-migrating spawners (35% loss) and downstream-migrating smolts (50%) and kelts. In addition, smolt production in areas upstream of HEP3 is far below carrying capacity. Thus, additional measures that not only facilitate movement of upstream spawners, but also reduce mortality and injuries of downstream migrants are urgently needed to create a self-sustaining fish population.

KEY WORDS: regulated river; holism; connectivity; brown trout; nature-like fishway; attraction efficiency; telemetry

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INTRODUCTION

Ecological connectivity, i.e. the functional 'exchange pathways of matter, energy and organisms' (Ward and Stanford, 1995), is an important feature of hydrologically intact rivers. Connectivity is active along four dimensions: longitudinal, vertical, lateral and temporal (Ward, 1989; Brunke and Gonser, 1997; Tockner *et al*., 1998). For fish, longitudinal connectivity is probably the most well-known dimension, involving upstream and downstream migration so that fish can move between feeding, spawning and winter habitats (Lucas and Baras, 2001). Flow regulation and building of dams and weirs interrupt connectivity (Ward and Stanford, 1995; Calles *et al*., 2007), which has lead to declines in many fish populations, accounting for more than 50% of the threatened fish species in Europe (Northcote, 1998). The environmental issues of hydropower are receiving more attention, however, as general environmental awareness is increasing and as the drawbacks of hydropower are being identified (Bratrich *et al*., 2004).

Today many forms of remedial measures are implemented in regulated rivers to ameliorate loss of ecological connectivity. For example fishways have been built at hydroelectric plants (HEPs) and other obstacles to re-establish longitudinal connectivity (Saltveit, 1993; Calles and Greenberg, 2005). Fishways are rarely functional for

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*Correspondence to: Olle Calles, Department of Biology, Karlstad University, S-651 88 Karlstad, Sweden. E-mail: olle.calles@gmail.com entire fish assemblages, primarily because: (1) fish cannot find their way to the fishway entrance (poor attraction efficiency, Rivinoja *et al*., 2001) or (2) the hydraulic conditions of the fishway exceed the fish's swimming ability (poor passage efficiency, Aarestrup *et al*., 2003). Even for fishways with high efficiencies, substantial delays or quiescent periods are common at river confluences and at power plant outlets (Chanseau *et al*., 1999; Gowans *et al*., 1999; Gowans *et al*., 2003; Thorstad *et al*., 2003). Moreover, in many cases the fish must pass several fishways before reaching spawning areas, and thus the efficiency of each fishway must be high and any delays must be limited, if the fishways are to be successful in re-establishing connectivity (Gowans *et al*., 2003). In most cases, however, the function of a fishway is never evaluated (Calles and Greenberg, 2005).

Many attempts at re-establishing longitudinal connectivity only address the issue of upstream passage. Large sums of money are being spent on trying to solve the upstream passage problems at hydroelectric facilities, disregarding the problems experienced by both juvenile and adult anadromous fish on their way to the sea (Arnekleiv *et al*., 2007). Smolt can be delayed, injured or even killed when attempting to pass hydroelectric facilities via turbines, bypass devices, spill gates, trash gates or trash racks (Montén, 1985; Matousek *et al*., 1994; Amiro and Jansen, 2000). In addition, kelts, after spawning return to the sea to recondition themselves before the next spawning event (Klemetsen *et al*., 2003). Unfortunately, little is known about kelts (Bardonnet and Bagliniere, 2000), and the problems they face as they pass power plants (Ferguson *et al*., 2002; Östergren and Rivinoja, 2008). Recent measures, however, have been directed at encouraging repeat spawning (Scruton *et al*., 2003; Wertheimer and Evans, 2005; Scruton *et al*., 2007).

The present study evaluates the success of a rehabilitation project with the goal of re-establishing longitudinal connectivity for anadromous brown trout (*Salmo trutta* L.) in the regulated river Emån, southeastern Sweden. In the river Emån sea trout migrate to the Baltic Sea, where they spend 1–4 years before returning to the river to spawn. When at sea, trout remain close to their home river, feeding in the coastal area. The Emån sea trout population is one of few wild and self-sustaining populations, supporting both small-scale commercial and important recreational fisheries. The Emån sea trout population is one of the largest in southeastern Sweden, and one of the few that has seen limited effects of hatchery stocking and as such it is of high conservation value.

In this study we use a holistic approach, studying the different life-stages of anadromous trout as they pass two hydroelectric facilities on their way upstream to spawning sites, using two recently constructed nature-like fishways, and downstream to the sea. Areas where many individuals are lost in their attempts to proceed upstream and downstream past the obstacles are identified and the underlying causes studied and analysed. Furthermore, we use the results from this evaluation to predict the potential annual production of trout molts in the newly-made available area upstream of the fishways and to determine what additional measures that are needed to maximize the rehabilitative effects of the new fishways.

MATERIAL AND METHODS

Study area

The study was conducted from May 2003 to June 2005 in the river Emån (57°07′59″N; 16°30′00″E), a river that has been regulated for approximately 100 years and has a long history of supporting a recreational and commercial fishery (Trybom, 1890; Klippinge, 1999). At present, the first definitive obstacle for anadromous species in the river Emån is located at Högsby, about 54 km upstream of the Baltic Sea. For fish to get that far, however, they first have to ascend vertical slot fishways at the hydropower plants in Emsfors (HEP 0, no turbines in operation) and Karlshammar (HEP 1), followed by the two nature-like fishways at Finsjö (HEPs 2–3), which were constructed in 2000 (Figure 1A). Since 2006, the gates at the dam at Emsfors are always kept open, allowing fish to pass freely.

HEP 3 is separated from HEP 2 by an 800 m long stretch of slow-flowing, deep water. At HEP 2, the entrance of the fishway is located at the tail-race of the power plant (Figure 1C, no. 2). Water from the power plant and the former channel conjoin approximately 350 m downstream of the power plant (Figure 1C, no. 1). At HEP 3 the entrance to the fishway is located in the former channel, approximately 250 m upstream of the tail-race, and fish have to pass a small waterfall (Figure 1B, no. 3) to reach the fishway (Figure 1B, no. 4). When large volumes of water are released into the adjacent tail-race or spill gate, the lowermost 30–40 m of both fishways are flooded. The relative discharge along the different migration routes past the power plants varied with power plant operation and

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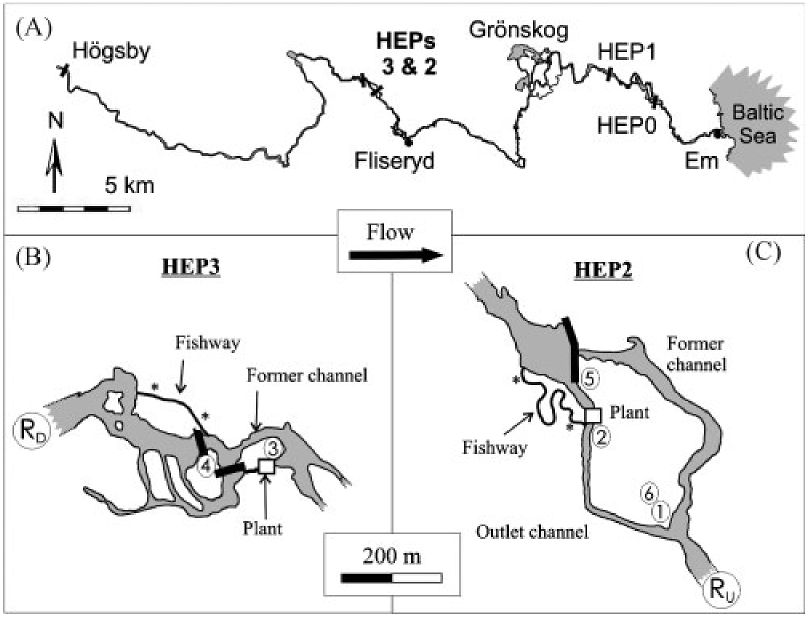

Figure 1. (A) Map showing the lower 54 km of the river Emån with fishways at the former hydroelectric plant (HEP) in Emsfors (HEP 0, 5.3 km from sea), and the operating HEPs at Karlshammar (HEP 1, 8.8 km), and lower (HEP 2, 28.8 km) and upper Finsjö (HEP 3, 29.6 km). (B) HEP 3 and (C) HEP 2, both with fishways with two PIT-antennae (∗) and the fixed telemetry stations as they were placed at fall (no. 1–3, i.e. automatic telemetry stations detecting spawners migrating upstream) and in spring (no. 4–6, automatic telemetry stations detecting smolt and kelt migrating downstream)

was expected to influence passage success, assuming that the highest discharge would attract more fish. When turbine discharge was lower than the spill discharge, most water was released into the former channels, attracting upstream migrants away from the fishway at HEP 2 and towards the fishway at HEP 3, and downstream migrants would have been expected to move into the former channels avoiding turbine passage (Figure 1).

The power plant at HEP 3 has a total capacity of 14 m^3 s^{-1} and is equipped with two twin-Francis units from 1919 (i.e. four runners, Table I). The power plant at HEP 2 has twice that capacity, using one large Kaplan runner. Smolt migration past the two facilities at HEP 1 and HEP 0 was not evaluated in this study, but HEP 1 is equipped with one Kaplan and one Francis runner, whereas HEP 0 has been inoperational for several years. Trash racks are present at

Table I. Characteristics of the power plants at Finsjö in the river Emån

Factor	HEP 2 (lower Finsjö)	HEP 3 (upper Finsjö)
Number of turbines	1	1
Manufacturer/brand	Kvaerner	KMW
Type of runner	Vertical Kaplan	Horizontal Francis[*]
Number of runners	1	4
Diameter of runner (mm)	2100	800
Number of blades runner^{-1}	4	16
Manufacturing year	1993	1919
Effect (MW)	2.15	0.6
Total capacity (m^3 s^{-1})	28	14
Rounds per minute	333	250
Annual production (GWh)	11.6	3.2
Head (m)	8.7	5.5
Spacing trash rack (mm)	30	20

[*] High specific speed.

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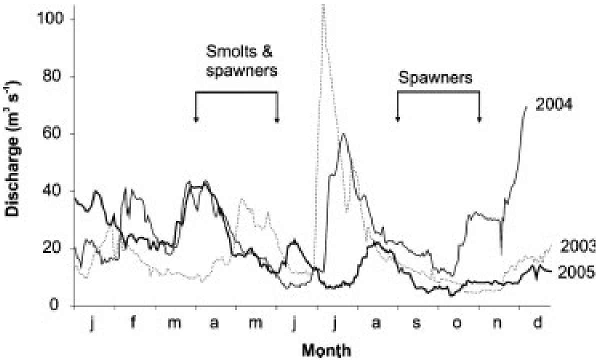

Figure 2. The daily mean discharge in the river Emån at Finsjö 2003–2005. The peak migration periods in spring and fall are indicated by the arrows

all power plants, with 20 and 30 mm spacing at HEPs 3 and 2, respectively. There are no devices guiding downstream-moving fish, but there are 1 m deep trash deflectors at both power plants in Finsjö and these might lead fish to the trash gates adjacent to the power intakes. If fish were to swim through the trash gates at both plants, they would fall several metres before striking a hard concrete surface. To evaluate the capacity of the trash deflectors as fish guiding devices, and to decrease the risk of injury for fish, wolf traps were constructed at the trash gates of HEP 3 (Figure 1B, no. 3) and HEP 2 (Figure 1C, no. 2). The gate at HEP 3 is 1.9 m wide and water is discharged at the surface. The discharge into this trap was approximately 0.3 $m^3 s^{-1}$ in 2004 and 0.5 $m^3 s^{-1}$ in 2005. The gate at HEP 2 is 3.5 m wide and water is discharged through a gate that opens at 0.5 m depth. The discharge into this trap was approximately 0.5 $m^3 s^{-1}$ in 2004 and 1.3 $m^3 s^{-1}$ in 2005. The relative discharge into the traps varied with total discharge through the turbines and ranged from 0 to 10% of total discharge flowing into the intake channels, depending on trap and year.

More information about the river Emån and the hydropower plants in the lower parts of the river can be found in Calles and Greenberg (2005, 2007). For information on the river and its long history of recreational fishing see Sjöstrand (1999) and Klippinge (1999).

Discharge and water temperature

Daily river and fishway discharge data at HEP 2 and HEP 3 were obtained from E.ON Sweden, the owner of the facilities (Figure 2). In addition the discharge in all the gates at both power plants ($N = 40$) was monitored during migration, i.e. April–May and September–October (Figure 3). Air and water temperatures were measured every 30 min using loggers (Tinytag Plus, Gemini data Loggers Ltd., UK).

The early phase of the spawning migration season in the river Emån is generally characterized by low flow conditions averaging 10.2 $m^3 s^{-1}$ in June–August 1986–1997. During the summers of 2003 and 2004, however, there were extremely high flow conditions in July (Figure 2). The spill water discharge during the main spawning migration period (September–October) was low at HEP 2 during both years and thus most of the time most water was released into the tail-race of the power plant, favouring fishway attraction (Figure 3A). For the upper plant (HEP 3) the situation was similar, but resulting in the opposite with regard to attraction, i.e. less water released as spill water and thus a low attraction to the fishway (Figure 3A). The fishway discharge during September and October was similar for both fishways with 1.5 $m^3 s^{-1}$ during 53 days (HEP 2) and 47 days (HEP 3) in 2003 and 43 days for both fishways in 2004. The rest of the time the discharge was 0.5 $m^3 s^{-1}$ for both fishways. The relative discharge in the fishway, as compared to the adjacent discharge source, was higher for HEP 3 than for HEP 2 (Figure 3A). At HEP 2, fishway discharge relative to the total discharge (power plant + fishway) was about three times higher in 2003 than in 2004.

The mean water temperature during the main spawning migration (September–October) was similar for both years (2003: $10.8 \pm 0.4°C$; 2004: $11.6 \pm 0.6°C$), but in 2003 the temperature rapidly decreased to 2.0°C during the

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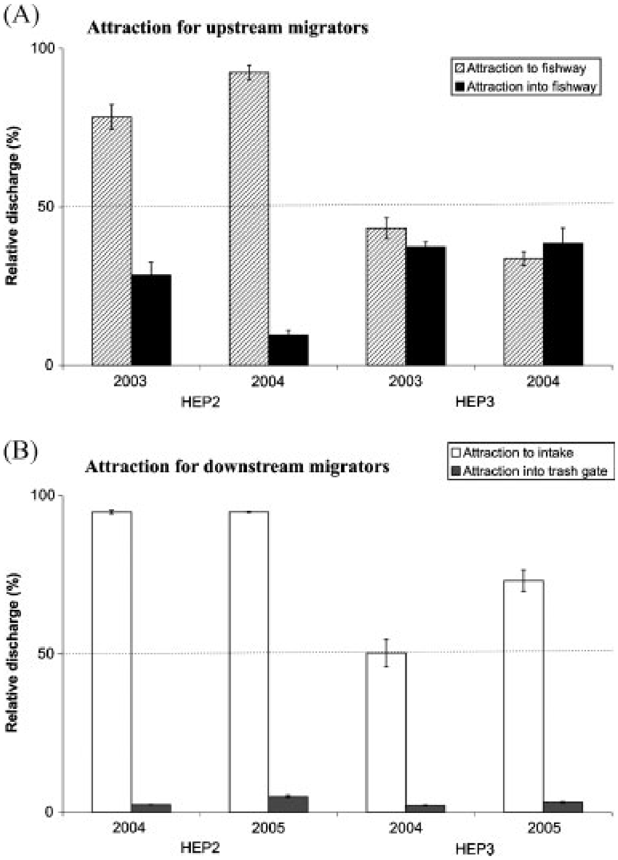

Figure 3. The relative discharge (% ± S.E.) along different routes for (A) upstream and (B) downstream migrating fish at HEP 2 and HEP 3 in fall 2003–2004 and spring 2004–2005. The percentage of discharge from the fishway or the route leading to the fishway/trash gate was compared to the corresponding discharge from the alternative route

last 2 weeks of October (mean 4.4 ± 0.5°C), whereas in 2004 the temperature remained at approximately 8°C during this period (mean 7.8 ± 0.1°C).

In 2001 and 2002, the fish had difficulty finding the HEP 3 fishway, resulting in several individuals remaining in the reservoir between the two power plants (Calles and Greenberg, 2005). To facilitate attraction to the fishway in 2004, the discharge at HEP 3 was manipulated to create artificial freshets in the former channel. The experiment was initiated in late September 2004 when we observed that fish could not locate the fishway. Freshets were released on four occasions, separated by 5, 6 and 10 days, respectively, and the irregular intervals and durations were a result of constraints related to power plant operation.

In 2004 and 2005, when downstream migration was studied, water was always spilled into the former channel at HEP 3. In 2004 the average relative discharge during the smolt migration period was about the same for the plant and the former channel, whereas in 2005 more water was released through the turbines (Figure 3B). The relative discharge into the trash gate, in relation to the turbine intake, was about 2–3% both years at HEP 3 (Figure 3B), and 2.5% (2004) to 5.0% (2005) at HEP 2. The water temperature in spring was similar for both 2004 and 2005, gradually increasing from 8°C in mid-April to 14°C by the end of May.

Tagging

Upstream migrating spawners were captured in the fishway at HEP 1, as described in Calles and Greenberg (2005), during 139 days in 2003 (14/5–27/6, 27/7–23/8, 27/8–31/10) and 126 days in 2004 (1/5–2/7, 3/8–4/10). Captured fish, without visible injuries, were anaesthetized using MS-222 (a benzocaine derivate), measured and

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Table II. Number, mean weight and mean length of PIT-tagged and PIT- and radio-tagged brown trout spawners at Karlshammar power plant, 2003–2004 in the river Emån

Year	Tagged	N	% Females	Length (mm)		Weight (kg)		Recaptures % (*N*)	Reached Finsjö % (*N*)
				Mean	Range	Mean	Range		
2003	PIT	194	49	681	500–940	3.91	1.4–9.3	18 (34)	11 (22+2)*
	PIT + Radio	20	55	667	520–890	3.68	1.1–7.0	15 (3)	−(0)
2004	PIT	98	41	720	490–970	4.56	1.0–10.3	20 (20)	20 (20 + 6)
	PIT + Radio	36	43	707	510–880	4.32	1.3–7.2	31 (11)	81 (29)**
Total		348	47	694	490–970	4.12	1.0–10.3	20 (68)	

*Individuals that reached Finsjö and the HEP 2 fishway in 2003 and 2004 (+N) were marked in previous years, but never recaptured at HEP 1 and hence excluded from the calculated proportions of fish.

**The radio-tagged trout in 2004 were transported to Finsjö by car.

weighed. A 3–4 mm long incision was made on the ventral body surface, just posterior to the tip of the left pectoral fin, into which a 32 mm PIT-tag (model RI-TRP-WR2B, 0.8 g, Texas Instruments, USA) was inserted subcutaneously (Table II). A subgroup of the spawners, 25 in 2003 and 35 in 2004, were also intragastrically radio-tagged (model F1820, 8 g, Advanced Telemetry Systems, USA). To reduce risk of regurgitation, a rubber ring of vulcanization tape was attached to each transmitter (Rivinoja *et al*., 2006). The tagged individuals represented 93 and 51% of the total number of fish passing HEP 1 in 2003 and 2004, respectively. Two-way ANOVA with year, sex and type of tagging as explanatory variables and length as the dependent variable ($F_{6,344} = 3.6$, $p = 0.0016$) showed that females were larger than males (710 vs. 679 mm, $F = 7.2$, $p = 0.008$), and individuals were smaller in 2003 than in 2004 (Table II, $F = 6.1$, $p = 0.014$), but that there was no effect of tagging type (Table II, $F = 0.48$, $p = 0.49$) or any interactions. The sex-ratio did not differ between the types of tagging (χ^2-test, 2003: df = 1, $\chi^2 = 0.07$, $p = 0.8$; 2004: df = 1, $\chi^2 = 0.03$, $p = 0.90$).

After tagging, the fish were released into an open cage located upstream of the fishway, which allowed the fish to continue their journey when they were ready. When the fishway was not used to trap fish, a photo-cell counter recorded all fish >500 mm as they passed the fishway at HEP 1. Calles and Greenberg (2005) found that only 14–19% of the PIT-tagged spawners released at HEP 1 reached HEP 2. Thus in 2003, we followed radio-tagged individuals as they swam upstream of HEP 1. In 2004, the radio-tagged individuals were transported by car from HEP 1 to HEP 2 and released approximately 400 m downstream of HEP 2 (Figure 1C R_U). This was done to increase the number of fish reaching HEP 2, thereby increasing the sample sizes for measuring attraction efficiencies of the fishways.

Smolts were caught using wolf traps installed at three spill gates at HEP 2 and HEP 3. The traps were checked daily from 15 April to 31 May during 2004 and 2005. Captured fish were anaesthetized using MS-222, measured and weighed. The degree of smoltification was classified as low, medium or high, based on the degree of body silverness, the lack of parr marks and fin colouration (Tanguy *et al*., 1994). The first 80 individuals that showed signs of smoltification (at least low) were tagged with radio transmitters (40 year^{-1}). The mean size of smolts did not differ between years, fish weighed 57.5 ± 4.8 g (S.E.) (*t*-test, $t_{73} = 1.08$, $p = 0.28$) and were 184 ± 4.3 mm long (*t*-test, $t_{74} = 1.83$, $p = 0.07$). In 2004 external tags were used (PIP-3, 0.55 g, Biotrack, Dorset, UK). The transmitters were pre-mounted on plastic spacer bars and attached to the back of the fish using dissolvable sutures, following the methods of Beaumont *et al*. (1996) with modifications by Crook (2004). In 2005 internal tags were used (model F1545, 0.9 g, Advanced Telemetry Systems, USA). The tag was inserted into the peritoneal cavity through an approximately 10 mm long incision that was then closed by two separate silk sutures. The antenna was lead through the body wall by means of a blunt needle. The procedure took 1.5–3 min. For both years, fish were tagged in the morning, held over the day (8–12 h) to check for post-tagging injuries, before releasing them into the main channel approximately 500 m upstream of HEP 3 (Figure 1B R_D). One individual died during recovery in 2004, and was omitted from the data set, and no individual died in 2005.

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Tracking

The movements of the fish were monitored continuously by three fixed telemetry stations (Advanced Telemetry Systems, ATS, Isanti, MN, USA), consisting of a receiver (R2100) and a Data Collection Computer (DCC) that was connected to a switching unit and two 4-element Yagi antennae. The fixed stations were positioned so that we could identify the route chosen when the fish had several routes to choose (Figure 1). Manual tracking by foot and by boat was used to locate individuals outside the range of the fixed stations (receiver R2100). All individuals were tracked manually at least once a day.

Swim-through PIT-antennae (2.5–3.0 × 1.0 m), covering the entire width of the channel, were placed at the entrances and exits of both fishways (Figure 1). The distance between the antennae was 300 m in the lower fishway and 100/70 m (2003/2004) in the upper fishway. Each antenna was connected to a reader (Series 2000 standard reader, Texas Instruments, USA) and either a data logger or a 'Compact Flash Unit' (CFU, Flinka Fiskar, Örkelljunga, Sweden). The units were supplied by main-line electricity when using computers and 12 V batteries when using CFUs. When a tag was present within the magnetic field generated by the antenna, the tag code, date and time were recorded and stored. Some antenna malfunctions occurred; nevertheless at least one antenna per channel was operational throughout the study. The detection range of each antenna was tested at least once a week, by holding a tag mounted to a stick at different distances from the antenna. The longitudinal detection range of the antennae varied from 0.3–1.0 m, which gave a total reading distance of 0.6–2.0 m as the antennae generate magnetic fields in both upstream and downstream directions. This was considered sufficient to detect all tagged fish.

Potential versus observed trout production

The stretch of river made available by the fishways at HEP 2 and HEP 3 is 24 km long and contains about 3.7 ha of suitable trout nursing grounds, corresponding to a 20% increase in reproduction area for trout in the river (Sjöstrand, 1999). The annual potential production of trout in this area was estimated, based on a mean productivity of 275 smolts ha^{-1} (Degerman *et al*., 2001). The observed production was quantified from electrofishing upstream of HEP 3 2001–2005, where mean $0+$ trout mean density was found to be 1500 ha^{-1} (Calles, 2006). The expected survival from 0+ to smolt was $p = 0.06$ (Degerman *et al*., 2001).

Data analysis and interpretation

All statistical analyses were performed using SAS software (SAS 9.1, SAS Institute Inc., Cary, NC, USA). Parametric tests were used when data met the assumptions for these tests, otherwise nonparametric tests were used. The fishway attraction efficiencies for spawners were determined by studying the radio-tagged individuals, whereas the passage efficiency was determined using both radio-tagged and PIT-tagged individuals.

RESULTS

Upstream migration

Of the 20 radio-tagged fish in 2003, three females regurgitated their radio transmitters immediately upon release at HEP 1 (15%), and were excluded from all further analyses. One female and one male made it to HEP 2 in 2.9 and 6.9 days, respectively (6.9 and 2.9 km day^{-1}), but neither of these entered the fishway. Of the radio-tagged fish in 2003, 88% stopped at sites downstream of HEP 2 identified as possible spawning grounds. As potential spawning habitat only comprised 2.5% of the total stream area the fish were showing positive selection for these sites (χ^2-test, df = 1, $\chi^2 = 23.1$, $p < 0.001$).

The median time required for the fish to move from HEP 1 to HEP 2 was 28 days in 2003 (range 4–83 days = 0.2–4.7 km day^{-1}) and 36 days in 2004 (range 3–93 days = 0.2–6.3 km day^{-1}). The proportion of PIT-tagged fish 2003–2004 that migrated to the fishways was higher for fish that had been there a previous year (44%) than for those that had never been there (13%; χ^2-test, df = 1, $\chi^2 = 6.8$, $p = 0.009$). Of the fish captured and PIT-tagged at HEP 1 in 2003, 22 individuals or 11% of the fish tagged were recorded at the HEP 2 fishway in 2003. In 2004, the corresponding proportion was 20% or 20 of the tagged fish, which was significantly higher than in 2003 (Table II,

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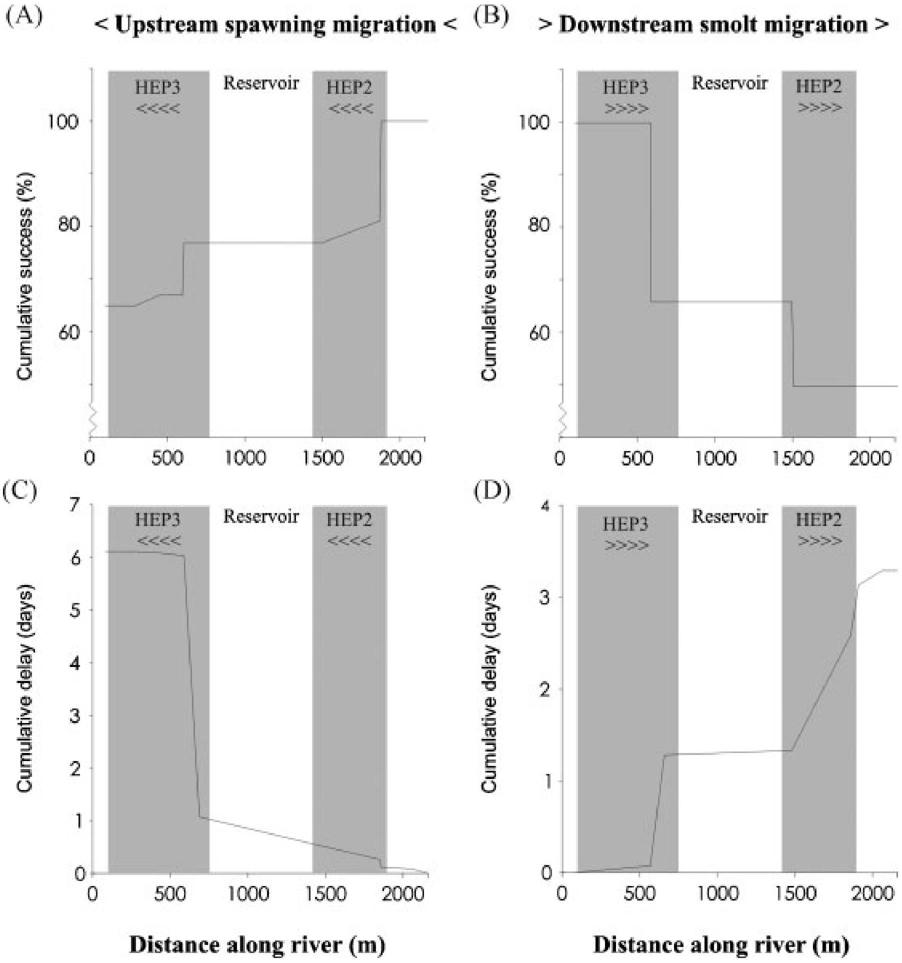

Figure 4. The cumulative success (A and B) and cumulative delay (C and D) for upstream migrating spawners in fall (A and C) and downstream migrating smolt in spring (B and D) at HEP 3 and HEP 2 in 2003–2005

χ^2-test, df = 1, $\chi^2 = 4.4$, $p = 0.040$). In addition another eight individuals that were marked in previous years, but never recaptured, entered the HEP 2 fishway in 2003 and 2004. The relative number of fish stopping downstream of Finsjö was hence nearly identical for radio-tagged fish in 2003 (88%) compared to what was observed for all PIT-tagged fish in 2003–2004 (mean 84%).

Attraction efficiency

The radio-tagged fish that made it to HEP 2 always selected the channel with the highest discharge at the time of arrival, i.e. the former channel in 2003 ($N = 2$) and the outlet channel in 2004 ($N = 36$, Figure 1C, no. 1). Consequently, attraction efficiency in 2004 (sample size too small in 2003) was 100% for the outlet channel (Figure 4A), and the median time from release until the fish actually entered the outlet channel was 2.1 h (Figure 4C). All individuals but one swam upstream to the tail-race area within 24 h (Figure 1C, from point 1 to 2). At the tail-race, the fish took a median of 3.2 h (Figure 4C) to ascend the fishway at HEP 2. There was considerable variation in the number of attempts made to enter the fishway (Table III), but 73% of the fish successfully ascended the fishway during their first visit to the tail-race. Attraction efficiency of the fishway at HEP 2 was 81% (Figure 4A). All 35 radio-tagged individuals swam into or near the fishway entrance. Six individuals spent 2–29

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Table III. The number of visits/attempts for radio-tagged trout at four different locations around the Finsjö power plants (HEP 2 and 3), 2004 in the river Emån, Sweden. The location number refers to illustrations in Figure 1

Location	HEP 2 (# visits)			HEP 3 (# visits)		
	Median	Range	Location	Median	Range	Location
Confluence area	1	1–56*	1	3	1–25	3
Route to fishway	1	1–56*		3	0–32	
Dead-end route	0			12	1–218	
Fishway area	1	1–56*	2	1	1–2	4
Fishway entrance	3	1–46		1**	1**	
Dead-end route	3	0–49		0**	0**	

*On all occasions, fish that visited the confluence area at HEP 2 continued along the route to the fishway and reached the fishway area, i.e. number of visits are indentical.

**All fish moved rapidly from the confluence into the fishway and no distinct visits, other than for passage, were detectable.

days below the power plant before either moving back downstream, regurgitating the transmitter or remaining in the tail-race until the end of the study.

The remaining 28 radio-tagged trout reached the upper power plant (HEP 3) in a median time of 9.5 h (79 m h^{-1}, range 1.4 h to 4 days). The majority of the fish appeared to have problems finding their way into the former channel past the small waterfall (Figure 1B, past point 3), as seen by the larger number of entrance attempts at the tail-race (dead-end route) than in the former channel (Table III, Wilcoxon signed ranks test, $Z_{22} = 3.8$, $p < 0.001$). The attraction problems at HEP 3 were further highlighted by the higher average number of visits to the tail-race area at HEP 3 compared to HEP 2 (Table III, Wilcoxon signed ranks test, $Z_{22} = 2.8$, $p = 0.006$), and by the longer time between arriving and entering the former channel/fishway at the HEP 3 than at HEP 2 (Figure 4C, note the steep increase of 80.3 h at about 650 m; Wilcoxon signed ranks test, $Z_{20} = 2.5$, $p = 0.011$). The individuals that made repeat visits to HEP 3 (75% compared to 22% of the same group of individuals at HEP 2) were observed to swim back and forth between HEP 3 and HEP 2.

The artificial freshets in 2004 had no direct effect on attraction efficiency of the former channel at HEP 3, 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 three out of four trials, but the difference was only significant in two out of four trials ($\chi^2 = 16.2$ and 37.1, df = 1, $p < 0.001$). After several weeks of decreasing discharge a natural freshet occurred in the river, and by 18 October the total capacity of the power plant was exceeded (i.e. >14 m^3 s^{-1}), generating an increased spill discharge into the former channel (Figure 2). This initiated increased activity among the trout and within 6 days all individuals, which up to this point had spent 6–30 days in the reservoir, left the area. During this natural freshet another five individuals entered the reservoir from HEP 2 and four of them swam rapidly to HEP 3 and successfully ascended the former channel and the fishway. As a result of the natural freshet, the final attraction efficiency for the former channel at HEP 3 in 2004 was 89% (25 of 28, Figure 4A). All 25 radio-tagged trout that passed the waterfall at HEP 3 in 2004 proceeded upstream and entered the fishway, i.e. resulting in an attraction efficiency of 100% for the fishway at HEP 3 (Figure 4A). The median time required for the fish to move from the waterfall into the fishway was 1.3 h (range 0.5–21.3 h, Figure 4C). The A.E. based on the number of PIT-tagged trout that had passed the fishway at HEP 2 and made it to the fishway at HEP 3 was 71% (17) in 2003 and 86% (18) in 2004. The time required to move between the fishways was lower in 2003 than 2004 (median 1.1 and 3.3 days respectively, Mann-Whitney, $U_{51} = 130$, $p = 0.009$).

Passage efficiency

In 2003 and 2004, a total of 50 PIT-tagged and 29 radio-tagged brown trout ascended the fishway at HEP 2 for a mean passage efficiency of 95%. In most cases a successful passage was achieved at the first attempt (i.e. they continued upstream after having passed the first PIT-antenna) and no difference in passage success was found

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between PIT-tagged and radio-tagged individuals in 2004 (χ^2-test, df = 1, $\chi^2 = 2.9$, $p = 0.09$). The median time required for the fish to move the 300 m between the two antennae was 2.1 h (141 m h^{-1}, range 1.4–21.4 h).

In 2003 and 2004, a total of 35 PIT-tagged and 25 radio-tagged brown trout ascended the fishway at HEP 3 for a mean passage efficiency of 97% (Figure 4A). In most cases a successful passage was achieved at the first attempt (i.e. they continued upstream after having passed the first PIT-antenna) and no difference in passage success was found between PIT-tagged and radio-tagged individuals in 2004 (both were 100%). The median time required for the fish to move between the two antennae was 28 min (range 18–53 min), which is equivalent to 163 m h^{-1} (range 79–238 m h^{-1}).

Attraction and passage efficiencies combined

When combining the attraction efficiencies observed for the radio-tagged fish in 2004 with the passage efficiencies observed for all fish in 2003–2004, the cumulative efficiency was 65% for both plants (Figure 4A). Based on the number of spawners tagged relative to the total number of spawners at HEP 1 we estimate that the mean number of trout spawners that swam past HEP 2 and HEP 3 in Finsjö each year was 25 individuals.

When comparing the two power plants the overall success was lower for HEP 2 (77%) than at HEP 3 (86%), but this difference was not significant (Figure 2A; χ^2-test, df = 1, $\chi^2 = 1.32$, $p = 0.25$). The total median delay was 21 times longer at HEP 3 than at HEP 2 (Figure 4C).

A larger proportion of the males than of the females successfully passed both power plants, 79 and 63% respectively, but the difference was not statistically significant ($\chi^2 = 0.9$, df = 1, $p = 0.35$). The radio-tagged brown trout that passed both power plants continued upstream and were observed at spawning grounds along the recolonized 24 km stretch of river, but with their numbers rapidly decreasing with distance upstream.

Downstream migration

Kelt. Approximately 58% of the kelts were observed moving downstream past HEPs 3 and 2 in the fall (28%) or in the spring the year after spawning (72%). The downstream movement occurred at similar water temperatures in fall (9.9 ± 0.8°C (S.E.)) and spring (10.0 ± 0.4°C), but the mean discharge during downstream passage was lower in the fall (16.4 ± 1.7 m^3 s^{-1}) than in the spring (23.8 ± 1.6 m^3 s^{-1}).

In spring 2004 all recorded downstream migration (11 fish) took place via the fishway at HEP 2, and the median date for using the fishways was 19 April. In spring 2005 the median date for downstream migration occurred on 6 May, and the kelts were observed migrating through the trash gate at HEP 3 (nine fish), the trash gate at HEP 2 (22 fish) and the fishway at HEP 2 (seven fish). Thus, 70% of the confirmed passages at HEP 2 took place through the trash gate, whereas at HEP 3 almost all passages occurred through spill gates in the former channel (i.e. Figure 1B: both sides of no. 4).

Smolt. Of the smolt that were radio-tagged and released upstream of HEP 3, 54% in 2004 and 45% in 2005 successfully passed both hydroelectric facilities, a non-significant difference between years (χ^2-test, $\chi^2 = 1.30$, df = 1, $p = 0.253$; Figure 4B). When looking at each facility separately, the passage success was higher for HEP 2 (76%) than for HEP 3 (66%), but this difference was not statistically significant (χ^2-test, $\chi^2 = 2.95$, df = 1, $p = 0.086$). The losses were attributed to turbine passage (13.9%) and other sources such as predation (25.0%) and desmoltification (12.0%), resulting in a total loss rate of 28.1% km^{-1}. The median capture date for smolt was 3 May in 2004 and 6 May in 2005.

In most cases the tagged smolts swam swiftly to the dams and then appeared to be ‘delayed’ before proceeding along the chosen route (Table IV, Figure 4D). At HEP 3 most fish chose the former channel, which was the route with the shortest delay and the highest success rate (Table IV). Turbine mortality for HEP 3 was consistent between years, with a loss of 35% (2004: 38%, $N = 8$; 2005: 33%, $N = 9$). For HEP 3 there was a notable difference between immediate and delayed success for smolt swimming through the turbines (39.6%) and the trash gate (52.8%), but not for the former channel (12.6%)(N.B. immediate success describes the individuals that left the site after passage and delayed success describes individuals that left Finsjö after passage). At HEP 2 most fish swam through the turbines, even though the delay was longer than for the less-used trash gate (Table IV). Turbine mortality in the single Kaplan turbine at HEP 2 averaged 11% (2004: 9%, $N = 23$; 2005: 13%, $N = 23$). The mortality rate for passage through the Francis turbines at HEP 3 was hence higher than for the Kaplan turbine at HEP 2 (χ^2-test,

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Table IV. The chosen route, median delay (the time from arrival to passage) and success for 80 radio-tagged trout smolt at the two power plants in Finsjö (HEP 2 and 3), 2004–2005, in the river Emån, Sweden. Choice and success are presented as the mean of the percentages observed in 2004 and 2005, where as the delay is the mean of the median values from 2004 and 2005. Immediate success were the individuals that left the site after passage and delayed success were individuals that left Finsjö after passage, i.e. only comparisons between routes for each plant is relevant

	HEP 3				HEP 2			
			Success (%)				Success (%)	
Route	Choice (%)	Delay (h)	Immediate	Delayed	Choice (%)	Delay (h)	Immediate	Delayed
Turbines	19.4	22.8	66.7	25.0	89.0	8.5	76.9	68.5
Trash gate	14.0	62.7	69.4	16.7	9.0	3.4	37.5	25.0
Former channel	57.7	1.6	76.4	63.8	2.0*	309.0	50.0	0
Did not pass	9.0	—	0	—	0	—	—	—
Total	100	4.5	66.3	43.8	100	5.1	76.1	65.0

*Only one individual that entered the fishway.

$\chi^2 = 12.02$, df $= 1$, $p = 0.001$). The delay for fish passing through the turbines or trash gate was higher at HEP 3 (median 42.8 h) than at HEP 2 (median 6.0 h, Table IV). The difference between immediate and delayed success was small for all routes at HEP 2 (Table IV).

The individuals that did not remain in the tail-race after passing through the turbines (turbine induced mortality) or continued their downstream migration (successful passage) were thought to have been lost due to predation or to desmoltification. In some cases this was verified by relocating the transmitter or the desmoltified individual, but in most cases these were merely educated guesses based on the movement pattern of the fish and/or the habitat type chosen by the fish (lotic vs. lentic). The losses due to predation and desmoltification combined comprised 26.3% of the total number of smolt at HEP 3 and 14.5% at HEP 2.

The fish guidance efficiency (FGE) for the trash diverters at Finsjö was 20% for HEP 3 (2 of 10) and 4% for HEP 2 (1 of 24) in 2004. In 2005, when the discharge into the gates was higher (Figure 3B), the efficiency increased to 50% at HEP 3 (9 of 18) and 14% at HEP 2 (4 of 28).

In 2005 a total of six fish (15%) made it to the sea, a journey of 28.8 km that took 5–20 days (median 5.1 days). None of these fish swam through the Francis turbines at HEP 3, but they swam through the Kaplan turbine at HEP 2. When compared to the number of individuals that successfully left HEP 2 in 2005 ($N = 18$), the success for smolt between Finsjö and the sea was 33.3% (2.3% loss km^{-1}).

The estimated potential annual productivity of smolts in the area upstream of Finsjö (HEP 3) was 1018 individuals. The observed production in this area, based on electrofishing surveys of 0+ 2001–2005 was 333 smolts. From these rather coarse estimates of potential and observed trout production in the river Emån, the production 2001–2005 was about 33% of what could theoretically be achieved.

Iteroparity

The number of return spawners at HEP 1 constituted 17% of the total catch in 2003 and 23% in 2004, and most were females (2003: 81%, $\chi^2 = 17.57$, df $= 1$, $p < 0.001$; 2004: 58%, $\chi^2 = 4.75$, df $= 1$, $p < 0.029$). This figure contrasts with an even sex ratio (46% females) among all brown trout captured and tagged at HEP 1 in 2001–2004 ($N_{\text{tot}} = 659$). The degree of iteroparity varied between tagging years and was lowest for the individuals tagged in 2001 (8%), followed by 2003 (13%) and 2002 (17%), i.e. not related to time since tagging occurred. 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 were second year recaptures ($N = 52$), but some individuals were third year recaptures ($N = 10$) and one female returned 4 years in a row.

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DISCUSSION

Our case-study of the river Emån illustrates the complexity of fish passage problems in regulated rivers. Although this kind of holistic evaluation of longitudinal connectivity is not possible to perform in all rivers targeted for remedial measures, the knowledge and experience obtained from this and similar studies should be used when planning different measures. Such an approach will contribute to avoiding one-way connectivity, a common feature of many rivers today. For the river Emån, our studies show that implementation of new nature-like fishways, considered as passable for most aquatic species (Eberstaller *et al.*, 1998), does not solve the issue of connectivity fully. As for many other rivers targeted for rehabilitative measures, no attempt to identify all measures needed to fully re-establish longitudinal connectivity in the river Emån was made before the first measures were implemented, i.e. similar to 'the field of dreams hypothesis' (Bond and Lake, 2003).

During 2001–2004 only 11–26% of the fish marked with PIT-tags at Karlshammar reached HEP 2 (Calles and Greenberg, 2005). The results from the 2003 telemetry study indicated that many of the migrants spawned downstream of HEP 2 in Finsjö. Once the fish arrived at HEP 2 some, not all, passed both fishways. This seems to be related to location of the fishways. At HEP 2 the fish have to be attracted away from the former channel, whereas at HEP 3 the fish have to be attracted towards the former channel. 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 HEP 2 and at the same time high enough to allow enough spill water to be released into the former channel at HEP 3. The discharge during the main spawning migration in 2003 and 2004 favoured fishway function at HEP 2 but not at HEP 3. In 2004 when the total discharge in the former channel at HEP 2 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 HEP 3, however, the delays were substantial as fish spending up to 30 days mainly in the tail-race and between the plants before ascending the former channel or returning downstream. Such movements between the waterfall and the tail-race at HEP 3 have previously been described as route-seeking behaviour (Karppinen *et al.*, 2002). In spite of the delays at the HEP 3, the attraction efficiency of the former channel/fishway was higher in the present study (71% in 2003, 86–89% in 2004) than in our previous study (50% in 2001, 53% in 2002) (Calles and Greenberg, 2005). The high attraction efficiency at HEP 3 in 2003–2004 might be related to the higher proportion of return spawners with previous experience of Finsjö in 2003–2004 than in 2001–2002. Another reason for observed differences in migratory behaviour between years could be related to differences in flow affecting both the spawners' tendency to migrate upstream and their capability and motivation to overcome obstacles on the way. Discharge was higher in 2003–2004 than in 2001–2002. The importance of high discharge for motivation for successful passage is illustrated by the higher relative number of individuals that successfully ascended Finsjö during the wet years 2003 and 2004 (67 and 76% respectively) than in the dry years 2001 and 2002 (46 and 47% respectively) (Jensen and Aass, 1995; Calles and Greenberg, 2005). Still we did not see any migratory response to the artificial freshets at HEP 3. This may have been because the releases were too short in duration and/or too small in amplitude (Thorstad and Heggberget, 1998). The effects of the last and largest artificial freshet, when the power plant was shut down and all water was released into the former channel, were obscured by the rain-induced natural freshet starting just days before. Still, the increased activity at the water fall during freshets is similar to effects observed in other studies (Thorstad and Heggberget, 1998), and the effect of the large natural freshet shows that an increase in flow initiates and stimulates migration (Arnekleiv and Kraabøl, 1996; Jonsson and Jonsson, 2002).

At both fishways, the delay was limited for most fish (<2 d for 85%), which probably reflects the fact that the fishways were easily found once the fish had managed to find the route leading to the fishway. Most fish appeared to try to enter the draft tube, but when failing to do so they started searching for an alternative route upstream. Thus, it appears that if the fishways are well situated, the fish will most likely find them (Bunt, 2001). Still, most fish at HEP 2 visited the entrance area of the fishway repeatedly before ascending. The observed reluctance to ascend a fishway after having located the entrance has been previously reported and the most common explanations are: (1) fish being discouraged or unmotivated to proceed upstream by the low relative flow from the fishway and (2) problems in finding the entrance orifice (Clay, 1995; Larinier, 1998; Gowans *et al.*, 1999; Karppinen *et al.*, 2002; Lundqvist *et al.*, 2008) or fish possibly sensing that these are man-made structures. At HEP 2 it is probably a matter of

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motivation, as all fish were observed close to the entrance shortly after arriving at the tail-race, with several visits to the entrance. Furthermore, the entrances of the fishways at Finsjö (HEP 2 and 3) are wide and deep (approximately 4 m wide and 1 m deep) with moderate water velocities, and there should not be any problems for fish to physically ascend the entrance once they know where it is. The reason for the shorter delay at the HEP 3 fishway may be that the spawners reach HEP 3 later in the spawning season at which time motivation is higher (Gowans *et al.*, 1999). Furthermore, if fish follow the former main channel upstream of the waterfall, they will automatically be led to and into the fishway, since the fishway entrance is an extension of the main channel. At HEP 2, the fishway entrance is not an extension of the main channel. Instead, it is 25 m downstream of the draft tube exit, oriented perpendicular to the direction of flow in the tail-race instead of the preferred close to parallell (Cowx and Welcomme, 1998). A potential problem with both fishways was the observed flooding of the lowermost parts of the fishways when large volumes of water were released in the adjacent competing tail-race or spill gate, which presumably makes it difficult for fish to locate the fishways and decreases their motivation to proceed upstream via that route (Clay, 1995; Karppinen *et al.*, 2002).

The passage efficiency and rate of ascent remained high for both fishways throughout the study, which agrees with our previous results (Calles and Greenberg, 2005; Calles and Greenberg, 2007). The overall efficiency for upstream migrating spawners at Finsjö in 2003–2004 was approximately 65%, which is considerably higher than <50% previously reported in Calles and Greenberg (2005), even though the study from 2001–2002 probably overestimated the total success since only fish that entered the fishway at HEP 2 was included in the calculations (i.e. A.E. of the HEP 2 fishway assumed to be 100 %). Many authors argue that minimum standards of 90–100% total efficiency should be achieved for a fishway to be considered as functional (Ferguson *et al.*, 2002; Lucas and Baras, 2001). This is not necessarily a reasonable goal since some fish may return downstream to correct for overshooting their natal sites (Bunt *et al.*, 1999; Boggs *et al.*, 2004). Furthermore, successful upstream passage of an obstacle does not necessarily imply a higher reproductive success when spawning grounds are present both upstream and downstream of the obstacle, which is the case for the Finsjö power plants.

Aspects other than attraction and passage efficiency of a fishway need to be addressed, such as the time required to pass the facility, which is often referred to as a delay. 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 post-spawning mortality (Shikhshabekov, 1971; Baras *et al.*, 1994; Jonsson *et al.*, 1997; Cowx and Welcomme, 1998; Chanseau *et al.*, 1999). Studies show that increased energy expenditures as small as 10% can have a detrimental effect on post-spawner survival (Jonsson *et al.*, 1997), which emphasizes the need to incorporate the effects of delay into evaluations of fishway function (Lundqvist *et al.*, 2008). The point in time in which so called ‘quiescent’ periods can be called delays has yet to be defined.

The timing for downstream migration by smolts and kelts was surprisingly similar, considering that other studies have found that kelts often migrate downstream earlier than smolts do (Klemetsen *et al.*, 2003). Differences in size and swimming capabilities of smolts and kelts create different types of problems, as most smolt passed through the trash racks and enter the turbines, whereas the kelts were too large to pass through the trash racks and instead they descended via the fishways and/or through the spill gates and trash gates.

The timing of spring descent in relation to water temperature appears to be similar to other studies from similar latitudes (Jonsson and Jonsson, 2002; Östergren and Rivinoja, 2008). In our study, most post-spawners descended the river in spring (72%) 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 to this may be that availability of winter habitat is greater in a large river than in a small one (Degerman *et al.*, 2001). The fish appear to follow the main current until they reach the power plant, and then they try to find an outlet downstream. In our previous study we interpreted the high percentage of kelts using the fishway for downstream passage as an indication of that they might be able to memorise migration routes (Calles and Greenberg, 2005), but the results from this study indicate that the fishway may be difficult to find and is only located when no other options are available.

The high proportion of tagged repeat spawners and their annual growth indicate that many fish do get out to sea to recondition, in spite of the observed downstream passage problems and delays. The female dominance among repeat spawners has been previously documented for Atlantic salmon (*Salmo salar* L.) and may relate to a higher energy expenditure during spawning by males, which consequently suffer higher post-spawning mortality (Niemelä *et al.*, 2000). Jonsson *et al.* (1997), however, attributed the difference in survival to males getting more injuries during spawning. Similar information on anadromous brown trout is scarce, but Berg *et al*. (1998), in a study of potamodromous brown trout, found that post-spawning mortality was higher for females than for males, which they related to the higher amount of energy expended by females at spawning.

Although relatively few smolts were caught, our study confirmed that smolts are now being produced upstream of HEP 2 and 3 at Finsjö. The results show that about 50% of the smolts that approach the power plants successfully pass both of them, and that survival was lower at HEP 3 (Francis runners) than at HEP 2 (Kaplan runner). In general, survival of fish passing through Francis turbines is low (Montén, 1985), and Matousek *et al*. (1994) reported survival rates of 71–100% and 61–89% for juvenile and adult rainbow trout, respectively, as they passed through Francis turbines at low head dams. Our survival rate of 65% at HEP 3 is consistent with this result, even if the total number of fish swimming through the turbine was low ($N = 17$). 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 HEP 3 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 fish have a low probability of being hit. This is supported by our results as survival was 89% at HEP 2. In addition, the large size of the runner and the relatively low head at HEP 2 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; Hadderingh and Bakker, 1998; Skalski *et al*., 2002). Survival of smolts passing through low-head, high-speed Kaplan runners comparable to the one found at HEP 2 may be as low as 22%, but with previous survival estimates ranging from 22–85%, our results fall only slightly outside of this range (Amiro and Jansen, 2000). Future studies are needed to determine the extent of delayed effects of turbine passage.

Predation is often a major cause of mortality for smolts, especially when passing through reservoirs (Jepsen *et al*., 2000; Olsson *et al*., 2001). Even though we cannot give precise estimates of the losses due to predation, the total loss that could not be attributed to turbine passage was 36.7%. We estimate that the loss due to predation was 25%, giving a loss rate of 13.9% km^{-1}, which is higher than estimates of 2.2–2.3% km^{-1} from unregulated parts of the river Emån (this study and Larsson, 1985). Smolt mortality attributed to predation in the Danish River Gudenå 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), indicating that the predation rate in our study is either very high or overestimated.

In spite of the higher mortality rate associated with the Francis runners at HEP 3, compared to the Kaplan runner at HEP 2, actual loss rates associated with the two power plants were similar as relatively few fish swam through the power plant at HEP 3 (19.4%) as compared to HEP 2 (89.0%). The availability of alternative passage routes allowed the fish to avoid the turbines at HEP 3. This suggests that passage success should be lower at HEP 3 during dry years as most flow will be led through the turbines (Hvidsten and Johnsen, 1997). Moreover, a scenario forcing all smolt to pass through the turbines would be devastating for the smolt run since our results probably underestimated the total turbine induced loss due to the difficulties in measuring delayed success. As a rough estimate of the delayed loss for HEP 3, only 40% of the fish that successfully passed through the turbines eventually left Finsjö as compared to 84% of the individuals that selected alternative routes. Also, of the six individuals that made it to the sea in 2005 not one had swam through the Francis turbines at HEP 3. The lower success for fish passing through turbines may be due to injuries incurred when passing the turbines or be due to the observed higher delay amongst these fish. The delay and/or injuries from the runner and trash rack may result in smolt loss when the affected individuals die or desmoltify and decide not to continue downstream (McCormick *et al*., 1998; Aarestrup and Koed, 2003; Olsson and Greenberg, 2004; Olsson *et al*., 2006). The observed delay may be related to turbulence at the trash racks and the effects this have on fish (Anonymous, 2005). The racks may have a repulsive effect and explain the higher delay observed for fish passing through the 20 mm rack at HEP 3 than the 30 mm rack at HEP 2 (less turbulence with larger gap size). The use of fine-spaced racks at turbine intakes, which often have been selected to reduce fish mortality may actually increase mortality since little attention has been paid to what approach velocities that different fish species are physically able to handle and thereafter provide fish with alternative routes when hindered or scared by the rack.

Conservational issues/Implications for management

The nature-like fishways at Finsjö have re-established longitudinal connectivity for salmonids in the river Emån. Our study has allowed us to identify problems that need to be considered when designing fishways. Location of the fishways is of paramount importance. In the river Emån, fish had most problems in finding the fishway at HEP 3, as seen by the longer time required to find their way into the channel leading to the fishway, presumably because flow in the former channel is generally low relative to the tail-race. In contrast, the fishway at HEP 2 was situated adjacent to the tail-race. This differential placement of multiple fishways within the same river may require well-defined flow conditions that will keep all fishways within a river fully functional. This can, of course, be quite difficult to attain as flow conditions are highly variable both within and between years. As a consequence, one need to consider when and where spill water is released. One recommendation is to oversize nature-like fishways, which can then take the large amounts of spill water released when intake capacity is exceeded, instead of releasing spill water into channels that attract fish away from fishways (Jungwirth, 1996). Alternatively, one could build more than one fishway at a dam, and in that way provide the fish with opportunities to navigate pass the dam regardless of flow conditions.

Another important issue is that many rivers have multiple dams, which means that the total efficiencies of all the fishways (i.e. the combined effect of attraction and passage efficiencies) need to be considered. If longitudinal connectivity is to be re-established along the entire river Emån, then one must consider the efficiency of eight fishways covering some 153 km, rather than the three that exist today. The low number of spawners reaching as far upstream as Finsjö and the overall efficiency of both fishways at HEP 2 and 3 combined indicates that recolonization of the river Emån upstream of Finsjö is likely to take many years (Bryant *et al*., 1999), especially when taking into account the large variation between years. The number of spawners that currently pass HEP 1 (about 50 kg females ha^{-} spawning ground) is considerably lower than the expected 300 kg ha^{-1} (Degerman *et al*., 2001), and our estimate of smolt production is only about 1/3 of that which is possible.

The rate at which this recolonization occurs could probably be accelerated by transplanting spawners upstream, as our study and other studies indicate that relocated salmonids show a low degree of backtracking (Heggberget *et al*., 1988). This is only a temporary solution, 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 efficiency per fishway is assumed to be 81%, the average we found at Finsjö (HEP 2 and 3 combined) 2003–2004, the annual number of spawning migrants successfully passing all eight fishways in the river Emån would be approximately 75 individuals or 19% of the total number of trout approaching the first power plant in the river (HEP 1). In both cases these are overestimates, 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). 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 HEP 3 are recolonized, thereby increasing the total area of rearing habitat in the river. Interestingly, the finding that adult trout with previous experience of the fishways at HEP 2 and 3 showed a greater tendency to return to Finsjö on their next visit, indicates that the recolonization rate will increase with time.

In many cases, re-establishment of connectivity has focused on getting spawners upstream of dams, with little effort directed towards the fate of the individuals and their progeny. Clearly, such remedial measures will have limited success if downstream migrants, both kelts and smolts, are unable to reach the sea. Special attention should be paid to return spawners since they are often dominated by large highly fecund females (Wootton, 1998; Jonsson and Jonsson, 1999; Niemelä *et al*., 2000). The proportion of return spawners has gradually increased during our study, with 3% recaptures in 2002 (Calles and Greenberg, 2005) and 23% in 2004, and this percentage may increase even more. A study of 27 Norwegian rivers showed that the proportion of return spawners can be as high as 69%, and tends to increase with river size and decreasing latitude (L'Abée-Lund *et al*., 1989). In addition to kelts, smolt loss must also be considered. Smolt loss at the power plants in the river Emån was substantial, and this was without being able to satisfactorily quantify the delayed effects of injury, which may also be high (Ferguson *et al*., 2006).

As the trout population in the river Emån relies on natural spawning alone, measures that facilitate iteroparity and smolt survival are important for the future success of the population (Boggs *et al*., 2004; Evans *et al*., 2004). Therefore, the most urgent measure is to provide downstream migrating fish with alternative routes with low risks of injury or mortality (Scruton *et al*., 2002, 2003; Scruton *et al*., 2007; Östergren and Rivinoja, 2008). The fact that

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both kelts and smolts migrate at the same time is encouraging, given the high cost of water needed for any future remedial measures. The observed guidance efficiencies of the trash diverters and gates (4–50%) were not sufficient, based on the recommendations of >80% by Ferguson *et al*. (1998), but higher efficiencies should be possible to achieve.

It will probably take many years before longitudinal connectivity is fully re-established in a regulated river like the river Emån. Smolt production in the newly opened areas is still low, far below the carrying capacity. In many cases, measures are not only required to facilitate upstream and downstream passage, but also to rehabilitate of spawning and rearing habitats (Bond and Lake, 2003). Thus, a holistic approach is needed to attain a fully functional lotic system, and many criteria have to be met to create self-sustaining, resilient fish communities (Katopodis, 2005; Palmer *et al*., 2005).

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