Behavior and Survival of Fish Migrating Downstream in Regulated Rivers

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Cover: A model of the structure of Atlantic salmon populations in the Vindelälven and Piteälven in northern Sweden.

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Behavior and Survival of Fish Migrating Downstream in Regulated Rivers

Abstract

Dams present obstacles to fish migrating between freshwater and marine habitats. This thesis evaluated downstream migrations of fish in five rivers in Sweden and North America, four of which were regulated (*i.e.*, dammed). It focused on species from the subfamily Salmoninae and addressed the following questions: **What is the survival of downstream migrating fishes passing turbines at dams?** Estimated survival of Atlantic salmon (*Salmo salar*) and sea trout (*S. trutta*) kelts (0.547-0.748) was significantly lower than smolts (0.903-0.947) at the Stornorrfors and Sikfors power stations in northern Sweden. Estimated survival of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) ranged from 0.814 to 0.946 at McNary Dam on the Columbia River, USA. **Does mortality associated with dam passage affect fish population productivity?** Yes. Salmon productivity was impacted by fish passing a single dam in two Swedish rivers, but the populations responded differently to strategies to mitigate dam passage mortality. Relative increases in female salmon escaping annually after 20 years were greater in the Piteälven River (68%) than the Vindelälven River (46%), when both smolts and kelts were protected and were four times greater (38 vs. 10%) when only kelts were protected. **What are the potential mechanisms of mortality associated with fish passing turbines at dams?** While results of some model studies suggested turbine blade strike was a major mechanism, assigning mortality to a specific mechanism or power station component was difficult. Studies at McNary Dam indicated potential impacts to fish sensory systems during turbine passage increased fish vulnerability to predation in the river below the dam, and this "delayed mortality" comprised from 46 to 70% of total mortality. A research program to identify fish injury thresholds to support the design of new turbines that could improve fish survival past dams is presented. **What are the potential strategies for mitigating mortality associated with fish passing turbines at dams?** Changing turbine operations alone did not significantly improve fish survival. Fish passage through a 3.9-km long system that bypassed fish around turbines at Bonneville Dam, USA, resulted in high fish survival (0.946), no injuries, mild stress responses, and fish passage times that were similar to water flow. Bypass design criteria for Pacific salmon are described. Water temperature and day length were key proximate factors controlling Atlantic salmon smolt migration timing; migrations in two study rivers were initiated around 8^{o} C. A model based on temperature predicted that the daily rate of smolts leaving rearing areas peaked near 12.6^{o} C. This information will allow timing past dams to be estimated and aid development of fish passage mitigation strategies in regulated rivers.

Keywords: survival, behavior, migration, salmon, trout, smolt, kelt, turbine

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Till svenska folket

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Ferguson, J., G. Ploskey, K. Leonardsson, R. Zabel, and H. Lundqvist. 2008. Combining turbine blade-strike and life cycle models to assess mitigation strategies for fish passing dams. *Canadian Journal of Fisheries & Aquatic Sciences* 65:1568-1585.

II. Ferguson, J., R. Absolon, T. Carlson, and B. Sandford. 2006. Evidence of delayed mortality on juvenile Pacific salmon passing through turbines at Columbia River dams. *Transactions of the American Fisheries Society* 135:139-150.

III. Ferguson, J., D. Baldwin, R. Peters, T. Carlson, A. Popper, A. Turnpenny, and H. Lundqvist. 2006. Studies to evaluate delayed mortality associated with passage of downstream migrating fishes through turbines, with implications for future turbine design. *In: Proceedings: 14th International Seminar on Hydropower Plants*, 22-24 November 2006, Vienna, Austria.

IV. Ferguson, J., B. Sandford, R. Reagan, L. Gilbreath, E. Meyer, R. Ledgerwood, and N. Adams. 2007. Bypass system modification at Bonneville Dam on the Columbia River improved the survival of juvenile salmon. *Transactions of the American Fisheries Society* 136:1487-1510.

V. Ferguson, J., K. Leonardsson, J. Anderson, L. Österdahl, and H. Lundqvist. Analysis of proximate factors affecting Atlantic salmon *(Salmo salar)* and sea trout *(S. trutta)* smolt migration initiation and timing. *Manuscript.*

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1 Introduction

Many animal species, including fishes, migrate in response to habitat conditions that vary spatially and temporally. I define migration as the seasonal or periodic, directed movement of animals in response to changes in weather or food availability to ensure reproduction. Approximately 1% of the known fish species are diadromous, and migrate between freshwater and marine habits through use of specialized physiological adaptations (McDowell 1988). The majority of these are anadromous, where individuals become sexually mature in marine habitats and migrate upstream as adults to spawn in freshwater, and where juveniles migrate downstream to marine habitats (Quinn 2005). Presumably fish migrate to take advantage of the higher foraging success, and resultant growth rates, found in marine waters (Northcote 1978). A smaller number of species are catadromous, where individuals grow and become sexually mature in freshwater and migrate downstream as adults, spawn in marine habitats, and migrate upstream as juveniles. Thus, habitat switching, or in the case of anadromy, the migration of juvenile fish from freshwater to marine habitats, constitutes an important adaptation that results in increased fitness to individuals and enhances reproductive success (Gross 1987). Many salmonids are anadromous, and anadromy is expressed in a large variety of life history patterns (Rounsefell 1958).

Within the Salmoninae subfamily of fishes, species in two of the seven genera have generally high economic and cultural value and are frequently studied: *Oncorhynchus* (Pacific salmon) and *Salmo* (Atlantic salmon and brown trout). Hereafter I refer to the anadromous form of brown trout (*S. trutta*) using its common name, sea trout. Most Pacific salmon are semelparous and undergo senescence and mortality after the first reproduction, whereas Atlantic salmon (*Salmo salar*), sea trout, and steelhead (*O. mykiss*) are iteroparous and can undergo repeat spawning. The frequency of repeat spawning varies among populations and years (Fleming

1996; Quinn 2005). Adults that do not die after spawning, re-smolt the following spring, and migrate downstream to re-enter marine habitats are termed "kelts."

Salmon eggs deposited in redds develop into alevins, which emerge in later winter or early spring and grow into parr. Parr rear in freshwater until undergoing the complex developmental transformation known as smoltification, that prepares the animal for seawater and initiates the active migration downstream (Hoar 1976). At this stage, juvenile salmon are termed "smolts." Proximate factors used by smolts to initiate migration include increases in river discharge (Jonsson 1991; Giannico and Healy 1998; Hembre *et al.* 2001), photoperiod (Eriksson *et al.* 1982), and water temperature (Fried *et al.* 1978; Jonsson and Rudd-Hansen 1985; Jonsson 1991). Both specific and relative temperature thresholds have been observed (*e.g.*, 10º C, Österdahl 1969; mean maximum daily temperature during a period preceding significant smolt movement, Solomon 1978; cumulative temperature, Zydlewski *et al.* 2005). Once initiated, migrations have been described as passive (Thorpe and Morgan 1978; Thorpe *et al.* 1981), active (Solomon 1978; Fängstam 1993; Peake and McKinley 1998), and a combination of both (Moser *et al.* 1991; Pavlov 1994).

Salmon are classified into two categories based on their freshwater life history patterns: stream type populations, where juveniles reside in freshwater for one or more years before initiating downstream migration (also called yearlings; *e.g.,* Atlantic salmon and sea trout), and ocean type populations, where juveniles migrate to the ocean during their first year of life (also called subyearlings; Healey 1991). Chinook salmon (*O. tshawytscha)* smolts display both stream and ocean type life history patterns, and individual populations can exhibit a great deal of variation within these basic themes (Quinn 2005). In general, all of these expressions of life history diversity result from individuals maximizing their fitness. For animals living in freshwater and marine environments, this diversity is important for population viability because it allows for a wider use of habitat and protects against short-term spatial and temporal environmental variability. The genetic diversity associated with such life history diversity provides the raw material for surviving long-term environmental change (McElhany *et al.*, 2000).

The Baltic Atlantic salmon is a genetically distinct stock (Ståhl 1987) that inhabits rivers in Sweden, Finland, Russia, Estonia, Latvia, Lithuania, and Poland (Christensen and Larsson 1979). Stock abundance has been negatively affected by many anthropogenic factors, including a high level of fisheries exploitation since WW II and the development of hydroelectric facilities and subsequent conversion of natural rivers into regulated systems (Karlsson and Karlström 1994). Approximately 71% of salmon populations in non-Russian rivers in the Baltic have been classified as extinct (World Wildlife Federation 2001). The majority of remaining wild Baltic Atlantic salmon are found in rivers that flow into the Gulf of Bothnia (Karlsson and Karlström 1994), which provide some of the best remaining habitat available to wild stocks (ICES 2005).

Worldwide, approximately 800,000 dams have been installed in rivers (World Commission on Dams 2000). While dams provide numerous societal benefits, they can have significant effects on the structure and function of river ecosystems (Ward and Stanford 1979; Winston *et al.* 1991; Reyes-Gavilán *et al.* 1996). Alterations of fish migration corridors by dams are often so pronounced they become integral parts of a species' life cycle. For example, members of the family Acipenseridae are characterized by unique life history patterns of slow growth, late maturation, and intermittent spawning. The family displays variable patterns of habitat use among freshwater, estuarine, and marine ecosystems (Auer 1996). White sturgeon (*Acipenser transmontanus*) in the Columbia River are potadromous, meaning they reside and reproduce wholly within freshwater. They ranged freely in the river prior to its development into a hydropower system, and undertook extensive seasonal migrations to take advantage of scattered and seasonally available food resources (Bajkov 1951). Today their habitat is partitioned into reservoirs and river reaches between hydroelectric dams, where the remaining spawning habitat is further reduced by hydropower system operations (Parsley and Beckman 1994). Beamsderfer *et al.* (1995) evaluated the population dynamics of white sturgeon stocks in lower Columbia River impoundments and found significant differences among reservoirs in sturgeon abundance, biomass, size composition, sex ratio, size of females at maturity, growth rate, condition factor, and rate of exploitation. They concluded that the potential yield from impounded populations was reduced by dam construction.

Accordingly, to fully understand the effects of dams on fish populations we must both quantify any impacts to individuals and consider how the impacts may affect overall population dynamics, and ultimately, population viability. Life cycle repercussions from alterations to migratory corridors may be especially important for iteroparous species given their complex life history structure (*e.g.*, Jonsson 1985; Niemelä *et al.* 2006).

Development of hydropower facilities in Sweden began in the early 1900s and was largely completed by 1975. These facilities employ the two most common types of turbines to produce electricity: Francis and Kaplan turbines (Fig. 1). Migrating fishes suffer mortality while passing these types of turbines (Schoeneman *et al.* 1961; Eicher Associates Inc. 1987; Muir *et al.* 2001; Ferguson *et al.* 2005), which can result in downward trends in populations (NRC 1996; Parrish *et al.* 1998; Williams *et al.* 2005). In Sweden, salmon and trout smolts migrating downstream typically pass dams through power stations because the dams are operated to maximize power production. For example, Rivinoja (2005) observed that 100% of radio tagged salmon smolts passed Norrfors Dam through the Stornorrfors Power Station in 2003, even when spill averaged 72 $m^3 \cdot s^{-1}$ or roughly 10% of powerhouse flow. Accordingly, I focused this thesis on the passage of fish through turbines at dams and its effect on populations.

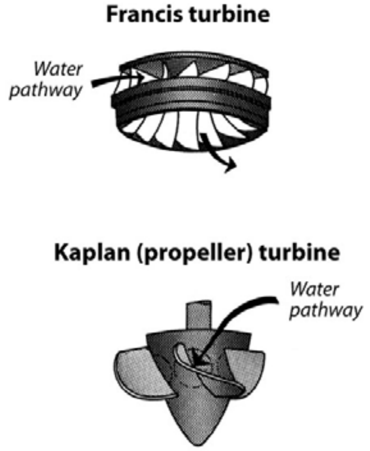

Figure 1. A schematic drawing of Francis and Kaplan turbine structures and water pathways.

Finally, there is a growing recognition of the need to restore ecological processes in regulated rivers (Stanford *et al.* 1996; Bushaw-Newton *et al.* 2002). Analytical tools to evaluate strategies that reduce impacts of regulated rivers on migratory fish populations will aid broader efforts to restore these processes and help conserve fish populations.

1.1 Thesis objectives

The objectives of this thesis were to improve our understanding of the behavior of fish as they migrate downstream in regulated rivers, quantify impacts to juveniles and adults passing dams and power stations, and develop analytical tools for use in formulating conservation measures. The thesis is comprised of five papers. Two of the papers report results of studies conducted on juvenile Pacific salmon. Data collected at Columbia River dams offered a robust source of detailed information on fish survival through turbines and fish bypass systems. This data was used to quantify impacts to fish when passing dams and to evaluate a mitigation strategy (Paper II, IV). Two additional papers analyzed Atlantic salmon and sea trout migrating in rivers in northern Sweden (Paper I, V). These focused on developing model approaches to identify mortality levels and population level impacts, and to improve our understanding of smolt behavior during the downstream migration. In the final paper, a program was developed to produce information needed to address the delayed mortality identified in Paper II. In contrast to the other papers, Paper III did not focus on any specific fish species, type of turbine, or river.

The information developed in the five papers was re-organized in the thesis to address the following questions:

1) What is the survival of downstream migrating fishes when passing turbines at dams?

2) Does mortality associated with dam passage affect fish population productivity?

3) What are the potential mechanisms of mortality associated with fish passing through turbines at dams?

4) What are the potential strategies for mitigating mortality that occurs when fish pass turbines at dams?

2 Materials and Methods

2.1 Study sites

Fish migrations in four Swedish rivers were studied: the Umeälven/Vindelälven, Piteälven, Rickleån, and Sävarån (Fig. 2). The Umeälven enters the Baltic Sea near the city of Umeå, is approximately 450 km long, and has a 26,815 km^2 watershed and a annual mean flow of 443 m^3·s^{-1}. The Stornorrfors Power Station is located 32 km upstream from the river mouth. It is the largest hydroelectric facility in Sweden and produces 600 MW of power through four Francis turbines. It has a flow capacity of 950 m^3·s^{-1} that is discharged through a 4.0-km long outlet tunnel. The Vindelälven is the largest tributary to the Umeälven, with an annual mean flow of 190 m^3·s^{-1}. It joins the Umeälven just upstream from the Stornorrfors Power Station and contains accessible habitat for wild salmon and trout spawning and rearing. From 1974 to 2007, a total of 57,146 adult salmon were counted at a fish ladder near the power station (annual mean = 1,681; ranged from 227 in 1986 to 5,995 fish in 2002), as were 1,446 sea trout (annual mean = 41; ranged from 8 in 1994 to 145 fish in 2004) (Paper I).

The Piteälven enters the Baltic Sea just below the Arctic Circle near the city of Piteå. The river is approximately 450 km long, and has a 11,285 km^2 watershed and a annual mean flow of 168 m^3·s^{-1}. However, much of the habitat in the Piteälven is not accessible to salmonids due to natural barriers. The Sikfors Power Station is located 40 km upstream from the river mouth. It has a total discharge capacity of 270 m^3·s^{-1} through two identical Kaplan turbines that operate at 19 m of head and produce 40 MW of power. Turbine discharge returns to the river through a 0.6-km long outlet tunnel. The river is free flowing upstream of the power station. From

1992 to 2007, a total of 9,504 adult salmon were counted at the fish ladder near the power station (annual mean = 731; ranged from 27 in 1993 to 1,628 fish in 2004) (Paper I).

The Rickleån originates in Lake Bygdeträsket approximately 50 km upstream from the sea and discharges into the Gulf of Bothnia just north of the city of Umeå. It has a 1,649 km^2 watershed with an annual mean flow of 16 m^3·s^{-1}. Several dams that present obstacles to salmon passage are located 15 km or further upstream from the mouth. A Wolf-type smolt trap was used 0.5 km from the river mouth to collect smolt migration timing data based on methods described in Österdahl (1969) (Paper V). A Wolf trap is typically used in small rivers and consists of a fine mesh screen that is angled downward slightly and positioned just downstream from an overflow weir. Water flow passes over the weir, and over (through) the screen, and downstream-migrating fish are captured in a collection box and held until they are examined to determine species, size, age, condition, timing, and abundance (Wolf 1951). The trap can be constructed to screen the entire river flow and thus can have high collection efficiencies.

The Sävarån is approximately 142 km long and has a 1,161 km^2 watershed with an annual mean flow of 12 m^3·s^{-1}. It empties into the Gulf of Bothnia north of Umeå and near the village of Sävar (Fig. 2). A rotary screw smolt trap was located 15 km upstream from the river mouth and used to collect smolt migration timing data from 2005 to 2007 based on methods described in Lundqvist *et al.* (2008) (Paper V). Rotary screw traps are commonly used in medium-to-large rivers for the live capture of salmon smolts to monitor species, size, age, condition, timing, and abundance (*e.g.*, Thedinga *et al.* 1994). The trap samples a portion of the river and consists of a cone covered in perforated plate that is mounted on a pontoon barge. The cone rotates around a center shaft, and downstream migrating fish are swept into the wide end of the cone (typically 1.5 to 2.4 m in diameter). Captured fish enter a live box at the rear of the trap for holding until examination. Trapping efficiencies can vary widely among species (Thedinga *et al.* 1994).

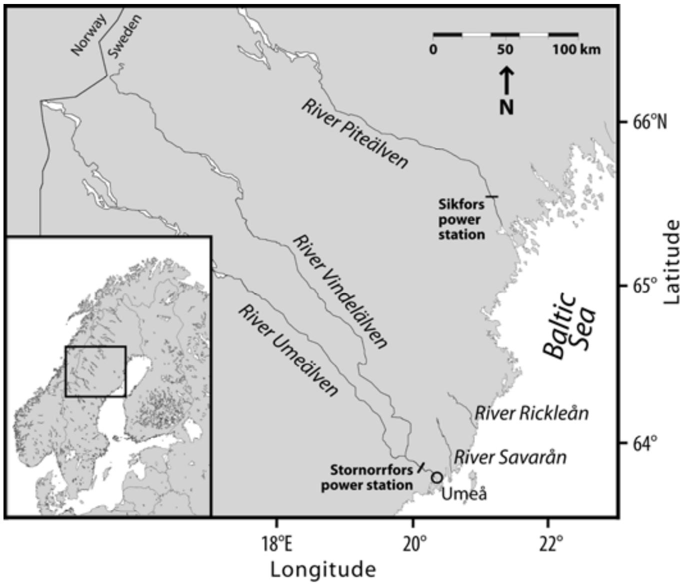

Figure 2. Rivers and power stations in northern Sweden that were studied.

A significant component of the thesis evaluated data collected at McNary Dam (river kilometer 467) and Bonneville Dam (river kilometer 235) on the Columbia River, USA (Fig. 3). The Columbia River has a 670,000 km^2 watershed with an annual mean flow of 7,500 $m^3 \cdot s^{-1}$, and is the fourth largest river in the United States as measured by flow. It has been heavily developed since the 1930s for hydropower production, flood control, commercial transportation, and irrigation (FCRPS 2001). It provides habitat for six species of Pacific salmon that must pass one to nine dams to access spawning and rearing habitats above the estuary. Each of the nine dams has a powerhouse outfitted with Kaplan turbines. Counts of adult salmon over the lowest dam (Bonneville Dam) have averaged more than 1 million fish annually since 2001 (USACE 2006). Historically, an estimated 8-10 million adults returned to the river each year prior to European contact (NRC 1996). Currently, an estimated 55% of historic Columbia River salmon populations have been extirpated (Gustafson *et al.* 2007) and 13 of 16 evolutionarily significant units (Waples 1991) are protected under the United States Endangered Species Act. In addition to the species that migrate through dams to reach suitable spawning and rearing habitat, several species of Pacific salmon inhabit the 235 km of free flowing river, as well as several large tributaries, located below Bonneville Dam (Fig. 3).

Figure 3. Map of the Columbia River showing the location of McNary and Bonneville dams.

2.2 Empirical study methods

The survival of yearling Chinook salmon migrating through turbines located at McNary Dam on the Columbia River was evaluated under two turbine operating conditions: maximum efficiency, which has turbines running within 1% of peak efficiency, and maximum load, wherein turbines operate outside the 1% range (Paper II). These operations were selected to evaluate two common turbine operations used during fish migration seasons. Maximum load is the operation that results in the highest power output, regardless of the volume of water flow through the turbine. Maximum efficiency is the point of operation where the maximum output of power is produced per unit of water flow through the turbine.

To evaluate survival, three mark recapture methods were used concurrently, meaning that test groups of differentially marked fish were released through the same release structures. Each day a group was released during one turbine operation, followed shortly thereafter by a second group released during the alternative operation; the first operation tested was alternated daily. Treatment fish were released equally among all three turbine intakes. Because fish marked using all three methods were released at the same locations within the test turbines, and under identical turbine operations, results among all three methods could be directly compared.

For the first marking method balloon tags were used to observe fish injuries and estimate survival after turbine passage (Normandeau Associates, Inc. 2003). This tag consisted of a small balloon externally attached to the dorsal musculature. Sodium bicarbonate powder in the balloon was activated prior to release by an injection of water. This allowed test fish to be released and pass through a turbine, after which the balloon inflated and fish were recovered from the water surface below the power station. Fish were then examined for injuries and held separately to observe short-term, direct mortality designated at 1 and 48 h. All recaptured fish were examined for descaling and injury, and those that died were necropsied to determine the probable cause of death. A nearly 100% recapture rate for balloon-tagged fish generally allowed study objectives to be met using smaller sample sizes.

Radio tags were the second method used. These tags weighed 1.4 g and measured 17 mm by 6 mm. They were surgically implanted into test fish using methods similar to those of Adams *et al.* (1998). Test fish were released into the turbines and detected at receiver arrays located 15, 41, and 46 km downstream from the power station. Finally, the third method of marking was a passive integrated transponder (PIT) tag which was inserted into the peritoneal cavity along with the radio tag (Prentice *et al.* 1990). PIT tags were detected at dams located below McNary Dam.

Detections of radio and PIT tagged fish were analyzed with the SURPH (survival under proportional hazards) software program for survival estimation (Lady *et al.* 2001) using the single release model (Cormack 1964; Jolly 1965; Seber 1965; Skalski *et al.* 1998, 2001). This model was applied using the complete capture history protocol of Burnham *et al.* (1987) to estimate survival and detection probabilities. For radio tagged fish, the geometric mean was used to estimate average relative survival, and treatment means of survival between two turbine operations were compared using two-factor weighted ANOVA (turbine flow and release day). Within each turbine operation, paired t tests were used to compare relative survival estimates to different detection sites downstream from the dam. Survival estimates based on radio and balloon tags were compared using a Z statistic, where the radio tag mean minus the balloon tag mean was divided by the square root of the sum of the radio and balloon tag calculated variances (Zar 1999). Survival means were compared using Z tests rather than t tests because the radio tag estimates were based on temporal replication, while the balloon tag estimates were calculated using pooled data and thus had no replicate-based degrees of freedom.

In Paper IV the performance of the original and new bypass systems were evaluated at the Bonneville Dam Second Powerhouse on the Columbia River. Four metrics were used for this evaluation. First, the survival of coded wire and radio tagged juvenile Pacific salmon was estimated. Fish were released into the bypass systems, collection channel, turbines, or tailrace and were detected or recaptured either 35 or 160 km downstream from the dam, depending on the study design. Survival was estimated using the following formula:

$$\hat{S} = \frac{T}{C} \tag{1}$$

Where T is the percentage of test fish recovered from releases made at powerhouse locations (turbine, bypass collection channel, and tailrace) and C is the percentage of test fish recovered or detected below the dam from releases made at a mid-river location 2.8 km downstream from the Bonneville Dam Second Powerhouse. The chi-square goodness-of-fit test (Zar 1999) was used to evaluate the assumption of downstream mixing of treatment and control groups (Burnham *et al.* 1987). Second, the physical condition of juvenile salmon was evaluated based on visual inspection of test fish for descaling, injury, and mortality after passage through the systems. Third, the timing of test fish was compared to water travel times. For both the physical condition and timing studies, fish were either tagged with a fin clip and recaptured in a net at the outlet to the original system, or PIT tagged and detected at a receiver located in the lower portion of the new bypass system. Fourth, the physiological condition of juvenile salmon was evaluated before and after passage through sections of the two bypass systems based on blood chemistry indicators of stress (cortisol and lactate). Data were analyzed using two-way ANOVA followed by a comparison of means using Fisher's protected least significant differences procedure (Peterson 1985).

2.3 Model study methods

Three types of models were used to evaluate fish migration behavior and survival. First, existing turbine blade-strike models from the gray literature were modified to incorporate specific turbine geometry and fish length data for Swedish rivers and power stations (Paper I). All three models were based on the mathematical probability that fish of a given length and travelling at a certain velocity and approach angle will pass between turbine blades as the turbine rotates (Bell 1991). Since the probability of turbine blade strike varies among species and power stations (Franke *et al.* 1997; Pavlov *et al.* 2002) due to differential responses related to fish length and age class, turbine type, project head, and project operation (Eicher Associates Inc. 1987; Čada 2001; Skalski *et al.* 2002), these variables were incorporated into the model formulations.

Salmon and trout smolt and kelt survival were estimated under the two turbine operations described in 2.2, that is, maximum load and maximum efficiency. At the Sikfors Power Station, maximum load is the normal mode of operation during the fish migration season. Maximum efficiency was modeled as an alternative operation at this power station based on the hypothesis that fish survival and hydraulic efficiency of turbine units are positively correlated (Ferguson *et al.* 2005). At the Stornorrfors Power Station, maximum efficiency is the normal mode of operation during the fish migration season, and this operation was compared to one based on maximum load, a typical operation at many power stations.

Second, age-structured, Leslie matrix models were used to estimate the responses of wild Atlantic salmon populations to strategies that mitigated mortality from turbine passage (Paper I). These models incorporated age-specific survival rates, fecundity, and life history variability in age of reproduction and proportion of repeated spawning. The models were based on the following formula:

$$\boldsymbol{n}(t+1) = \boldsymbol{A}\,(t) \cdot \boldsymbol{n}\,(t) \tag{2}$$

where the vector $\boldsymbol{n}$(t) represents the number of individuals at the end of time step t at each age, and $\boldsymbol{A}(t)$ is a 9 x 9 population projection matrix that varies at each time step (Caswell 2001). Each element of the matrix, a_{ij}, represents the transition of i-year-olds (columns) to j-year-olds (rows) during the yearly time step. The models predicted salmon population responses to three hypothetical scenarios each designed to eliminate any mortality from turbine blade strike for an alternate subset of age classes: (1) juveniles, (2) adults, and (3) both juveniles and adults. Results of these scenarios were compared to results from a “base case” that represented current conditions and included effects from turbine blade strike mortality. Differences represented effects of mortality in different age classes on the populations. The differences were expressed as absolute and relative changes in population growth rate (λ), and increased annual adult female salmon escapement over a dam after 20 years.

Third, Atlantic salmon smolt migration rates in the Rickleån and Sävarån were evaluated by developing sigmoid and logistic regression models based on water temperature and day length. Our goal was to build a predictive model based on easily measured environmental metrics that could be used to determine when to install smolt-monitoring traps at various locations throughout a watershed, or when to operate fish passage mitigation measures at dams (spill or bypass systems) to optimize their utility.

The sigmoidal model was:

$$r_S = \frac{r_{\max}}{1+\exp\left(\left(\theta_0-\theta\right)/b\right)} \tag{3}$$

where r_s is the daily rate of migration (fraction leaving the rearing areas each day), $r_{\max}$ is the maximum daily rate of fish leaving their rearing areas, Θ is water temperature each day, Θ_0 is the temperature at the midpoint in the distribution, b is the slope of the curve. The distribution of rates developed by the model was sigmoidal in shape.

In the logistic regression model, we used standard logistic regression with Rickleån salmon smolt data as the dependent variable, and water temperature and day length as independent variables. These variables have been related to the onset of the smolt migrations in other systems (*e.g.*, Jonsson and Rudd-Hansen 1985; Hembre *et al.* 2001; Bryne *et al.* 2003). The goal of the logistic regression was to parameterize a function for r_{LR} of the form:

$$r_{LR} = \frac{1}{1+\exp\left(\beta_0+\beta_1 X_1+\beta_2 X_2+\ldots\right)} \tag{4}$$

where β_{i} are coefficients, and X_{i} are temperature, day length and their interaction. We used Akaike's information criterion (AIC) to select the most appropriate sub-model in competition with the full model (Burnham and Anderson 2002).

Next, we formulated a continuous time model to predict salmon smolt migration timing and patterns in the Sävarån for 2005 to 2007, based on the best logistic regression and sigmoid models using the Rickleån smolt collection data. The continuous time model was formulated as:

$$N(t) = N_0 * (1-r)^t \tag{5}$$

where N is the total number of smolts available each day to leave (migrate) from the rearing area, r is the rate (fraction) of smolts leaving each day, t is time, and N_0 is the initial number of smolts (*i.e.*, the total number of smolts collected each year). To investigate whether smolt travel time may have affected model predictions of arrival timing, we evaluated whether different time lags improved model fits by delaying predicted smolt arrival timing at the Sävarån trap by 1, 2, or 3 days.

The five papers that were incorporated into the thesis can be summarized as follows:

Paper I: Turbine blade-strike and life cycle models were used to estimate effects on Atlantic salmon populations from smolt and kelt mortality due to passage through turbines at the Stornorrfors Power Station (Vindelälven) and Sikfors Power Station (Piteälven) in Sweden.

Paper II: Balloon, radio, and PIT tags were used to estimate the survival of yearling Chinook salmon through turbines at McNary Dam on the Columbia River under two turbine operating conditions.

Paper III: A research program was presented to address the delayed passage mortality identified in Paper II and aid the design of new turbines that reduce impacts to downstream migrating fishes compared to current designs.

Paper IV: Yearling and subyearling Chinook salmon and coho (*O. kisutch*) salmon survival and passage through two juvenile fish bypass systems at Bonneville Dam on the Columbia River was evaluated and related to engineering criteria used to design the systems.

Paper V: Mathematical models of Atlantic salmon migration rates were developed based on analysis of how salmon smolts responded to water temperature and day length in the Rickleån and Sävarån in Sweden.

3 Results – summary of papers

Mean blade-strike survival of Atlantic salmon and sea trout kelts was significantly lower than that of smolts, and ranged from 0.547 to 0.748 for kelts and from 0.903 to 0.947 for smolts. For both types of turbines evaluated (Francis and Kaplan) there were no significant differences in fish survival between the two turbine operating conditions of maximum unit load and maximum efficiency, or between the two species for both smolts and adults (Paper I).

Based on life cycle modeling, salmon populations in the two rivers responded differently to strategies for mitigating blade-strike mortality. Population growth rates increased up to 3% and were relatively similar for the two rivers. However, the relative increase in the number of female salmon escaping above a dam annually after 20 years was greater in the Piteälven than the Vindelälven when both smolts and kelts were protected (68 vs. 46%), and was approximately four times greater when kelts alone were protected (38 vs. 10%). Sensitivity analyses of the "base case" scenarios, or existing conditions, demonstrated the importance of life cycle model parameters varied considerably between the two rivers. In the Vindelälven, population responses were primarily sensitive to the dam passage rate of adults migrating upstream. In contrast, responses in the Piteälven were associated with several parameters, including adult dam passage rate, 2-sea winter (SW) and 3-SW kelt repeat spawn rate, and the dam passage mortality of age-2 and age-3 smolts.

We found no differences in the survival of juvenile Pacific salmon through turbines under the two operations tested, but strong evidence of delayed mortality from turbine passage. Survival estimates based on radio tag data (0.814-0.871) were significantly lower than those based on balloon tag data (0.930-0.946) under both operations ($0.001 \leq P \leq 0.038$). Based on these differences we estimated that delayed mortality comprised from 46 to 70% of the total estimated mortality to fish during passage through turbines at McNary Dam. A literature review suggested the delayed mortality was likely caused by sublethal impacts to fish sensory systems which increased the vulnerability of salmon smolts to predators in the tailrace (Paper II).

Paper III outlined a research program designed to evaluate the delayed mortality identified in Paper II. Such a program would quantify the physical environment fish are exposed to during passage through hydroelectric turbines by relating "doses" in terms of physical impacts to fish sensory systems. Any sensory system impacts that effected the animal's ability to survive would be evaluated through use of secondary challenges such as predator trials. These effects on individuals would then be linked to their populations through use of life cycle models.

Paper IV evaluated two fish bypass systems at Bonneville Dam on the Columbia River. Survival of subyearling Chinook salmon released into the original system ranged from 0.774 to 0.911 and was significantly lower ($P < 0.05$) than survival of test fish released into turbines and the area immediately below the powerhouse where bypass system flow re-entered the river. Yearling and subyearling Chinook salmon and yearling coho salmon released into the bypass system were injured ($\leq 3.08\%$) or descaled (8.5-28.6%). Also, levels of blood plasma cortisol and lactate in both yearling and subyearling Chinook salmon were significantly higher after passage through the system compared to levels in fish released directly into a net located over the bypass exit. The system was then extensively modified using updated design criteria, and the site where juvenile fish re-entered the river was relocated 2.8 km further downstream to reduce predation on bypassed fish by the dominant predator in the area, northern pikeminnow (*Ptychocheilus oregonensis*). Based on studies conducted from 1999 to 2001, the new bypass system resulted in virtually no injuries to fish, fish passage times that were generally similar to water travel times, and mild stress responses from which fish recovered quickly. Mean estimated survival of subyearling Chinook salmon passing through the new bypass system was 0.946 in 2001, an unusually low flow year.

Paper V we observed that salmon smolts initiated migrations at similar water temperatures in both rivers (7.6 and 8.0º C), and had similar midpoints in migration rate distribution curves developed using the sigmoid model (12.4 and 12.8º C). However, the estimated maximum rate of smolts leaving their rearing areas was higher in the Sävarån ($0.36 \cdot d^{-1}$) than in the Rickleån ($0.23 \cdot d^{-1}$), and the sigmoidal model only captured the initiation of salmon smolt migrations in the Sävarån, and under predicted the slope and maximum rate (Fig. 4).

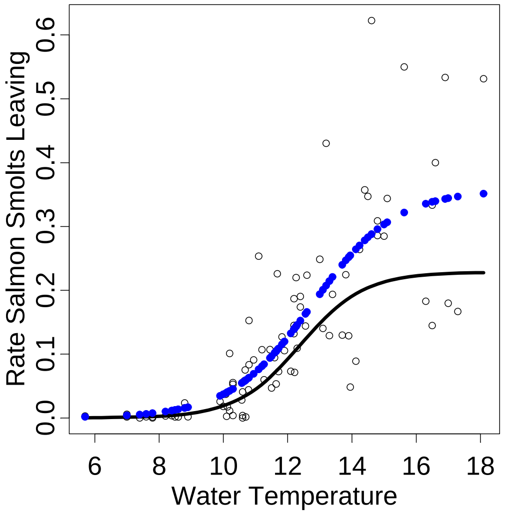

Figure 4. Sigmoidal model predictions of the rates of salmon smolts migrating in the Sävarån relative to water temperature, 2005 to 2007. The solid black line is the rate predicted by applying Rickleån model coefficients to Sävarån temperature data. Solid black dots are the rates predicted by fitting the sigmoidal model to the Sävarån River smolt count and temperature data. Open circles are the actual (observed) daily rates of salmon smolts migrating in the Sävarån.

Results from logistic regression modeling indicated that the best model according to AIC was:

$$r_{LR} = \frac{1}{1+\exp\left(\beta_0 + \beta_1 WT + \beta_2 DL + \beta_3 WT \times DL\right)} \tag{6}$$

where r_{LR} is the daily rate of smolts leaving the rearing areas, *WT* is water temperature, and *DL* is day length. Predicted smolt migration timing and patterns were compared between the sigmoid model (Eq. 3) and logistic regression model (Eq. 6) using the continuous time model (Eq. 5). These comparisons indicated that the logistic model provided a better fit to the observed Sävarån data in 2 of 3 years (2005 and 2006), and provided a similar, but slightly poorer fit than did the maximum daily rate model in 2007. Overall, adding day length and the product of water temperature and day length to the logistic regression model provided increased predictive capability over a model based on temperature only (Fig. 5).

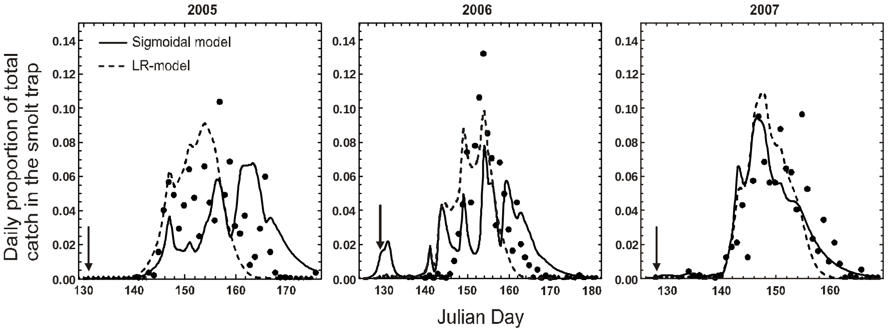

Figure 5. Plots of the fit of sigmoidal (solid line) and logistic regression (dotted line) model predictions of daily salmon smolt migration rates in the Sävarån, 2005-2007. Solid dots represent observed rates. Arrows indicate dates when trapping operations started each year.

Interestingly, median and peak migration dates of salmon smolts were different in the two rivers studied, and were approximately 9 days later in the Rickleån. In addition, trout smolts responded differently to water temperatures in the Sävarån than did salmon smolts, and began migrating when water temperatures reached 5.5º C, compared to 8.0º C for salmon. Also, the respective median and peak collections were 2.5 and 7.0 days earlier for trout than for salmon.

Discussion

4.1 What is the survival of fish passing turbines at dams?

At the Stornorrfors Power Station, estimated mortality of salmon and trout smolts based on blade-strike models was 6.8 and 8.5%, respectively, under the typical turbine operation of maximum efficiency. These rates were similar to the 8% mortality estimated by Montén (1985) based on marked salmon released into the power station as juveniles and recaptured in fisheries. The similarity in results between the two estimation methods suggests that blade strike was the primary mechanism of mortality for juvenile fish passing these turbines.

However, Montén (1985) also reported that salmon smolt mortality was 25% through the entire Stornorrfors Power Station including the turbine and a 4-km long outlet tunnel where he released additional groups of fish. This higher empirical estimate of mortality suggests that the blade-strike model underestimated total mortality at this power station. It also suggests that mortality from passage through the outlet tunnel or mortality mechanisms other than strike compromised a significant component of total mortality.

At the Sikfors Power Station, the blade-strike model estimate of mortality was 8.6% for juvenile salmon and trout and was significantly lower than the empirical estimate of 19.2% reported by Rivinoja (2005). Since Rivinoja (2005) did not partition the treatment reach as Montén had done, a direct comparison of estimated survival at this power station through only the turbines using both approaches was not possible. The treatment reach used by Rivinoja (2005) included the turbines, a 0.6-km long outlet tunnel, and 4 km of river downstream from the power station.

Francis turbines are typically used at locations involving higher project head which results in higher water velocities through the passageways. Francis turbines also have more blades (15–17) than Kaplan turbines (4–6) (Fig. 1), which results in higher fish mortality rates through Francis than Kaplan turbines (Eicher Associates Inc. 1987). Surprisingly, estimated mortality of salmon and trout smolts and kelts was similar between both types of turbines evaluated, based on blade-strike modeling. The lack of any difference between the two types of turbines tested likely resulted from the high rotation speed of Kaplan turbines at the Sikfors Power Station which increased the probability of fish striking a blade. At this power station, turbines rotate at 167 rpm and blades pass a stationary point in the turbine 11 times per second. Similar turbines at Columbia River dams rotate at approximately 75 rpm. Overall, the mortality estimates developed here using blade-strike and mark recapture methods were within ranges reported in analyses of similar metadata (Eicher Associates 1987; Bickford and Skalski 2000).

4.2 Does mortality associated with dam passage affect fish population productivity?

Results of blade-strike modeling indicated that kelt mortality was significantly higher than smolt mortality, but that measures to protect both juvenile and adult salmon from turbines in the Piteälven and Vindelälven increased population growth rates and the number of females escaping above each dam (Paper I). This indicated that losses of smolts and kelts during passage through a single dam were significant enough to affect salmon population productivity in both rivers.

However, salmon populations in each study river responded differently to theoretical mitigation measures. Although these measures produced more female salmon in the Vindelälven than the Piteälven on an absolute basis, the relative response of salmon in the Piteälven was greater, especially when kelt mortality was eliminated. This differential response may have resulted from several factors. First, the Piteälven salmon population started at a much lower initial abundance level. Here, protecting both smolts and kelts from turbine-induced mortality resulted in an additional escapement of females that would approximately double the estimated production of smolts observed in 2005, achieve 86% of the estimated production capacity of the available habitat, and exceed the interim management goal of increasing wild salmon production in Baltic rivers to 50% of their capacity (ICES 2005).

Second, this may have resulted from the assumptions that 100% of adults migrated upstream passed the Sikfors Power Station, but only 30% were assumed to pass a fish ladder near the Stornorrfors Power Station based on Rivinoja (2005). Results of sensitivity analyses conducted in Paper I showed that variability in the number of female salmon produced in the Vindelälven after 20 years was highly dependent on the rate of adults passing over Norrfors Dam. However, the results reported were for the base case only, and we did no sensitivity analyses after applying alternative management scenarios. Additional model studies will be needed to estimate the degree to which differential responses between the two populations depended on the assumption that only 30% of adults returning to the Vindelälven entered the population. Resolution of this important adult passage issue will undoubtedly affect how salmon populations in the Vindelälven respond to potential mitigation strategies.

While not specifically analyzed here, another factor to consider when interpreting these results is that there is more habitat to produce smolts in the Vindelälven (1,242 ha; 95% PI: 917-1,776) than in the Piteälven (425 ha; 95% PI: 359-511), and the potential to produce smolts from this habitat is greater in the Vindelälven (most probable number = 83,000; 95% PI: 32,000-1,960,000) than in the Piteälven (most probable number = 46,000; 95% PI: 32,000-67,000). In 2005, an estimated 97,000 salmon smolts were produced in the Vindelälven, compared to 7,000 in the Piteälven (ICES 2005).

The life cycle model developed in Paper I was based partly on adult count data. This is a common type of data used in population viability analyses, and one frequently available to resource managers. Density independent models are commonly used because their simplicity makes them applicable to a variety of data sets, and provides a straightforward method to obtain quantitative measures of population variability from count data (Morris and Doak 2002). We chose a density independent approach because salmon smolt production was estimated to be well below the carrying capacity of the available habitat (ICES 2005), and because of evidence the populations are controlled primarily by Baltic Sea fisheries (Romakkaniemi *et al.* 2003). We felt this approach was reliable given this information and at this stage of model development. However, using a density independent model requires that four assumptions be addressed (Morris and Doak 2002):

1) The mean (u) and variance (σ^2) of the log population growth rate are both constant. Three major factors can cause this assumption to be incorrect: density dependence, demographic stochasticity, and temporal trends in environmental conditions. We assumed density dependence was not affecting population growth rate. We did not test for demographic stochasticity. If present, it can be accounted for by adjusting the quasi-extinction threshold to a sufficiently high threshold, although in our analysis we did not evaluate treatment effects on population extinction thresholds. Also, we did not explicitly test to see if there were temporal trends in environmental conditions. However, we were not aware of any large environmental trends during the time period modeled (1995-2004).

2) No environmental autocorrelation. This assumption primarily affects extinction risk, which was not estimated. However, we had no information to suggest that a bad (or good) year of environmental conditions was followed by a similar year, but did not conduct the Durbin-Watson d statistic tests to see if autocorrelation was present in the data.

3) No catastrophes or bonanzas. We were not aware of any acute changes in population size over a short period of time due to catastrophes such as

ice storms, landslides, or droughts, or a bonanza such as an extremely productive marine environment.

4) No observation error. The count data were collected at dams by hatchery (Stornorrfors) or dam (Sikfors) personnel, and we had no reason to suspect their procedures changed within the count period modeled.

We used an age-structured, Leslie matrix model to estimate the responses of wild Atlantic salmon populations to strategies that mitigated mortality assigned to turbine passage. We chose an age-structured model for several reasons: first, the count data was provided in an age format (*e.g.*, 2-SW, 3-SW, etc.), second, we had experience with life cycle model studies on Pacific salmon that used age-structured models (e.g., Kareiva *et al.* 2000), third, recording salmon in terms of their age is a common designation system (Quinn 2005). Salmon are characterized by phenomenal growth rates, and size in fact is a key metric used at many counting facilities to assign fish into age class distributions. As discussed above, there were no indications from the available data that growth of the populations modeled was density dependent. In this situation, an age-structured model could be rescaled into a size-structured model by transforming the age data into the corresponding size at that age, but would provide similar results. In addition, density independent models have been used in cases where populations are recovering, and density dependence was thought not to be an important factor (*e.g.*, Kareiva *et al.* 2000). Thus, although size classified and density dependent models are commonly used in viability analyses (Caswell 2001), in this case we found no strong basis for departing from using an age-structured, density independent model.

4.3 What are the potential mechanisms of mortality associated with fish passing through turbines at dams?

The basic concept of a hydro-mechanical turbine, is that energy stored in the water behind a dam in the form of head, is converted into kinetic energy that acts on the blades causing the turbine (including the stator) to rotate. This causes electricity to be produced by the generator, similar to an automobile generator except that it is turned by a fan belt. Water passageways within the turbine are designed to turn and accelerate flow so that the maximum amount of energy possible is transferred to the turbine blades from the head and motion of the water. Fish entering turbines are accelerated with the directed water flow, passed over the blades, decelerated in the area below the blades, and exit the draft tube in the bulk flow, which now swirls as it enters the area below the power station. Thus, the potential forces acting on fish that may cause injury and mortality are:

1) mechanical, where a fish can strike stationary flow guiding structure (vanes) or water control gates, or the rotating blades themselves; 2) hydraulic, as fish are susceptible to shearing forces within the turbine or the change in water velocity over a given distance, and turbulence, which is the fluctuation in water velocity at a point in a flow field; 3) pressure, as all fish are exposed to a sudden drop in pressure downstream from turbine blades that can cause injuries to organs such as the swim bladder; and 4) noise, as the turbine environment is quite noisy from the flow forces and possibly cavitation.

Effects on fish from passing through turbines can be both immediate and delayed. Immediate mortality can be estimated through use of strike models (Paper I) and balloon tags (Paper II). Delayed mortality is the mortality among fish that experienced low (sublethal) levels of physical stress or injury during dam passage and subsequently died from increased susceptibility to disease or predation (Čada 2001). In Paper II we concluded the observed delayed mortality was likely caused by predation on fish affected by sublethal impacts to fish sensory systems. Impaired sensory systems could result in: 1) failure to detect predators; 2) poor fast-start performance; 3) the inability to shoal effectively; 4) increased conspicuousness of the prey; 5) effects on fish equilibrium; and 6) negative buoyancy upon entering the tailrace.

The overwhelming majority of studies on fish passage through dams or river reaches have focused on estimating overall passage survival (*e.g.*, Mathur *et al.* 1994; Skalski *et al.* 1998; Muir *et al.* 2001). For turbine passage, this "fish in, fish out" approach has continued since studies first started in the early 1940s (*e.g.*, Montén 1985), and includes the blade-strike modeling discussed here. While this is a useful approach for estimating the relative magnitude of mortality to fish passing turbines, it provides little information as to the actual mechanisms acting on fish and how to reduce their effects.

A few researchers have attempted to relate findings to physical conditions within the turbines. Mathur *et al.* (1996) concluded that eliminating gaps between turbine hubs and blades may enhance fish survival, and Coutant and Whitney (2000) attempted to relate fish behavior to turbine passage conditions. The approach taken in Paper II made further progress in relating physical exposures to survival, where results from different mark recapture methods were compared and evaluated relative to measurements taken of the physical environment to which fish were exposed when passing through test turbines. However, due to its scope and specialized nature, the additional research needed to investigate these effects will likely have to be conducted by a consortium of government agencies, academia, and industry interests. Such a program should: 1) quantify the physical environment to which fish are exposed during passage through hydroelectric turbines in terms of each mechanism of mortality (strike, pressure change, shear, turbulence, and noise); 2) relate the “doses” of these physical effects to fish sensory system impacts through laboratory studies; 3) relate any sensory system impacts to the animal’s ability to survive its environment through use of secondary challenges such as predator trials; and 4) link any effects on individuals to their populations through life cycle model studies (Paper III).

4.4 What are the potential strategies for mitigating mortality to fish from passing turbines at dams?

The simplest strategy for mitigating fish mortality from passage through power stations would be use turbine operations that are safer for fish. However, results of blade-strike modeling indicated that alternative turbine operations had no significant effect on salmon and trout smolt or kelt mortality at the Stornorrfors and Sikfors power stations. Also, there was no statistical difference in the survival of juvenile Chinook salmon between turbine operations based on both balloon and radio tag studies at McNary Dam on the Columbia River. These findings suggest that changing turbine operations alone will not significantly improve the productivity of salmon and sea trout populations in the rivers studied. Additional measures will be needed to address stock conservation goals, such as installing surface-oriented guidance structures or outlets through spillways or powerhouses (Ferguson *et al.* 1998; Scruton *et al.* 2002; Johnson *et al.* 2005; Scruton *et al.* 2008) to reduce the proportion of juveniles and kelts passing through turbines.

Blade-strike models incorporated mortality due to strike but not other potential mechanisms of mortality (pressure, shear, turbulence, and noise). Thus, applying their results warrants some caution. An alternative approach to evaluating whether different turbine operations at the Stornorrfors and Sikfors power stations provide better (or worse) passage conditions would be to use mark recapture methods that incorporate effects on fish from exposure to the entire turbine environment, outlet tunnels, and delayed effects expressed in the river environment below the power station, such as radio and PIT tags.

Supporting the need for further testing of turbine operations using mark recapture studies are results from a meta-analysis of survival data that evaluated fish survival relative to turbine unit operating efficiency (Skalski *et al.* 2002). It showed that peak survival did not necessarily coincide with peak unit efficiency and that results varied among turbines, requiring the need for detailed studies in each situation to determine the best operation for fish survival. Skalski *et al.* (2002) noted that differences between maximum survival and survival at peak turbine unit efficiency were 3.2% or less. Therefore, detecting small differences in survival among treatments using mark recapture techniques will require large sample sizes and sufficient replication.

Another mitigation strategy used at some locations is to intentionally pass river flow through the spillway during the fish migration season (*e.g.*, Muir *et al.* 2001). This strategy reduces overall dam passage mortality by allowing smolts and kelts to pass the dam through spill, a route of passage that is typically safer for fish than turbines (Ferguson *et al.* 2005). However, use of the strategy is site specific and dependent on hydraulic patterns in the forebay (fish need to approach close to the spillway to find the mitigation flow being spilled), the proximity of the spillway to the power station (closer is better because most of the river flow, and thus fish, are approaching the power station), the location of the spillway relative to the thalwag or deepest point of the river channel (the closer the spillway is to the thalwag the better), and the physical configuration of the spillway and stilling basin.

As discussed above, it does not appear that spill will be an effective mitigation strategy at the Stornorrfors Power Station (Rivinoja 2005). However, the effectiveness of using spill to reduce turbine passage mortality is less clear at the Sikfors Power Station. Rivinoja (2005) observed that 85% of radio tagged salmon and trout smolts (n = 40) passed the station in 2003 when spill through deep gates averaged 19% of river flow, but that none of the 60 salmon smolts that were radio tagged in 2004 passed through the spillway during 4% spill through surface oriented outlets. Over the past 10 years, spill volume has averaged 46% of total river flow at this dam during the smolt migration period; however, passage behavior data under these conditions are unavailable. Spill is used as a major mitigation measure at Columbia Rivers dams (Ferguson *et al.* 2005), and potentially may be an effective mitigation measure at hydroelectric facilities in Sweden other than those discussed here.

Another mitigation strategy is to route downstream migrating fish around dams in specially designed bypass systems. Based on Paper IV, survival, physical condition, passage timing, and blood physiological indicators of stress were all useful metrics for assessing the performance of both bypass systems tested. Each measure provided different types of information. Survival through the bypass system and river environment below the bypass exit may be the single most important measure of overall system performance. Determining what level of survival is acceptable will depend on the legal and political framework within which the bypass system is being judged and the status of fish populations using the system. Salmon managers in the Pacific Northwest region of the US expect fish survival through bypass systems to be higher than 95%.

Rates of physical injury to eyes or operculum should be low (< 1%). Scale loss is a concern since loss of mucus or scale layers can affect osmoregulation and sea water tolerance (Bouck and Smith 1979), and increase disease susceptibility. Descaling rates vary among species, and scale loss can increase through the migration period as the smoltification process progresses. Taking these factors into consideration, salmon managers in the Pacific Northwest expect descaling rates to be lower than 3% (Ceballos *et al.* 1993). Injury and descaling rates above these levels indicate that a bypass system component is not operating correctly.

Physiological indicators of stress and passage timing are more subtle measures of overall system performance that can provide additional insight into how fish behave and react to a system. Blood chemistry indicators should follow a normal pattern of increase and decline within 24 hours of bypass passage (Wedemeyer 1976; Gadomski *et al.* 1994; Mesa *et al.* 1994; Sharpe *et al.* 1998). High levels or slow recovery periods indicate problems exist with the bypass system. Fish passage times are expected to be close to, but somewhat longer than, water particle travel times as fish sense and orient to bypass flow and system components. Unusually long times would indicate that hydraulic conditions within the bypass are poor and are allowing fish to find sanctuaries and delay movement through the system.

In Paper V, two different trapping systems were used to collect smolt migration information. In the Sävarån, a rotary screw trap sampled a portion of the river. In the Rickleån, a Wolf trap sampled the entire river. Both types of smolt collection facilities provided data that was adequate for analyzing migration timing and responses to environmental variables. In addition, adding day length and the product of water temperature and day length to the logistic regression model provided increased predictive capability over models based on temperature only. Adding day length appeared to provide a stabilizing factor to the model compared to one based on just water temperature, which can vary within seasons and between years. Results of lagging smolt counts by up to 3 days to account for smolt travel times from rearing areas to the trap also improved the fit on predictions based on the logistic regression model. Thus, salmon smolts in the Sävarån appear to be rearing in areas that require from 1 to 3 days travel time before reaching the smolt collection trap. Further research on the location of fish rearing areas and travel times will aid additional model refinement. Overall, the logistic regression model, which is based on easily measured or known parameters (water temperature and day length), offers a starting point for predicting salmon smolt migrations in coastal rivers in northern Sweden.

4.5 Applicability of results

The results presented above must also be considered in three broader contexts: 1) how applicable are the tools developed here to other species; 2) can the analytical tools be developed further; and 3) how might the effects of observed direct and delayed dam passage mortality discussed here, relate to the population dynamics of other migrating species?

The turbine blade-strike models used in Paper I have been used only on salmonids to the best of my knowledge. However, passage effects are a concern for many other species, and some have been studied empirically including northern pike (*Esox lucius)*, Atlantic eel (*Anguilla anguilla*), American shad (*Alosa sapidissima*), and minnow (*Phoxinus phoxinus*) (Montén 1985; Heisey *et al*. 1992; Pavlov *et al.* 2002). The strike models can easily be applied to other power stations and species because they have simple input parameters that are commonly available. However, as discussed above, their drawback is that they only address the probability of fish striking rotating machinery, and do not account for the many other potential causes of mortality to fish when passing turbines, which may be a greater consideration for other species. The models can be used to make inferences regarding relative levels of mortality among treatments but may not produce accurate estimates of overall passage mortality. Further studies comparing model and empirical estimates will be required to more fully understand their accuracy among species and locations, including the role of turbine outlet tunnels in estimates of overall turbine mortality.

The combined model approach outlined in Paper I was designed to address two goals. First, provide specific information on the effects of dam passage on salmon and trout populations in the Piteälven and Vindelälven for use in developing mitigation strategies. In this context, the method developed was very specific. Second, develop an approach for use on different species and in data-poor situations. While hydroelectric development has matured in North America and Western Europe, it is expanding rapidly in Southeast Asia, Central Asia, and the Middle East as emerging economies in these areas develop. The combined model approach appears versatile and adaptable to many species and situations, given its relatively simple structure and requirement for input data that are generally available.

The modeling approach developed in Paper I was density independent. However, density dependent mechanisms are widely viewed as affecting many aspects of population regulation such as habitat selection, growth, predation, reproduction, and intra- and inter-specific competition (Wootton 1998). Understanding the role of these aspects of density dependence in population regulation is important for population conservation and natural resource management (*e.g.*, Fagan *et al.* 2001; Greene and Beechie 2004). Developing a combined model using density dependent models may broaden the approach further to include species and questions additional to those studied here. For example, Scheuerell *et al.* (2006) used a density dependent life cycle model to evaluate how Pacific salmon populations responded to changes to habitat, hatchery production, and harvest rates. Similarly, in some situations it may be important to understand the benefits of implementing strategies for mitigating fish passage mortality relative to other conservation measures. In these cases, using density dependent models may help determine the most biologically effective conservation approaches for a species of interest.

The majority of data available on fish passage survival through turbines is based on mark recapture techniques (radio, balloon, and PIT tags)(*e.g.*, Paper II, IV; Skalski *et al.* 2002), not blade-strike models. Results from empirical studies offer another source of data for life cycle modeling and studies of populations using the approach discussed in Paper I. For example, based on the estimated mortality of 19.2% for salmon smolts passing the Sikfors Power Station developed by Rivinoja (2005), the relative increase in the number of female salmon passing Sikfors Dam when smolts, and both smolts and kelts, experienced no turbine related mortality would be 122.2 and 200.9%, respectively. These were substantially larger than the increases of 23 and 68% reported in Paper I for these conditions.

Results from Paper I indicated that kelt mortality was substantially higher than smolt mortality for both species evaluated (Atlantic salmon and sea trout) and both types of turbines (Francis and Kaplan). Fish passage mortality through turbines is size dependent as large fish have a higher probability of striking rotating machinery during passage. The analysis also showed that passing a single dam can impact fish population productivity. These results have several implications for how dam passage mortality may affect population dynamics of migrating species in general. They suggest that the adult life stages of potadromous species that undertake migrations for feeding or to complete the life cycle, all iteroparous anadromous species, and all catadromous species in regulated rivers are at greater risk than are smaller individuals or semelparous contingents. Indeed, Montén (1985) reported that injuries (combined injury and mortality) to adult Atlantic eels ranged from 40 to 100% at several power stations in Sweden.

The susceptibility of older age classes (larger fish) to differential mortality can affect population abundance, reproductive potential, and the productivity of any species. One might think of it as being analogous to fishing mortality, for which there is a rich source of literature on population level effects (*e.g.,* Hilborn and Walters, 2001). For iteroparous species, the differential mortality may also affect population viability and persistence.

Recently, conservation biology principles and theory have been applied to salmon populations by McElhany *et al.* (2000) who suggest that a salmon population needs a certain level of abundance, spatial structure, diversity, and growth rate to be viable. They define a viable population as "an independent population …that has a negligible risk of extinction due to threats from demographic variation, local environmental variation, and genetic diversity changes over a 100 year time frame." Thus, size- and age-class dependent differential turbine passage mortality may affect fish population viability and resilience. Resilience is the capacity of a system to absorb disturbances, shocks and stresses. Measures of resilience include resistance to a disturbance and how quickly a system returns to a state of equilibrium after the disturbance (Holling and Meffe 1996). When the system is a population, the concept of resilience would suggest that life history diversity spreads risk and thereby protects a species from stochastic events. Dodson *et al.* 1998 suggest that persistence is an additional component of salmon population viability.

Moreover, Hilborn *et al.* (2003) found that the sockeye salmon fishery in Bristol Bay Alaska was sustained by the biocomplexity of stock structure, where individual populations displayed a diverse array of life history characteristics and were thus differentially affected by changes in climatic conditions during the past century. However, the net result of the complexity was that the population maintained its overall productivity throughout the time period. To summarize, some have argued that reducing the natural variation in ecological systems leads to loss of biological diversity, diminished resources, and ultimately, to social and economic issues (Holling and Meffe 1996).

Paper II concluded that delayed turbine passage mortality is a large component of overall mortality and was likely caused by sublethal impacts to fish sensory systems from exposure to physical conditions within the turbine. This suggests that other species of fish, whether they are anadromous, catadromous, or potadromous, will likely be impacted by exposure to conditions within turbines because they have similar sensory systems, although the level of impact will vary with fish species, size, and type of turbine. Studies using the approach developed in Paper II (*i.e.*, concurrent testing with balloon and radio tagged fish) will be needed to quantify whether delayed mortality comprises a similar proportion of total mortality for other species.

This conclusion also suggests that power station operators, turbine manufacturers, and fishery managers must address sublethal impacts to fish when developing improved turbine designs for passing fish more safely. The approach outlined in Paper III for evaluating delayed mortality was presented at a turbine engineering conference because turbine manufacturers are asked to develop safer turbines by their clients, and I wanted to communicate the approach to the primary users of this type of information. The approach is not species specific whatsoever. It offers an alternative to the status quo which is focused simply on estimating mortality, or at best, observing fish after turbine passage and retrospectively identifying causes of injury (strike, pressure, or shear) based on assumed relationships (*e.g.*, Normandeau Associates *et al*. 2003). Paper III uses a dose-response approach similar to that used in toxicology studies to identify injury thresholds. Impacts to individuals would then be determined through laboratory studies, and impacts on populations through model studies. The program was intended to produce the types of information needed to develop new turbine designs that would result in passage exposures below fish injury thresholds. Turbines based on such information could be installed at new power stations or when aging turbines at many existing power stations are replaced.

The evaluation metrics used in Paper IV (survival, condition, physiological indicators of stress and travel time) are generic and could be applied to any type of passage structure or species that migrates within river ecosystems or between freshwater and marine habitats. The design criteria identified in Paper IV are highly specific to Pacific salmon but are broadly applicable throughout their geographic range. While the criteria may not apply to other genera and families, they offer a basis for developing similar design criteria for species in the genus *Salmo*. One shortcoming of the criteria is that they are poorly developed for downstream migrating adult Pacific salmon. Adult criteria for steelhead and species in the genus *Salmo* should be developed due to their use of iteroparity as a life history strategy.

Paper IV described what can happen when a state-of-the-art, but untested, mitigation strategy is implemented at a dam. In this case, the original juvenile fish bypass system performed more poorly than the passage route it was designed to mitigate (turbines). This has several implications. First, untested mitigation strategies implemented at dams may result in increased, not decreased, downward pressures on fish populations, and can led to the types of population level effects discussed above. Second, attention to design criteria is essential when developing mitigation facilities. For this reason, along with the fact that they represent 35 years of “trail and error” bioengineering experiments never reported in peer reviewed literature, the design criteria used in both bypass systems tested were incorporated into Paper IV. Third, post-construction studies should be conducted to verify that a facility is performing as expected. The poor performance of the bypass system at Bonneville Dam curtailed power station operations until the issue was resolved. It took eight years of biological testing over a 14-year period to determine the cause of the problems and install a solution, at a cost of roughly $70 M.

Finally, the results in Paper V are specific to Atlantic salmon smolt migrations in the forest rivers of northern Sweden. They may be applicable to trout and salmon in other (and possibly larger) Baltic rivers, but further analysis will be needed to answer this question. The approach of using water temperature and day length as metrics for determining the rate at which salmon smolts will leave their rearing areas could be tested in other rivers, although salmonids are highly locally adapted (Taylor 1991) and the actual temperature threshold will vary among populations and locations (Hvidsten *et al.* 1995; 1998).

5 Conclusions

1. Estimated survival of Atlantic salmon and sea trout kelts was significantly lower than that of smolts passing the Stornorrfors Power Station (Umeälven) and Sikfors Power Station (Piteälven) based on blade-strike model studies. Estimated mean survival ranged from 0.547 to 0.748 for kelts and from 0.903 to 0.947 for smolts (Paper I).

2. Salmon population growth rates and the number of females escaping above dams in the Vindelälven and Piteälven increased when smolt and kelt mortality was eliminated. In the Piteälven, salmon population growth rates increased by 2.8%, and 68% more females escaped above the dam annually after 20 years. In the Vindelälven, salmon population growth rates increased by 1.8% and 46% more females escaped above the dam annually after the same period (Paper I).

3. Salmon populations in Vindelälven and Piteälven responded differently to strategies for mitigating mortality caused by fish striking turbine blades. The relative increase in the number of female salmon escaping above a dam annually after 20 years was greater in Piteälven than Vindelälven when both smolts and kelts were protected (68 vs. 46%), and was approximately four times greater when kelts alone were protected (38 vs. 10%). These differences were not predicted by results from blade-strike model studies. They show the value in analyzing population level effects on fish from passing dams compared to simply estimating dam passage mortality, and that population level responses to potential dam passage mitigation measures should be evaluated for each population and river of interest (Paper I).

4. The survival of juvenile Pacific salmon through turbines at McNary Dam on the Columbia River was not different between two operations

tested. However, radio tag estimates were significantly lower than balloon tag estimates under both operations, and based on differences in estimated survival between the two evaluation methods used, delayed mortality comprised from 46 to 70% of the overall mortality that was measured. A literature review suggested the delayed mortality was likely caused by sublethal impacts to fish sensory systems which increased their vulnerability to predation in river reaches below that dam (Paper II).

5. Overall, the point estimates of mortality from empirical and model studies reported here provided little information on the actual mechanisms of mortality, or how to redesign turbines to improve the physical conditions fish experience (strike, pressure, shear, turbulence, and noise) to reduce direct or delayed mortality. Although we observed significant differences in physical conditions test fish were exposed to during passage through different turbine operations in Paper II, more studies will be required to identify linkages between physical exposures and injury levels.

6. Use of updated engineering criteria for designing bypass systems that routed downstream migrating fish away from turbine intakes and around a dam on the Columbia River resulted in high fish survival, virtually no injuries, fish passage times that were generally similar to water travel times, and mild stress responses from which fish recovered quickly. These systems can improve survival, but close attention must be paid to their design for them to function properly. Survival, physical condition, passage timing, and blood physiological indicators of stress were all useful metrics for assessing the performance of fish bypass systems (Paper IV).

7. Salmon smolt median and peak migration dates were different in the two rivers studied and approximately 9 days later in the Rickleån compared to the Sävarån. This observed shift in migration timing may have resulted from differences between the two time periods studied, such that environmental cues smolts used for migration initiation were advanced in the most recent decade compared to the 1960s due to warmer water temperatures. The logistic regression model provided a better fit to data from the Sävarån in 2 of 3 years (2005 and 2006), and was only slightly poorer at fitting the data than was the sigmoidal model in 2007. Sea trout smolts responded differently to water temperatures in the Sävarån than did Atlantic salmon smolts and initiated their migrations when water temperatures reached 5.5º C, compared to 8.0º C for salmon; median and peak trout collections were 2.5 and 7.0 days earlier than salmon, respectively (Paper V).

8. The analytical tools and approaches developed here provided specific information on salmon passage issues in the Piteälven, Vindelälven, Sävarån and Rickleån rivers of northern Sweden and at two dams on the Columbia River. However, their primary value may lie in their versatility and applicability to other situations as well. The blade-strike models appear quite adaptable to other species and power stations for making relative assessments among treatments, due to their simple input requirements. The combined blade-strike and life cycle model identified effects on fish populations from dam passage. Use of a combination of metrics (fish condition, survival, and passage timing) when evaluating facilities that route juvenile fish around power stations could be readily applied to studies of facilities at other locations and species, due to its generic nature. The engineering and hydraulic criteria developed used to design successful Pacific salmon juvenile fish bypass facilities offer a starting for similar criteria for other salmonid species as well. Finally, the model of Atlantic salmon smolt migration developed for the Sävarån may be useful in predicting migrations in other rivers in northern Sweden and the Baltic region.

6 Management implications

Results of studies described in this thesis lead to the following recommendations:

1. Actions taken to protect salmon migrating downstream in Piteälven may produce a proportionately greater response from the existing population and available habitat than would similar actions in Vindelälven. However, this conclusion is based on existing conditions, where only 30% of the adult salmon migrating upstream in the Umeälven were assumed to have passed Norrfors Dam. Further studies of the effect this passage condition has on these results should be conducted using methods described here, especially considering that steps are underway to improve adult passage conditions at Norrfors Dam and Stornorrfors Power Station.

2. The conclusion that salmon in the Piteälven may produce a proportionately greater response to potential mitigation scenarios should be revisited once more precise estimates are available of the production capacity of habitat in the Vindelälven. Implementing a smolt monitoring program in this river would allow more precise indices of annual smolt production to be developed. This information would reduce the uncertainty as to whether the current smolt production level is near, or below, capacity. Improved estimates will aid the interpretation of results from studies that indicated differences in population level responses between the two rivers. It would also allow the migration timing model described in Paper V to be tested against smolt timing information from the Vindelälven, a large "mountain" river. While unrelated to the thesis directly, such a program would enable additional information to be obtained on smolt growth through scale and otolith analysis, on population structure through genetic and otolith microchemistry analysis, and on inter-annual variability in population productivity (smolt to adult return rates). Such a program could be based on a series of smolt monitoring facilities located throughout the

watershed, or in facilities designed to bypass smolts around the Norrfors Dam and Stornorrfors Power Station complex.

3. Life cycle models could be used to explore whether density dependent factors are controlling salmon in the Vindelälven and Piteälven. For the Vindelälven, both existing and future (improved) adult passage conditions at Norrfors Dam could be evaluated, along with the range in estimated smolt production capacity of the habitat. The results would allow the sensitivity of results presented here to be judged in terms of model selection and parameterization.

4. The contribution of kelts to the overall productivity of salmon in the Piteälven appeared high, and kelts may make similar contributions to salmon in the Vindelälven once adult passage issues are resolved at the Norrfors Dam. Given this and their apparent high rate of mortality when passing through turbines, additional studies on this component of salmon and trout populations in these rivers should be considered. These could include estimating route-specific dam passage survival (turbines and spillways) through mark recapture studies, and model studies for evaluating the contribution of kelts to overall population productivity and persistence.

5. It appears unlikely that modifying turbine operations at Stornorrfors and Sikfors will significantly improve the survival of smolts or kelts passing these power stations. To reach stock conservation goals, additional measures will likely be required to reduce the proportion of fish passing turbines, such as spilling river flow or installing fish bypass systems.

6. The potential influences of turbine outlet tunnels on downstream migrating fish have not been well documented. The effects on fish from exiting turbine draft tubes in high energy, turbulent flow and passing through tunnels that lack any light for visual orientation should be studied. At the Stornorrfors Power Station, additional field studies will be required to quantify effects to fish from passage through its turbine outlet tunnel and resolve apparent discrepancies between empirical and model estimates of turbine mortality. In combination with mark recapture studies and to help interpret their results, sensors could also be released through the outlet tunnel to record the magnitude and duration of physical conditions (pressure, turbulence, and wall strike) that fish may experience during passage.

7. Delayed mortality should be incorporated into the experimental designs of fish passage survival studies when overall accuracy in the estimates is an objective. While including 15 km of river below a power station captured

much of the delayed mortality at a Columbia River dam, this distance should be verified for Swedish rivers by conducting experiments based on the study design described in Paper II, where multiple receiver arrays were located downstream from a power station to partition mortality effects among river reaches. The distance needed to fully recover from turbine passage will likely vary with fish species, age class, type of turbine, presence of outlet tunnels, river system, and the species of predators and their abundance in river reaches below the stations.

8. Implementing the research program outlined in Paper III would aid the development of safer turbine designs for migratory fish.

9. The hydraulic and engineering criteria described in Paper IV for Pacific salmon offer a starting point for designing similar systems for Atlantic salmon, sea trout, and other salmonid species. However, a thorough literature review should be conducted to determine if adjustments to these criteria are needed for the species of interest. For example, Atlantic salmon and sea trout smolts are larger than Pacific salmon smolts. In addition, bypass system design criteria for adults migrating downstream in regulated rivers needs to be developed for both *Salmo* and *Oncorhynchus*.

7 Swedish summary – Sammanfattning

Ferguson, J. W. 2008. Beteende och överlevnad hos nedströmsvandrande fiskar i reglerade älvar. Doktorsavhandling. ISSN: 1652-6880. ISBN: 978-91-85913-56-5. Originaltitel: Behavior and Survival of Fish Migrating Downstream in Regulated Rivers.

Dammar utgör ofta hinder för fiskvandring mellan sötvatten och havet. I denna avhandling utvärderades nedströmsvandring av fisk i fem älvar i Sverige och USA, varav fyra var kraftverksreglerade. Arbetet fokuserades på arter inom underfamiljen Salmoninae och följande frågor belystes: **Hur stor är överlevnaden av nedströmsvandrande fiskar som passerar turbiner vid kraftverksdammar?** Den skattade överlevnaden av utlekt (kelt) Atlantlax (*Salmo salar*) och öring (*S. trutta*) var 0,547-0,748, därmed signifikant lägre än överlevnaden för smolt, 0,903-0,947, vid de svenska kraftverken i Umeälven (Stornorrfors) och Piteälven (Sikfors). Överlevnaden av juvenil kungslax (*Oncorhynchus tshawytscha*) var mellan 0,814 och 0,946 vid McNary-dammen i Columbiafloden, USA. **Påverkas populationstillväxten av fiskdödlighet som uppstår vid kraftverkspassage?** Ja. Laxens möjliga populationsökningstakt påverkades negativt av dödlighet orsakad av kraftverkspassage vid bägge av de studerade svenska älvarna, dock med olika grad av respons vid minskade passageförluster (potentiellt åstadkommen med nedströmsavledning). Den relativa ökningen i det årliga antalet återvändande honor efter 20 år var högre i Piteälven (68%) än i Vindelälven (46%), förutsatt att både smolt och kelt kan avledas utan dödlighet, motsvarande differens var fyra gånger (38% jämfört med 10%) om endast kelt avleds. **Vilka faktorer ger upphov till fiskdödlighet vid kraftverkspassage?** Även om vissa modeller har visat att den största dödligheten uppstår då fisk träffas av turbinblad, är det svårt att relatera dödlighet till enskilda mekanismer eller kraftverksenheter. Studier vid McNary-dammen visade på skador hos fiskens sensoriska system vid turbinpassage, vilket ökade predationsrisken efter passage och gav upphov till en indirekt fördröjd dödlighet från 46% till 70% av den totala dödligheten. I syfte att utveckla turbiner med högre fisköverlevnad, presenteras forskning rörande gränsvärden av skador som medför dödlighet. **Vilka åtgärder kan vidtas för att minimera kraftverksdödligheten för nedströmsvandrande fisk?** Att förändra turbindriften i sig gav ensamt inte någon betydande högre överlevnad. Fiskpassage genom en speciellt konstruerad 3,9 km lång nedströmsavledaren vid Bonneville Dam i USA, resulterade i hög överlevnad (0,946), inga skador och obetydlig stress. Passagetiderna för fisk motsvarade samtidigt vattnets transporttid. Olika former av avledningskriterier för Stillahavslaxar presenteras. En modell för två svenska älvar demonstrerade att vattentemperaturen var en nyckelfaktor som utlöste och styrde smoltens vandringstider hos Atlantlax, initierad vid runt 8°C och beräknad vara som intensivast kring 12,6°C. Med denna information kan man förutse när fisken anländer till kraftverk och dammar vilket bidrar till att utveckla lämpliga strategier i syfte att öka överlevnaden för nedströmsvandrande fisk i reglerade älvar.

***Nyckelord**: överlevnad, beteende, migration, lax, öring smolt, kelt, turbin*

8 Finnish summary – Tiivistelmä

Ferguson, J. W. 2008. Alavirtaan vaeltavien kalojen käyttäytyminen ja säilyvyys rakennetuissa joissa. Doctor's dissertation. ISSN: 1652-6880. ISBN: 978-91-85913-56-5.

Padot estävät kalojen vaelluksia merellisten ja makean veden habitaattien välillä. Tässä työssä arvioitiin kalojen alavirtaan vaelluksia Ruotsin ja Pohjois-Amerikan viidessä joessa, joista neljä oli padottu. Työ keskittyi Salmoninae-alaheimon lajeihin ja haki vastauksia seuraaviin kysymyksiin: **Mikä on säilyvyys kaloilla, jotka laskeutuvat alavirtaan padoilla sijaitsevien turbiinien kautta?** Atlantin lohen (*Salmo salar*) ja meritaimenen (*S. trutta*) kuteneiden aikuisten (talvikkojen) arvioitu säilyvyys (0,547-0,748) oli merkitsevästi heikompi kuin vaelluspoikasten (smolttien) säilyvyys (0,903-0,947) Pohjois-Ruotsin Stornorrforsin ja Sikforsin voimalaitoksilla. Nuorten kuningaslohille *(Oncorhynchus tshawytscha)* arvioitu säilyvyys USA:n Kolumbiajoen McNary-padolla oli vastaavasti 0,814-0,946. **Vaikuttaako padon läpi kulkeutumisen aiheuttama kuolevuus kalapopulaation tuottoon?** Kyllä. Padon läpi kulkeutuminen vaikutti lohen tuottoon kahdessa ruotsalaisessa joessa, mutta populaatiot reagoivat eri tavoin kuolevuuden vähentämisstrategioihin. Mallinnuksen perusteella padon ylittävien naaraslohien vuotuisen määrän suhteellinen lisäys 20 vuoden kuluttua oli Pitejoessa 68 % ja Vindeljoessa 46 %, kun sekä smolttien että talvikkojen kuolevuus minimoitiin. Kun yksin talvikkojen vaellustappiot minimoitiin, oli lisäys vastaavasti 38 % ja 10 %. **Mitkä ovat mahdolliset kuolevuuden mekanismit, jotka liittyvät turbiinien läpi kulkeutumiseen?** Vaikka eräiden mallikokeiden tulokset viittasivat siihen, että turbiinin siiven aiheuttama mekaaninen vaurio oli pääasiallinen mekanismi, on kuolevuuden liittäminen tiettyyn mekanismiin tai voimalaitoksen osaan vaikeaa. McNaryn padolla tehdyt tutkimukset

antavat viitteitä siitä, että kalan aistijärjestelmään kohdistuvat vaikutukset niiden kulkeutuessa turbiinien kautta lisäävät alttiutta saalistukselle padon alapuolella. Tämä "viivästynyt kuolevuus" muodosti 46-70 % kokonaiskuolevuudesta. Työssä esitetään kalojen vaurioitumisen reunaehdot tunnistava tutkimusohjelma käytettäväksi kalaystävällisempiä turbiineja kehitettäessä. **Mitkä ovat mahdolliset keinot patojen läpi kulkeutumisen aiheuttaman kuolevuuden vähentämisessä?** Turbiinien käytön muuttaminen ei yksinään parantanut merkitsevästi kalojen säilyvyyttä. Kalojen ohjaaminen 3,9 km pituisen ohitusuoman kautta Bonnevillen padolla, USA:ssa, johti suureen säilyvyyteen (0,946). Kalat eivät vaurioituneet, stressivasteet olivat pienet ja kalojen vaellusnopeus vastasi veden nopeutta. Ohitusuoman suunnittelukriteerit Tyynenmeren lohelle esitetään. Veden lämpötila oli avaintekijä, joka kontrolloi Atlantin lohen vaelluksen ajoitusta: vaellus kahdessa joessa alkoi veden lämpötilan ollessa noin 8° C ja lämpötilaan perustuva malli ennusti vaellukselle lähtevien smolttien määrän saavuttavan huippunsa lämpötilan ollessa 12,6° C. Tämä tieto auttaa määrittämään ajankohdat, jolloin padot ohitetaan ja näin kehittämään menetelmiä alasvaelluksen haitallisten vaikutusten vähentämiseksi rakennetuissa joissa.

Avainsanat: säilyvyys, käyttäytyminen, vaellus, lohi, taimen, smoltti, talvikko, turbiini

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Finally, this thesis is dedicated to the people of Sweden. I hope the information contained herein will assist their efforts to rebuild the wonderful wild salmon and trout populations native to the beautiful Baltic Sea.

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