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Atlantic Salmon Migration Past Barriers

Thesis for the degree of Philosophiae Doctor

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Norwegian University of Science and Technology
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Atlantic salmon migration past barriers

A dissertation

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Philosophiae Doctor (PhD)

By

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“*When the strength of the current in a spate is considered,*

and also the sinuous course a Salmon must take in order to avoid the strong rapids,

this power of swimming must be considered as extraordinary.”

(William Scrope, Tweed, 1843)

Acknowledgements

The completion of this PhD-project is a terminal for a somewhat untraditional combination of interests and a winding professional career. My father took me to the rivers and streams and my first small trout was landed the year I turned five. Thanks a lot to him and my mother for introducing me to outdoor activities in my early life. I first stepped into a salmon river when I was 12, but little did I know, even when I graduated as a waste water engineer, that these fascinating animals would eventually turn to become my profession. The road went through consulting hydraulic engineering and a number of years as a river hydraulics researcher before I was given the opportunity to study the migration of the salmon on my own for four unstained years.

The research studies presented in this thesis was funded by the Norwegian Research Council's RENERGI Programme (project no. 177893), with economic contributions from Norwegian hydro power companies, the Norwegian Directorate for Nature Management and the Norwegian Water Resources and Energy Directorate. Thanks go to all those involved for the realization of this project.

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Abstract

The Atlantic salmon depend on successful migration between essential habitats in freshwater and the ocean. However, during both downstream and upstream migration the fish encounter natural or manmade obstacles which can block or delay their migration and migration through hydropower turbine can cause severe mortality. This PhD-study has focused the salmon migration challenges, upstream and downstream, based on studies in Norwegian rivers, and the results are presented in four scientific papers. A study of all the 344 Atlantic salmon fishways in Norway was conducted to investigate the state and function of the fishways and to identify links between passage efficiency and physical characteristics of the construction and the river site. The results showed that 66 % of the Norwegian fishways were passing fish effectively. No correlation was found between fishway functionality and their height, length or technical design. Functional fishways were found at river sites with larger discharge than dysfunctional fishways and efficiency was better among fishways passing man-made obstacles. These findings indicate that fishways in smaller rivers and fishways without supervision and funding from hydropower companies suffer from lack of sufficient attention. While entrance design problems are reported to be a main challenge in many fish pass projects, this was not the same situation among Norwegian fishways. On the other hand, many fishways were not functional because of long time lack of maintenance or damages from physical strain.

Downstream migration of juvenile Atlantic salmon past a hydropower intake in a Norwegian river was studied by use of radio tagged fish during three spring seasons. The results showed that it was possible to create models for both the smolt timing and for the route choice at the intake, where the fish could enter the intake or choose a bypass section. Route choice was controlled by both total river discharge and proportion of discharge in the bypass. Additionally, a model could be developed to describe the effect of strobe lights at the intake. This model demonstrated that more fish chose the bypass when the strobe lights were on during night, while no such effect was found during daytime. Further, a hydropower simulation model was calibrated for the same river. By use of this model, it was shown that river discharge and partition could be optimized to increase bypass migration according to the route choice model. Both reservoir manipulation and manipulation of discharge partition at the intake was simulated and showed that bypass migration could be increased from 20 to 80

% in selected years. The use of models to describe downstream migration represents a useful tool for planning of fish-friendly hydropower production and the methods are most likely applicable to other rivers and regions.

In a case study of man-made weirs on a residual flow river reach the delaying impact from the weirs on upstream migration was studied. Adult Atlantic salmon were enumerated in an upstream fish ladder before and after removal of two concrete weirs. The point of time for peak migration was more than one month earlier after the removal, indicating that even small obstacles may imply significant migration delay. Additionally, the weir removal changed the physical habitat from a lake habitat to a riverine habitat. Consequently, a large increase in spawning and subsequent juvenile densities was observed immediately after restoration.

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List of original papers

The present thesis is based on the following scientific papers, which will be referred to by their roman numbers in the following:

Paper I: Atlantic salmon fishways: The Norwegian experiences
Fjeldstad, H. P.
Submitted manuscript

Paper II: A concept for improving Atlantic salmon smolt migration past hydro power intakes
Fjeldstad, H. P., Uglem, I., Diserud, O. H., Fiske, P., Forseth, T., Kvingedal, E., Hvidsten, N. A., Økland, F. & Järnegren, J. A.
In review: Journal of Fish Biology

Paper III: Optimizing Atlantic salmon smolt survival by use of hydropower simulation modelling in a regulated river
Fjeldstad, H. P., Alfredsen, K., & Boissy, T.
Manuscript

Paper IV: Removal of weirs and the influence on physical habitat for salmonids in a Norwegian river
Fjeldstad, H. P, Barlaup, B. T., Stickler, M., Babrielsen, S. E. & Alfredsen, K. (2011).
River Research and Applications

Note:

All the papers have been written by the author of this thesis and the use of the manuscripts is accepted by all co-authors and the editor of *River Research and Applications.*

Chapter one

INTRODUCTION

Just like a pilgrim, the Atlantic salmon is a long distance traveler, not to a holy place, but their life cycle depends on the anadromous migration between their breeding grounds and feeding in the ocean. Combined with its beauty, size and power, these spectacular migrations, upstream and seaward, have given the salmon an iconic status in addition to its economic and recreational value. At the same time, the dependence of migration between essential habitats implies a particular vulnerability (Johnsen *et al.,* 2011). Historically, Atlantic salmon was distributed in more than 2600 watersheds on both sides of the North Atlantic (WWF, 2001). In North-America, populations were spread from Ungava Bay on the west side of Labrador in Canada and down south to the Long Island Sound near New York City (NEFSC, 2006). In Europe, the range stretched from the Kola Peninsula in Russia and all the way down to Portugal. Today, research reports an overall decline in salmon populations (ICES, 2011). Nearly 90 % of the known, healthy populations are presently found in Norway, Iceland, Ireland and Scotland and based on the number of distinct populations and total occurrence, Norway is the core area for the Atlantic salmon (WWF, 2001). However, the decline in salmon stocks is noticeable also here. From a long list of reasons, 77 Norwegian salmon populations are already threatened or gone extinct, and 114 are classified as vulnerable or as reduced (Hansen *et al.* 2007). This thesis project has focused on Atlantic salmon migration challenges, based on studies in Norwegian rivers. Some of these challenges are particularly caused by anthropogenic impacts. Such impacts, in the thesis represented by hydropower development, are and will remain a challenge for the existence of the salmon populations in the future.

Conservation of the Atlantic salmon relies on comprehensive and multidisciplinary actions in the years to come. For animals which utilize habitats over a large geographic range, negative anthropogenic impacts are often complex and consequently, they can be difficult to mitigate. Therefore, enhancing and maintaining conditions for salmon migration, and thereby sustain production areas, is crucial for the future existence of healthy salmon populations.

UPSTREAM MIGRATION

Endler (1977) considered migration as “relatively long-distance movements made by large numbers of individuals in approximately the same direction at approximately the same time… usually followed by a regular return migration.” This is a rather precise framing for the Atlantic salmon migrations. During its oceanic return migration, the adult Atlantic salmon can move with estimated speeds of 50-100 km day^{-1} relative to the ground (Hansen & Quinn, 1998) and it returns with a precise orientation to its home river (Hansen *et al*., 1993). On its upstream journey the salmon encounter obstacles and barriers that delay or block the migration routes (Mills, 1989; Thorstad *et al*., 2003; Thorstad *et al*., 2005). The salmon appear to display a high degree of local homing within the river, which is regarded as a main reason for the motivation to overcome such hindrances (Harden Jones, 1968; Stasko *et al.,* 1973). The ability of swimming and leaping is strongly dependent on water temperature, and cold water can delay migration past waterfalls and fish passes significantly (Bell, 1973). Local hydraulic conditions around a migration obstacle depend on discharge, and fish passing often takes place in certain discharge windows (Jensen *et al.*, 1986; Rivinoja *et al*., 2001). Water quality, turbidity and weather conditions are additional factors that can influence migration, and these variables often correlate with river discharge (Banks, 1969). Intrinsic factors, such as maturation state or energy state may also influence the migration pattern and motivation from such factors may increase when spawning time approaches (Johnsen *et al.*, 1998; Gowans *et al*., 1999; Thorstad *et al*., 2011).

Construction of fish passage facilities for Atlantic salmon has long traditions. The oldest existing fishway in Europe is found in Ireland (from 1852), and already in 1806 the first fishway was constructed in the United States (Grande, 2010). The oldest fishway in Norway was blasted in rock in 1872 and in the beginning the fishways were likely used as a measure to increase population size and fishing opportunities. Since then, man-made fragmentation of river systems has taken place in the majority of large rivers in the world (Nilsson *et al*., 2005) and one consequence of this is loss of habitat connectivity. Construction of dams and weirs is a major threat to riverine fish populations (Petts 1984; Ward, 1989; Larinier, 2001) and is particularly harmful to diadromous fishes (Scruton *et al.,* 2008). Parallel to the industrial development and increasing anthropogenic impacts, a large number of fish passes of various technical designs have been constructed (Clay, 1995) to try to mitigate fragmentation. There is a long list of Atlantic salmon fishway successes, and the salmon with its abilities and motivation, is certainly willing to use a suitable fishway. Two fish ladders were constructed in the Ballisodare River in Ireland in 1855 and before this, less than 20 salmon were caught yearly in the river. In 1858 the number had increased to 1457 fish and in 1870 the fishery yield was 9750 salmon (Landmark, 1884). At the same time, contrary examples demonstrate that fishway migration can be challenging. Outlets of hydropower stations seems to represent a particular problem and Rivinoja *et al.* (2001, 2005) suggested that only 26 % of the migrating fish in River Umeå in Sweden passed the fish ladder past Stornorrfors power plant. In River Garonne in France Croze *et al*. (2008) found that only 47 % of radio tagged salmon succeeded in passing through the fish lift at the Golfech-Malause hydroelectric complex, while all the tagged fish visited the tailrace area by a median of three times. This suggested that the fishway entrance was not sufficiently attractive. Noonan *et al*., (2011) reviewed 65 papers on fish passage and found a passing success of 61.7 % for salmonids (and only 21.1 % for non-salmonids). Also, they found that passing success increased with fishway length and with water velocities and that pool and weir, pool and slot and natural fishways were more efficient than Denil and locks/elevators. Altogether, past research suggests that the problems must be solved with a combination of knowledge on biological aspects, such as fish behaviour and capabilities, and engineering knowledge, such as hydraulic conditions, physical strain and civil works (Katopodis, 1992; Grande, 2010; Williams *et al.,* 2011). Finally, good functionality over time requires that the constructions are regularly inspected and maintained.

Figure 2. Beautiful and efficient fishway in River Bergebyelva, Finnmark, Norway.

DOWNSTREAM MIGRATION

Even though some juvenile Atlantic salmon never migrate to the sea (Hendry *et al*., 2004), the majority complete their seaward migration during spring and early summer. (As an iteroparous species the salmon display a significant rate of adult post spawners, called kelts, which return downstream to a repeated feeding period in the ocean but this part of the life cycle will not be focused in the following). Hvidsten *et al*. (1998) suggested that the peak smolt migration corresponds with sea water temperature attaining 8 ˚C and a synchronized migration to reach the sea at the correct moment is vital for the smolt survival (Hvidsten *et al*., 1995; Rikardsen & Dempson, 2011). Hence, timing of the smolt migration is later in northern rivers (Davidsen *et al*., 2005). After a physiological pre-adaption to the marine life cycle (Høgåsen, 1998), the seaward migration is triggered by river specific hydrological and geographical characters, such as river discharge and water temperature (Jonsson & Ruud-Hansen, 1985; Hvidsten *et al*., 1995; McCormick *et al*., 1998). Predation from birds and fishes is expected to have a selective effect on migration behaviour (Mather, 1998), which might explain the findings of nocturnal migration in areas with dark nights (Hansen &

Jonsson, 1985; Hvidsten *et al.,* 1995), while this does not seem to be the case in areas with light nights (Veselov *et al*., 1998, Davidsen *et al*., 2005). Reports from other studies suggest that daytime migration is also common in temperate regions but Ibbotson *et al*. (2006) demonstrated that this is mostly at water temperatures above 12 ˚C, when swimming capacity is good. The smolts often migrate in groups and resent research has suggested that these groups can also have a kin-structure (Olsén *et al*., 2004).

Smolt migration through hydropower turbines involves direct blade strike mortality (Montén, 1985) and delayed mortality from other sub-lethal effects (Ferguson *et al.*, 2006). The mortality rate depends strongly on the turbine design and can be related to turbine tuning (Montén, 1985; Skalski *et al.,* 2002). Preventing smolts from entering deleterious hydropower intakes is challenging, since the bulk of the total discharge is typically diverted through the turbines and the smolts appear to follow the main discharge (Scruton *et al.* 2003; Rivinoja *et al.,* 2004). Bypass spill of water can reduce turbine migration (Scruton *et al*., 2008), but good design of the spillway system is crucial, as the smolt seems to be attracted to the bypass only if it is located in the immediate proximity of the intake (Kraabøl *et al*., 2008). A second measure to prevent turbine migration is to construct some kind of physical screening system (Scruton *et al*., 2003). For instance, large screening systems are in use in front of the intakes of the dams in Columbia River (Washington). Such systems are expensive, and floods and floating debris can clog or destroy the screens. Effective bypassing of smolts past intakes requires extensive and site-specific knowledge about the infrastructure, hydraulic conditions and fish behaviour (Williams *et al*., 2011). Finally, successful bypass migration depends on certain monitoring or estimates of the smolt timing. This is particularly important if flood spill is needed, since bypass success is often related to the magnitude and timing of spill water discharge (Fjeldstad *et al.,* 2011).

AIMS OF THESIS

Understanding the mechanisms and solving the problems connected to the Atlantic salmon migrations implies collaboration between biologists, engineers and managing authorities. In this PhD study, a multidisciplinary approach has been employed focusing on i) upstream migration problems in Norwegian rivers and ii) development of model tools that contribute to increase smolt survival past hydropower intakes. The following detailed aims were defined to provide answers to key questions connected to the challenges associated with the salmon migrations:

- What lessons on design and functionality can be learnt from more than 100 years of Atlantic salmon fishway constructions in Norway?
- Which are the main fishway problems, what problems have been solved, and which challenges should be addressed in the future?
- How do man-made weirs influence upstream Atlantic salmon migration patterns, and what are the consequences of such weirs on the physical salmon habitat?
- Which are the physical variables that control downstream smolt migration and route choice at hydropower intakes in regulated rivers, and how can this knowledge be used to adapt hydropower operation in order to reduce migration through turbines?
- How can smolt survival at intakes be increased, combined with cost effective power production through the use of hydropower simulation models?

Chapter two

MATERIALS AND METHODS

Study sites

The study presented in Paper I covers all the 344 Atlantic salmon fishways in Norway. Out of these, altogether 89 rivers were visited on-site from northern Finnmark county (71° N, 29° E) to southern Vest Agder county (58° N, 7° E). With some exceptions, selection of the visited sites was generally based on the potential population increase caused by an efficient fishway at that particular site, judged by local river authorities. Hence, largest attention was paid to fishways with the largest potential. No consideration was given to the virtual function of the fishway or to any technical characteristics or size of the project. The size of the visited rivers ranged from a mean annual flow of 170 m^3s^{-1} down to 1 m^3s^{-1}.

The smolt studies in Paper II and III were carried out in the River Mandalselva, southern Norway (58.0° N, 7.0° E). The site was selected as one of the Norwegian rivers with a hydropower intake on its anadromous reach combined with an important salmon population. The river has a mean annual flow of 88 m^3s^{-1} and the anadromous reach is 47 km long. The catchment covers 1800 km^2 and is regulated by a number of reservoirs and six power plants, the two lowermost on the anadromous reach. The field study reach in Paper II covered the lowermost reservoir Mannflåvann with its hydropower intake and bypass reach, which is approximately 6 km long. Except from flood events, the discharge in the bypass was 3 m^3s^{-1} during the smolt migration periods. Smolts were radio tagged and released 3 km upstream of the reservoir. Tracking of fish was also covering this river reach. The hydropower simulations in Paper III covered the entire catchment with a complete representation of the hydropower system.

The study of weir removal presented in Paper IV was carried out in the river Nidelva, south-east of Norway (58.6° N, 8.7° E). This is one of the Norwegian rivers where man-made weirs were constructed on the anadromous reach for aesthetical reasons. The catchment covers an area of 4000 km^2 with a mean annual flow of 110 m^3s^{-1}. The river is regulated by ten hydropower plants with respective reservoirs, and the study site covered a 2.6 km long residual flow reach downstream of the lowermost hydropower dam at Rykene, only a few kilometres from the ocean. Minimum flow in the study reach was 5 m^3s^{-1} in summer and 1 m^3s^{-1} in winter and three concrete weirs had changed the physical conditions on the reach into a lake habitat.

Tagging and tracking of smolts

Radio telemetry experiments were conducted to monitor individual behaviour of downstream migrating smolts in a regulated river system during three seasons and the observed smolt movements could be linked to the physical variables recorded on the study reach. Two different radio transmitters, manufactured by Advanced Telemetry Systems, USA, were used as tags. The fish were anaesthetised during inserting of the tags and the operation lasted 2-3 minutes for each fish (Figure 2). All handling and tagging was conducted according to the Norwegian regulations for treatment and welfare of animals. Manual tracking of tagged fish was conducted from the banks of the river and lake by use of portable antennas and coordinates of individual fish were plotted on daily maps. In addition, fixed antenna stations tracked tagged fish continuously. The fixed stations had a range of 250-900 meters, depending on topographic characteristics.

Figure 2. Radio tagging (upper picture) and tracking of Atlantic salmon smolt at the banks of River Mandalselva. Lower photograph by Ingebrigt Uglem.

Modelling of smolt migration

The use of models to describe smolt behaviour in a regulated river system make it possible to predict such behaviour in the future, and thereby implement operational strategies which in turn can minimize smolt mortality. Two migration models were developed in the study presented in Paper II. First, smolt migration timing was modelled with generalized linear models (Poisson log-linear models; McCullagh & Nelder, 1989). Smolt catch data from a screw trap (Thedinga *et al*., 1994) was used as input to the model in addition to data for river discharge, water temperature and Julian day. The number of smolts migrating at each single day represented the response variable. Second, smolt migration route choice at a hydropower intake was modelled by a generalized linear model (GLM) of the binomial family (Dobson, 1990) since the observed response variable is a two-level factor (migration through tunnel or bypass). The modelling and testing was performed with the statistical software "R" (R Development Core Team, 2009) for both models. The study presented in Paper III used the two smolt migration models from Paper II in combination with the nMag hydropower simulation model (Killingtveit & Sælthun, 1995). This model calculates power production and thereby the corresponding river discharge within the frames of runoff, hydropower infrastructure, reservoir volumes, market price on electricity and any defined restrictions. Typical restrictions are environmental flows and reservoir filling curves. A model was calibrated for the River Mandal river hydropower system and different strategies were tested to optimize smolt survival past the hydropower intake by manipulation of the production regime.

Effects of habitat adjustments

In paper IV, removal of concrete weirs and the influence on upstream migration and physical habitat was presented. Planning and construction works for the removal of the weirs were supported by results from hydraulic modelling and biological investigations before and after removal of the weirs was used to verify the impacts on the salmon. Spawning activity in the study reach was monitored by scuba diving during five winter seasons before weir removal and during three seasons after removal. In the same period, salmonid eggs were sampled from redds and identified to species level by genetic analysis (Mork & Heggberget, 1984; Vuorinen & Piironen, 1984). Densities of juvenile Atlantic salmon were estimated by use of electrofishing following the method described by Bohlin et al. (1989). Hydraulic modelling of water velocities and depths were conducted with the River2D hydraulic model (Steffler, 2000), with topography data mapped by use of a differential GPS-system and depth soundings. Finally, migration data for adult Atlantic salmon were collected by daily enumerations in a fish ladder upstream the study reach. Here, all fish were counted manually and data for species, sex and length was recorded.

Additional data collection and data analysis

The findings presented in Paper I was based partly on qualitative judgments of fishway functionality, conducted by local river authorities and partly by analysis of quantitative data for characteristics of each fishway and river site. Mean annual river flow for each of the 344 fishway sites was obtained by a combination of methods. A part of the sites were close to gauging stations operated by The Norwegian Water Resources and Energy Directorate (NVE) and data from these stations could be used directly. In addition, national maps of specific runoff produced by NVE and data for catchment sizes were used to calculate river discharges. In the remaining cases, discharges were found in books and reports. Enumeration data for adult migrating salmon in a number of fishways were provided from stakeholders, river keepers, colleague scientists and The Norwegian directorate for Nature Management.

In Paper II and III, existing data for runoff and river discharge was available from NVE and the power company (Agder Energi) while air temperatures were provided by The Norwegian Meteorological Institute. Additional data for water temperatures were given from Norwegian Institute for Water Research and recordings from a Heraeus model M310 sensor (Heraeus Sensor Technology GmbH, Germany), and two Onset Computer Cooperation sensors (Onset Computer Corporation, Massachusetts, USA).

Additional calculations and statistical testing were conducted by use of Windows Excel spreadsheets and Minitab 16 (Minitab Inc. Pennsylvania, USA). Graphs and illustrations have been made in SigmaPlot 11.0 (Systat Software Inc. 2008).

Chapter three

STRUCTURE OF THE SCIENTIFIC WORK

The present PhD thesis addresses vital challenges associated with upstream and downstream Atlantic salmon migration, based on multidisciplinary studies in Norwegian rivers. Given the dramatic decline in salmon populations worldwide, findings from such studies are important for future fish management and to better understand how human activities can be combined with viable salmon populations. The upstream migration in Norwegian fishways is the first topic of this thesis. Up to date information about all the existing fishways for Atlantic salmon in Norway is collected in order to create an overview of their state, function, successes and typical reasons for dysfunction (Paper I). This paper represents a review of Norwegian fishways and shows the characteristics, history and intensions of fish pass construction in Norway. The next part of the work focus on the juvenile seaward migration, and a three years telemetry study of downstream smolt migration is presented in Paper II. This paper suggests two different statistical models which describe i) the timing of the seasonal migration and ii) the choice of route, either through a safe bypass or into a hydropower plant intake. The objective of Paper III is to demonstrate how a hydropower simulation model can be used to modify the production regime in order to maximize the proportion of smolt migration through the bypass described in Paper II. A number of different simulated discharge series from the hydropower simulation model is used as input to the migration models in Paper II to describe scenarios for smolt survival during 22 seasons. The last section of the scientific work is a case study on weir removal as a measure for improved migration conditions. Paper IV presents a study where upstream migration is enhanced by reduction of man-made obstacles, in this case by ultimately removing two concrete weirs. This study also demonstrates positive side effects of the weir removal, for instance improved habitats for spawning and rearing of juveniles.

The following paragraphs include main findings from each paper.

RESULTS OF THE PAPERS IN SUMMARY

Paper I: Atlantic salmon fishways: The Norwegian experiences

Construction of fish passes for Atlantic salmon thrived in Norway during 1870's, promoted by prior successful projects both on the British Isles and in North America. Since then, a general escalation of completed projects has contributed to a large increase of available production areas, with an exceptional large number of passes constructed between 1960 and

1980. Altogether 344 fish passes for Atlantic salmon were identified along the entire coast, the majority designed as concrete pool and weir ladders with surface notches or blasted pools in rock. Of these ladders, 89 were visited on-site in order to verify their design, state and function. Altogether 66 % of the Norwegian ladders were judged to be fully functional, while 21 % were dysfunctional and 8 % had unknown function. In addition, 5 % of the ladders were categorized as partly functional. Functionality was not correlated with river size or magnitude of the water drop at the respective site, and entrance problems were only regarded as the main reason for dysfunction at 5 % of the sites. Also, dysfunction did not seem to be related to technical design inside the ladder and was not more frequent in larger (longer) than in smaller ladders. The majority of dysfunctional fish passes suffered from construction damages and general lack of maintenance. This trend did not demonstrate that the ladders in question were no longer prioritized, but rather a consequence of a large number of constructions that are now 30-50 years old. Even though the focus of fish pass construction has shifted over the years, from increasing fishery yields to conservation of declining salmon population, it is recommended that the pace of maintenance must be increased to catch up with the present forces of nature. Additionally, in order to verify the virtual function of the ladders and as a measure for monitoring and management of the wild salmon populations, enumeration and surveillance systems should be considered in a larger part of the fish passes. A fish ladder provides a physical opportunity for certain monitoring, and such systems were only present in 18 % of the Norwegian ladders.

Paper II: A concept for improving Atlantic salmon smolt migration past hydro power intakes

The general controlling variables for the timing of downstream smolt migration have been described by previous studies, but the timing is specific for each river and population. Also, the route choice at hydropower plant intakes is strongly related to the site-specific topography and hydraulics. However, the fact that smolts tend to follow the bulk discharge seems to remain a global challenge. Based on smolt catches from a screw trap over seven years, a model was developed that described the migration timing in River Mandalselva. The best model fit was obtained with a set of parameters for river discharge, water temperature, changes in these two variables from the previous day and Julian date. Further, approximately 250 smolts were tracked during their downstream migration by use of radio transmitters through three spring seasons. The main objective was to see if bypass spill could increase safe migration around the turbines, and when flood spill gave the best response. Findings from this study showed that the route choice could be described by a statistical model and that the choice was influenced by total river discharge and proportion of the total discharge spilled in a bypass. Large total discharge was negatively correlated with bypass migration, while increased bypass spill increased bypass migration. Additionally, more fish migrated at night, indicating that flood spill gives the best effect at night, when electricity prices are also lower. In the last season of the study, strobe lights were installed on each side of the hydropower intake, intended to scare smolts from entering. The study showed that the strobe lights gave a significantly increased bypass migration when they were used at night, while no such effect could be seen during the light hours. Recommendations from the study has later been used as guidelines for environmentally friendly power production and video surveillance data will eventually be used to evaluate the results.

Paper III: Optimizing Atlantic salmon smolt survival by use of hydropower simulation modelling in a regulated river

Power production is planned by use of market price expectations and hydropower simulation models, the latter representing the physical catchment and its power production infrastructure. In this study a hydropower simulation model for River Mandalselva and its six power plants was fitted to observed production data to analyze the smolt migration in a 22 years period. Combined with the smolt timing model and route choice model from Paper II, different release strategies were tested, aiming at increased smolt migration in the bypass at the intake described in Paper II. The second objective was to explore the economic consequences of the different strategies. The hydropower model simulates short term discharges accurately, and also provides possibilities for long term planning. For example, given the data for the snow pack in the catchment, release strategies for the reservoirs can be adapted to mitigate assumed negative effects on the route choice for the smolts. Not surprisingly, initial simulations showed that smolt survival could be increased by a general increase of residual flow in the bypass from 3 to 15 m^3s^{-1} but at a cost of 14 € per extra fish in the bypass. By looking at eight selected years and simulating increased flood spill in the bypass of 50 m^3s^{-1} in target periods, the bypass migration increased on average from 21 to 51% at the expense of 7 € per extra fish in the bypass. Another simulation showed that bypass migration could be increased from 19 to 80 % and from 26 to 76 % in two selected years when release from an upstream reservoir was postponed one month combined with an increased bypass flow from 3 to 15 m^3s^{-1}. This simulation implied a cost of 4-5 € per extra fish in the bypass. This study demonstrates that smolt survival can significantly be manipulated by use of the above mentioned models and that the power company can utilize their own modeling tools to optimize their power production within the frames of a given requirement for smolt survival.

Paper IV: Removal of weirs and the influence on physical habitat for salmonids in a Norwegian river

In this study, a residual flow reach on a heavily regulated Norwegian river was investigated. The reach is the corridor for upstream migrating adult salmon and all fish is enumerated in a fish ladder upstream of the reach. Three concrete weirs, approximately 1.5- 2 meters high, were constructed on the reach at a time when the salmon was extirpated and esthetical objectives dominated the planning, and this had created a lake habitat between the weirs. Biological monitoring started in 2002, because the physical habitat on the reach was regarded as unsuited for Atlantic salmon when it returned in the beginning of the 1990's as water quality was re-established at a sustainable level. The biological data indicated that spawning was scarce in the reach and previous telemetry studies showed that adult fish hesitated to migrate through, even though fish ladders were found at each weir site. Consequently, a hydraulic model was used to plan partly and complete removal of two of the weirs, and in 2007 the constructions were completely removed. Analyses of the enumeration data from the ladder upstream showed that the migration peak came more than one month earlier after the weirs were removed, indicating that the weirs had represented physical migration barriers and that the effect of this was not fully compensated by the ladders past the weirs. Additionally, biological monitoring demonstrated that salmon spawning sites were recreated in the old bed substratum and were occupied immediately the first season after weir removal, when water velocities increased to more suitable levels for spawning. Accordingly, juvenile Atlantic salmon densities increased dramatically on the reach.

Chapter four

DISCUSSION AND CONCLUSION

While downstream smolt migration problems are mostly linked to hydropower intakes, upstream migration barriers can be both man-made and natural hindrances. The main objective of the PhD project has been to study main migration challenges for Atlantic salmon in Norwegian rivers, and to suggest methods and solutions to enhance migration past physical barriers. That means, how can delay, blocking and mortality be reduced at barriers? Based on the questions asked in the introduction, the main conclusions from the study are summarized in the following paragraphs.

1. Construction of fishways for Atlantic salmon in Norway has opened approximately 2000 km of new production areas since the start in 1872 and today, almost 350 fishways for salmon are found along the entire coast. The positive effects of many of these projects are significant (e.g. Figure 3), and the salmon demonstrate an incredible motivation and ability to overcome barriers.

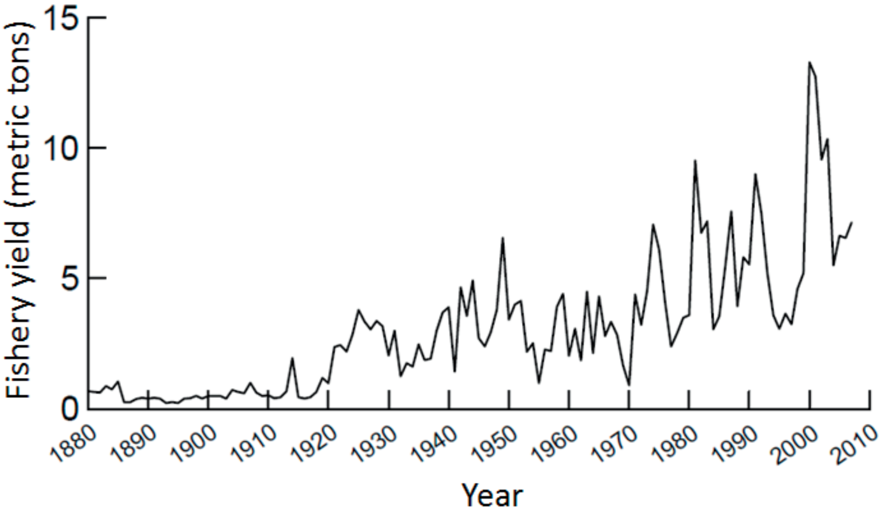

Figure 3. Fishery yields in River Målselva, where a pool and weir fish ladder was opened in 1910. While a few hundred kilos was caught yearly before 1910, the average yearly catch was close to 6000 kg the last 30 years.

The vast majority of Norwegian fishways are pool and weir type ladders and this design has proved to be successful. Length and height of the fishways was not correlated with passing efficiency. In fact, some of Europe's longest and highest fishways were found among the fully functional Norwegian ladders. Also, pool and weir type ladders constructed inside completely dark tunnels over long distance did not seem to delay the migration. Altogether 66 % of the fishways were judged to have good function, which is slightly higher than international findings (Noonan *et al.*, 2011). Even if a considerable number of the Norwegian fishways pass man-made constructions, such as hydropower dams, approximately 75 % of the fishways in Norway are established past natural waterfalls (Grande, 2010). Another typical characteristic is that 70 % of them are found in small rivers, at sites with a mean annual river flow smaller than 20 m^3s^{-1}. Entrance problems and hydraulic problems inside the fishways were identified in a relatively small part of the fishways (6 %). As entrance problems is regarded as a main problem elsewhere (Rivinoja *et al.*, 2001, Croze *et al.*, 2008) it is possible that this important issue has been solved in many Norwegian projects, maybe because of the small size of the rivers. Another explanation could be that fishways that is reported as damaged and not properly maintained masks possible entrance problems. The main reason for dysfunction was physical damages to the constructions and lack of maintenance.

2. Water temperature, river discharge and Julian day were the main controlling variables for the timing of the smolt migration, and route choice at hydropower intakes could be manipulated with bypass spill of water. Conservation of healthy Atlantic salmon population in regulated rivers requires that hydropower production schemes and infrastructure is adapted to this downstream smolt behaviour. Without mitigating measures, the majority of the downstream migrating smolts will choose to enter intakes and depending on turbine design, this route can lead to significant mortality. These findings suggest that studies of local behaviour of downstream migrating smolts related to physical variables are crucial for planning of the mitigating measures. Further, development of modelling tools can predict timing and migration success through bypass systems and thereby increase survival rates significantly (Figure 4).

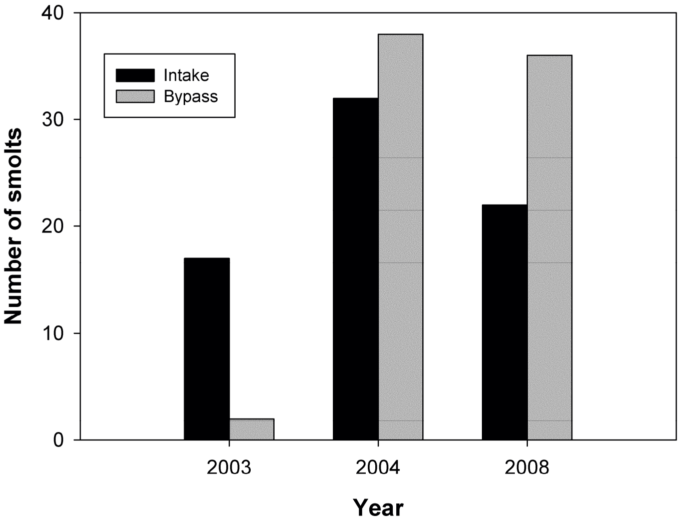

Figure 4. Number of radio tagged salmon smolts that chose to migrate through a bypass system (gray bars) or into a hydropower intake (black bars) three different seasons. In 2003, a minimum discharge of only 3 m^3s^{-1} *was released to the bypass system and only 11 % of the smolts chose that route. In 2008 64 % of the smolts chose the bypass, when bypass discharge was manipulated according to recommendations from a statistical model.*

By use of strobe lights in front of hydropower intakes, smolt migration into the tunnel can be reduced in the dark hours. Scaring of juvenile salmon has been demonstrated in earlier studies (Johnson *et al.*, 2005) and is particularly important in temperate regions with nocturnal migration patterns. The night hours also corresponds with reduced prices on electricity and consequently the period when flood spill to bypass systems involve lowest costs.

3. Hydropower simulation models, which are in use by hydropower companies in most hydropower systems, can be used to enhance smolt migration into bypass systems, by manipulating reservoir release in targeted periods. Such manipulations must be based on local knowledge about the migration timing and relation between smolt route choice and discharge partition at the specific hydropower intake. Spill of bypass discharge is fundamental for bypass migration and a main topic is to identify the timing and magnitude of the sufficient amount.

4. Physical barriers, such as man-made weirs, can delay upstream salmon migration significantly, even if the construction is provided with fishways. Removal of two concrete weirs in a Norwegian river demonstrated that the migration peak in an upstream fish ladder came one month earlier after the weirs were removed. Particularly, this can be the case on residual flow reaches where the river discharge is small. In regulated Norwegian rivers, weirs have been constructed for aesthetical reasons or as a measure to increase wetted area for aquatic life. Consequently, in rivers with migrating fish, the use of weirs should be re-considered. Also, spawning and juvenile salmon densities increased dramatically as the weir removal had changed the physical conditions to a riverine habitat. The use of hydraulic models, combined with biological monitoring, represents a useful method to visualize and plan such habitat adjustments.

RECOMMANDATIONS AND FURTHER WORK

Open migration corridors, upstream and downstream, are essential for viable Atlantic salmon populations in the future. Management of the salmon as an endangered species relies on immediate actions on a wide scale as anthropogenic threats are presently restricting the distribution range and reducing the number of populations. A fundamental issue in the future must be to bring more knowledge about fish migrations on the table and to take this knowledge in use. To reach this goal, future research studies must to large extent be carried out in multidisciplinary scientific environments. The benefits of collaboration between biologists and engineers have fortunately been recognized and this has been demonstrated in this and other resent research studies. The next step should be to incorporate the knowledge in operational management to a larger extent. That assignment is challenging as nature management can include conflicts with other interests, such as energy production, land-use, industry and other infrastructure. To maintain and enhance Atlantic salmon migration in Norway, the following main issues should be addressed in future:

1. The main reason for fishway dysfunction in Norway is long-time lack of maintenance or damages from physical strain. The current lag of maintenance and repair requires a short term investment plan to improve functionality of existing fishways. Subsequently, future maintenance procedures should include emergency action plans when fishways are damaged at crucial sites, and regular scheduled inspections of all prioritized constructions. Altogether, the proven success of fishways for salmon should urge more extensive use of such constructions as a management tool to conserve and re-establish the remaining salmon populations in Norway.

2. The typical Norwegian fishway today is a concrete pool and weir ladder. This design has been successful for salmon migration in Norwegian rivers under most conditions. Still, at sites with large fluctuations in upstream water level the function can be reduced in periods resulting in too much or two little water in the fishway. In future projects this should be solved by use of more flexible intake solutions. Knowledge on this topic partly exists internationally and further development and testing of different designs in laboratory should be used to optimize water intake solutions.

3. Successful downstream smolt migration past hydropower dams remains a general challenge and requires thorough local mapping of the site. In this study, relations between smolt route choice and physical variables at an intake were described by a statistical model, but the mechanisms are not completely understood. In the future, detailed topographic mapping and hydraulic modelling, combined with radio tagging experiments could give more insight to the fish behaviour. Based on this knowledge, an adequate bypass migration system should be established at all sites were adult fish are allowed to pass. This is a question of animal welfare and not only a measure for conservation of the population.

4. Enumeration systems are present in 18 % of Norwegian fishways. Data from such systems gives vital information for future management of the salmon populations, and the fishways represent sites where exact enumeration is physically feasible. Therefore, an increased number of such systems should be considered. Additionally, enumeration data and running collection of data for juvenile salmon densities, detailed catches, spawning redds etc. should be reported continuously to the fishway database described in this thesis. Such data could support the judgment of fishway function.

5. This PhD-study has shown that even small weirs delay upstream salmon migration significantly, and the damming effects of such weirs possibly obstruct or delay downstream migration as well. The focus of river restoration has shifted from aesthetic targets towards holistic biological functionality and removal of such constructions should be considered to a larger extent.

6. As part of this PhD-project, an experimental fishway downstream a hydropower plant was constructed, including a sonar monitoring system (DIDSON). The objective of this study was to increase the knowledge about adult salmon behaviour and preferences at fishway entrances.

Nature research is not always easy and because of different practical problems, one of them some tremendous flood periods, results from these studies could not support significant conclusions so far. This shows that long term studies are required and hopefully, further research can be conducted in the experimental fishway, resulting in new knowledge about fishways passing hydropower dams.

While upstream Atlantic salmon migration has received long time and extensive research attention, the downstream migration past hydropower intakes is still a main challenge. Further development of this field of competence is important. Finally, the conservation of the worlds remaining salmon populations relies on a comprehensive action plan for restoration of migration corridors, new fishway projects and maintenance of our existing constructions. This is a challenge were we can do something.

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Appendix A

Original publications

Paper I

Atlantic salmon fishways: The Norwegian experiences

Paper II

A concept for improving Atlantic salmon smolt migration past hydro power intakes

A concept for improving Atlantic salmon smolt migration past hydro power intakes

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Running title: Atlantic salmon smolt past hydro power intake

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ABSTRACT

Mortality associated with salmonid smolt migration through hydropower turbines is a major challenge for sustaining viable fish populations in regulated rivers. In the present study cost effective (in terms of reducing loss of power production) measures for increasing bypass migration were developed and tested by establishing statistical models for timing of smolt migration and favourable diversion of water to the bypass and the effects of strobe lights were evaluated. Initial tracking of radio tagged smolts showed very low bypass migration under normal hydropower operations. Bypass migration increased when bypass discharge was experimentally increased and a model was developed that described relationships between total river discharge, bypass diversion and smolt migration route. Further improvements were obtained by installing two strobe lights at the tunnel entrance that increased bypass migration during night, but not during daytime. According to the behaviour of radio tagged fish, the implemented measures contributed to increasing the annual proportion of bypass migration from 11 % to 64 %, and according to model predictions to 60-74 % when the hydropower facilities were operated according to the developed models. To ensure correct timing of discharge diversion a smolt migration model was developed that based on environmental variables could successfully predict the general pattern of migration timing. The presented concept for improving smolt migration past hydro power intakes should be applicable in many systems where migration past hydropower installations cannot easily be solved by screening systems.

Key words: Atlantic salmon smolt, telemetry, downstream migration, hydropower intake, migration timing.

INTRODUCTION

Loss of habitat connectivity due to construction of dams is a major threat to riverine fish populations (Ward, 1989; Larinier, 2001). On a global scale more than 40 000 dams higher than 15 m have been built (World Commission on Dams, 2000). These dams restrict fish migrations and alter the natural habitat for many fish species. This problem is particularly evident for anadromous fishes for which viable populations depend on successful migration from breeding grounds to the ocean and return migrations to spawning grounds. Upstream migrations across dams may be ensured by construction of fish ways for which there are several design solutions (EPRI, 2002). These may also be used during downstream seawards migration, but in hydropower facilities migration through turbines are common because the bulk of the total discharge is typically diverted through the turbines. Hydropower turbines represent a major problem for migrating juveniles, causing direct mortality due to blade strike (see for example Monten, 1985 and resent studies by Rivinoja, 2005), shear injuries (Mathur *et al*., 2000) and sub-lethal effects (Ferguson *et al.,* 2006) causing delayed mortality or reduced future reproductive success.

Hydropower dams have caused the extinction or significantly reduced numerous populations of anadromous salmonid fishes, both for Pacific species (*Onchorhyncus*) along the west coast of North American and Atlantic species (*Salmo*) along the east coast and in Europe (Ridell, 2003; Hindar *et al*., 2003). Re-establishment of migration routes is essential to re-introduce or enhance these populations across their distribution areas. While research and implementation of upstream migration solutions is extensive, and indeed often successful (Scruton *et al.,* 2008), seaward migration of juveniles (smolts) remain a major challenge in many river systems. Salmonid smolts are small and numerous, and they appear to follow the main discharge (Rivinoja, 2005) often leading them into the hydropower intake and turbines. Prediction of timing of the smolt run is a crucial foundation for the planning of fish-friendly power production. Subsequently, successful diversion of smolts into bypass systems often relies on diverting large parts of the river discharge into the bypass, at the cost of power production, or large scale and often expensive screening systems (Johnson & Dauble, 2006; Scruton *et al.,* 2008). The latter may be particularly challenging in systems with organic debris or where power intakes and bypass systems are not within immediate proximity.

Based on a case study of smolt migration of Atlantic salmon (*Samlo salar,* L.) in a Norwegian river a concept for successful bypass of salmon smolts was explored based on the following elements: 1) Establishment of a numerical model to predict timing of migration from environmental factors allowing correct timing of mitigating measures. 2) Optimal diversion of water to the bypass system that influence the choice of migration route and 3) the use of strobe lights as a measure to increase bypass migration.

The overarching goal was to ensure successful smolt migration while minimizing loss of power production and avoiding large and costly screening systems. The present paper reports on mitigating measures that, according to the behavior of radio tagged fish have contributed to increasing the proportion of bypass migration from 11 % in 2003 to 64 % in 2008, and according to model predictions to 60 % and 74 % in 2009 and 2010.

MATERIALS AND METHODS

STUDY SITE

The study was carried out in the River Mandal, southern Norway (58°N, 7°E, Fig. 1). The catchment covers an area of 1800 km^2 and is one of the largest rivers in southern Norway with a mean annual discharge of 88 m^3s^{-1} and a length of 115 km. Atlantic salmon and brown trout, (S*almo trutta* L.) can migrate from the sea and 47 km up to the natural waterfall of Kavfossen. European perch (*Perca fluviatilis*), European eel (*Anguilla anguilla*) and brook trout (*Salvelinus fontinalis*) are also common in the watercourse. Salmon fisheries in the river have historically been among the most productive in Norway until the beginning of last century, when acid precipitation caused extensive fish mortality (from 1914) and around 1970 the salmon stock was considered as extirpated whereas brown trout was close to extinction. From 1997 the river has been limed from two automatic lime dosage plants. A new salmon stock (strayers from other rivers and release of eggs and fry with parents from a nearby river) rapidly increased in size, and the catch peaked at 10 metric tons in 2001. The present salmon stock in the River Mandal is a genetically blend, with likely weak or no links to the original stock (Hesthagen *et al.,* 2010). Assumedly, this will affect the pattern of migration and further adaptation to the local environment is expected.

Six hydro power plants are situated in the river and its tributaries with natural and artificial lakes serving as reservoirs for the plants. Two of the power plants, Bjelland and Laudal, are located on the anadromous reach of the river (Fig. 1). Both plants utilize main parts of the river discharge, leaving a limited residual flow in the bypass for fish migration, except for shorter periods with flood events. Bjelland is situated close to the upper migration barrier, while about one third of the salmon production is likely to take place upstream of the intake of the Laudal power plant (Ugedal *et al*., 2006). The intake to Laudal power plant is situated in the Lake Mannflåvatn (4 km long with a reservoir capacity of 1.5 mill m^3). The water level in the Lake Mannflåvatn (67 m.a.s.l) is controlled by a two meter high and 50 meters wide horizontal concrete dam located at the natural outlet crest of the lake, approximately 300 meters downstream (south) from the plant intake (Fig. 1). The concrete dam is also the entry to the 6 km bypass for migration of fish. The present minimum residual discharge between Lake Mannflåvatn and the outlet from Laudal power plant is 1.5 m^3s^{-1} in winter and 3 m^3s^{-1} in summer (May-October). The residual discharge is controlled through a sluice gate in the left side of the dam. The gate has a flow capacity of 13 m^3s^{-1} and exceeding discharge will flood the crest of the dam.

From the intake a rock tunnel, parallel to the residual flow reach, leads production water to the two Francis turbines in Laudal power plant (maximum 110 m^3s^{-1}). The junction point between the residual flow and the tailrace is situated immediately downstream of the plant. Based on turbine specifications and “rules of thumb” for blade strike probability (Montén, 1985) in the order of 70 % smolt mortality is assumed for smolts entering the turbines. Thus, the power station represents a major challenge for reestablishment of the salmon population upstream the Lake Mannflåvatn.

STUDY DESIGN

The study consisted of four major parts: 1) Observations and modelling of timing of smolt migration based on data from a smolt trap operated from 2004 to 2008, 2) mapping of migration route without any manipulations during 2003, 3) mapping and modelling of migration route with manipulation of flow diversion between the hydropower intake and bypass in 2004 and 4) mapping of migration route in 2008 after installation of strobe lights at the intake tunnel, a floating boom barrier outside the intake and flow manipulations according to the model developed in 2004. Mapping of migration route was performed by radio tagging and manual and automatic tracking of smolts. Finally, the developed models were used to estimate bypass migration during 2009 and 2010 when the power station was operated according to developed recommendations.

PHYSICAL VARIABLES

Smolt migration in River Mandal takes place around the month of May. The period is characterized by increasing water temperature and spring floods caused by snow melt. Typically, during spring, the hydro power plant at Laudal will utilize the plant capacity flow, except for the restriction of the 3 m^3s^{-1} minimum flow to the bypass section. Additional flood spill from heavy rain or snow melt is common. The power company provided hourly discharge data for the production flow and in the bypass from their gauging system. (Fig. 2).

Water temperature in the period before, and during, the smolt run is considered one of the controlling variables for the timing of the smolt migration (Jonsson & Ruud-Hansen, 1985). Hourly temperature data from the different power stations was provided by the power company. Additional temperature data at Hesså (Fig. 1) were obtained from two Onset Computer Cooperation sensors and logged every 15 minutes as part of this study (Fig. 3). 2003 was considerably colder than 2004 while 2008 was intermediate and all three years showed the typical temperature increase during the smolt run.

TIMING OF SMOLT MIGRATION

Salmon smolts were caught on their natural run by a floating rotary screw trap (see Thedinga *et al*., 1994) at Hesså, approximately 3 km upstream of the river outlet to the Lake Mannflåvatn (Fig. 1). The trap was located in a constriction of the river, allowing the trap opening to cover a maximum cross section area and inspected every morning at 8 am in the smolt migration period from 2004 to 2008. The screw trap was in use on average 47 days each season and a total of 2419 smolt were caught (Table I).

The smolt migration was modelled with generalized linear models (Poisson log-linear models; McCullagh & Nelder, 1989). Catch data from the trap and data for discharge, water temperature, change in discharge and temperature from previous day and Julian day years was input to the model. Days with trap out of use were omitted from the material. The number of smolts migrating at each single day represented the response variable. All tests were executed with the “R” software package (R Development Core Team, 2009). It was assumed that the total number of smolts caught in the trap represented the total stock and the remaining number, divided on the remaining days of the defined migration period, was used as a model offset. This implied that the estimated number of migratory fish depended on the available number smolts left upstream. The choice between different models was conducted with AIC (Akaike, 1974). After each smolt run the model was verified and adapted with catch data.

MAPPING OF MIGRATION ROUTE

Tagging and tracking of salmon smolts

Atlantic salmon smolts were captured, tagged with radio transmitters and tracked through the smolt run periods of 2003, 2004 and 2008. The main focus of the tracking was to monitor the migration route of individual fish and to link the migration behaviour to physical variables, such as temperatures and discharges and to mitigations introduced in 2004 and 2008.

Weight, fork length and an index of smoltification (1 = smolt sized parr but with clear parr marks, 1.5 = parr with weak parr marks and weak silvering, 2 = weak but visible parr marks and evident silvering on the sides, 2.5 = very weak parr marks and silvered sides, and 3 = no parr marks, complete silvering and pigmentation only along pectoral, dorsal and caudal fins) was recorded for each fish. Parr classified to smolt index 1 were not tagged.

Two different radio transmitters were used as tags. The smallest, model F1410, Advanced Telemetry Systems, ATS, USA (7 x 15 mm, weight in air of 1.0 g, weight in water of 0.6 g, guaranteed battery life of 14 days) and the largest, ATS model F1420 (8 x 16 mm, weight in air of 1.3 g, weight in water of 0.8 g, guaranteed battery life of 28 days). Frequencies were in the range of 142.000-142.500 MHz for both transmitter models. Each fish was identified by a unique frequency and pulse rate (25-45 pulses pr. minute). The fish were anaesthetised by a 3-minute immersion in an aqueous solution of 2-phenoxy-ethanol (EEC No 204-589-7, 0.5 ml/l water). A one cm incision was made on the ventral surface posterior to the pelvic girdle using a scalpel. The transmitter was inserted through the incision and pushed forward into the body cavity. The antenna was pushed through the body wall using a hollow needle, allowing the antennae to exit the body cavity. The incision was closed using two independent silk sutures (4/0 Ethicon). The operation lasted 2-3 minutes. The gills of the fish were regularly irrigated with fresh water during surgery. Tagged fish were transferred to a recovery container. When recovered and normal swimming capability was observed, the fish were released into the river. All handling and tagging was conducted according to the Norwegian regulations for treatment and welfare of animals. A total of 50, 95 and 96 tagged fish were released in 2003, 2004 and 2008 respectively (Table II).

Manual tracking of tagged fish was carried out from the banks of the river and lake using a portable antennae (ATS radio receiver, model R2100). In addition, fixed antennae stations (9-element Yagi) with data loggers (SRX_400, Lotek Wireless Inc.) were established for continuous tracking of tagged fish (Fig. 1). One station was placed next to the power plant intake (logging station 1) and one station in the bypass section, approximately 1600 meters downstream of the dam at Lake Mannflåvatn (logging station 2). Station 1 had a range of 300-950 meters upstream and 200-550 meters downstream, while station 2 had a range of 250-350 meters upstream and 200-250 meters downstream. The range was estimated with dummy transmitters placed at 15-20 cm depth. One additional antennae station was established in 2008, approximately 3 km downstream of the release site, just upstream Lake Mannflåvatn (logging station 3). The range of this station was tested with dummy transmitters at several meters depth to ensure that tagged fish was observed when they passed in deeper parts of the transect. This station was able to provide more accurate information on when the smolts entered the lake. Fish positions were plotted on daily map sheets in scale 1:50 000 with 200 meters precision. In the area close to the hydro power intake the positions were plotted with 50 meters precision.

Data from manual tracking of tagged fish combined with data from automatic logging stations were compiled for analysis of fish movements and to determine migration route. Daily, manual tracking was used to estimate when fish left the release site and fish location within the Lake Mannflåvatn. Fish arrival at the outlet of the lake was estimated based on data from logging station 1 in combination with manual tracking. Logging station 2 (in the bypass) monitored the individuals migrating this route, while fish that were registered and instantly lost at the logging station 1 (and not identified on the station in the bypass) were defined as having migrated into the tunnel. In periods when water discharge was manipulated and in periods when fish were presumed to leave the lake, intensive manual tracking was performed in the bypass section to verify that fish did not pass without being detected by the bypass logging station.

2003 – mapping of migration route without flow manipulations

The smolt migration observations from 2003 represented the river system without mitigations with respect to power production. The Laudal power plant was almost continuously running at a 80-100 m^3s^{-1} discharge (Fig. 3). The discharge in the bypass section was 3 m^3s^{-1} for most of the migration period except for two shorter periods, between 13-16 May (max 33 m^3s^{-1}) and between 24-27 May (max 55 m^3s^{-1}). The radio tagged smolts were released on 7 May in the river just upstream of the inlet to Lake Mannflåvatn. Approximately 100 fish were caught by standard procedure electro fishing (Bohlin et al., 1990) in the upstream tributary Kosåna the day before and the largest 50 individuals were selected for the experiment. The fish were immediately transported in an oxygenated tank downstream to the inlet of Lake Mannflåvatn where they were held in cages in the river before being released. Radio tagged fish were tracked and located manually every day from the release site and down to the outlet of Lake Mannflåvatn between 7 May and 6 June in 2003.

2004 – mapping of migration route with flow manipulations

Since most of the tagged fish migrated into the hydro power intake in 2003, the study in 2004 focused on hydrological and hydraulic factors likely to increase the proportion of smolts that migrate through the bypass. Salmon smolts were caught on their natural run in the rotary screw trap at Hesså (Fig. 1), in the period between 28 April and 22 May. The fish were taken from the trap chamber and placed into floating storage baskets. After a few days retention time the fish were tagged and released just downstream of the trap. The fish were radio tagged and tracked and located manually between 29 April and 31 May. Additional manual inspection was performed in the bypass section 1-4 times a day in high discharge periods in 2004.

2004 was characterized by long periods with minimum flows in the bypass section. During four periods the partition between the hydro power intake and the bypass was manipulated to give artificial freshets to the bypass (Fig. 2). The first two periods lasted approximately 50 hours and peaked at 50 m^3s^{-1} while the two next periods lasted approximately 35 hours and peaked at 25 m^3s^{-1} and 35 m^3s^{-1}, respectively. Between the freshets minimum flow was established in the bypass for 2-6 days.

2008 – mapping of migration route with additional physical measures

In 2008 two fish were caught by electric fishing in Kosåna, while the rest were captured in the rotary screw trap. Tagging was performed using the same procedures as previous seasons. All fish were radio tagged between 30 April and 29 May (Table II). 76 fish were released at Hesså while the last 20 were released directly into Lake Mannflåvatn (Fig. 1). Radio tagged fish were tracked and located manually between 30 April and 15 June. Manual tracking of the bypass section was irregular.

It has been suggested that the use of screening systems (Scruton *et al.,* 2008) and strobe lights (Johnson *et al*., 2005) can guide or scare fish away from intakes. Thus, in 2008 a floating boom was introduced in front of the intake tunnel and one submerged strobe light on each side of the tunnel entrance, both facing upstream towards a point in the middle of the intake streamline. The boom formed a semicircle approximately 15-20 meters from the tunnel and had a one meter deep rubber skirt penetrating 80 cm into the water. The strobe lights were flashing every second day from 12 noon to 12 noon in the period from 10 May to 21 June. During the days when strobe lights were on the lights flashed for 5 minutes, and then turned off for 5 minutes, and so on for 24 hours. This procedure was selected under the assumption that it would reduce the risk of habituation (Patrick *et al.,* 1985).

A larger flood volume during the spring of 2008 provided long periods with flood spill and high discharges in the bypass section (Fig. 2). The discharge in the bypass was generally between 20 and 60 m^3s^{-1} and was not reduced to 3 m^3s^{-1} until mid June. At the start of the smolt run, the total flow reached 500 m^3s^{-1}. Flow through the turbines was reduced in 25 periods during the study period, as part of the experiments. The flow was generally reduced from the evening to the next morning as smolts are assumed to descend mainly at night (Ibbotson *et al*., 2006). The size and duration of flow reduction was on average 52 m^3s^{-1} (SD 21) and 10 hours, (SD 3.3). Reductions in turbine flow did not instantly increase the bypass flow with the equivalent value, because bypass flow is controlled by the water level in the lake, which is delayed with several hours due to the reservoir filling curve.

MIGRATION ROUTE MODELLING

MIGRATION ROUTE MODELLING

The purpose of the route modelling was to describe the probability for fish to choose the bypass instead of the intake to the power plant, based on data for water discharge through the different waterways and other physical variables that may influence this choice. The smolt migration route choice was modelled by a generalized linear model (GLM) of the binomial family (Dobson, 1990) since the observed response variable is a two-level factor (migration through tunnel or bypass). The modelling was performed with the statistical software “R” (R Development Core Team, 2009). The data set for 2003 was relatively small, and since only two fish went through the bypass under extreme condition we excluded the 2003 figures from further analysis. The data sets for 2004 and 2008 were implemented in the modelling work.

MODEL PREDICTIONS FOR BYPASS MIGRATION IN 2009 AND 2010

Based on the conclusions from the studies in 2003, 2004 and 2008 the river management authorities, stakeholders and power company agreed on using the developed models and physical mitigations in 2009 and 2010. The impacts of the suggested power plant operation (and strobe light/floating boom) on route choice were not verified with a radio tagging project and consequently, the following analyses only serves as illustration of potential effects, pending field validation.

During the main smolt migration period in 2009 and 2010, the division of water between Laudal power plant and the bypass was manipulated to maximize bypass migration according to the established model (based on the 2004 and 2008 data). During the manipulation period from 6 to 25 May in 2009, the average total flow was 62 (± 18SD) m^3s^{-1}. In 2010 flow manipulations were performed between 5-26 May and, the total discharge averaged 41 (± 12SD) m^3s^{-1}. The bypass discharge was increased during night in both years. In 2009, the average bypass flow was 14 % of the total during day and 33 % during night, while the corresponding proportions in 2010 where 25 % and 54 %. Based on the smolt trap catches, the periods of discharge manipulations were estimated to cover 77 % of the migrating smolts in 2009 and 67 % in 2010. Data on the water discharge diversion in these two years and data on number of captured smolts in the trap at Hesså was used as input to the model of route choice to estimate proportion of smolts that migrated through the bypass. Also, for comparison the number of smolts in the bypass under a minimum bypass flow regime was estimated. The distribution between day and night migration was assumed to be similar to that observed in 2004. Similarly, arrival times at the Lake Mannflåvatn outlet were estimated from the median migration time observed in 2004. Since the water discharge in 2009 and 2010 were considered to be quite similar to 2004, migration parameters from this year were applied for predictions rather than using data resulting from the very high flow conditions in 2008.

RESULTS

MODELING OF MIGRATION TIMING

Based on the smolt catches from the different years it was found that the timing of the smolt migration could be successfully modelled by water temperature and discharge and changes in these variables. Migration was also strongly related to Julian day and the predictions depended on the estimated remaining number of available smolts. The following model was fitted to estimate the number of migrating smolts (Table III):

$$\begin{aligned}\ln(\mathit{Smolts}) = {} & \ln\left(\mathit{MeanSmoltNumber}\right) + \mathit{Const} + \beta_1 \times \mathit{Tempsum} + \beta_2 \times \mathit{Temp} + \\ & \beta_3 \times \mathit{Tempdiff} + \beta_4 \times \mathit{Discharge} + \beta_5 \times \mathit{Dischargediff} + \beta_6 \times \ln\left(\mathit{Discharge}\right) + \\ & \beta_7 \times \ln\left(\mathit{Temp}\right) + \beta_8 \times \mathit{Days}\end{aligned}$$

where

Smolts is the estimated number of smolts that migrate that day,

MeanSmoltnumber is the mean number of smolts per day not yet caught in the trap (the total number of smolts caught after each day divided by the number of days left of the migration period),

Tempsum is the accumulated degree days from March 1,

Temp is the water temperature that day,

Tempdiff is the change in water temperature that day,

Discharge is the water discharge at the site that day,

Dischargediff is the change in water discharge from the previous day, and
Days is the number of days since April 1.

This model had an AIC value of 2004, and a R^2 of 0.60 (R^2_{val} = 0.46). While the model fitted the smolt catches well, it underestimated the observed early migration peak in 2007 (Fig. 4). The days when 25, 50 and 75 % of the smolt migration had passed was also predicted well by the model (Fig. 5), except for 2007. However, the model did predict an earlier smolt migration in 2007 than in the other years. A number of simpler models with fewer parameters were fitted. They were all rejected because their AIC values (ranging from 2041 to 2253) were substantially larger than the AIC value of the chosen model.

CHOICE OF MIGRATION ROUTE

In 2003, a large part (32%) of the tagged fish did not migrate from the release site (Table IV). Of the remaining 34 individuals, 19 migrated out from the lake (via the bypass or the turbines; hereafter termed migrants or migratory fish). The migrants had larger fork length (t=2.17, p=0.036), and had higher smolt indexes (t=3.24, p=0.002) than tagged fishes that remained in the river or lake after tagging. Also the migrants left the release site at half the time of the fish that stopped elsewhere in the river system (t=-2.13, p=0.048). Of the 19 migrants 17 (89 %) entered the hydro power intake between 11-26 May and two (11 %) migrated into the bypass at 25 May and 26 May (Fig. 6). This demonstrated that the intake attracted migrating smolts and prevented safe migration to the sea under the prevailing hydrological conditions during spring 2003. Two rain episodes increased the bypass discharge (Fig. 2), but the effect on migration route was small. Eight smolts migrated from the lake during the first episode, all through the turbines. Another six smolts migrated during the second episode, four through the turbines and two in the bypass. Another five smolts migrated through the turbines before and between the two episodes.

During the spring 2004, diversion of discharge between the power station and the bypass was actively manipulated at four occasions, creating situations that was assumed to be both favourable and unfavourable for bypass migration. 38 smolts migrated the bypass and 32 entered the intake (Table IV). Hence, 54 % of the smolts that eventually left Lake Mannflåvatn migrated through the bypass, a large increase from the year before (Fig. 6). The remaining 20 (22 %) did not migrate. 14 of these 20 had left the release site while six remained at the site (possibly dead). The smolts that went into the intake had smaller smolt index (likely less mature as smolts) than those that went through the bypass (t=2.17, p=0.034). Fish that entered the bypass stayed longer in the lake (t=-2.34, p=0.024) than the fish entering the intake tunnel. These findings indicate that the most mature smolts may have a higher probability of selecting the bypass. Migration through the intake (day: 25 %, night: 75 %) tended to be more diurnal than in the bypass (day: 47 %, night: 53 %), (Chi^2-test, $\chi^2 = 3.72$; p=0.054). Because periods with medium or high total discharge were shorter than periods with small total discharge, this was adjusted in the analyses by dividing the total number of migratory fish by the amount of time of the actual discharge intervals (Fig. 7). A migration route model was developed by using the explanatory variables total discharge (*Total*), proportion of total discharge in the bypass (*Share*), and the smolt index (*SI*).

$$\log it(\pi) = \log\left(\frac{\pi}{1-\pi}\right) = \beta_1 \times Total + \beta_2 \times Share + \beta_3 \times SI ,$$

where

π is the probability that a fish migrate through the bypass (estimated parameter values in Table V). The factors $[\beta_2, \beta_3]$ were marginally insignificant but were included in the model as we suggest they have a mechanistic relation to migration route. Because smolt index is independent of flow partition and not a variable that can be "regulated", a simplified model was developed, based on total discharge (Total) and the proportion of discharge in the bypass (Share) (Table V). In order to visualise the probability for smolt to select the bypass, a probability matrix was established based on the two-variable model (Table VI).

In 2008, a total of 61 of 96 (64 %) individuals were recorded when they migrated through either the bypass or the intake tunnel (Table IV). Of the 61 migrants 49 were released at Hesså while 12 were released in the lake, representing 64 % and 60 % of the two batches respectively. Due to somewhat difficult logging conditions, it is likely that 8-10 fish migrated without sufficient recordings at the fixed logging stations and these fish were not included in the analysis. Additionally, three smolts migrated the bypass at uncertain point of time and were also excluded from further analyses. Of the remaining 35 individuals, 20 smolts were still observed in the lake at the end of the study period. Similarly to 2003, migratory fish was larger than non-migratory ($p=0.034$ for length and $p=0.051$ for mass).

The water discharge in the River Mandal in spring 2008 was generally very high, and much higher than in both 2003 and 2004 (Fig. 2) and attempts to develop a common model for 2004 and 2008 failed. The latter attempts are also questionable because pooling observations with non-overlapping ranges (in this case discharge) into one dataset may give dubious results. Different factors or mechanisms may influence the choice of migration route at very different discharges and in addition, strobe lights, a barrier (boom) and new flow manipulations were introduced in 2008.

In contrast, effects of the strobe lights were strong and could be modelled. Because manipulations of flow diversion between the power station and bypass were done during night (by reduction of production flow), separate models were fitted for Night (from 22:00 to 04:59, n=44) and Day (from 05:00 to 21:59; n=14). The strobe lights were by design independent from the rest of the variables (on and off every second day) so the effect of them could be evaluated separately. The model showed that the strobe lights had no effect during daytime (the lighter hours) whereas they had a strong effect during night. For the 24 hour periods when the strobe lights were off, approximately the same number of smolts went into the intake as through the bypass, and the proportions of migrations for Day and Night for both migration route alternatives were equal (Table VII). When the strobe lights were on, the number of migrations during daytime was approximately the same through both routes as when the lights were off, i.e. the lights had no effect during the day. In contrast, during the night much fewer smolts entered the tunnel and more migrated through the bypass.

The model for the effect of strobe lights on the migration route choice during night was:

$$Logit(\pi) = Log\left(\frac{\pi}{1-\pi}\right) = 0.167 + 1.22 \times SL$$

where π is the probability to choose the bypass when migrating during night and SL is the strobe lights (Off = 0, On = 1) (p = 0.078). The probability of bypass migration during the night increased from 0.54 (strobe lights off) to 0.80 (lights on) and the predictions for tunnel migration fits well with the observations.

More extensive modelling attempts, with a suite of explanatory variables such as total discharge and proportional discharge through the bypass in addition to strobe lights, failed to significantly improve the model for migration route choice during night in 2008. For the smolts that migrated during the lighter hours (Day) in 2008, an acceptable model for migration route choice was not obtained.

More fish migrated at night (from 22:00 to 04:59) than during day all the three years. In 2003, 12 of the 19 (63 %) left the lake at night (22:00 – 04:59) (Fig. 8). The next year, 44 out of 70 migrants (63 %) went out during night. In 2008 the same figure increased to 69 % even though the night here represents only 7 of 24 hours. Hence, migration was more than five times more likely to occur during the night than during the day.

MODEL PREDICTIONS FOR BYPASS MIGRATION IN 2009 AND 2010

In 2004, the number of smolts that migrated out of Lake Mannflåvatn during day and night hours were similar, hence 50% of the smolts registered in the traps in 2009 and 2010 were assumed to migrate during night. The time used from the smolt trap to the outlet of Lake Mannflåvatn was set to three days, corresponding to the median migration time in 2004.

Assuming that the effect of water discharge conditions on the choice of migration route was the same in 2009 and 2010 as in 2004, and ignoring the effect of strobe lights, the predicted proportion of smolts migrating throught the bypass given by the simplified model (Table V) was 49 % in 2009 and 67 % in 2010. Both higher total discharge and higher proportion of bypass flow induced the higher estimates for 2010. However, based on the 2008 migration data, a significant effect of the strobe lights during the night hours was revealed. Adding the estimated effect of strobe lights to the simplified route model, the predicted proportion of smolts migrating through the bypass increase to 60 % in 2009 and 74 % in 2010. If only a minimum residual discharge had been allowed in the bypass, the predicted number of smolts in the bypass would have been 51 % and 62 % in these two years (including the strobe light effect). Hence, based on model predictions, the mitigating water flow manipulations have increased the number of bypass migration by 18-19 % in both these periods.

The predictions of bypass migrations are sensitive to the assumption of equal proportion of smolts migrating during night versus day, since both higher bypass flow during night and an effect of strobe light only at the dark hours increase the probalility of smolt swimming though the bypass. In 2008, approximately 75 % of the registered smolts migrated during night. Applying these proportions in the above calculations, including the effect of strobe lights, increase the predicted proportion in the bypass to 71 % in 2009 and 83 % in 2010. Field validation of these model predictions have not been performed.

DISCUSSION

Fish-friendly power production is a matter of economic costs and it is important that mitigating measures such as spill of water is implemented at the correct time for maximum efficiency at minimum costs. The developed smolt timing model is a useful tool in this context. The model could successfully predict 25, 50 and 75 % migration, although predictions were poorer for the cold spring of 2007. The environmental variables influencing migration timing (discharge and water temperature, and changes in these from the previous day) are similar to those found in other studies (Hvidsten *et al.,* 1995; Whalen *et al.,* 1999). The number of parameters in our model is higher than the number of parameters in previous studies (for example six in Hvidsten et al, 1995 which used the same type of model). However, the model was selected because it gave a considerably lower AIC value than any of the alternative tested models with fewer parameters. In addition, mean migration speed (from the release site to the Lake Mannflåvatn, and through the lake to the tunnel area) from the telemetry studies can be used to predict when the majority of the smolts arrive at the intake tunnel. Finally, it is interesting to note that in the order of 60-70 % of the smolts left the lake during nighttime (the seven hours from 22:00-04:59), indicating that measures would be most effective when implemented at night. The pattern of predominately nocturnal migration of Atlantic salmon smolt has been repeatedly shown (Olsén *et al.,* 2004; Riley *et al*., 2007; Hvidsten *et al*., 1995), with notable exceptions at high temperatures (Ibbotson *et al*., 2006; Moore *et al.,* 1995) and at high latitudes with midnight sun (Davidsen *et al.,* 2005).

The proportion of radio tagged migrating smolts in the bypass increased from 11 % in 2003 to 54 % in 2004 and further to 64 % in 2008. Parts of this change is likely due to the differences in discharge conditions among years, but it is evident from the analyses and developed models that the tested mitigating measures affected migration route choice. Higher number of tagged individuals could have improved the power of the analyses. However, this number was constrained by both costs and national regulations regarding animal experiments.

Under the prevailing hydrological conditions during the smolt run in 2003 (full production at Laudal power plant and minimum residual discharge) it is evident from the observed migration route choices that the smolts experienced high mortality from turbine impacts. Because such conditions is common during spring in this river, successful reestablishment of a self sustaining and exploitable (by angling) salmon population upstream of the power station intake depends upon measures that increase bypass migration and thus smolt survival.

By increasing the discharge into the bypass a large increase in smolt migration through the bypass section was observed in 2004. The developed migration route choice model showed that bypass migration generally decreased with increasing total discharge but increased with increasing diversion of the total flow to the bypass. These findings suggest that power production planning for low discharge during spring and spill of water into the bypass during smolt migration can increase the smolt survival significantly. Due to limited reservoir capacity, however, spring discharge cannot be significantly reduced under many hydrological conditions (large snowmelts or rainfalls) and the necessary spill of water during high discharge conditions will significantly reduce power production at Laudal power plant. Thus, other measures to increase bypass migration are highly profitable.

The spring flood during the smolt run in 2008 was large and a model for the effects of discharge partitioning between the turbine intake and bypass could not be developed. Thus, it appears that flow partition was not particularly important for route choice under the high discharge conditions in 2008. There might be a threshold value for “sufficient” discharge in the bypass and, flow partition as a parameter may not be the relevant explanatory variable for route choice under such conditions. Further analyses and measurements of the site specific hydraulic conditions and water velocity patterns around the intake can probably increase the understanding of these mechanisms. The boom that was introduced in 2008 may also have influenced the migration route, but the effect could not be analysed since it is confounded with among year differences. However, a separate effect from the strobe lights was demonstrated during the dark hours, reducing the number of smolts that entered the intake tunnel significantly during night. Thus, in accordance with other studies on the effects of strobe lights (Johnson & Ploskey, 1998) it is likely to assume that the lights scared migrating smolts away from the intake area.

In addition to the environmental variables and the strobe light, the degree of smoltification appeared to influence migration route. Fish that migrated the bypass were, judging from their morphology, more typical smolts at the time of tagging than those that migrated through the tunnel. Moreover, smolt that migrated the bypass stayed longer in the lake. The latter effect may also be related to smoltification because maturation is expected to progress during the spring.

Implanting radio transmitters may affect fish behaviour. Moore *et al.* (1990) found no effects of radio tagging on physiological parameters or swimming behaviour in Atlantic salmon juveniles or smolts. In contrast, McCleave & Stred (1975) and Peake *et al.* (1997) found negative effects on swimming capacity in some of their groups. Thus, the most likely negative effect of tagging in the present study would be a reduced swimming capacity. However, the relatively high rate of movements observed indicate that the swimming capacity was not considerably affected. A number of fish were lost during the study, indicating that battery longevity and radio range were limiting factors.

The developed models for timing of the smolt run, the effect of flow partitioning at typical discharge levels and the effects of the strobe lights were combined to predict migration route during 2009 and 2010 when the developed knowledge was used as guide for fish friendly power production (spill of water and strobe lights in operation every day). Predictions indicated that a high proportion (60-74 %) of the smolts migrated through the bypass. However, such predictions need to be validated by further migration studies, currently under planning. If proven successful, the presented concept for improving smolt migration past hydro power intakes should be applicable in many cases where migration past hydropower installations cannot easily be solved by screening systems. Elements such as flow partitioning and strobe lights could by themselves be useful in other smolt guiding systems.

ACKNOWLEDGEMENTS

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TABLES

Table I. Number of smolts caught in the smolt trap at Hesså and the number of days when the trap was operational during 2004-2008.

	2004	**2005**	**2006**	**2007**	**2008**
Number of smolts caught in rotary screw trap	568	447	562	537	305
Number of catch days	47	47	57	38	48

Table II. The number of radio tagged smolts, dates and site of release and biological characteristics for the smolts (average and SD for fork length, body weight, smolt index [see main text] and condition factor) in 2003, 2004 and 2008.

Date of release		**Release site**	**Fork length (mm)**		**Weight (g)**		**Smolt index**		**c-factor**	
	N		**Av**	**SD**	**Av**	**SD**	**Av**	**SD**	**Av**	**SD**
Total 2003:										
May 5	**50**	Mannflå	**12.5**	**1.3**	**17**	**5.1**	**2.3**	**0.5**	**0.86**	**0.11**
2004										
apr.29	6	Hesså	14	1.1	19.8	4.5	2.3	0.4	0.72	0.06
May 3	19	Mannflå	14.1	0.8	21.4	3.7	2.8	0.3	0.75	0.05
May 5-11	53	Hesså								
May 16	10	Mannflå	14.3	0.5	22.7	3	2.7	0.2	0.77	0.03
May 22	18	Lake Mannflåvatn	14.1	0.8	20.7	4.1	2.9	0.3	0.73	0.05
Total 2004:	**95**		**14.4**	**0.9**	**23**	**5.3**	**2.7**	**0.3**	**0.76**	**0.05**
Total 2008:										
April 30-May 29	**96**	**Hesså**	**14.5**	**1.3**	**23.5**	**7.1**	**2.5**	**0.4**	**0.75**	**0.07**

Table III. Estimated coefficients for different variables in the smolt migration model. Paramteres are given both for the model including data from all years (Total model; with estimated X^2), and for subsets of data where the tabulated years where omitted. The later is used for model validation. All coefficients had $p<0.001$. R^2 estimated by regression for the total model = 0.60, R^2 estimated by regression for the validated models = 0.46.

		Model without years (for validation)					
Coefficient	**Total model**	**2004**	**2005**	**2006**	**2007**	**2008**	**X^2 total model**
Intercept	-14.585	-15.162	-13.294	-20.423	-13.471	-15.052	425.107
β_1	0.006	0.007	0.006	0.014	0.004	0.006	69.293
β_2	-1.025	-0.646	-1.089	-1.604	-1.214	-1.081	158.385
β_3	0.349	0.43	0.374	0.295	0.267	0.373	70.68
β_4	-0.03	-0.035	-0.027	-0.027	-0.025	-0.03	170.201
β_5	0.029	0.026	0.031	0.024	0.036	0.029	490.853
β_6	1.912	2.497	1.613	2.257	1.211	1.962	164.099
β_7	8.822	7.037	8.862	13.928	9.691	9.084	238.298
β_8	-0.049	-0.075	-0.047	-0.142	-0.016	-0.05	75.085

Table IV. Main figures for the movements of tagged smolts in 2003, 2004 and 2008. Bold figures add up total number of tagged smolts each year. The three last rows indicate time of migration and days spent in the lake for the fish that eventually migrated out of the lake.

	2003	**2004**	**2008**
Number of smolts not leaving release site	16	6	8
Number of smolts left in the lake/river at the end of the study	15	14	27
Lost signals		5	
Number of smolts migrating through bypass reach	2	38	39
Number of smolts migrating into intake	17	32	22
Total number of tagged smolts	**50**	**95**	**96**
Number of smolts migrating at night (22:00-04:59)	12	44	40
Number of smolts migrating during day (05:00-21:59)	7	26	18
Days spent in the lake (only migrants included)	9.9	-	6.8

Table V. Estimated coefficients for the different variables in the migration route choice model for 2004. Parameters for the three-variable model is listed first, with parameters for the simplified (two-variable) model following under.

Variable	**Coefficients**	**Estimate**	**SE**	**z**	**p**
Three-variable model:					
	Intercept	-3.370	2.630	-1.280	0.199
Total flow [m^3 s^{-1}]	β_1	-0.032	0.010	-3.180	0.002
Proportion of flow in bypass	β_2	0.030	0.016	1.860	0.063
Smolt index	β_3	1.660	0.950	1.750	0.080
Two-variable model:					
	Intercept	1.140	0.622	1.380	0.067
Total flow [m^3 s^{-1}]	β_1	-0.032	0.010	-3.260	0.001
Proportion of flow in bypass	β_2	0.031	0.016	2.000	0.045

Table VI. Proportion (%) of smolts migrating bypass as function of total discharge and proportion of total discharge in bypass, as predicted by the two-variable model in Table V. Dark grey: high proportion of smolts in bypass,. medium grey: medium proportion, light grey: relatively small proportion. Numbers in italic in white fields are not practically applicable but are included to give a general picture of the model.

Proportion of total discharge in bypass (%)	**Total discharge (m^3 s^{-1})**											
	20	**30**	**40**	**50**	**60**	**70**	**80**	**90**	**100**	**110**	**120**	**130**
10	70	63	55	47	39	31	25	19	14	*11*	*8*	*6*
20	76	70	63	55	46	38	31	24	19	*14*	*11*	*8*
30	82	76	70	62	54	46	38	31	24	*19*	*14*	*11*
40	86	81	76	69	62	54	46	38	30	*24*	*18*	*14*
50	89	86	81	76	69	62	54	45	37	*30*	*24*	*18*
60	92	89	86	81	75	69	61	53	45	*37*	*30*	*23*
70	94	92	89	85	81	75	68	*61*	*53*	*45*	*37*	*29*
80	96	94	92	89	85	81	*75*	*68*	*61*	*53*	*44*	*36*

Table VII. Migration route choices for 2008, split into smolt numbers migrating during periods with strobe lights off or on, and into migrations during day or night.

Strobe lights	**Off**			**On**		
	Day	**Night**	**Total**	**Day**	**Night**	**Total**
Bypass	3	13	16	4	16	20
Intake	3	11	14	4	4	8
Total	6	24	30	8	20	28

FIGURE CAPTIONS

Fig. 1. The River Mandal and the study area with logging stations and capture and release sites indicated Rectangular covers the bypass section.

Fig. 2. Water discharge from Lake Mannflåvatn in 2003, 2004 and 2008 in the period from 1 May to 15 June.

Fig. 3. Water temperature at Bjelland in 2003, 2004 and 2008 in the period from 20 April to 20 June.

Fig. 4. Migration patterns at the rotary screw trap at Hesså in five different years. Predictions from the total model and predictions from models fitted without the year in question is also shown.

Fig. 5. Predicted day of 25, 50 and 75 % smolt migration from the model and from the observations. The one-to-one line is drawn to show where the plots are supposed to fall if the model predictions are similar to the observations. The 2007 data are marked in the figures.

Fig. 6. Number of smolts migrating into the intake and bypass each of the years 2003, 2004 and 2008.

Fig. 7. Migration of radio tagged smolts in tunnel and bypass between 7 May and 5 June in 2004. ***(a)*** *Proportion of smolts at different total discharge of total number of tagged (and migrated) smolts, and* ***(b)*** *Smolt migration rates for intake and bypass at different discharges as proportion of migratory fish related to the period of time when the actual discharge interval was present. Large values can indicate large smolt number or short periods with that actual discharge, and vice versa.* ***(c)*** *Proportion of total number of migrated individuals at different proportions of total discharge in bypass.* ***(d)*** *Proportion of migrated individuals in tunnel or bypass within each total discharge interval.*

Fig. 8. Frequency of smolts migrating at different hours of the day in 2003, 2004 and 2008.

FIGURES

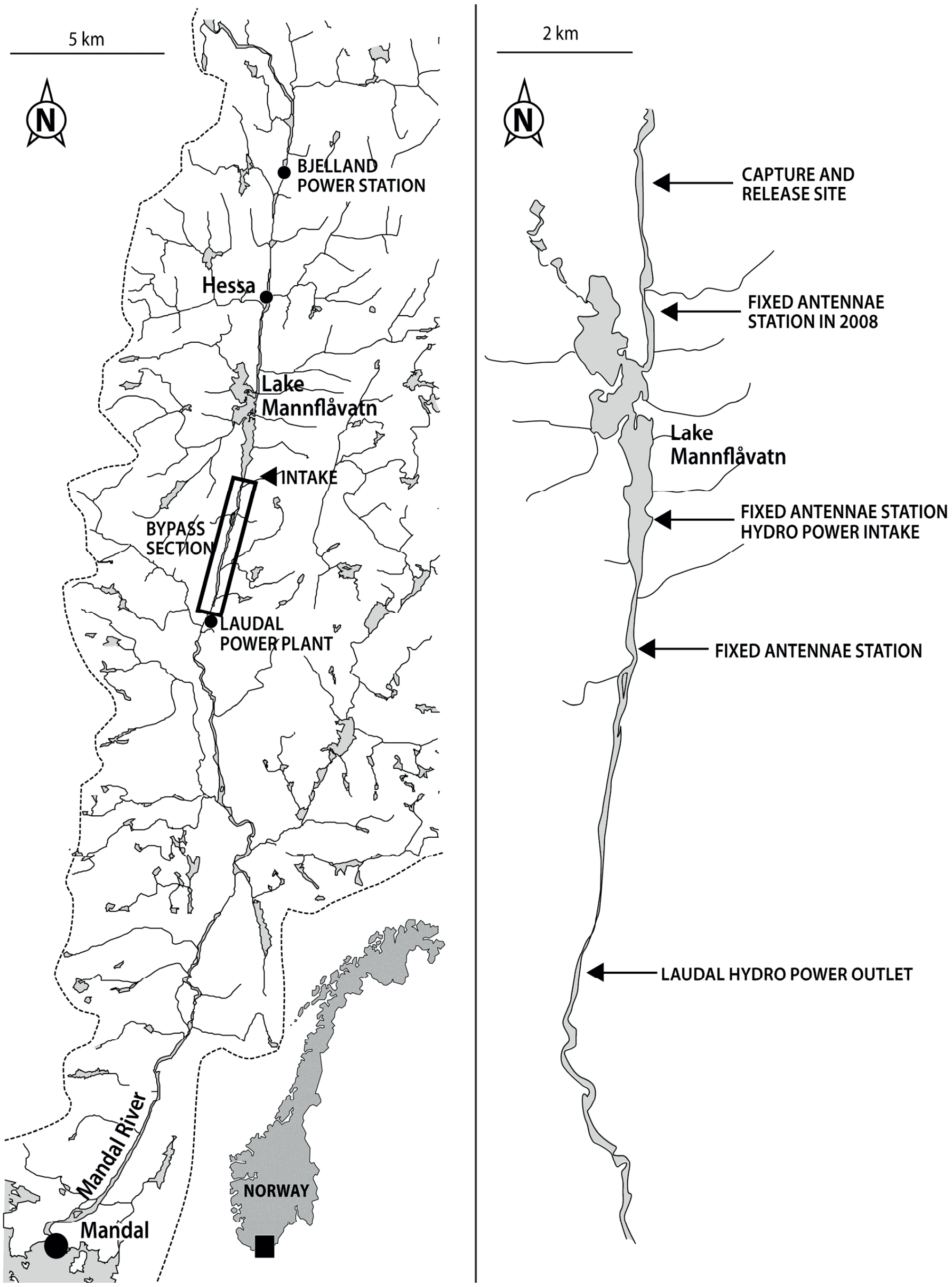

Figure 1

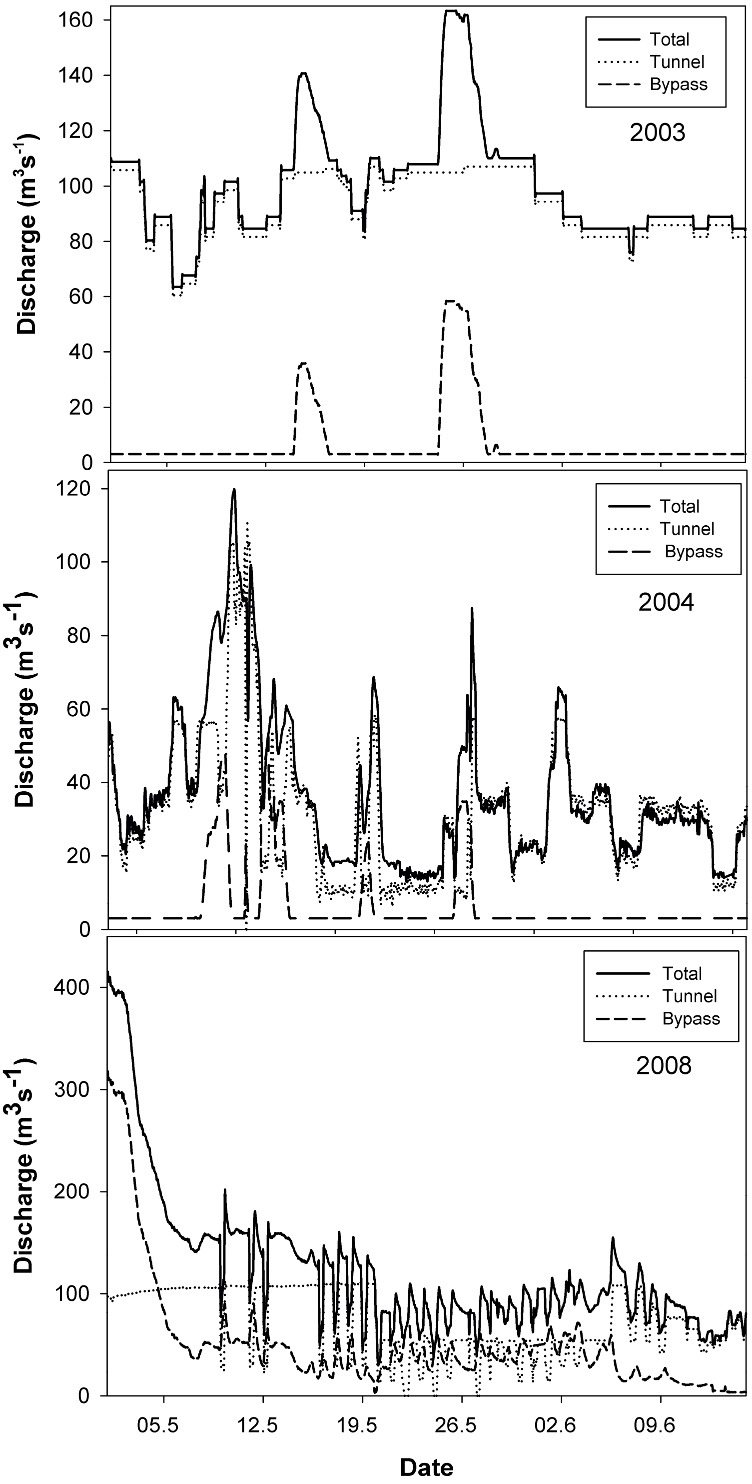
Total
Tunnel
Bypass
2003
Discharge (m^{3}s^{-1})
0
20
40
60
80
100
120
140
160
2004
0
20
40
60
80
100
120
2008
0
100
200
300
400
05.5
12.5
19.5
26.5
02.6
09.6
Date

Figure 2

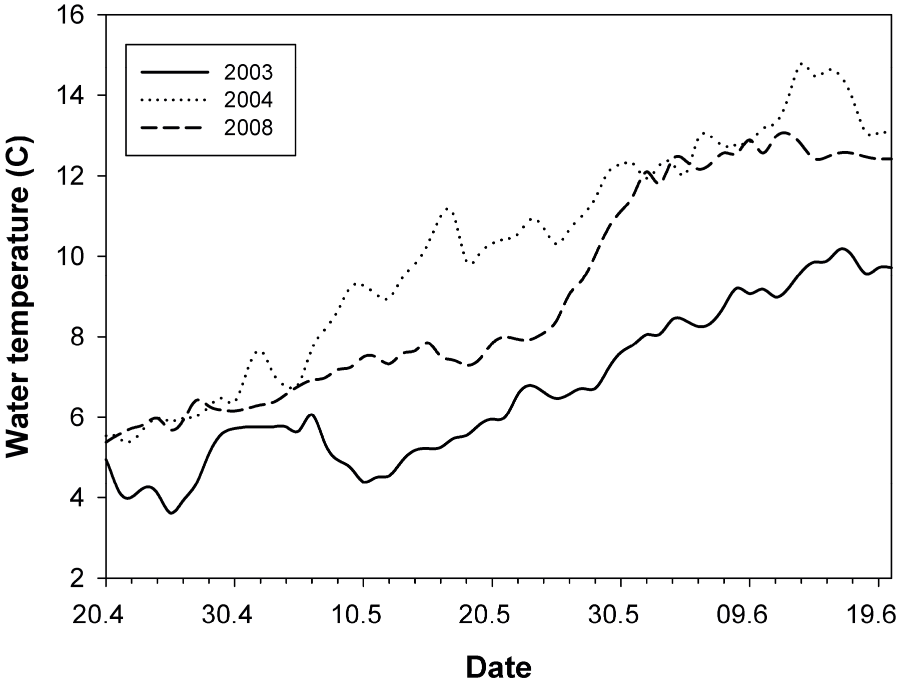
16
14
12
10
8
6
4
2
Water temperature (C)
2003
2004
2008
20.4
30.4
10.5
20.5
30.5
09.6
19.6
Date

Figure 3

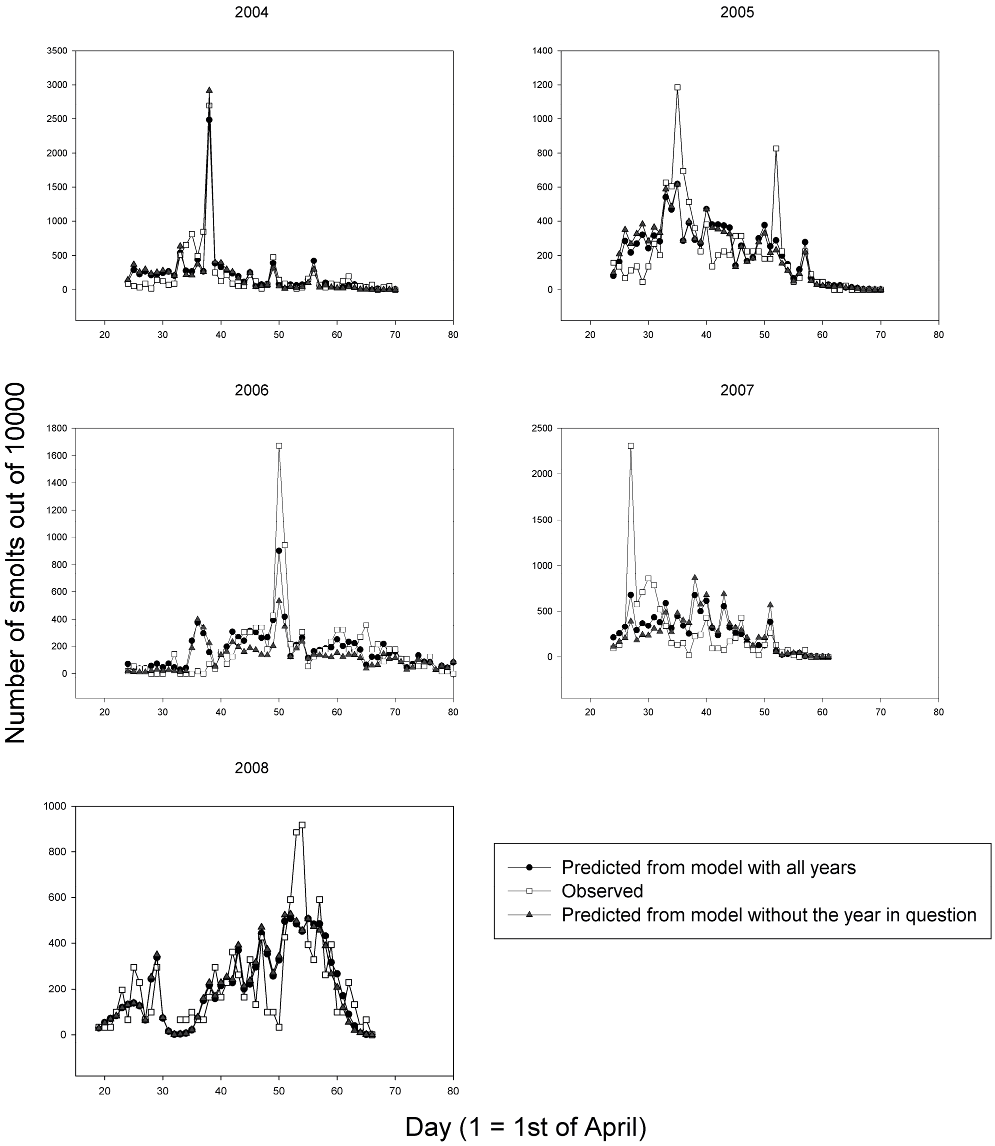
2004
3500
3000
2500
2000
1500
1000
500
0
20
30
40
50
60
70
80
2005
1400
1200
1000
800
600
400
200
0
20
30
40
50
60
70
80
2006
1800
1600
1400
1200
1000
800
600
400
200
0
20
30
40
50
60
70
80
2007
2500
2000
1500
1000
500
0
20
30
40
50
60
70
80
2008
1000
800
600
400
200
0
20
30
40
50
60
70
80
Predicted from model with all years
Observed
Predicted from model without the year in question
Number of smolts out of 10000
Day (1 = 1st of April)

Figure 4

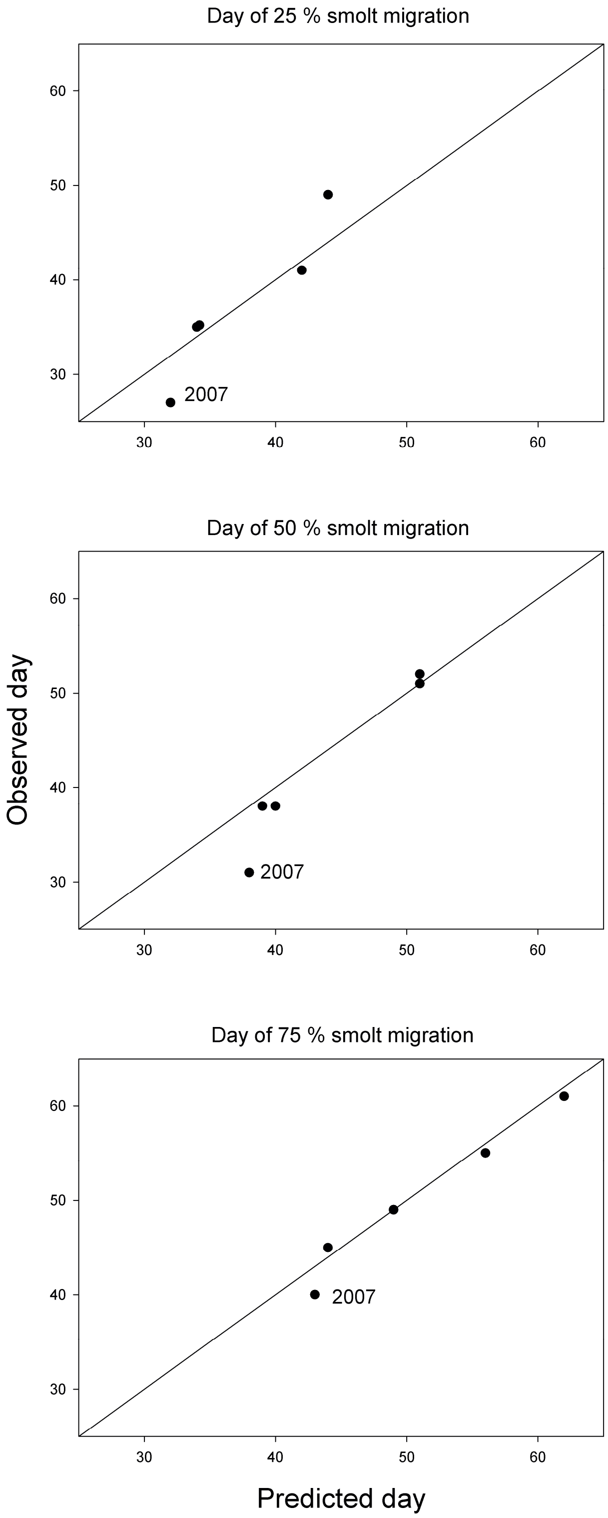
Day of 25 % smolt migration
2007
Day of 50 % smolt migration
2007
Day of 75 % smolt migration
2007
Observed day
Predicted day
30
40
50
60

Figure 5

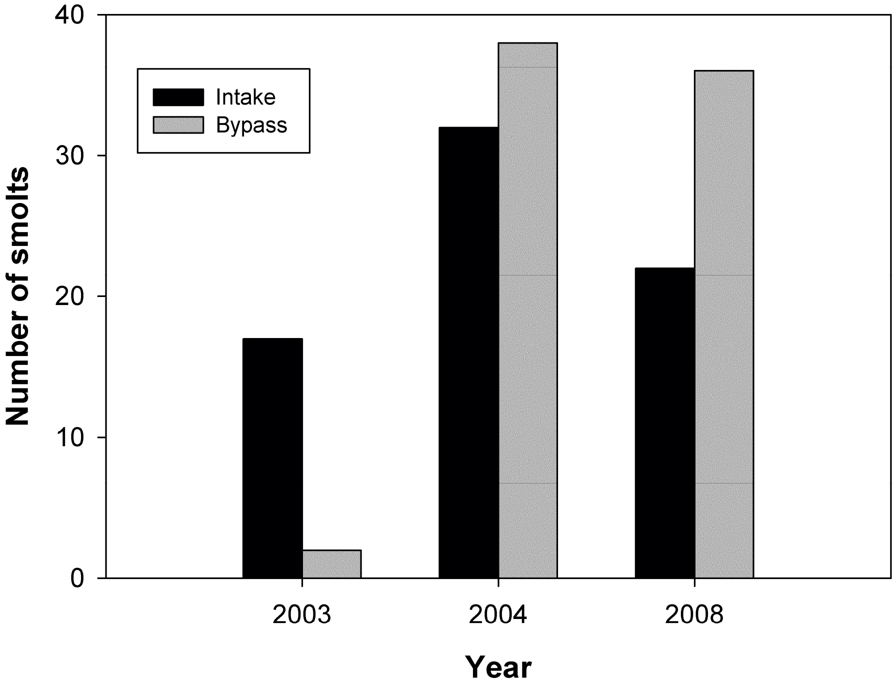
40
30
20
10
0
Number of smolts
Intake
Bypass
2003
2004
2008
Year

Figure 6

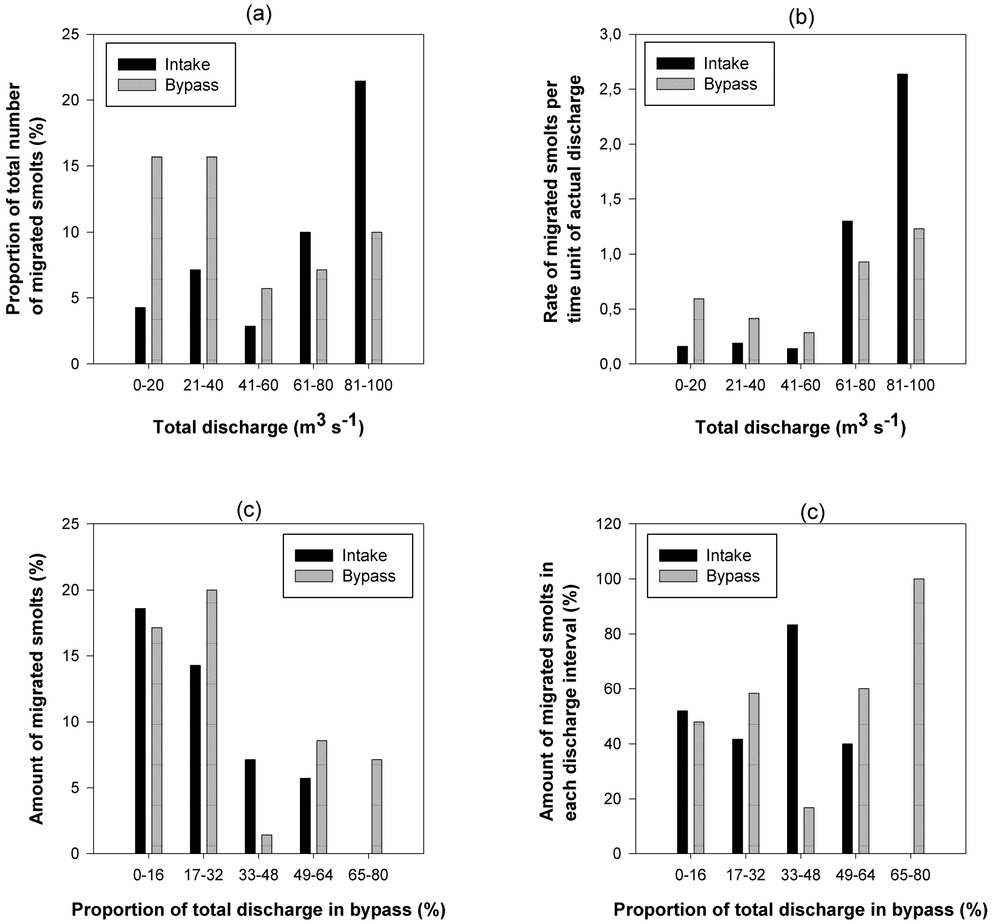
(a)
Intake
Bypass
Proportion of total number of migrated smolts (%)
0
5
10
15
20
25
0-20
21-40
41-60
61-80
81-100
Total discharge ($m^3 s^{-1}$)
(b)
Intake
Bypass
Rate of migrated smolts per time unit of actual discharge
0,0
0,5
1,0
1,5
2,0
2,5
3,0
0-20
21-40
41-60
61-80
81-100
Total discharge ($m^3 s^{-1}$)
(c)
Intake
Bypass
Amount of migrated smolts (%)
0
5
10
15
20
25
0-16
17-32
33-48
49-64
65-80
Proportion of total discharge in bypass (%)
(c)
Intake
Bypass
Amount of migrated smolts in each discharge interval (%)
0
20
40
60
80
100
120
0-16
17-32
33-48
49-64
65-80
Proportion of total discharge in bypass (%)

Figure 7

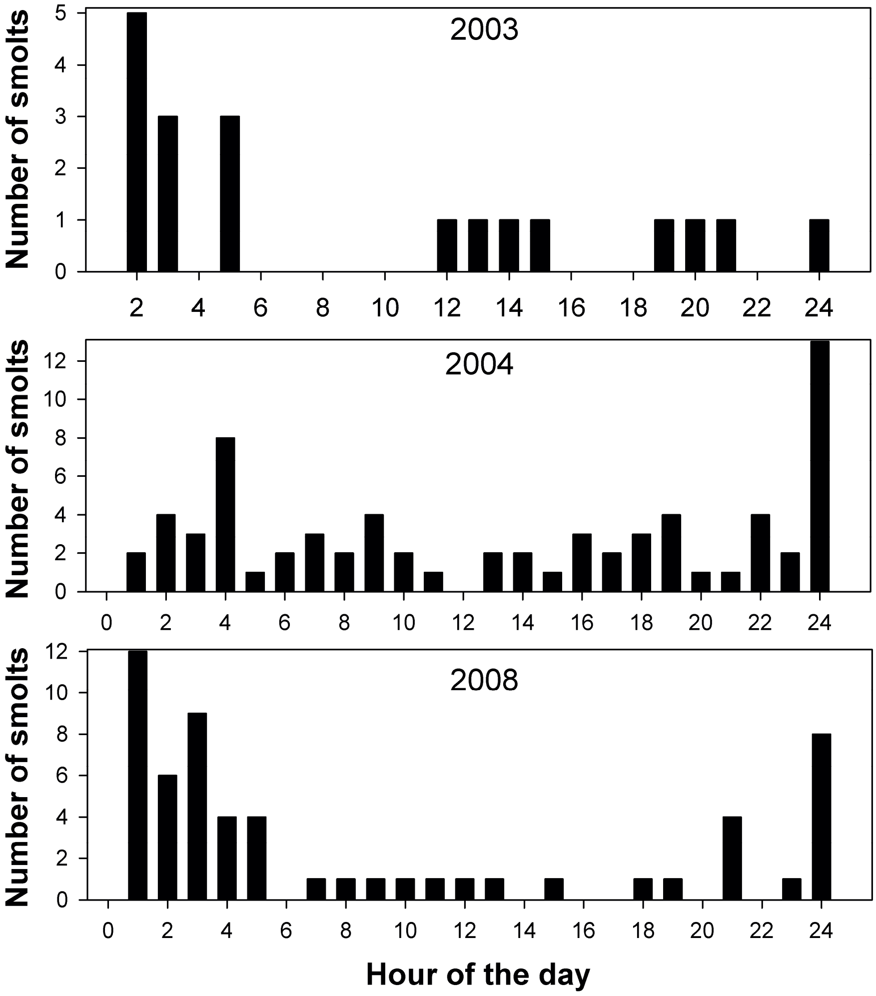
2003
2004
2008
Number of smolts
0
1
2
3
4
5
0
2
4
6
8
10
12
0
2
4
6
8
10
12
14
16
18
20
22
24
Hour of the day

Figure 8

Paper III

Optimizing Atlantic salmon smolt survival by use of hydropower simulation modelling in a regulated river

Is not included due to copyright

Paper IV

Removal of weirs and the influence on physical habitat for salmonids in a Norwegian river

Is not included due to copyright