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Riina Huusko

DOWNSTREAM MIGRATION OF SALMON SMOLTS IN REGULATED RIVERS: FACTORS AFFECTING SURVIVAL AND BEHAVIOUR

UNIVERSITY OF OULU GRADUATE SCHOOL;
UNIVERSITY OF OULU,
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DOWNSTREAM MIGRATION OF SALMON SMOLTS IN REGULATED RIVERS: FACTORS AFFECTING SURVIVAL AND BEHAVIOUR

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Abstract

Atlantic salmon is one of the most widely known migratory fish species whose populations have declined because of hydropower installations. Attempts have been made to preserve salmon stocks in regulated rivers by building fishways for adult fish migrating upstream, but downstream migration of salmon smolts has been almost totally ignored. Instead, captive breeding programmes and extensive stocking of hatchery-reared salmon smolts have been initiated to compensate for highly reduced natural production and to maintain salmon yields. In recent decades, demands to reduce the environmental effects of hydropower production, together with public awareness of decreasing recapture rate and yield of stocked salmon, have increased calls for rebuilding wild salmon stocks in rivers modified for hydropower production. As a consequence, survival of salmon smolts during downstream migration and the effects of hatchery rearing and stocking methods are now research topics of high importance. This thesis examined the need for modifications to the current standard hatchery rearing and release methods, determined the effects of commonly used tagging methods and investigated the impacts of river regulation on the survival and behaviour of downstream migrating smolts by applying telemetry techniques. Modifications made to the standard rearing processes noticeably affected the physiology, behaviour and survival of salmon smolts. In addition, the timing of release was shown to be a key factor for the survival of released smolts. Therefore, comprehensive rearing of smolts, and improving current release methods, especially to match the timing of release to the migration window of wild smolts, are high priorities. Observations in semi-natural environments indicated that commonly used tagging methods had only slight effects on the survival of smolts, so they can be freely used to examine smolt performance. However, more information on rearing and stocking processes and tagging methods is still needed to fully verify the present findings in field conditions. Finally, increasing smolt survival during their downstream migration in regulated rivers is an urgent issue, as survival of smolts was found to be six-fold lower within a river section with five hydropower dams than in a corresponding section of a free-flowing river. In future salmon stock rebuilding actions in regulated rivers, safeguarding downstream migration of smolts should be considered as an equally important issue to safeguarding upstream migration of spawners.

Keywords: fish tags, hatchery-rearing, hydropower, migration speed, telemetry

Huusko, Riina, Lohen vaelluspoikaset rakennetuissa joissa: selviytymiseen ja käyttäytymiseen vaikuttavat tekijät.
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Tiivistelmä

Lohen kannat ovat taantuneet jokien vesivoimarakentamisen seurauksena. Rakennettujen jokien katkenneita vaellusyhteyksiä on pyritty avaamaan rakentamalla kalateitä ylävirtaan vaeltavia aikuisia lohia varten, mutta alavirtaan vaeltavat kalat ovat jääneet lähes huomiotta. Samanaikaisesti kalankasvatus ja massiiviset poikasistutukset ovat olleet suuressa roolissa lohikantojen ylläpitämisessä. Viime vuosikymmeninä istutustulosten heikkeneminen ja toisaalta yleisemminkin lisääntynyt kiinnostus ympäristöasioita kohtaan ovat lisänneet halukkuutta palauttaa lohikantojen luontaista lisääntymistä rakennettuihin jokiin. Tämän seurauksena kasvatus- ja istutusmenetelmien vaikutukset lohen poikasiin sekä vaelluksen onnistuminen rakennetuilla joilla ovatkin nousseet tärkeiksi tutkimusaiheiksi. Väitöskirjani tavoitteena oli selvittää telemetriatekniikoiden avulla nykyisin käytössä olevien kasvatus- ja istutusmenetelmien, yleisesti käytössä olevien kalamerkintätapojen sekä joen patoamisen vaikutusta lohen vaelluspoikasten jokivaelluksen onnistumiseen. Poikaskasvatuksen aikaiset muutokset vaikuttivat vaelluspoikasten kokoon, fysiologiaan ja käyttäytymiseen. Lisäksi kasvatuskäytäntöjä muuttamalla saatiin tuotettua enemmän luonnonpoikasia muistuttavia istukkaita kuin perinteisellä kasvatusmenetelmällä. Istutusajankohta osoittautui myös tärkeäksi selittäjäksi vaelluspoikasten eloonjäännissä. Kasvatusmenetelmien muuttaminen paremmin luonnonolosuhteita vastaaviksi ja istutusajankohdan sovittaminen luonnonpoikasten luonnolliseen vaellusaikaan olisivat tarpeellisia muutoksia nykyisiin kasvatus- ja istutuskäytäntöihin. Yleisesti käytössä olevat kalamerkintätavat soveltuvat vaelluspoikastutkimuksiin, sillä eri merkintämenetelmien vaikutukset vaelluspoikasten kasvuun ja käyttäytymiseen olivat vähäisiä kokeellisissa olosuhteissa tehdyssä tutkimuksessa. Lisää tietoa kuitenkin tarvitaan kasvatus- ja istutusmenetelmien sekä merkintätapojen vaikutuksista luonnonolosuhteissa. Lohen vaelluspoikasten selviytymistä alasvaelluksesta rakennetuilla joilla tulee parantaa merkittävästi, sillä vapaasti virtaavassa joessa vaelluspoikasten selviytymisen havaittiin olevan kuusinkertainen rakennettuun jokeen verrattuna. Lohikantojen palauttamishankkeissa on palaavien aikuislohien kutuvaelluksen rinnalla kiinnitettävä erityistä huomiota myös vaelluspoikasten jokivaelluksen onnistumiseen.

Asiasanat: kalamerkit, laitoskasvatus, telemetria, vaellusnopeus, vesivoima

For dad and mom

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27.11.2017 Riina Huusko

List of original articles

This thesis is based on the following publications, which are referred throughout the text by their Roman numerals:

I Vainikka, A., Huusko, R., Hyvärinen, P., Korhonen P. K., Laaksonen, T., Koskela, J., Vielma, J., Hirvonen H., & Salminen, M. (2012). Food restriction prior to release reduces precocious maturity and improves migration tendency of Atlantic salmon (*Salmo salar*) smolts. Canadian Journal of Fisheries and Aquatic Science, 69(12), 1981–1993.

II Karppinen, P., Jounela, P., Huusko, R., & Erkinaro, J. (2014). Effects of release timing on migration behaviour and survival of hatchery-reared Atlantic salmon smolts in a regulated river. Ecology of Freshwater Fish 23(3), 438–452.

III Huusko, R., Huusko, A., Mäki-Petäys, A., Orell, P., & Erkinaro, J. (2016). Effects of tagging on migration behaviour, survival and growth of hatchery-reared Atlantic salmon smolts. Fisheries Management and Ecology, 23(5), 367–375.

IV Huusko, R., Hyvärinen, P., Jaukkuri, M., Mäki-Petäys, A., Orell, P., & Erkinaro, J. (2017). Survival and migration speed of radio-tagged Atlantic salmon (*Salmo salar* L.) smolts in two large rivers: one without and one with dams. Canadian Journal of Fisheries and Aquatic Science, https://doi.org/10.1139/cjfas-2017-0134

Own contribution

The original idea for this work was originated from Aki Mäki-Petäys, Jaakko Erkinaro, Panu Orell and Pekka Hyvärinen. I contributed to collecting field data and processing data for the analyses in all subprojects, and I assisted writing introduction and discussion in Papers I and II. I had the main responsibility for the analysis and writing in Papers III and IV. All the authors edited the final manuscripts, and agreed with their contents.

Contents

1 Introduction

Fish migration involves synchronised movement between and among reproductive, feeding or/and seasonal refuges, which increases the fitness of individuals during different stages of the life cycle (Gross *et al.* 1988, Dingle & Drake 2007, Brönmark *et al.* 2008). The scale of fish migration varies from metres to thousands of kilometres, depending on the species and the life history strategy, and can occur in freshwaters, marine environments, or between freshwater and marine habitats (Lucas & Baras 2001, Morais & Daverat 2016). Environmental variations can lead to large individual- and population-level variations in the timing of migration, depending on stage of the life cycle (Jonsson & Jonsson 1993, Klemetsen *et al.* 2003).

Human activities, such as damming of rivers, deterioration of water quality and overfishing, have affected fish migrations around the world. In particular, hydropower dams have blocked the longitudinal connectivity between freshwater and marine habitats and have caused declines or even local extinction of diadromous fish species (Jonsson *et al.* 1999, Hall *et al.* 2011, Erkinaro *et al.* 2011, Brown *et al.* 2013). However, particularly in recent decades, increased environmental awareness and public pressure to reduce the negative environmental effects of hydropower developments have resulted in demands to rebuild migratory fish populations in rivers dammed for hydropower production (Erkinaro *et al.* 2011, Opperman *et al.* 2011, Brown *et al.* 2013).

Atlantic salmon (*Salmo salar* L.) is one of the most widely known migratory fish species, with great economic and social importance. Atlantic salmon has an anadromous and iteroparous life cycle, with adult fish ascending their natal river for reproduction and post-spawners (kelts) and juveniles (smolts) descending towards marine feeding grounds (Klemetsen *et al.* 2003). Hydropower developments have caused lack of connectivity and degradation of suitable habitats, resulting in a decline in Atlantic salmon populations throughout the distribution range of the species (Saunders *et al.* 2006, Erkinaro *et al.* 2011). This is also the situation in the Baltic Sea area, where most of the salmon rivers have been harnessed for hydroelectricity and, due to loss of migration routes at hydropower dams, natural reproduction of salmon stocks has ceased (Erkinaro *et al.* 2011). Captive breeding programmes and extensive stocking of hatchery-reared salmon smolts have been initiated to compensate for reduced or lost salmon production, as well as for the commercial fishery. However, in recent decades the recapture rate of hatchery-reared salmon has declined, with a concurrent increase in wild salmon production (Romakkaniemi *et al.* 2003, ICES 2010). As a consequence, the massive stocking efforts have been questioned and there is an increasing interest in rebuilding naturally reproducing salmon populations in regulated rivers.

Establishing longitudinal connectivity in both the upstream and downstream direction in rivers with hydropower dams and impoundments is often a prerequisite for naturally reproducing fish stocks, and the need for fish passage facilities has been recognised for a long time (Clay 1995, Williams *et al.* 2011). However, most fishways developed to date have been designed to only facilitate upstream migration of commercially and recreationally valuable fish, such as adult salmonids. Meanwhile, the needs of downstream migrating juveniles and spent salmonids have been ignored (Arnekleiv *et al.* 2007, Williams *et al.* 2011, Katopodis & Williams 2012). It has previously been believed that, downstream migrating fish are able to bypass dams easily through hydropower turbines or spillways, but a number of studies in regulated rivers have shown that passing through dams in the downstream direction clearly decreases the survival of downstream migrants (Holbrook *et al.* 2011, Norrgård *et al.* 2013). However, the mortality of downstream migrating fish can be high even in free-flowing rivers e.g. due to predation (Thorstad *et al.* 2012). Moreover, mortality estimates for the vast majority of regulated rivers are biased by the fact that they indicate the situation only after dam construction, while the potential survival in these rivers in their natural state is unknown. An accurate estimate of the natural survival of downstream migrating salmonids would hence provide an important reference point against which the results from regulated rivers could be compared. One possibility to quantify the survival could be to measure migration success simultaneously in regulated and free-flowing rivers that are as comparable as possible in terms of basic environmental characteristics, such as river size, climate, geographical location and ecology and species composition. However, only one study in which such a pairwise comparison has been applied has been published so far (Welch *et al.* 2008).

Survival of downstream migrants in a regulated river is heavily influenced by (1) the level of direct and delayed mortality of fish passing through the turbines of the hydropower plant, (2) mortality of fish using alternative passage routes around the hydropower plant, (3) predation pressure in reservoirs, (4) migration delay and predation in the river section above the hydropower dam and (5) cumulative effects in rivers with multiple hydropower dams (Coutant & Whitney 2000, Thorstad *et al.* 2012).

The mortality induced by direct and delayed turbines is usually caused by collision with turbine structures (Mathur *et al.* 1996, Ferguson *et al.* 2006), barotrauma (Cramer & Oligher 1964, Stephenson *et al.* 2010) or due to increased stress (Mathews *et al.* 1986). Sublethal injuries during turbine passage may increase predation probability during later phases of river migration (Coutant & Whitney 2000, Ferguson *et al.* 2006) and may affect survival even after sea entry (Budy *et al.* 2002, Zydlewski *et al.* 2010, Stich *et al.* 2015). For example, abundant loss of scales may result in reduced osmoregulatory ability of salmon smolts, increasing their mortality later in the sea (Zydlewski *et al.* 2010). Overall turbine-induced mortality depends on turbine type and often the risk of mortality increases with increasing fish length (Ferguson *et al.* 2008). Water supersaturation below some hydropower dams may also lead to mortality induced by gas bubble disease (Ruggles 1980). Fish using alternative migration routes, such as spillways, may have the same mortality and causes of injury as seen in turbine-induced mortality, but the injuries are often less severe and the mortality rate is usually lower than in turbine passage (Ruggles 1980).

Reservoirs and impoundments often form slowly flowing, even lentic, habitats, which may favour predatory fish species that normally do not occur in faster flowing river sections (Jepsen *et al.* 1998, Olsson *et al.* 2001). In addition to providing habitats preferred by predators, the slow flow in reservoirs may delay downstream migration and thereby increase the vulnerability of migrants to predation (Jepsen *et al.* 1998, Aarestrup *et al.* 1999, Jepsen *et al.* 2000). A delay just above the hydropower dam, due to fish not finding the downstream passage route or hesitating to enter the turbine intake, may similarly increase predation risk (Jepsen *et al.* 1998). As an added consequence of delays, fish may not enter the sea at the optimal time (McCormick *et al.* 1998, Stich *et al.* 2015). The timing of sea entry is very crucial for downstream migrating salmonid juveniles, which need to enter the sea within an optimal time window where the environmental conditions (food availability and predation pressure) are favourable for survival (McCormick *et al.* 1998, Stich *et al.* 2015).

In addition to securing migration routes, rebuilding a lost fish population in a regulated river calls for several other supporting measures, at least in the beginning of the process. For example, stocking-programs and/or fishing restrictions in both the sea and the river may have to be implemented (Mäki-Petäys *et al.* 2012). These actions need to be well-planned, because for example producing fish for stocking requires an efficient hatchery rearing programme to avoid rearing-induced negative effects on fish performance (Einum & Fleming

2001, Araki *et al.* 2007). Moreover, the rebuilding of a weak or extinct salmon population will often take decades and releases of hatchery-reared salmon may be needed for a long time, at least as regards stockings of eggs and fry in spawning areas and parr and smolts in production areas, in order to have imprinted fish returning to spawn in the 'natal' river (Aprahamian *et al.* 2003). Many studies have shown that hatchery-reared juvenile salmon differ physiologically, morphologically and behaviourally from their wild conspecifics (*e.g.* Weber & Fausch 2003, Jonsson & Jonsson 2006). These differences have been shown to reduce survival (Hyvärinen & Rodewald 2013), which may be caused *e.g.* by the fact that hatchery-reared smolts have no experience of avoiding predators (Einum & Fleming 1997) and/or they have weaker swimming ability (Anttila 2009). On the other hand, the adoption of a migratory life-history strategy may depend on individual condition, growth rate and hormonal status of fish (e.g. Berglund 1995, Hutchings & Jones 1998, Brodersen *et al.* 2008) and, as a consequence, the hatchery-rearing methods aiming at producing large, viable smolts in minimal time may have negative impacts on migration behaviour, such as migration activity or speed of smolts (Lans *et al.* 2011, Larsson *et al.* 2012, Orell *et al.* in press). To improve the quality of hatchery fish, new rearing methods have been developed within the past decade, for example endurance training (Anttila *et al.* 2011), changes in feeding regimes (Norrgård *et al.* 2014, Paper I), enriched rearing (Hyvärinen & Rodewald 2013, Korhonen *et al.* 2014) and reduced rearing density (Larsen *et al.* 2016, Rosengren *et al.* 2017). In addition to hatchery rearing methods, aspects of the release, such as release procedures and timing, may affect the survival and behaviour of the parr and smolts, and therefore needs to be adjusted to local conditions (Rodewald 2013).

The majority of studies performed to date on the migration success and behaviour of fish in regulated rivers have been based on tagged individuals, with several different tagging methods being used. The key to a successful study with tagged fish is to attach the tag without negatively affecting the physiology or behaviour of the fish, or affecting the risk of fish mortality (Baras & Lagardére 1995, Bridger & Booth 2003, Rub *et al.* 2014). The effects of conventional (*i.e.* non-electronic) and telemetry (*i.e.* electronic and/or transmitting) tags on salmon parr and smolts have been studied for decades. It has been shown that tagging has variable effects on fish, and tag loss can vary between, and even within tagging methods (Hansen 1988, Moffett *et al.* 1997, Peake *et al.* 1997, Larsen *et al.* 2013, Rub *et al.* 2014, Jepsen *et al.* 2015). However, only few studies have compared the effects of different tag types on the behaviour of the smolt during their downstream migration (see Hockersmith *et al.* 2003).

2 Aims of the thesis

The main aim of this thesis was to examine different factors that affect the survival of Atlantic salmon smolts in regulated rivers. The work sought to 1) identify the need for changes in current hatchery rearing and release methods to improve the performance of reared smolts, 2) examine the effects of commonly used tagging methods on the salmon smolts and 3) quantify the impacts of river regulation on the survival and behaviour of salmon smolts during their river migration.

More specifically, the first objective was to study how changes in the feeding regime of juvenile salmon, applied during different phases of hatchery rearing, affected the physiology and behaviour of salmon smolts (Paper I). The second objective was to determine the effects of timing of release on the survival and migration behaviour of hatchery-reared salmon smolts by releasing smolts at different dates during the spring at the lowermost reservoir of the regulated River Oulujoki during three successive years (Paper II). The third specific objective was to examine the effects of tagging by four commercially produced and widely used tag types on survival, growth and behaviour of smolts in semi-natural arenas (Paper III). The fourth and final objective of this thesis was to estimate the effects of river regulation on the survival of salmon smolts by comparing the migration of different types of hatchery fish (reared both by standard practices and by an enriched rearing method in a hatchery and semi-wild fish (hatchery-reared fish stocked at fry stage into a river and captured as smolts) between two neighbouring large rivers: the free-flowing River Tornionjoki and the heavily regulated River Kemijoki (Paper IV).

3 Materials & Methods

3.1 Study rivers

The rivers Oulujoki (Papers I, II) and Kemijoki (Paper IV) were once productive Atlantic salmon rivers flowing into the Bothnian Bay of northern Finland (Fig. 1, Table 1). However, construction of multiple dams in the main stem of these rivers in the 1940s effectively blocked migration routes for migratory fish, causing the extirpation of salmon stocks in these rivers (Table 1). In both of the rivers, salmon stocks are currently maintained by massive, annual compensatory release of smolts by the power companies. The smolts are mainly released at the river mouth, except for one-third of the River Oulujoki smolts, which are released below the second dam, 35 km from the river mouth. In recent decades, restoration of naturally reproducing populations has been a management target in both of these rivers, partly because of increasing concerns about declining recapture rates and yield of tagged smolts from the compensatory releases.

The River Tornionjoki is the largest unregulated river in the Baltic Sea Basin, supporting a large wild salmon population (Romakkaniemi *et al.* 2003). It is the neighbouring watershed to the River Kemijoki, which flows to the Bothian Bay at the city of Tornio, about 15 km west of the mouth of River Kemijoki (Fig. 1, Table 1).

Table 1. Hydrological characteristics and number of dams in the rivers studied in this thesis.

River	Catchment area (km^2)	Length of main stem (km)	Dams[1]	Discharge[2] (m^3/s)
Oulujoki	22 841	102	7	274
Kemijoki	51 127	298	8	607
Tornionjoki	40 157	180	0	400

[1]Number of dams in the main stem,

[2]Mean for 1991-2000

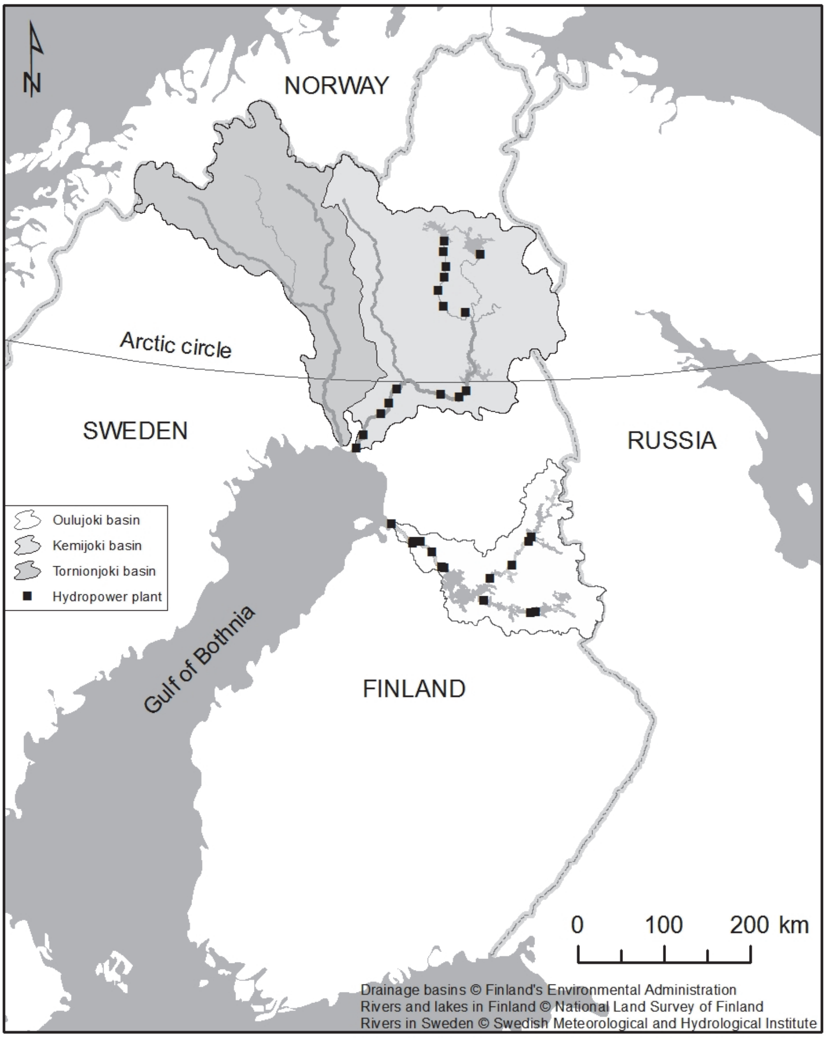

Fig. 1. Main system of the three rivers in Northern Finland studied in this thesis (the rivers Oulujoki, Kemijoki and Tornionjoki). Black squares indicate the location of hydropower plants in the regulated rivers Oulujoki and Kemijoki.

3.2 Experimental facilities

Eight outdoor semi-natural circular channels were used for experimental studies on the migration timing and behaviour of salmon smolts. These semi-natural channels were located at the Kainuu Fisheries Research Station (www.kfrs.fi, Natural Resources Institute Finland (Luke): 64°23′20′′N, 27°30′23′′E). Each circular channel had gravel on the bottom and directional water flow, and was equipped with four passive integrated transponder (PIT) reader antennae placed at equal distances (for more details, see Papers I, III), to investigate fish movements.

Smolts were also released into the Merikoski fishway, which was equipped with three PIT reader antennae in the doorways between the steps of the fishway (for details see Paper I). The Merikoski fishway is located at the lowermost hydropower plant of the River Oulujoki, about 2 km upstream from the river mouth.

3.3 Tagging methods

Telemetry was used in all the investigations, because this method enables tracking of individual fish movement. A PIT tag was implanted into fish to investigate the effects of rearing (Paper I) or tagging (Paper III) on salmon smolts. The study fish were surgically tagged with the PIT tags (for details see Paper I, III) and their movements were tracked in semi-natural channels or in a fishway during the migration season. In addition to PIT tagging, tagging with an anchor T-tag, Carlin tag and dummy radio transmitter were used as treatments in a study examining tagging effects on the performance of smolts (for details see Paper III). The anchor T-tag was also used to examine return rates of salmon reared in different diet treatments (for details see Paper I).

Survival and migration behaviour of the smolt during downstream migration in the rivers were studied using radio-telemetry (Papers II, IV). Fish were tagged surgically with a radio transmitter (for details see Papers II, IV) and their movements were tracked with automatic listening stations along the study rivers. In addition, the fish were also tracked manually during the study period to find the terminal location of the salmon smolts at the end of the study.

Tagging was carried out by trained, experienced operators and according to animal experiment legislation in Finland (licences ESLH-2008-04178/Ym-23, EVISA-2458-04.10-03.2011 and EVISA/3109/04.10.07/2015).

3.4 The experiments

A total of 2249 hatchery-reared two-year old Atlantic salmon smolts and 115 semi-wild smolts were used in the different experiments reported in this thesis (Table 2).

Effects of feed and feeding regimes in the hatchery (Paper I) were studied using salmon of Oulujoki stock and the fish were reared at the Kainuu Fisheries Research Station using four different diets. At the beginning of the feeding experiment, a total of 1000 juvenile salmon were tagged with PIT tags for individual identification and smolts were divided randomly into diet groups. The control fish were reared by standard methods (HR), using a standard commercial feed and feed ration (for details see Paper I). The spring diet (SD) involved manipulation on both feed composition (lipid-reduced) and feed ration (50% of normal) during a 45-day period in spring one year prior to smolting. The winter diet (WD) fish were fed only once a week (reducing total food availability by 85%) during 7 months prior to stocking (from October 2008 to May 2009). A combination of the spring and winter diets (CD) was applied to the fourth diet group (see Table 1 in Paper I). The hormonal onset of maturation in spring inhibits simultaneous but not subsequent smoltification in salmon (Shrimpton & McCormick 2002). Therefore, manipulation of food availability at specific times was used to control the occurrence of smoltification and precocious maturation of salmon smolts. The applied diet periods were based on previous studies, which indicated that springtime feed restriction would reduce precocious maturation of male parr (*e.g.* Rowe *et al.* 1991, Thorpe 1994, Berglund 1995) and that a reduction in feed ration in winter would improve the smoltification process and migration activity of salmon smolts (Lans *et al.* 2011, Larsson *et al.* 2012). The fish were measured for total length and mass four times during the experiment. Movements of the HR and WD fish were monitored from 21-22 October 2008 to 20-21 July 2009 the semi-natural circular channels at the Kainuu Fisheries Research Station. In addition, fish from all groups were stocked to the Merikoski fishway daily between 29 May and 1 June 2009, to investigate the migration tendency of the fish. PIT antennae were used until the end of September 2009. However, stocked smolts were not detected after 15 July 2009.

In order to examine the effects of timing of release on salmon smolts (Paper II), a total of 221 two-year old, hatchery-reared salmon smolts were used in a three-year study (Table 1 in Paper II). The smolts belonged to the Oulujoki hatchery stock and were produced at the Montta hatchery (64°49′14′′N, 26°0´28´´E) by standard rearing methods. The smolts were tagged with radio transmitters and had 2-4 days recovery time before release. The releases into the River Oulujoki took place at different times during the spring (10, 18 and 22 May in 2007; 2, 23 May and 2 June in 2008, 29 April and 24 May in 2009). The main release sites were below the Montta hydropower dam (three release groups in 2007 and 2008, one release group in 2009) and above the Pyhäkoski hydropower dam (three release groups in 2008) in the River Oulujoki. In 2009, the first group of tagged fish were among the compensatory smolts from the hatchery released directly into the river. In 2007 and 2008, the first group of tagged fish was released 1-2 weeks after the standard compensatory releases.

A total of 800 2-year-old salmon smolts of Oulujoki hatchery stock origin were used to investigate tagging effects (Paper III). The smolts were reared using standard rearing methods at the Kainuu Fisheries Research Station. The fish were divided randomly into groups of 160 fish and tagged with one of the four tag types (see section 3.3), or left untagged as a growth control. All the tagged fish carried a PIT tag for movement monitoring in the circular channels using PIT tag antennas. The PIT-tagged treatment group (PT) had only a PIT tag. The other treatment groups were tagged with an additional dummy radiotransmitter (RT), an anchor T-tag (TT) or a Carlin tag (CT) (Table 2). Movements of the tagged smolts were monitored with PIT antennae from 24 May to 25 June 2013. Fish were measured before and after the movement monitoring.

Salmon smolts of Tornionjoki brood stock were used for comparisons between the regulated River Kemijoki and the free-flowing River Tornionjoki. All these smolts were from the same original batch of eggs, the brood stock consisting of 26 females and 10 males captured from the River Tornionjoki in 2012. The fish were reared at the Kainuu Fisheries Research Station, using an enriched rearing method. The greatest differences in enriched rearing compared with the standard rearing method are that cover or shelters are provided for the fish and that changes are made in flow direction and velocity (for details, see Hyvärinen & Rodewald 2013). Semi-wild smolts used in the study were also reared in the same tanks as hatchery smolts, but released into a tributary of the River Ounasjoki (the largest tributary of the River Kemijoki) as fry or parr (for details see Paper IV). In the River Tornionjoki, a total of 115 hatchery-reared salmon smolts (ER) were released for the study. In the River Kemijoki, a total of 228 salmon smolts, including both hatchery-reared smolts (ER; 113 fish) and semi-wild smolts (SW) stocked as 0+ fry (44 fish) or 1-year-old parr (71 fish), were released into the tributary river (Table 2). These treatments were applied to reveal potential differences in migration propensity and performance between smolts of hatchery origin but reared either in enriched hatchery conditions or in wild environment until smolt stage.

Table 2. Data on the Atlantic salmon smolts tagged for movement tracking and released into different rivers.

Study site and study years	Treatment[1]	Tag type	Release groups (n)	Number of fish (n)	Length (mm)	Paper
River Oulujoki						II
2007	HR	Radio	3	60	237	
2008	HR	Radio	6	120	224	
2009	HR	Radio	2	41	212	
River Kemijoki						IV
2015	ER	Radio	3	113	182	
	SW	Radio	3	115	149	
River Tornionjoki						IV
2015	ER	Radio	3	115	184	
Merikoski fishway						I
2009	HR	PIT	3	595	195	
	SD	PIT	3	585	187	
	WD	PIT	3	625	189	
	CD	PIT	3	551	178	
Semi-natural channels						
2009	HR	PIT	1	400	169	I
	WD	PIT	1	400	169	
2013	HR	PIT	1	160	216	III
	HR	PIT+Radio	1	160	214	
	HR	PIT+T	1	160	209	
	HR	PIT+Carlin	1	160	210	

[1]Origin of the fish, HR = hatchery-reared with standard methods, ER = hatchery-reared with enriched methods, SW = semi-wild, SD = hatchery-reared with food restriction during spring one year prior to stocking, WD = hatchery-reared with food restriction during winter prior to stocking, CD = hatchery-reared with food restriction in both spring and winter diet in the same fish.

3.5 Statistical analysis

3.5.1 Physical differences between smolt groups

Differences in total length (mm) and mass (g) between treatment-groups were analysed using parametric or nonparametric tests in SYSTAT (Paper I) or R (R

Core Team 2016; Papers III, IV). The variables were natural log-transformed (ln (x+1)) prior to analysis to meet the normality assumption.

The untagged fish were used as a control when analysing the tagging effects on fish growth using nested Analysis of Variance (Ruohonen 1998). The models were built separately for both response variables (total length and body mass), and a channel effect was controlled for by entering it as a factor nested within the treatment.

3.5.2 Migration behaviour at semi-natural study sites

In Paper I, the Mann-Whitney U test was used for comparisons of migration behaviour between different feeding groups in the semi-natural circular channels. In addition, the migration tendency of feeding groups was compared by logistic regression from smolts released into the Merikoski fishway. For this analysis, the fish were classified into two classes: (1) fish that left within two days of stocking and (2) fish that stayed in the fishway longer than two days. The statistical analyses in Paper I were performed using SPSS 16.0 (SPSS Inc.) and R (R Core Team 2016).

In Paper III, a generalized linear mixed-effects model (GLM) (Zuur *et al.* 2009) was used due to the response variable being poisson distributed to analyse the effects of tagging on the migration behaviour of salmon smolts. The treatment group tagged only PIT was used as a reference against which the other treatments were compared. The tagging groups were used as a fixed variable, and the effect of channel was controlled for by including it as a random variable in the model. The models were constructed separately for each of the movement variables, using R (R Core Team 2016).

3.5.3 Survival and migration speed

In Paper II, survival of salmon smolts was defined by records from automatic listening stations: if a fish was not recorded at the downstream listening station by the end of study, it was defined as dead. For estimating survival of the smolts, a lazy Bayesian rule learning algorithm (Zheng & Webb 2000) was used. The model is suitable for the correlated predictors (release date, river flow, water temperature and fish length) and hence it was used here. In addition, the lazy Bayesian rule model was used, because there were not strong *a priori* assumptions on the relationships between survival and predictors. Migration speed of smolts (km/day) was calculated between each automatic listening station and the MP5' algorithm (Quilan 1992, Wang & Witten 1997) was used for estimating the migration speed in relation to fish length, release day, river flow, water temperature and year. The MP5' model constructs trees of regression models and it is generally used for estimating a continuous response with multiple predictors. The local effects on migration speed with correlated predictors can be exploited using the M5P' model. RapidMiner Enterprise Edition 5.2.008 supplemented with Weka extension (Mierswa *et al.* 2006, http://rapid-i.com) was used for the statistical analyses in Paper II.

In Paper IV, the estimated survival of smolts in the free-flowing River Tornionjoki and regulated River Kemijoki (Table 1, Fig. 1) was compared using Cormack-Jolly-Seber (CJS) mark-recapture models, which can estimate both survival and detection probability in the same model (Lebreton *et al.* 1992). Both rivers were divided into two sections for comparisons: an upper free-flowing section in both rivers, and a lower section with five hydropower plants in the River Kemijoki and none in the River Tornionjoki. Survival of smolts was also compared between release groups (stocked as 2-year-old smolts, 1-year-old parr or 0+ fry) along the reaches of the River Kemijoki using the CJS models. In addition to survival, the migration speed (body length per second, BL/s) was calculated for the upper and lower sections of both rivers using the time of individual smolts between the automatic listening stations. The linear mixed-effects models (Zuur *et al.* 2009) were fitted to test differences in migration speed between rivers or smolt groups. The models were fitted separately for upper and lower sections of the study rivers, using R (R Core Team 2016).

4 Results and Discussion

4.1 Effects of changes in hatchery rearing methods on salmon smolts

The results indicated that even a relatively short feed restriction period in spring reduced the proportion of precociously mature male parr by almost 50% (Paper I), which was a greater decrease than observed previously by Berglund (1995). Precocious maturation in the autumn decreased the likelihood of both visual smoltification and start of early migration in the spring, as is also shown in previous studies (Fängstam *et al.* 1993 and references therein). Frequency of precocious maturation is known to vary between years and hatcheries (Lundqvist *et al.* 1988, Kallio-Nyberg *et al.* 2009). This thesus shown that springtime feed restriction shows promise in reducing precocious maturation in the hatchery environment.

Based on the PIT-tracking in semi-natural environments, feed reduction during the winter period prior to release increased both the migration speed and the precision of migration in the downstream direction, supporting previous findings for salmon (Lans *et al.* 2011) and brown trout (Wysujack *et al.* 2009, Larsson *et al.* 2012). In semi-natural channels, fish in the winter diet treatment reached the migration activity threshold two weeks earlier than fish in the standard diet treatment. In addition, smolts for which feeding were reduced during the winter period left their release site earlier than smolts from the spring diet group in the Merikoski fishway. Both observations suggest that low food availability in winter may increase the motivation for migration and force juvenile salmon to search for better feeding opportunities.

Despite the promising results in terms of a decrease in autumnal precocious maturation and in the start of the migration, feed restriction did not significantly increase the tag return rates or the numbers of returning spawners. However, tag return rates were very low in all feeding groups (on average 0.2%), indicating that the survival of reared post-smolts is poor and that released smolts may suffer from domestication or other factors not considered in this study (see also Jokikokko *et al.* 2006, Araki *et al.* 2007, Kallio-Nyberg *et al.* 2009). In addition to poor return rates, feed restriction had negative effects on fin erosion and mortality in the hatchery.

The survival and migration behaviour of the enriched reared smolts was not different from that of the semi-wild smolts in the regulated River Kemijoki (Paper IV). Hyvärinen and Rodewald (2013) found that survival of enriched reared smolts during the smolt run in the River Tornionjoki was two-fold higher than that of smolts reared by the standard method. In addition to studies in the natural environment, the effects of the enriched rearing method have been compared with those of standard rearing at different phases of rearing, and have also been studied under experimental conditions (Korhonen *et al* 2014 and references therein). The results have shown many benefits of enriching methods on the fish, such as decreased parasite load (Aalto-Araneda 2014) and lower incidence of disease (Korhonen *et al.* 2014). In an experimental study, Rodewald *et al.* (2011) showed that after release to a semi-natural channel, salmon parr produced by enriched rearing started to use natural food (insects) faster than parr produced by standard rearing. These findings suggest that the quality of the hatchery-reared salmon parr and smolts can be improved.

4.2 Effects of timing of release on salmon smolt migration

Survival probabilities of hatchery-reared smolts released into a regulated river increased with increasing water temperature and later release day (Paper II). These results confirm earlier findings that increasing water temperature and day length are the most important factors for the smoltification process (Hoar 1988, Jonsson 1991, McCormick *et al.* 1998, Veselov *et al.* 1998, Byrne *et al.* 2003, Otero *et al.* 2014). In addition, several studies have suggested that smoltification state at release time affects the survival of the stocked smolts (McCormick & Saunders 1987, Virtanen *et al.* 1991, Boeuf 1993, Staurnes *et al.* 1993, Lundqvist *et al.* 1994, McCormick *et al.* 1998, McKinnell & Lundqvist 2000, Zydlewski *et al.* 2005). The results in Paper II clearly demonstrated that releases into the River Oulujoki in early spring, *i.e.* at cold water temperature, decreased smolt survival during river migration by delaying the start of migration and lowering migration speed, making the smolts more susceptible to predation. The estimated survival probability clearly increased above a threshold temperature of 5.9 °C and a threshold release day of 16 May (Julian date 138), and was highest when the water temperature was above 10.1 °C (Paper II). Earlier studies on the effects of timing of release have been based on either trapping of descending smolts in rivers (Kennedy *et al.* 1984, Strand & Finstad 2007) or, more commonly, tag returns of recaptured adult fish in the sea (Staurnes *et al.* 1993, Lundqvist *et al.*

1994, McKinnell & Lundqvist 2000, Jutila *et al.* 2005). Despite the difference in method used, the results from these earlier studies also suggest that survival of smolts increases when they are released at water temperature close to or above 10 °C (Lundqvist & Eriksson 1985, Jutila *et al.* 2005, Ferguson 2008; Vähä *et al.* 2008, Otero *et al.* 2014). In fact, it was found in Paper II that the return rates for compensatory stocking in the River Oulujoki declined as the timing of release shifted to early spring with colder water temperatures (Fig. 5 in Paper II).

In Paper II, the effect of river flow on the estimated survival probability varied a lot (see Table 2 in Paper II). In general, high discharge seemed to increase swimming speed and survival of smolts. In some earlier studies, increasing river discharge has been found to trigger the migration of smolts (Jonsson 1991, McCormick *et al.* 1998, Byrne *et al.* 2003). Furthermore, Whalen *et al.* (1999) found that an increase in water flow increases migration activity during the time when smolt physiology is optimal for sea water adaptation (measured by gill Na^{+},K^{+} -ATPase activity), but that changes in river flow before or after the optimal time window do not affect migration activity. River flow may not determine the overall migration window, but it may affect smolt movement within the migration season. Differences in smolt migration propensity were observed at different phases during the migration window in the River Kemijoki and River Tornionjoki (Paper IV) indicating that the smolt migration window is sensitive to environmental conditions and survival can vary during the migration season.

In addition to timing of release, release procedure is reported to be important for fish survival (Rodewald 2013). Typically smolts are transported and released into the new environment directly from the transport tanks. However, when a soft release type is used instead, where fish are first allowed to recover from the transport and handling stress by acclimatising to the new environment in cages, the subsequent survival of the fish has been found to be higher (Rodewald 2013). In this thesis, the both conventional release type (Papers I, II) and soft type (Paper IV) was used.

4.3 Tagging effects on salmon smolts

Tagging did not increase the mortality of salmon smolts and the tag wounds were well-healed during the study period (Paper III). Similarly, previous PIT tagging studies report healing within a relatively short period (Zydlewski *et al.* 2001, Larsen *et al.* 2013). However, visual observations at the end of the study indicated that the wound area showed slight inflammation in 29.4% of T-anchor-tagged fish, 20.0% of Carlin-tagged fish and 10.6% of radio-tagged fish (compared with 0% of PIT-tagged fish) (Paper III). It has been reported previously, that tag parts like a swinging tag label or antenna that move when the fish is swimming or maintaining position against water flow may slow the healing of the insertion area (Jepsen *et al.* 2008*a*). Moreover, observations on Carlin-tagged rainbow trout (*Oncorhynchus mykiss*) indicate that the fish may suffer greater injuries if the tag is not secured just below the dorsal fin (McAllister *et al.* 1992). However, the high healing rates of tag wounds in the Paper III indicated proper installation of the external tags.

Tag retention rates were relatively high in all tagging treatments (Paper III). All PIT tags were retained during the study, as found in previous studies using 23 mm PIT tags on > 90 mm juvenile salmon (Larsen *et al.* 2013). Tag loss was highest in the radiotagging treatment, with four (2.5%) expelled dummy transmitters during the one month duration of the experiment. However, a visible change in the abdomen of the radio-tagged fish was observed, indicating a possible early phase of the tag expelling process, and tag loss rates in the radiotagging treatment could thus have increased during a longer study period (Jepsen *et al.* 2008*b*, Sandstrom *et al.* 2013). Overall, many previous studies have reported higher tag loss rates for different types of anchor tags, Carling tags or surgically implanted transmitters (McAllister *et al.* 1992, Lacroix *et al.* 2004, Welch *et al.* 2007, Jepsen *et al.* 2008*b*) than observed in the present study. However, many of these studies have had a clearly longer monitoring period compared to the present study.

In general, the migration behaviour of salmon smolts was almost similar in all tagging treatments: smolts started active movement in the downstream direction in mid-June with increasing water temperature. However, smolts from the Carlin tag and radio transmitter treatments started their migration slightly later and had lower maximum activity per day compared with PIT only-tagged fish. The Carlin tagging and radio transmitter tagging were considered harsher tagging treatments than the others (see Material & Methods in Paper III), most probably causing stronger stress reactions and affecting the swimming capacity of smolts.

4.4 Comparing survival of salmon smolts in a regulated river and a free-flowing river

Survival probability of Atlantic salmon smolts was six-fold lower in the regulated section of the River Kemijoki compared to a corresponding free-flowing section of the River Tornionjoki. However, smolt survival along the free-flowing upper section was similar in both rivers (Fig. 3 in Paper IV). These differences in smolt survival suggest that decreased survival can be attributed to hydropower plants and flow regulation of the River Kemijoki. The results also confirm earlier finding that smolt survival is higher along a free-flowing compared with a dammed section of the same river (Holbrook *et al.* 2011, Norrgård *et al.* 2013, Stich *et al.* 2015). In fact, the findings in Paper IV are also comparable with earlier Carlin tag return rates from the sea in the same rivers: in a study by Vehanen *et al.* (1993), the return rate was 7-10% for salmon smolts released in the River Tornionjoki, compared with <2% for smolts released in the River Ounasjoki.

Decreased smolt survival has been linked to the duration of exposure to predation by piscivorous fish and avian predators, and therefore migration speed of the smolts is considered to be one of the key factors for high survival (Jepsen *et al.* 1998, Hyvärinen & Rodewald 2013, Paper II). In regulated rivers, predation pressure has been reported to be high in areas with the decreasing water velocity, *e.g.* in reservoirs (Jepsen *et al.* 1998, Thorstad *et al.* 2012) and near dams (Venditti 2000). The decreased water velocity due to damming also causes a delay or a total stop to smolt migration (Plumb *et al.* 2006, Scruton *et al.* 2007, Nyqvist *et al.* 2017). The results in Paper IV supported these earlier findings, as migration speed was lowest in the regulated section of the River Kemijoki, with observations of delays and stops above dams (Fig. 4 & 5 in Paper IV).

In addition to increased predation, decreased survival depends on direct turbine mortality and sublethal injuries caused by passage through the turbine (Ferguson *et al.* 2008, Holbrook *et al.* 2011). These effects vary between hydropower plants, depending on the structures and design of the dam (Coutant & Whitney 2000). For example, the turbine type in the hydropower plant has a clear effect on turbine mortality and injuries (Ferguson *et al.* 2008). Based on manual tracking observations, direct turbine mortality in the River Kemijoki was relatively low but smolts seemed to be unwilling to migrate through the next turbines after the first (upstream) hydropower plant (see Fig. 5 in Paper IV). However, the exact causes of mortality remain uncertain if the smolts are not actually seen dead after the turbine passage or if their causes of mortality are not otherwise reliably verified.

The low survival rates (14%) observed in this thesis call for actions to secure the downstream migration of smolts in regulated rivers. In fact, many types of downstream passage facilities have been developed during recent decades (Larinier & Travade 2002). However, measuring the passage efficiency of such facilities usually takes several years, often including continuous enhancements of the downstream passage facility (Johnson *et al.* 2000, Williams *et al.* 2001, Scruton *et al.* 2003, Scruton *et al.* 2008). Moreover, it seems highly likely that functional solutions will vary between dams and rivers (Larinier & Travade 2002, Scruton *et al.* 2008).

5 Conclusions: Future studies and implications for management

Managed introduction into spawning areas (eggs, fry) and production areas (parr, smolt) are often needed for a long time as a supporting measure when rebuilding a lost salmon population (*e.g.* Mäki-Petäys *et al.* 2012). Moreover, a well-planned hatchery rearing programme that produces viable fish for stocking and appropriate release methods are important for increasing the survival of the fish after release. The first overall aim of this thesis was to obtain a general view of how rearing methods affect the physiology and behaviour of salmon smolts, and how survival after stocking is affected by the timing of release.

Based on the results of this thesis, modifications to standard rearing can have obvious effects on the physiology and behaviour of salmon smolts (Papers I, IV). The results obtained for feed restriction (Paper I) are encouraging, showing that precocious sexual maturation of male parr can be reduced and that the overall migration propensity of smolts can be improved by changes in feeding regimes applied at a certain sensitive period. However, these rearing methods also have unwanted impacts, such as increased mortality rates and fin erosion. Furthermore, tag return rates did not differ between standard and feed-restricted fish. In this regard, if the target is to produce good quality smolts for stocking purposes, there is an obvious need to further optimise the feed restriction schedule or develop more comprehensive rearing methods.

The studies on salmon smolts reared using the enriched rearing method indicated that their migration did not differ from the semi-wild individual (Paper IV). These results together with earlier studies (*e.g.* Hyvärinen & Rodewald 2013) indicate that enriched rearing method have the potential for improving the quality of the hatchery-produced fish. These findings suggest that the enriched rearing method could be one option to produce fish for stocking purposes, but more studies are still needed to analyse various effects and implications of this rearing method and its performance in field conditions.

The timing of release was shown to be one of the key factors for survival of the released smolts (Papers II, IV). The natural smolt migration window is often reported to be at water temperature of about 10 °C (McCormick *et al.* 1998). It was show that the migration window of stocked salmon smolts is also determined by water temperature, as the smolts released too early into cold water showed delayed start of migration and had higher mortality than smolts released later in spring (Paper II). On the other hand, it was also shown that releasing smolts too late during the migration period causes reduced survival and migration speed and that regional environmental conditions during the smolt migration window affect the survival of stocked smolts (Paper IV). Therefore, if the goal is to maximise the survival of released smolts after stocking, the release time should be matched to the natural smolt migration window of the target river and releases may need to be carried out several times during the spring.

In the development of new rearing or release methods, it is important to keep practical aspects in mind. The solutions should be useful in different kinds of hatchery environments and production volumes. For example, preliminary tests on the enriched rearing method have been initiated in different commercial hatcheries in Finland (Korhonen *et al.* 2014), but more studies and experience on this method are needed. Furthermore, the hatcheries rearing fish for stocking purposes should be required to perform more rearing and release tests, in order to refine these processes to ensure that after the release, fish in the target river system are highly viable.

The number of smolts surviving river migration and arriving to the sea is considered one of most important measures of viable salmon populations, because post-smolt survival in the sea has declined during recent decades (ICES 2010). To this end, the second aim of this thesis was to investigate the magnitude of the effects of river regulation on smolt survival. The effects of tagging on salmon smolt survival and behaviour were also investigated, to reveal whether the methodology used in migrations studies could potentially affect the outcomes.

Knowledge of the effects of different tag types on fish performance is crucial for drawing accurate conclusions from tagging studies. Based the results of this thesis, the effects of the most frequently used tagging techniques are not severe and it appears that all the tag types tested are suitable for at least short-term studies of fish performance. However, more knowledge of the effects of tagging on fish in natural conditions is needed.

In a regulated river with five power stations, the survival of smolts during river migration was six-fold lower than in a comparable natural river (Paper IV). Problems in smolt migration seem to be especially prevalent in heavily regulated rivers, where survival was observed to be only 4-14% (Paper IV, Huusko *et al.* 2012). The increased mortality in a regulated river is due to the effects of hydropower dams and turbines, such as direct turbine mortality (Mathur *et al.* 1996, Ferguson *et al.* 2006), barotraumas (Cramer & Oligher 1964, Stephenson *et al.* 2010) and delays (Venditti *et al.* 2000) above dams. It is evident that all these effects accumulate in heavily regulated rivers (Paper IV). However, the roles of different elements contributing to mortality are difficult to separate. In the future, more detailed information is needed on the various potential sources of mortality and causes of migration delays in regulated river, such as the impacts of different turbine intake depths or the effect of earlier passage experience on consequent migration motivation.

The low survival rates, observed in this thesis, call for actions to secure the downstream migration of smolts in regulated rivers. Various downstream passage facilities have been developed, but measuring passage efficiency usually takes several years. Based on the present findings, it seems highly likely that functional solutions will vary between dams and rivers. Thus, future studies about the behaviour of salmon smolts above hydropower dams in changing flow conditions are urgently needed. A better understanding of the processes guiding the behaviour of smolts, especially their preferred swimming pathways near the dams may help to develop efficient passage facilities without applying the 'trial and error' principle that may take many years or even decades.

References

Aalto-Araneda, M. (2014). Vaihtelevan kasvatusympäristön ja emotaustan vaikutus tarttuviin lois- ja bakteeri-tauteihin sekä niiden aiheuttamaan kuolleisuuteen Itämeren lohen (*Salmo salar*) istukaskasvatuksessa. Licentiate thesis of Veterinary, University of Helsinki. In Finnish.

Aarrestrup, K., Jepsen, N., Rasmussen, G., & Økland, F. (1999). Movements of two strains of radio tagged Atlantic salmon, *Salmo salar* L., smolts through a reservoir. Fisheries Management and Ecology, 6(2), 97–107. doi: 10.1046/j.1365.2400.1999.00132.x

Anttila, K. (2009). Swimming muscles of wild, trained and reared fish: aspects of contraction machinery and energy metabolism. Acta Universitatis Ouluensis. A Scientiae rerum naturalium 526.

Anttila, K., Jokikokko, E., Erkinaro, J., Järvilehto, M., & Mänttäri, S. (2011). Effects of training on functional parameters of muscles in reared Atlantic salmon smolts: connection to downstream migration pattern. Journal of Fish Biology, 78(2), 552–566. doi:10.1111/j.1095-8649.2010.02871

Aprahamian, M. W., Smith, K. M., McGinnity, P., McKelvey, S., & Taylor, J. (2003). Restocking of salmonids – opportunities and limitations. Fisheries Research, 62(2), 211–227. doi:10.1016/S0165-7836(02)00163-7

Araki, H., Cooper, B., & Blouin, M. S. (2007). Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science, 318(5847), 100–103. doi:10.1126/science.1145621

Arnekleiv, J. V., Kraabol, M., & Museth, J. (2007). Efforts to aid downstream migrating brown trout (*Salmo trutta* L.) kelts and smolts passing a hydroelectric dam and a spillway. Hydrobiologia, 582(1), 5–15. doi:10.1007/s10750-006-0547-8

Baras, E., & Lagardére, J.-P. (1995). Fish telemetry in aquaculture: reviews and perspectives. Aquaculture International, 3(2), 77–102. doi:10.1007/BF00117876

Bates, B., Maechler, M., Bolker, B. M., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1.-7

Berglund, I. (1995). Effects of size and spring growth on sexual maturation in 1+ Atlantic salmon (*Salmo salar*) parr: interactions with smoltification. Canadian Journal of Fiaheries and Aquatic Science, 52(12), 2682–2694. doi:10.1139/f95-857

Bridger, C. J., & Booth, R. K. (2003). The effects of biotelemetry transmitter presence and attachment procedures on fish physiology and behavior. Reviews in Freshwater Sciences, 11(1), 13–34. doi:10.1080/16226510390856510

Brodersen, J., Nilsson, P. A., Hansson, L.-A., Skov, C., & Brönmark, C. (2008). Condition-dependent individual decision-making determines cyprinid partial migration. Ecology, 89(5), 1195–1200. Doi:10.1890/07-1318,1

Brönmark, C., Skov, C., Brodersen, J., Nilsson, P. A., & Hansson, L.-A. (2008). Seasonal migration determined by a trade-off between predator avoidance and growth. PLoS ONE 3, e1957. doi:10.1371/journal.pone.0001957

Brown, J. J., Limburg, K. E., Waldman, J. R., Stephenson, K.., Glenn, E. P., Juanes, F., & Jordaan, A. (2013). Fish and hydropower on the U.S. Atlantic coast: failed fisheries policies from half-way technologies. Conservation Letters, 6(4), 280–286. doi:10.1111/conl.12000

Budy, P., Thiede, G. P., Bouwes, N., Petrosky, C. E., & Schaller, H. (2002). Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. North American Journal of Fisheries Management 22(1), 35–51. doi:10.1577/1548-8675(2002)022<0035:ELDMOS>2.0.CO;2

Clay, C.H. (1995). Design of fishways and other fish facilities. Boca Raton, FL:CRC-Press.

Cramer, F. K., & Oligher, R. C. (1964). Passing fish through hydraulic turbines. Transactions of the American Fisheries Society, 93(3), 243–259. doi:10.1577/1548-8659(1964)93[243:PFTHT]2.0.CO;2

Coutant, C. C., & Whitney, R. R. (2000). Fish behavior in relation to passage through hydropower turbines: a review. Transactions of the American Fisheries Society, 129(2), 351–380. doi:10.1577/1548-8659(2000)129<0351:FBIRTP>2.0.CO;2

Dingle, H., & Drake, V.A. (2007). What is migration? BioScience, 57(2), 113–121. doi:10.1641/B570206

Gross, M. R, Coleman, R. M., & McDowall, R. M. (1988). Aquatic productivity and the evolution of diadromous fish migration. Science, 239, 1291–1293. doi: 10.1126/science.239.4845.1291

Einum, S., & Fleming, I.A. (1997). Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. Journal of Fish Biology, 50(3), 634–651. doi: 10.1111/j.1095-8649.1997.tb01955.x

Erkinaro, J., Laine, A., Mäki-Petäys, A., Karjalainen, T. P., Laajala, E., Hirvonen, A., … Yrjänä, T. (2011). Restoring migratory salmonid populations in regulated rivers in the northernmost Baltic Sea area, Northern Finland – biological, technical and social challenges. Journal of Applied Ichthyology, 27(Suppl. 3), 45–52. doi:10.111/j.1439-0426.2011.01851.x

Ferguson, J. W. (2008). Behavior and survival of fish migrating downstream in regulated rivers. Doctoral thesis, Swedish University of Agricultural Sciences, Umeå.

Ferguson, J. W., Absolon, R. F., Carlson, T. J., & Sandford, B. P. (2006). Evidence of delayed mortality on juvenile Pacific salmon passing through turbines at Columbia River dams. Transactions of the American Fisheries Society, 135(1), 139–150. doi:10.1577/T05-080.1

Ferguson, J. W., Ploskey, G. R., Leonardsson, K., Zabel, R. W., & Lundqvist, H. (2008). Combining turbine blade-strike and life cycle models to assess mitigation strategies for fish passing dams. Canadian Journal of Fisheries and Aquatic Science, 65(8), 1568–1585. doi:10.1139/F08-078

Fängstam, H., Berglund, I., Sjöberg, M., & Lundqvist, H. (1993). Effect of size and early sexual maturity on downstream migration during smolting in Baltic salmon (*Salmo salar*). Journal of Fish Biology, 43(4), 517–529. doi:10.1111/j.1095-8649.1993.tb00436.x

Hall, C. J., Jordaan, A., & Frisk, M. G. (2011). The historic influence of dams on diadromous fish habitat with a focus on river herring and hydrologic longitudinal connectivity. Landscape Ecology, 26(1), 95–107. doi: 10.1007/s10980-010-9539-1

Hansen, L. P. (1988). Effects of Carlin tagging and fin clipping on survival of Atlantic salmon (*Salmo salar* L.) released as smolts. Aquaculture, 70(4), 391–394. doi:10.1016/0044-8486(88)90122-6

Hockersmith, E. E., Muir, W. D., Smith, S. G., Sandford, B. P., Perry, R. W., Adams, N. S., & Rondorf, D. W. (2003). Comparison of migration rate and survival between radio-tagged and PIT-tagged migrant yearling Chinook salmon in the Snake and Columbia rivers. North American Journal of Fisheries Management, 23(2), 404–413. doi:10.1577/1548-8675(2003)023<0404:COMRAS>2.0.CO;2

Holbrook, C. M., Kinnison, M. T., & Zydlewski, J. (2011). Survival of migrating Atlantic salmon smolts through the Penobscot River, Maine: a prerestoration assessment. Transactions of the American Fisheries Society, 140(5), 1255–1268. doi:10.1080/00028487.2011.618356

Hutchings, J. A., & Jones, M. E. B. (1998). Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. Canadian Journal of Fisheries and Aquatic Science, 55(Suppl. 1), 22–47. doi:10.1139/d98-004

Huusko, R., Orell, P., van der Meer, O., Jaukkuri, M., & Mäki-Petäys, A. (2012). Lohen vaelluspoikasten radiotelemetriaseuranta Iijoella vuosina 2010–2011. Working report, Finnish Game and Fisheries Research Institute. In Finnish. Retrieved from: http://urn.fi/URN:ISBN:978-951-776-932-7

Hyvärinen, P., & Rodewald, P. (2013). Enriched rearing improves survival of hatchery-reared Atlantic salmon smolts during migration in the River Tornionjoki. Canadian Journal of Aquatic and Fisheries Science, 70(9), 1386–1395. doi:10.1139/cjfas-2013-0147

Jepsen, N., Aarestrup, K., Økland, F., & Rasmussen, G. (1998). Survival of radio-tagged Atlantic salmon (*Salmo salar*) and trout (*Salmo trutta*) smolts passing a reservoir during seaward migrating. Hydrobiologia, 371/372, 347–353. doi:10.1023/A:1017047527478

Jepsen, N., Christoffersen, M., Munksgaard, T. (2008*a*). The level of predation used as an indicator of tagging/handling effects. Fisheries Management and Ecology, 15(5–6), 365–368. doi:10.1111/j.1365-2400.2008.00623.x

Jepsen, N., Mikkelsen, J. S., & Koed, A. (2008*b*). Effects of tag and suture type on survival and growth of brown trout with surgically implanted telemetry tags in the wild. Journal of Fish Biology, 72(3), 594–602. doi:10.1111/j.1095-8649.2007.01724.x

Jepsen, N., Pedersen, S., & Thorstad, E. (2000). Behavioural interactions between prey (trout smolts) and predators (pike and pikeperch) in an impounded river. Regulated Rivers: Research and Management, 16(2), 189–198. doi:10.1002/(SICI)1099-1646(200003/04)16:2<189::AID-RRR570>3.0.CO;2-N

Jepsen, N., Thorstad, E. B., Havn, T., & Lucas, M. C. (2015). The use of external electronic tags on fish: an evaluation of tag retention and tagging effects. Animal Biolotelemetry, 3(1), 49. doi:10.1186/s40317-015-0086-z

Jokikokko, E., Kallio-Nyberg, I., Saloniemi, I., & Jutila, E. (2006). The survival of semi-wild, wild and hatchery-reared Atlantic salmon smolts of the Simojoki River in the Baltic Sea. Journal of Fish Biology, 68(2), 430–442. doi:10.1111/j.0022-1112.2006.00892.x

Johnson, G. E., Adams, N. S., Johnson, R L., Rondorf, D. W., Dauble, D. D., & Barila, T. Y. (2000). Evaluation of the prototype surface bypass for salmonids smolts in spring 1996 and 1997 at Lower Granite Dam on the Snake River, Washington. Transactions of the American Fisheries Society, 129(2), 381–397. doi:10.1577/1548-8659(2000)129<0381:EOTPSB>2.0.CO;2

Jonsson, B., & Jonsson, N. (1993). Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries, 3(4), 348–365. doi:10.1007/BF00043384

Jonsson, B., & Jonsson, N. 2006. Cultured salmon in nature: a review of their ecology and interaction with wild fish. ICES Journal of Marine Sciences, 63(7), 1162–1181. doi: 10.1016/j.icesjms.2006.03.004

Jonsson, B., Waples, R., &Friedland, K. (1999). Extinction considerations for diadromous fishes. ICES Journal of Marine Science: Journal du Conseil, 56(4), 405–409. doi:10.1006/jmsc.1999.0483

Jutila, E., Jokikokko, E., & Julkunen, M. (2005). The smolt run and postsmolt survival of Atlantic salmon, *Salmo salar* L., in relation to early summer water temperatures in the northern Baltic Sea. Ecology of Freshwater Fish, 14(1), 69–78. doi:10.1111/j.1600-0633.2005.00079.x

Kallio-Nyberg, I., Salminen, M., Saloniemi, I., & Kannala-Fisk, L. (2009). Marine survival of reared Atlantic salmon in the Baltic Sea: the effect of smolt traits and annual factors. Fisheries Research, 96(2–3), 289–295. doi:10.1016/j.fishres.2008.12.009

Katopodis, C., & Williams, J. G. (2012). The development of fish passage research in a historical context. Ecological Engineering, 48, 8–18. doi:10.1016/j.ecoleng.2011.07.004

Kennedy, G. J. A., Strange, C. D., Anderson, R. J. D., & Johnston, P. M. (1984). Experiments on the descent and feeding of hatchery-reared Salmon smolts (*Salmo salar* L.) in the River Bush. Aquaculture Research, 15(1), 15–25. doi:10.1111/j.1365-2109.1984.tb00578.x

Klemetsen, A., Amundsen, P. A., Dempson, J. B., Jonsson, B., Jonsson, N., O'connell, M. F., & Mortensen, E. (2003). Atalntic salmon *Salmo salar* (L.), brown trout *Salmo trutta* (L.) and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish, 12(1), 1–59. doi:10.1034/j.1600-0633.2003.00010.x

Korhonen, P. K., Hyvärinen, P., & Leinonen, A. (2014). Lohikalojen istukaspoikasten virikekasvatus - käytännön kokemuksia. Working report, Finnish Game and Fisheries Research Institute. In Finnish. Retrieved from: http://urn.fi/URN:ISBN:ISBN 978-952-303-178-4

Lacroix, L. A., Knox, D., & McCurdy, P. (2004). Effects of implanted dummy acoustic transmitters on juvenile Atlantic salmon. Transactions of the American Fisheries Society, 133(1), 211–220. doi:10.1577/T03-071

Lans, L., Greenberg, L.A., Karlsson, J., Calles, O., Schmitz, M., & Bergman, E. (2011). The effect of ration size on migration by hatchery-raised Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). Ecology of Freshwater Fish, 20(4), 548–557. doi:10.1111/j.1600-0633.2011.00503.x

Larinier, M., & Travade, F. (2002). Downstream migration: problems and facilities. Bulletin Français de la Pêche et de la Pisciculture, 364 (Suppl), 181–207. doi:10.1051/kmae/2002102

Larsen, M. H., Johnsson, J. I., Näslund, J., Thomassen, S. T., & Aarestrup, K. (2016). Reduced rearing density increases postrelease migration success of Atlantic salmon (Salmo salar) smolts. Canadian Journal of Fisheries and Aquatic Science, 73(5), 804–810. doi:10.1139/cjfas-2014-0563

Larsen, M. H., Thorn, A. N., Skov, C., & Aarestrup, K. (2013). Effects of passive integrated transponder tags on survival and growth of juvenile Atlantic salmon *Salmo salar*. Animal Biotelemetry, 1(1), 1–8. doi:10.1186/2050-3385-1-19

Larsson, S., Serrano, I., Eriksson, L.-O., & Fleming, I. (2012). Effects of muscle lipid concentrtion on wild and hatchery brown trout (Salmo trutta) smolt migration. Canadian Journal of Fisheries and Aquatic Science, 69(1), 1–12. doi:10.1139/f2011-128

Lebreton, J.-D., Burnham, K. P., Clobert, J., & Anderson, R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs, 62(1), 67–118. doi:10.2307/2937171

Lucas, M., & Baras, E. (2001). Migration of Freshwater Fishes. Oxford: Blackwell Publishing Ltd.

Lundqvist, H., Clarke, W. C., & Johansson, H. (1988). The influence of precocious sexual maturation on survival to adulthood of river stocked Baltic salmon. Ecography, 11(1) 60–69. doi:10.1111/j.1600-0587.1988.tb00781.x

Lundqvist, H., & Eriksson, L.-O. (1985). Annual rhythms of swimming behaviour and seawater adaptation in young Baltic salmon, *Salmo salar*, associated with smolting. Environmental Biology of Fishes, 14(4), 259–267. doi: 10.1007/BF00002629

Lundqvist, H., McKinnell, S., Fängstam, H., & Berglund, I. (1994). The effect of time, size and sex on recapture rates and yield after river releases of *Salmo salar* smolts. Aquaculture, 121(1–3), 245–257. doi:10.1016/0044-8486(94)90024-8

Mäki-Petäys, A., van der Meer, O., Ramakkaniemi, A., Orell, P., Rivinoja, P., & Erkinaro, J. (2012). Lohikantojen palauttaminen rakennetuille joille - mallinnustyökalu tuki- ja säätelytoimien biologiseen arviointiin. Working report, Finnish Game and Fisheries Research Institute. In Finnish. Retrieved from: http://urn.fi/URN:ISBN:978-951-776-872-6

Matthews, G. M., Park, D. L., Achord, S., & Ruehle, T. E. (1986). Static seawater challenge test to measure relative stress levels in spring Chinook salmon smolts. Transactions of the American Fisheries Society, 115(2), 236–244. doi:10.1577/1548-8659(1986)115<236:SSCTTM>2.0.CO;2

Mathur, D., Heisey, P. G., Euston, E. T., Skalski, J. R., & Hays, S. (1996). Turbine passage survival estimation for Chinook salmon smolts (*Oncorhynchus tshawytscha*) at a large dam on the Columbia River. Canadian Journal of Fisheries and Aquatic Science, 53(3), 542–549. doi:10.1139/f95-206

McAllister, K. W., McAllister, P. E., Simon, R. C., & Werner, J. K. (1992). Performance of nine external tags on hatchery-reared rainbow trout. Transactions of the American Fisheries Society, 121(2), 192–198. doi:10.1577/1548-8659(1992)121<0192:PONETO>2.3.CO;2

McCormick, S. D., Hansem, L. P., Quinn, T. P., & Saunders, R. L. (1998). Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Science. 55(Suppl. 1), 77–92. doi:10.1139/d98-011

McKinnell, S. M., & Lundqvist, H. (2000). Unstable release strategies in reared Atlantic salmon, *Salmo salar* L. Fisheries Management and Ecology, 7(3), 211–224. doi:10.1046/j.1365-2400.2000.00172.x

Mierswa, I., Wurst, M., Klinkenberg, R., Scholz, M., & Euler, T. (2006). Yale: Rapid prototyping for complex data mining tasks. Proceeding of the 12th ACM SIGKDD international conference on knowledge discovery and data mining (KDD-06), 2006.

Moffett, I. J. J., Crozier, W. W., & Kennedy, G. J. A. (1997). A comparison of five external marks for Atlantic salmon, *Salmo salar* L. Fisheries Management and Ecology, 4(1), 49–53. doi:10.1046/j.1365-2400.1997.d01-163.x

Morais, P., & Daverat, F. (2016). An Introduction to Fish Migration. Boca Raton, FL: CRC-Press.

Norrgård, J. R., Greenberg, L. A., Piccolo, J. J. Schmitz, M., & Bergman, E. (2013). Multiplicative loss of landlocked Atlantic salmon *Salmo salar* L. smolts during downstream migration trough multiple dams. River Research and Applications, 29(10), 1306–1317. doi:10.1002/rra.2616.

Norrgård, J. R., Bergman, E., Schmitz, M., & Greenberg, L. (2014). Effects of feeding regimes and early maturation on migratory behaviour of landlocked hatchery-reared Atlantic salmon *Salmo salar* smolts. Journal of Fish Biology, 85(4), 1060–1073. doi:10.1111/jfb.12522

Nyqvist, D., Greenberg, L., Goerig, E., Calles, O., Bergman, E., Ardren, W. R., & Castro-Santos, T. (2017). Migratory delay leads to reduced passage success of Atlantic salmon smolts at a hydroelectric dam. Ecology of Freshwater Fish, 26(4), 707–718. doi:10.1111/eff12318

Olsson, I. C., Greenberg, L. A., & Eklöv, A. G. (2001). Effects of an artifial pond on migrating brown trout smolts. North American Journal of Fisheries Management, 21(3), 498–506. doi:10.1577/1548-8675(2001)021<0498:EOAAPO>2.0.CO;2

Otero, J., L'Abée-Lund, J. H., Castro-Santos, T., Leonardsson, K., Storvik, G. O., Jonsson, B., … Vøllestad, L. A. (2014). Basin-scale phenology and effects of climate variability on global timing on initial seaward migration of Atlantic salmon (*Salmo salar*). Global Change Biology 20(1), 61–75. doi:10.1111/gcb.12363

Opperman, J. J., Royte, J., Banks, J., Day, L. R., & Apse, C. (2011). The Penobscot River, Maine, USA: a basin-scale approach to balancing power generation and ecosystem restoration. Ecology & Society, 16(3), 7. doi:10.5751/ES-04117-160307

Orell, P. Erkinaro, J., Kiljunen, M., Torniainen, J., Sutela, T., Jaukkuri, M., & Mäki-Petäys, A. Short sea migration and precocious maturation in reared Atlantic salmon post-smolts in the northern Baltic Sea. ICES Journal of Marine Science (in press)

Quinlan, J. R. (1992). Learning with continuous classes. Proceedings of the Australian Joint Conference on Artificial Intelligence. Singapore: World Scientific, 343–348.

Peake, S., McKinley, R. S., Scruton, D. A. & Moccia, R. (1997). Influence of transmitter attachment procedures on swimming performance of wild and hatchery-reared Atlantic salmon smolts. Transactions of the American Fisheries Society, 126(4), 707–714. doi:10.1577/1548-8659(1997)126<0707:IOTAPO>2.3.CO;2

Plumb, J. M., Perry, R. W., Adams, N. S., & Rondorf, D. W. (2006). The effects of the river impoundment and hatchery rearing on the migration behavior of juvenile steelhead in the lower Snake River, Washington. North American Journal of Fisheries Management, 26(2), 438–452. doi:10.1577/M04-177.1

R Core Team (2016). R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. Available from https://www.R-project.org/

Rodewald, P. (2013). Effects of broodstock origin, rearing environment and release method on post-stocking performance of Atlantic salmon. Doctoral thesis, University of Helsinki.

Rodewald, P., Hyvärinen, P. & Hirvonen, H. (2011). Wild origin and enriched environment promote foraging rate and learning to forage on natural prey of captive reared Atlantic salmon parr. Ecology of Freshwater Fish, 20(4), 569–579. doi:10.1111/j.1600-0633.2011.00505.x

Romakkaniemi, A., Perä, I., Karlsson, L., Jutila, E., Carlsson, U., & Pakarinen, T. (2003). Development of wild Atlantic salmon stocks in the rivers of the northern Baltic Sea in response to management measures. ICES Journal of Marine Science, 60(2), 329–342. doi:10.1016/S1054-3139(03)00020-1

Rosengren, M., Kvingedal, E., Näslund, J., Johnsson, J. I., & Sundell, K. (2017). Born to be wild: effects of rearing density and environmental enrichment on stress, welfare, and smolt migration in hatchery-reared Atlantic salmon. Canadian Journal of Fisheries and Aquatic Sciences, 74(3), 396–405. doi:10.1139/cjfas-2015-01015

Rowe, D. K., Thorpe, J. E., & Shanks, A. M. (1991). Role of fat stores in the maturation of male Atlantic salmon (Salmo salar) parr. Canadian Journal of Fisheries and Aquatic Science, 48(3), 405–413. doi:10.1139/f91-052

Rub, A. M. W., Jepsen, N., Liedtke, T. L., Moser, M. L., & Weber, E. P. (2014). Surgical insertion of transmitters and telemetry methods in fisheries research. American Journal of Veterinary Research, 75(4), 402–412. doi:10.2460/ajvr.75.4.402

Ruggles, C. P. (1980). A review of downstream migration of Atlantic salmon. Canadian Technical Report of Fisheries and Aquatic Society, 952, 1–27.

Ruohonen, K. (1998). Individual measurements and nested designs in aquaculture experiments: a simulation study. Aquaculture, 165(1–2), 149–157. doi:10.1016/S0044-8486(98)00252-X

Sandstrom, P. T., Ammann, A. J., Michel, C., Singer, G., Chapman, E. D., Lindley, S., … Klimley, A. P. (2013). Growth, survival, and tag retention of steelhead trout (*Oncorhynchus mykiss*) and its application to survival estimates. Environmental Biology of Fishes, 96(2–3), 145–164. doi:10.1007/s10641-012-0051-0

Saunders, R., Hachey, M. A., & Fay, C. W. (2006). Maine's diadromous fish community: past, present, and implications for Atlantic salmon recovery. Fisheries, 31(11), 537–547. doi:10.1577/1548-8446(2006)31[537:MDFC]2.0.CO;2

Scruton, D. A., McKinley, R. S., Kouwen, N., Eddy, W., & Booth, R. K. (2003). Improvement and optimization of fish guidance efficiency (FGE) at a behavioural fish protection system for downstream migrating Atlantic salmon (*Salmo salar*) smolts. River Research and Applications, 19(5–6), 605–617. doi: 10.1002/rra.735

Scruton, D. A., Pennell, C. J., Bourgeois, C. E., Goosney, R. F., Porter, T. R., & Clarke, K. D. (2007). Assessment of a retrofitted downstream fish bypass system for wild Atlantic salmon (*Salmo salar*) smolts and kelts at hydroelectric facility on the Exploits River, Newfoundland, Canada. Hydrobiologia, 582(1), 155–169. doi:10.1007/s10750-006-0557-6

Scruton, D. A., Pennell, C. J., Bourgeois, C. E., Goosney, R. F., King, L., Booth, R. K., … Clarke, K. D. (2008). Hydroelectricity and fish: a synopsis of comprehensive studies of upstream and downstream passage of anadromous wild Atlantic salmon, *Salmo salar*, on the Exploits River, Canada. Hydrobiologia, 609(1), 225–239. doi: 10.1007/s10750-008-9410-4

Shrimpton,J. M., & McCormick, S. D. (2002). Seasonal changes in androgen levels in stream- and hatchery-reared Atlantic salmon parr and their relationship to smolting. Journal of Fish Biology, 61(5), 1294–1304. doi:10.1111/j.1095-8649.2002.tb02472.x

Staurnes, M., Lysfjörd, G., Hansen, L. P., & Heggberget, T. G. (1993). Recapture rates of hatchery-reared Atlantic salmon (*Salmo salar*) releted to smolt development and time of release. Aquaculture, 118(3–4), 327–337. doi:10.1016/0044-8486(93)90467-D

Stephenson, J. R., Gingerich, A. J., Brown, R. S., Pflugrath, B. D., Deng, Z., Carlson, T. J., … Seaburg, A. G. (2010). Assessing barotrauma in neutrally and negatively buoyant juvenile salmonids exposed to simulated hydro-turbine passage using a mobile aquatic barotrauma laboratory. Fisheries Research, 106(3), 271–278. doi:10.1016/j.fishres.2010.08.006

Stich, D. S., Kinnison, M. T., Kocik, J. F., & Zydlewski, J. D. (2015). Initation of migration and movement rates of Atlantic salmon smolts in fresh water. Canadian Journal of Fisheries and Aquatic Science, 72(9), 1339–1351. doi:10.1139/cjfas-2014-0570

Strand, R., & Finstad, B. (2007). Migratory behaviour in relation to smolt development and releasing strategies in Atlantic salmon (*Salmo salar* L.) smolts. Aquaculture, 273(2–3), 277–283. doi:10.1016/j.aquaculture.2007.10.010

Thorpe, J. E. (1994). Reproductive strategies in Atlantic salmon, *Salmo salar* L. Aquaculture Research, 25(1), 77–87. doi:10.1111/j.1365-2109.1994.tb00668.x

Thorstad, E., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H., & Finstad, B. (2012). A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. Journal of Fish Biology, 81(2), 500–542. doi:10.1111/j.1095-8649.2012.03370.x

Vähä, J.-P., Erkinaro, J., Niemelä, E., & Primmer, C. R. (2008). Temporally stable genetic structure and low migration in an Atlantic salmon population complex: implications for conservation and management. Evolutionary Application, 1(1), 137–154. doi:10.1111/j.1752-4571.2007.00007.x

Vehanen, T., Pasanen, P., Lehtinen, E., & Simola, O. (1993). Report on salmon (Salmo salar L.) tagging experiments performed by Taivalkoski State Aquaculture in 1973–1988. Kalatutkimuksia, Finnish Game and Fisheries Research Institute. In Finnish.

Venditti, D. A., Rondorf, D. W., & kraut, J. M. (2000). Migration behavior and forebay delay of radio-tagged juvenile Chinook salmon in a lower Snake River impoundment. North American Journal of Fieheries Management, 20(1), 41–52. doi:10.1577/1548-8675(2000)020<0041:MBAFDO>2.0.CO;2

Wang, Y., & Witten, I. H. (1997). Indroduction of model trees for predicting continuous classes. Proceeding of the poster papers of European Conference on machine learning, Prague: University of Economics, Faculty of Informatics and Statistics.

Weber, E. D., & Fausch, K. D. (2003). Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition. Canadian Journal of Fisheries and Aquatic Science, 60(8), 1018–1036. doi:10.1139/f03-087

Welch, D. W., Batten, S. D., & Ward, B. R. (2007). Growth, survival, and tag retention of steelhead trout (*O. mykiss*) surgically implanted with dummy acoustic tags. Hydrobiologia, 582(1), 289–299. doi: 10.1007/s10750-006-0553-x

Welch, D. W., Rechisky, E. L., Melnychuk, M. C., Porter, A. D., Walters, C. J., Clemets, S., … Schreck, C. (2008). Survival of migrating salmon smolts in large rivers with and without dams. PLoS Biology, 6:e265. doi:10.1371/journal.plio.0060265

Whalen, K. G., Parrish, D. L., & McCormick, S. D. (1999). Migration timing of Atlantic salmon smolts relative to environmental and physiological factors. Transactions of the American Fisheries Society, 128(2), 289–301. doi:10.1577/1548-8659(1999)128<0289:MTOASS>2.0.CO;2

Williams, J. G., Armstrong, G., Katopodis, C., Larinier, M., & Travade, F. (2011). Thinking like a fish: a key ingredient for development of effective fish passage facilities at river obstructions. River Research and Applications, 28(4), 407–417. doi:10.1002/rra.1551

Williams, J. G., Smith, S. G., & Muir, W. D. (2001). Survival estimates for downstream migrant yearling juvenile salmonids through the Snake and Columbia Rivers hydropower system, 1966-1980 and 1993-1999. North Ameican Journal of Fisheries Management, 21(2), 310–317. doi:10.1577/1548-8675(2001)021<0310:SEFDMY>2.0.CO;2

Wysujack, K., Greenberg, L. A., Bergman, E., & Olsson, I. C. (2009). The role of the environment in partial migration: food availability affects the adoption a migratory tactic in brown trout *Salmo trutta*. Ecology of Freshwater Fish, 18(1), 52–59. doi:10.1111/j.1600-0633.2008.00322.x

Zheng, Z., & Webb, G. I. (2005). A comparative study of semi-naïve bayes methods in classification learning. In: Simoff, S. J., Williams, G. J., Galloway, J., & Kolyshkina, I. (eds.) Proceeding of the 4th Australasian Data Mining Conference, 5–6th December, 2005, Sydney, Australia.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). Mixed Effects Models and Extensions in Ecology with R. New York: Springer-Verlag.

Zydlewski, G. B., Haro, A., Whalen, K. G., & McCormick, S. D., (2001). Performance of stationary and portable passive transponder detection systems for monitoring of fish movements. Journal of Fish Biology, 58(5), 1471–1475. doi:10.1111/j.1095-8649.2001.tb02302.x

Zydlewski, J., Zydlewski, G., & Danner, G. R. (2010). Descaling injury impairs the osmoregulatory ability of Atlantic salmon smolts entering seawater. Transactions of the American Fisheries Society, 139(1), 129–136. doi:10.1577/T09-054.

Original articles

I Vainikka, A., Huusko, R., Hyvärinen, P., Korhonen P. K., Laaksonen, T., Koskela, J., Vielma, J., Hirvonen H., & Salminen, M. (2012). Food restriction prior to release reduces precocious maturity and improves migration tendency of Atlantic salmon (*Salmo salar*) smolts. Canadian Journal of Fisheries and Aquatic Science, 69(12), 1981–1993.

II Karppinen, P., Jounela, P., Huusko, R., & Erkinaro, J. (2014). Effects of release timing on migration behavior and survival of hatchery-reared Atlantic salmon smolts in a regulated river. Ecology of Freshwater Fish, 23(3), 438–452.

III Huusko, R., Huusko, A., Mäki-Petäys, A., Orell, P., & Erkinaro, J. (2016). Effects of tagging on migration behavior, survival and growth of hatchery-reared Atlantic salmon smolts. Fisheries Management and Ecology, 23(5), 367–375.

IV Huusko, R., Hyvärinen, P., Jaukkuri, M., Mäki-Petäys, A., Orell, P., & Erkinaro, J. (2017). Survival and migration speed of radio-tagged Atlantic salmon (*Salmo salar* L.) smolts in two large rivers: one without and one with dams. Canadian Journal of Fisheries and Aquatic Science, https://doi.org/10.1139/cjfas-2017-0134

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