Effects of feeding regimes on phenotype and performance in Atlantic salmon

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Cover: Hatchery-reared Atlantic salmon juvenile
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Abstract

Atlantic salmon populations have declined worldwide across their distribution. This is partly due to hydro power development that has degraded freshwater habitat and cut off the migration routes between the freshwater habitat and the sea. To prevent extinctions, and to compensate fisheries for decreased natural production, supplementary rearing and releases of hatchery-reared fish are common. However, the survival of released hatchery-reared fish has been lower compared to wild fish, and since the middle 1990s the survival has decreased even more. The decrease in survival coincides with a large increase in smolt size and an increasingly deviant phenotype compared to wild smolts. In this thesis I examine how different feeding regimes used in the hatchery can affect the size and the energetic state of hatchery-reared salmon. I test the effects of a more wild-like phenotype on downstream migration as smolts and monitor their adult return rates from the sea. Large scale feeding experiments were done in a hatchery environment and smaller scale experiments were done in an adjacent research laboratory. Different marking techniques such as passive integrated transponder (PIT)-, and acoustic tags, were used to monitor fish movement and adult return rates. By using restricted feed rations and periods of starvation, phenotypically wild-like smolts, in terms of body size and energetic state, could be produced. Fish with strongly restricted feed rations suffered from severe dorsal fin damage and higher mortality. Moderate feed restrictions did not affect fin damage nor mortality. Lower energetic state increased the migration speed in experimental streams. In the river, lower energetic state and increased smolt length increased the sea entry. However, the most important factor for successful sea entry was the discharge in the river. Modelling of individual smolt characteristics showed that smolts of intermediate size had the highest probability of adult return from the sea. My results suggest that in order to have the highest return rates, hatchery-reared smolts should be slightly larger compared to wild smolts, but not as large as the smolts commonly released from hatcheries. Moderate feed restrictions for larger two year old fish, appear to be enough to improve smolt migration and increase the sea age at maturity. In addition, moderate feed restrictions for larger two year old fish would likely increase their adult return rates.

Keywords: Atlantic salmon, energetic state, feed restriction, fin damage, life history, migration, return rate, smolt, starvation, wild-like

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Abstract

Laxen har påverkats negativt av vattenkraftsutbyggnad som förstört lek- och uppväxtområden i sötvatten och skurit av vandringsvägar mellan sötvatten och födoområden i havet. För att kompensera fisket för lägre naturlig produktion av lax har vattenkraftsbolagen blivit ålagda att odla och sätta ut laxsmolt. Jämfört med vild lax är överlevnaden hos den odlade laxen lägre när de släppts ut och skillnaden i överlevnad har ökat sedan mitten av 1990-talet. Den minskande överlevnaden för odlad fisk sammanfaller med en period då storleken på smolten vid utsättningen har ökat markant i jämförelse med den vilda smolten. I avhandlingen har jag undersökt om olika foderregimer kan användas i odlingen för att minska storleken på odlad smolt. Jag har också testat effekten av en fysiologiskt mer vild-lik smolt på smoltvandring och andelen vuxen fisk som senare återvänder från havet till älven. Resultaten visar att det är möjligt att producera en smolt i samma storlek och med lika stor energireserv som en vild smolt men då måste utfodringen begränsas kraftigt vilket i sin tur leder till allvarliga fenskador och ökad dödlighet. Vid mindre foderbegränsningar påverkades inte fenskador och dödlighet. En mindre energireserv hade positiv effekt på smoltvandringen i de kontrollerade försöken och i älven. I älven var det dock vattenflödet i den gamla älvfåran som hade störst inverkan på hur stor andel av smolten som nådde havet. När det var lägre flöde en längre period var det färre fiskar som nådde havet. Sannolikheten att återvända som vuxen lax från havet påverkades av smoltens storlek vid utsättningen och sambandet var puckelformat. Detta indikerade att den odlade smolten bör vara något större än den vilda smolten, men mindre än den nuvarande odlade smolten som sätts ut idag, för att ha störst chans att återvända från havet som vuxen. Måttliga foderbegränsningar för de största tvååriga fiskarna verkar vara tillräckligt för att förbättra smoltvandringen och minska andelen som kommer tillbaka redan efter ett år i havet. Det är också möjligt att måttliga foderbegränsningar för de största fiskarna kan öka det totala antalet fiskar som återvänder eftersom smolten i mellanstorlek hade störst sannolikhet att återvända från havet som vuxna.

Nyckelord: Atlantlax, energistatus, fenskador, foderbegränsning, livshistoria, smolt, svält, vandring, vildlik, överlevnad

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Preface

“So weird! How can someone spend so much time researching such a small an uninteresting thing?!” My thoughts at the professor installation talk of Hans Lundqvist in 1999 *The complex threats against the wild River Vindelälven salmon*. Since then, things have definitely changed and now I’m the weird one...!

Dedication

Till Edward, Theo och Colin - ni är det bästa jag vet!

Talk about a dream, try to make it real.
Bruce Springsteen

Contents

List of publications

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

I Persson, L. & Alanärä, A. (2014). The effect of shelter on welfare of juvenile Atlantic salmon *Salmo salar* reared under a feed restriction regimen. *Journal of Fish Biology* 85 (3), pp. 645-656.

II Persson, L., Leonardsson, K., and Alanärä, A. Manipulation of the energetic state of Atlantic salmon *Salmo salar* juveniles and the effect on migration speed. (Submitted manuscript).

III Persson, L., Kagervall, A., Leonardsson, K., Royan, M., and Alanärä, A. The effect of body size and energetic state on smolt migration in Atlantic salmon. (Manuscript).

IV Persson, L., Leonardsson, K., and Alanärä, A. Higher adult return rates from the sea of intermediate sized hatchery-reared Atlantic salmon smolts. (Manuscript).

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The contribution of L. Persson to the papers included in this thesis was as follows:

I Participated in planning of the experiment, did most of the field work and the data analyses, and wrote most of the manuscript.

II Participated in planning of the experiment, did most of the field work and the data analyses, and wrote most of the manuscript.

III Participated in planning of the experiment, did most of the field work and the data analyses, and wrote most of the manuscript.

IV Participated in the planning of the experiment, did some of the field work, analysed data together with AA and KL, and wrote most of the manuscript.

1 Introduction

Atlantic salmon (*Salmo salar*) is an anadromous fish that conducts extensive migrations between freshwater and marine habitats to complete its life-cycle (figure 1). Atlantic salmon are iteroparous, which means that they can reproduce more than once. The adults return to their natal rivers to spawn after one or more years in the sea. They spawn during the fall and the eggs hatch the following spring. The newly hatched alevins stay in the gravel until their yolk-sac has been absorbed and then swim up as fry and start to feed. At the end of the summer the fry develop into juvenile fish called parr and the parr rear in the river for one or more years before they smoltify (Jonsson & Jonsson, 2011a). The smoltification process prepares salmon for a life in the sea. The downstream migration as smolts usually occurs during spring when the smolts migrate to the sea where the feeding-, and growth conditions are better (McCormick *et al.*, 1998). Some males become sexually mature as parr and stay in the river and take part in the spawning. Previously mature male parr can later smoltify and migrate to the sea in the same way as immature fish (Jonsson & Jonsson, 2011a; Lundqvist, 1983). There are some examples of landlocked or resident populations of Atlantic salmon that complete their life-cycle without migrating to the sea (Klemetsen *et al.*, 2003).

Atlantic salmon and other salmonid populations have declined due to habitat degradation, over-exploitation, and hydropower development among other things. Supportive breeding and propagation is widely used to avoid extinctions and support commercial and recreational fisheries (Jonsson & Jonsson, 2011b). In the Baltic Sea area, large scale release programs of hatchery-reared Atlantic salmon have been in place since the 1950s. They are mainly based on legal obligations of the power plant companies to compensate fisheries for loss of natural smolt production caused by hydropower developments (Kallio-Nyberg *et al.*, 2013).

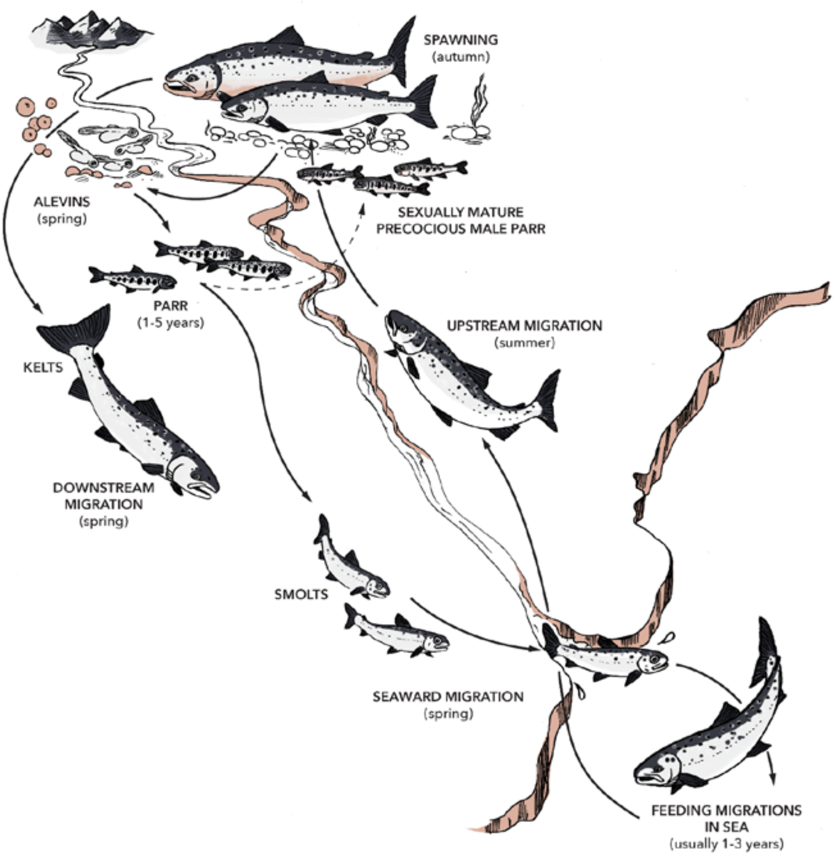

Figure 1. Life cycle of Atlantic salmon. Modified from Lundqvist (1983) by Johanna Hägglund.

The magnitude of compensation is often expressed as number of fish released and decided based on the estimated fisheries catch before exploitation (Anon., 1956). For production of hatchery-reared fish, the broodstock of adult fish are either kept in captivity or caught in the wild every year. When the fish are ready to spawn they are stripped for eggs or milt and the eggs are artificially fertilized and incubated in hatcheries. Eggs can be planted into streams and rivers, juveniles can be released at various stages of their freshwater phase, or be released at the river mouth as post-smolts. Atlantic salmon are often stocked as smolts to limit density induced competition with wild fish[1] and/or to surpass the carrying capacity of the river when for example juvenile habitat is missing or

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[1] Wild fish: natural fertilization, fish born and reared naturally in the wild.

highly limited (Jonsson & Jonsson, 2009). In the Baltic Sea, approximately 4.6 million hatchery-reared smolts are released annually (ICES, 2017).

Even though released fish are derived from wild and local populations they suffer from higher mortality compared to wild fish, which is likely due to the difference between the hatchery conditions and the natural habitat in the wild (Johnsson *et al.*, 2014). In hatcheries, feed is abundant, diseases are treated, and there are no predators, which together make life as a juvenile easier for a hatchery-reared fish compared to a wild fish. On the other hand fish are reared at unnatural high densities, feed is distributed in a way that promotes competition, and they are continuously disturbed by humans, which together make life challenging in the hatchery (Huntingford, 2004). The different conditions between the wild and the hatchery environment generates behavioural adaptations to captivity that may be detrimental for the survival of hatchery-reared fish after release into the wild (Einum & Fleming, 2001). For example, the captive environment promotes aggressive and bold behaviour that is advantageous in a predator-free environment but may be fatal when predators are present (Huntingford, 2004).

Lower survival compared to wild fish has been reported several times for hatchery-reared fish after release into the wild (Aarestrup *et al.*, 2014; Chittenden *et al.*, 2008; Jonsson *et al.*, 2003). During the 1980s and 1990s the survival of hatchery-reared Atlantic salmon to adulthood was estimated to about half of wild fish and survival was positively correlated with smolt size (Jokikokko *et al.*, 2006; Kallio-Nyberg *et al.*, 2004). The positive effect of size was partly thought to be due to lower vulnerability to size-dependent predation (Kallio-Nyberg *et al.*, 2009). The mortality during the freshwater migration phase is often associated with predation, which can be high on newly stocked smolts (Thorstad *et al.*, 2012; Kekäläinen *et al.*, 2008; Jepsen *et al.*, 1998). The post-smolt stage in the sea is considered a key life stage and is also associated with high mortality (Friedland *et al.*, 2009). After the middle of 1990s, the estimated post-smolt survival decreased until 2005 (ICES, 2017). The difference in survival to adulthood between hatchery-reared and wild fish increased and Siira *et al.* (2006) estimated that the return rates to the Gulf of Bothnia of hatchery-reared fish was up to 4.5 times lower than the return rates of wild fish. Due to improvements of the rearing technique in the hatcheries and development of the feed over time, the size of the smolts have increased, and especially so after the year 2000 (Hedman, 2011; Eriksson *et al.*, 2008). The positive effect of a larger smolt size on survival in hatchery-reared fish seems to have disappeared after the year 2000 (Kallio-Nyberg *et al.*, 2009). Rather the increase in size of hatchery-reared fish over time coincides with the decreasing trend in re-capture rates (Eriksson *et al.*, 2008). A decreasing trend in recapture rates may indicate reduced quality of hatchery-reared fish but is also influenced by lower willingness of fishers to report tags of recaptured fish and lower fishing intensity (Petersson *et al.*, 2013).

Size-wise, the hatchery-reared smolts differ a lot from the equivalent wild smolts (Lans *et al.*, 2011; Eriksson *et al.*, 2008). It has been speculated that the hatchery-rearing produces fish that are unwilling to leave the river (Thorstad *et al.*, 2011), and that the larger size and the high energetic state of hatchery-reared fish decrease their motivation to migrate after release (Serrano *et al.*, 2009). Hatchery-reared fish can be up to five times larger and have three-four times more body lipids compared to wild fish (Lans *et al.*, 2011). The phenotypical differences between hatchery-reared and wild fish has been recognized as a potential explanation for the poor performance of hatchery-reared fish in the wild (Stringwell *et al.*, 2014; Einum & Fleming, 2001). Several authors have argued for a production of a phenotypically more wild-like smolt (Jensen *et al.*, 2016; Thorstad *et al.*, 2011; Jonsson & Jonsson, 2009).

Compared to wild fish, hatchery-reared fish have lower sea age at maturity since a larger fraction of hatchery-reared fish return to the river as grilse after only one winter at sea (Jensen *et al.*, 2016; Kallio-Nyberg *et al.*, 2015). A positive relation was found between marine growth in the Gulf of Finland and the Bothnian Sea and the grilse fraction (Salminen, 1997). The larger fraction of grilse in hatchery-reared populations of the Baltic Sea, may be related to the large size of hatchery-reared post-smolts. It has been suggested that large post-smolts are able to switch to piscivory earlier than small post-smolts and therefore utilize the feeding opportunities in the Bothnian Sea more efficiently (Salminen *et al.*, 2001).

Feed restrictions and feed with different dietary lipid content can be used to manipulate the size and the energetic state of hatchery-reared fish (Shearer *et al.*, 1997), and feed restrictions in the hatchery have had positive effects on smolt migration in Atlantic salmon (Norrgård *et al.*, 2014b; Vainikka *et al.*, 2012; Lans *et al.*, 2011) and brown trout (*Salmo trutta*) (Davidsen *et al.*, 2014; Larsson *et al.*, 2012; Wysujack *et al.*, 2009). Since the predation on newly released smolts can be high (Thorstad *et al.*, 2012; Kekäläinen *et al.*, 2008), a fast initiation of the migration and a fast transit through the river may be positive for the survival of hatchery-reared fish.

Feed restrictions in the hatchery usually increase aggression among juvenile salmonids since the juveniles in the wild are territorial and defend feeding territories (Brännäs & Alanärä, 1994; Storebakken & Austreng, 1987). Increased aggression often results in more fin damage form nipping (Canon Jones *et al.*, 2011; Latremouille, 2003). Turnbull *et al.* (1998) reported that most attacks were directed towards the caudal and the dorsal fin, and Vainikka *et al.* (2012) reported increased dorsal fin damage in feed restricted Atlantic salmon juveniles. Enrichment has been found to improve fin quality in juvenile Atlantic salmon (Näslund *et al.*, 2013) and in juvenile steelhead (*Oncorhynchus mykiss*) (Berejikian & Tezak, 2005), possibly due to the effect of visual isolation and fewer aggressive interactions.

1.1.1 Aims and objectives

The overall aim with this thesis was to find ways to improve the quality of hatchery-reared smolts so that their adult return rates would increase. The main objectives were to use different feeding regimes in the hatchery to produce a more wild-like smolt in terms of body size and energetic state, and to evaluate if a phenotypically more wild-like smolt performed better during smolt migration and had higher adult return rates compared to conventionally reared smolts.

My main research questions are:

- How are the body size and energetic state of two year Atlantic salmon affected by feed restrictions (paper I, II, and IV), feed with different dietary lipid content (paper II), and periods of starvation (paper II)?
- Can shelter within the rearing environment be used to mitigate negative effects of restricted feed rations on fin damage (paper I)?
- How do a wild-like body size and energetic state affect the swimming and migration speed of a hatchery-reared two year old smolt in experimental streams (paper II)?
- How do the smolt size and the energetic state affect the sea entry rate after release into the river (paper III)?
- At what smolt size and energetic state is the probability of adult return from the sea the highest (IV)?

The studies were approved by the Swedish Ethical Committee for Animal in Research, Ethical application A112-10.

2 Method and materials

2.1.1 Study system

I have conducted my studies at the Norrfors hatchery and the adjacent research laboratory located in Norrfors (63° 53´ N; 20° 1´ E) next to the River Umeälven close to the city of Umeå, Sweden. The hatchery is managed by the power company Vattenfall Vattenkraft AB and the research laboratory is managed by the Swedish University of Agricultural Sciences. The hatchery annually releases one and two year old Atlantic salmon and sea run brown trout smolts into the river to compensate for the hydropower development and the damming of the River Umeälven. The River Umeälven originates from the mountain area in the western Sweden and is regulated by several hydropower plants. The last power plant Stornorrfors has its dam about 30 km from the coast of the Gulf of Bothnia. Above this dam, the 450 km long and unexploited tributary River Vindelälven enters the River Umeälven (figure 2). The River Vindelälven has wild populations of Atlantic salmon and sea run brown trout. Upstream and downstream migration of fish pass the Stornorrfors power plant is facilitated by an 8 km long bypass channel (the old river bed) and a fish ladder at the hydro power dam in Norrfors. The fish ladder is open between 20 May and 1 Oct and the minimum discharge is 10 m^3 s^{-1} during this period. The hatchery-reared population of Atlantic salmon is derived from a mix of hatchery-reared and wild returning spawners caught every year at the fish ladder. The main growth season in the hatchery is approximately between June and the end of September.

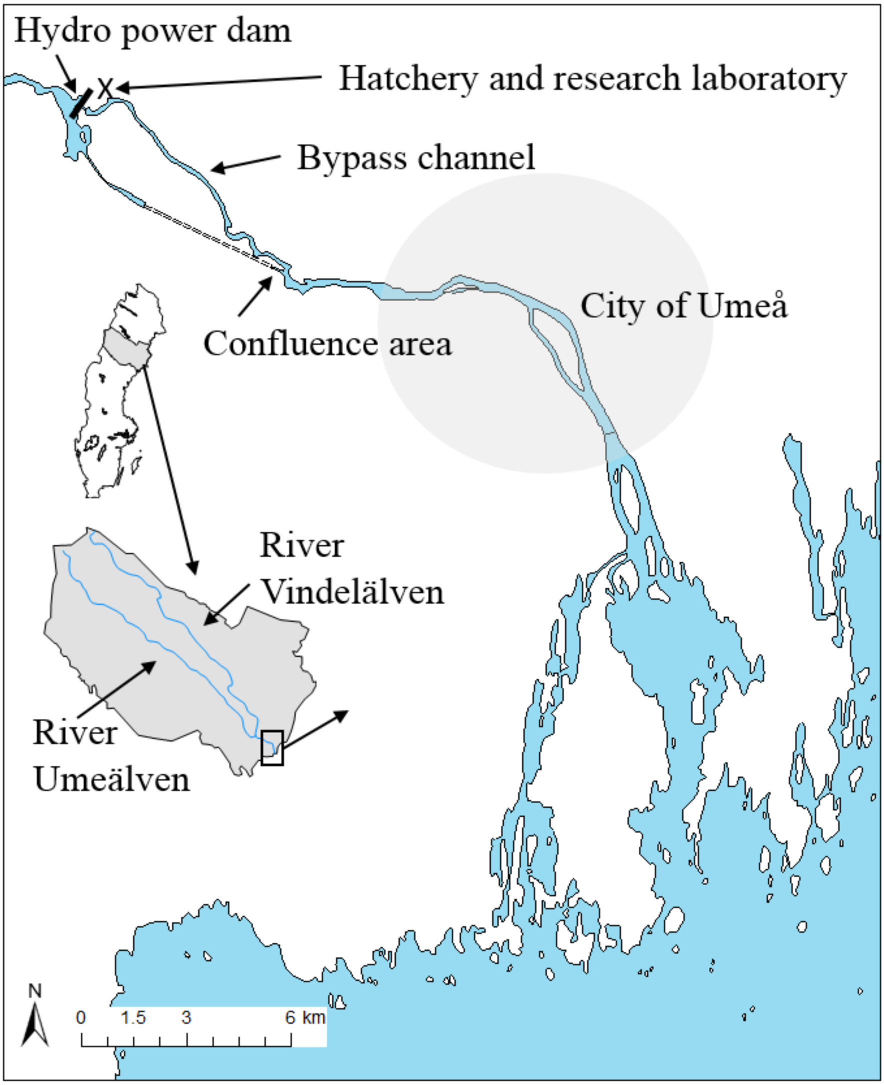

Figure 2. Geographic location of the study area and a detailed map of the lower part of the River Umeälven. The confluence area is where the water from the hydropower plant and the water from the bypass channel reunite, approximately 22 km from the coast. The River Vindelälven enters the River Umeälven approximately 10 km upstream the hydro power dam at Norrfors.

2.1.2 Fish in the different experiments

After the first summer in the hatchery the 0+ fish are size graded and the largest fish are released the following spring as one year old smolts. The medium and small fish are kept in the hatchery for another year and released as two year old smolts. Feed restrictions were applied during the second year. In the experiments in the research laboratory fish from the same grading were used whereas in the large scale experiment in the hatchery, fish from both medium and small grading were used. In 2010, there was only one replicate per feed treatment and size grading (medium/small) due to lack of fish graded as medium. In 2011, two replicates per feed treatment and size grading were used, and in 2012, only fish graded as medium were used with two replicates per feed treatment (table 1).

For the experiments in the laboratory fish were conventionally reared in the hatchery during their first year and moved into the research laboratory during spring before the start of their second growth season. In the first experiment in the laboratory during 2011, all fish were tagged with passive integrated transponder (PIT) tags and about 120 were put into each of the 16 tanks available. Half of the tanks were equipped with an "extra" bottom (figure 3) and feed restrictions were applied in a 2 x 2 factorial design. In the second experiment in the laboratory during 2012, about 126 fish were put into each tank and feed restrictions and feed with different dietary lipid contents (9 or 15 %) were used in a 2 x 2 factorial design. After the growth season half of the fish were starved until the following spring when fish were tagged with PIT-tags and used to study smolt migration in experimental streams in 2013.

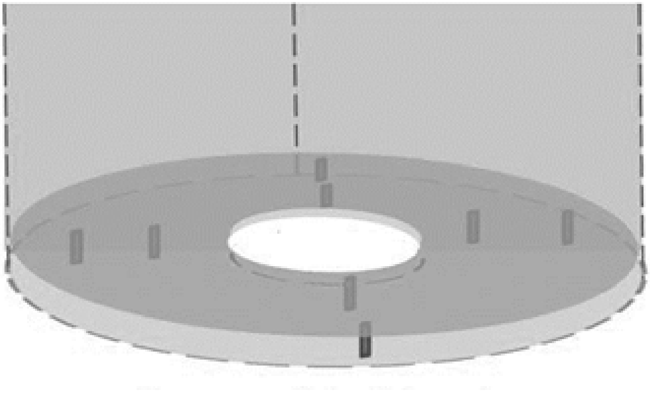

Figure 3. Illustration of the shelter when placed in the tank. The tank and the shelter had a diameter of 1 m, the circular hole for the drainage had a diameter of 30 cm, and the distance between the bottom of the tank and the shelter was 5 cm.

To evaluate effects of feed restrictions on the smolt migration in the river, fish from the large scale feeding experiment (2010 – 2012), as well as fish from the smaller scale experiment in the laboratory during 2011, were used in the river migration study between 2011 and 2013. To evaluate the effects of feed restrictions on adult return rates and life history in terms of sea age at maturity, fish from the large scale feeding experiment, as well as fish that were to be released as one year old smolts, were tagged with PIT-tags and released from the hatchery between 2011 and 2013.

Wild Atlantic salmon smolts from River Vindelälven were tagged and monitored within the European Data Collection Framework (ICES, 2017). To make comparisons with wild fish, data from the monitoring program were used between 2011 and 2013. In 2011, wild fish were also included in the river migration study.

2.1.3 Rearing tanks

In the hatchery, the circular rearing tanks had a diameter of 11 m and the water depth was approximately 40 cm. In the research laboratory the water depth of the rearing tanks was approximately the same, 40 cm, and the diameter of the tanks was 1 m. The water flow through the tanks in the research laboratory was approximately 30 l per minute, the mean light at the water surface was approximately 150 lx and the light:dark cycle followed the ambient photoperiod. Dead fish were removed daily and the tanks in the research laboratory were cleaned when deemed necessary.

2.1.4 Theoretical energy need

Fish in hatcheries are usually fed to satiation to prevent fin damage (Latremouille, 2003) and the feed rations recommended by the feed manufacturers often include feed waste. The theoretical energy need of salmon can be calculated and then the feed rations can be adjusted to decrease the growth of the fish and result in a smaller sized smolt. The digestible energy need (DEN, kJ $DE * g^{-1}$, (Alanärä *et al.*, 2001)), describes the amount of energy (kJ DE) the fish needs to eat to gain 1 g of weight and DEN is calculated as follows:

$$DEN = \frac{FI * DE}{W_2 - W_1}$$

where FI is the feed intake (g) and DE is the digestible energy content of the feed (kJg^{-1}). Information on DEN for salmon was found in Bailey and Alanärä (2006) and expressed as follows:

$$DEN = 10.77 + 1.05 * Ln\,(W)$$

The theoretical energy requirement (TER) can be calculated as follows:

$$TER = DEN * W_i$$

where W_i is the daily weight increase (g). The daily weight increase was calculated by using the thermal unit growth coefficient (TGC) (Iwama & Tautz, 1981). Values of TGC were obtained from analysis of previous growth records in the Norrfors hatchery (unpublished data). The average TGC value during the main growth season (June – September) between 1999 and 2010 was 1.6 (± 0.3). The daily weight increase can be estimated by using the following equation:

$$W_2 = (W_1^{\frac{1}{3}} + [\frac{TGC}{1000} * T])^3$$

where W_2 is the weight after one day (g), W_1 is the initial weight (g), and T is the water temperature (°C). TER is used to calculate the daily feed allowance as follows:

$$FA = \frac{n * TER}{DE}$$

where FA is the fish’s feed requirement (g day^{-1}) and n is the number of fish in the rearing unit.

2.1.5 Feed rations

In the large scale feeding experiment in the hatchery, the feed allowance model, which describes the feed requirement for optimal growth without feed waste, was multiplied by a correction factor. For feed restricted groups the correction factor was 0.7 in 2010 and 2011, and 0.6 in 2012, and for control groups it was 1.2 to assure feeding to satiation. In the research laboratory the correction factor was 0.5 in the first experiment and 0.65 in the second experiment for the feed restricted groups, and 1.2 for control groups.

In the large scale feeding experiment in the hatchery it was complicated to adjust the feeding system so that the daily feed rations corresponded to the desired levels; hence the resulting amounts of feed became larger than anticipated, especially the first year. In the research laboratory the feed was provided with automatic drum feeders from ArvoTec and the first year the rotating drums were not suitable for the low feed rations (due to relatively low number of fish in the tanks). Therefore, the resulting amount of feed for fish in the research laboratory became much smaller than anticipated. Before the start of the second feeding experiment in the research laboratory in 2012, the rotating drums were changed and the feed rations set slightly higher than the previous year. With the new rotating drums the feeding situation improved but the rations were still too small for the rotating drums to provide the feed at the desired level. Thus, real control groups fed ab libitum were missing in the laboratory experiments.

2.1.6 Handling of fish and assessment

In the large scale feeding experiment in the hatchery, the hatchery staff reported the initial weight of the fish and routinely assessed a subsample of 100 or 200 individuals from each tank and treatment to calibrate the settings of the feeding system and adjust feed rations. At assessment, the fish were anaesthetized with tricaine methanesulfonate (MS-222) and total length (to the nearest mm) and weight (to the nearest g) were recorded as well as occurrence of sexually mature males with running milt. Fin damage was assessed according to a three graded scale, modified from the six graded scale provided by Hoyle *et al.* (2007), based on the deterioration of the fin where 1 was an intact or almost intact fin; 2 was a moderate fin damage < 50 % of the fin eroded; 3 was severe fin damage > 50 % of the fin eroded. For analysis of fin damage in the hatchery, the fin damage scores were summed to create a fin index of the combined degree of fin damages: a fish with intact fins, i.e. score 1 on all assessed fins, got a fin index of 3 (1+1+1); and a fish with severe fin damage on all assessed fins, i.e. score 3 on all assessed fins, got a fin index of 9 (3+3+3).

In the research laboratory, fish were assessed at the start and the end of the experiment and fork length (to the nearest mm), weight (to the nearest g), and fin damage were recorded as well as the occurrence of sexually mature males with running milt. In the experiment with shelter in 2011, fin damage was in focus and therefore the fin status of the dorsal, caudal, and pectoral fins was assessed on a six graded scale between 0 (no damage) and 5 (severe damage) according to Hoyle *et al.* (2007). During the second feeding experiment in the research laboratory in 2012, the modified three graded scale was used to assess fin damage. To update the feed ration calculations in the research laboratory, which were changed weekly based on the theoretical weight increase of the fish, weighing of fish in groups was done in August in both years.

A subsample of fish from the feeding experiments in the hatchery and the research laboratory were euthanized and frozen for later body lipid and protein analyses. For detailed method of lipid and protein analyses please see paper I or II.

2.1.7 Tagging of fish

In all experiments, 12 mm passive integrated transponder (PIT) tags (Allflex BIO.12.B.03/TX708HQ) have been used to identify individuals, monitor fish movement in the experimental streams, and monitor adult return rates. For the large scale feeding experiment fish were tagged with PIT-tags in March or April the same year they were released (paper IV). In the first feeding experiment in the laboratory, fish were tagged with PIT-tags in the end of June before the start of the experiment (paper I). For the second feeding experiment fish were not individually tagged for the growth experiment but approximately half of the fish were tagged with PIT-tags the subsequent spring (April) to be included in the migration experiment in the experimental streams (paper II). In the river migration study coded acoustic transmitters (LP-7.3, 69 kHz,Thelma Biotel, mass in air 1.9 g) were used to monitor the downstream migration (paper III). Hatchery-reared fish were tagged with acoustic transmitters in the beginning of May in all three years and wild fish were tagged on two occasions; 25 May and 7 June in 2011.

The average weight of the fish from the feed restricted and the control groups in the large scale hatchery experiment did not differ after the first year and the difference was small after the second year. To increase the difference in size between tagged groups, feed restricted groups from the small grading and control groups of fish from medium grading were tagged in 2011 and 2012 (table 1). The groups are denoted small for small grading and restricted feed ration and medium for medium grading and control feed ration. The feed restricted group in 2013 (medium grading) was also denoted small since the average weight of the fish was similar to the other small groups. The same groups that were PIT-tagged from the large scale hatchery experiment were used in the river migration study with one exception: a group of fish from small grading that had not been included in the feeding experiment was tagged in 2011. In addition to the tagged groups of fish from the large scale hatchery experiment, a group of fish from the research laboratory was tagged and included in the river migration study in 2012 (table 1).

At tagging, the fish were anaesthetized with MS-222 and a scalpel was used to make an incision to insert the PIT-tag into the body cavity. To surgically implant the acoustic transmitter, the anesthetized fish was placed ventral side up on a wetted towel in a u-shape on a surgery table and an incision was made with a scalpel between the pectoral fin and the pelvic girdle and the transmitter inserted into the body cavity. The incision was closed by two interrupted sutures (silk, EH7149G 4/0 FS-2, Johnson and Johnson). The tagging of hatchery-reared two year old smolts with acoustic transmitters was done in the beginning of May approximately two weeks before release.

Wild fish were tagged with PIT-tags according to the same procedure as hatchery-reared fish but the tagging was done continuously during the trapping period (approximately between the middle of May and the beginning of July each year). The smolt trap was emptied in the morning and fish were tagged during the day and left to recover for a few hours before they were released into the river again. The wild fish that were tagged with acoustic transmitters were also tagged the same day they had been trapped (25 May and 7 June) according to the same surgical procedure as the hatchery-reared fish. After tagging with the acoustic transmitters, wild fish were transported to the release site and put into a net pen in the river to recover for approximately eight hours until they were released. The release site was located in the same area right below the hydro power dam where the hatchery-reared fish were released (see below).

The same information that was assessed previously in the large scale feeding experiment in the hatchery, as well as in the laboratory, was recorded at the time of tagging. For wild fish total length was recorded for all fish and weight was recorded on a subsample (ca 150 fish year^{-1}).

2.1.8 Calculated variables

Fulton's condition factor (K)(Ricker, 1975) was calculated for all fish as follows:

$$K = 100\,000 * W * L_F^{-3}$$

where W is the weight (g) and L_F is the fork length (mm). For fish in the large scale feeding experiment and for wild fish, total length (L_T) was converted to fork length (L_F) by using unpublished data on 326 hatchery-reared fish and 54 wild fish, where both L_T and L_F had been recorded. The equation was found using linear regression for hatchery-reared fish ($R^2 = 0.99$):

$$L_F = L_T * 0.95 - 1.17$$

and for wild fish ($R^2 = 0.98$):

$$L_F = L_T * 0.91 + 2.74$$

Since there were large differences in initial average size of the fish among tanks in the large scale feeding experiment, effects on growth in terms of specific growth rate (SGR) were analysed. Specific growth rate (SGR) (Ricker, 1979) was calculated as follows:

$$SGR = \frac{lnW_2 - lnW_1}{\Delta t} * 100$$

where W_2 is the final weight (g), W_1 is the initial weight (g), and Δt is the number of days between weightings. For the subsample of fish that was used to analyse body lipids and proteins, the energetic state of the fish was calculated by adding the calorific values of lipids and proteins. Lipids were given a value of 39 kJ g^{-1} and proteins 24 kJ g^{-1} (Jobling, 1994).

Due to difficulties achieving the desired feed rations in both the hatchery and the research laboratory, the obtained feed rations expressed as % body weight day^{-1} were calculated. The calculation was based on the feed allowance model described above but the daily weight increment was based on the obtained TGC values for each group of fish instead of the fixed value of 1.6. TGC values for each group were estimated by simulating the theoretical daily growth rate needed to achieve the observed final body weight after one growth season. In the hatchery, the feed rations included feed waste.

2.1.9 Releases

All hatchery-reared experimental fish were released into the river together with the conventionally reared fish. The fish were released through the drainage pipe in the hatchery and therefore no handling of the fish was needed. The drainage pipe from the hatchery drains into the bypass channel right below the dam approximately 30 km from the coast. Two year old smolts were released around the 25 May each year and one year old fish were released later. The later release of one year old fish was due to legal requirements of a visual assessment of smolt status to approve that the one year old fish were ready to migrate. Hence, the release date of one year old fish differed among years and was 9 July in 2011, 26 June 2012, and 17 June in 2013.

2.1.10 Experimental streams

Experimental streams were constructed within two hatchery-rearing tanks. For the migration study, fish were randomly netted from each tank in the research laboratory and carried in large buckets to the experimental streams in the hatchery. The study was done between the 20 and 30 May, which corresponded to the time when the two year old smolts were released form the hatchery (23 May). Fish were put into the experimental streams and their movements were registered using two PIT-tag antennas per stream for four days and then the fish were replaced with new fish. This was repeated three times which created six replicate groups of fish. For a more detailed method description of the analyses of PIT-tag data please see paper II.

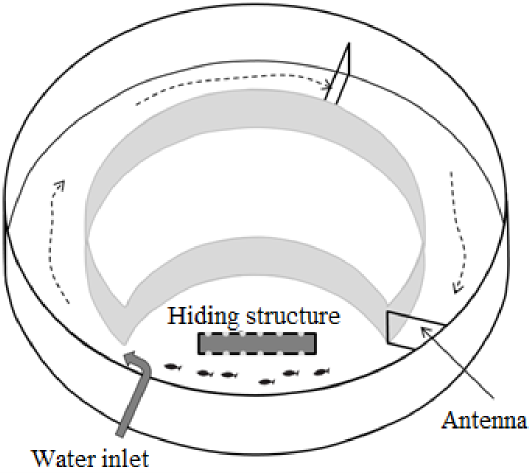

Figure 4. Schematic view of one of the experimental streams used to study downstream migration of individual Atlantic salmon smolt. The direction of the water current is shown by hatched arrows. Two antennas, covering the whole width of the stream, were positioned about 8 m from each other. The antennas were weird to a reader unit and a data logging computer.

2.1.11 Statistical analyses

ANOVA was used to evaluate the effects of different treatments on growth measures, fin damage, and mortality in the experiments in the hatchery and the research laboratory. ANOVA was also used to evaluate the effect of treatment on migration speed in the experimental streams. Tukey HSD test and student's t-test were used to identify significant differences. Student's t-test was also used to evaluate effects of starvation on relative weight loss and drop in condition factor.

Linear regression was used to evaluate the relationship between condition factor and energetic state of the fish and to evaluate the effects of condition factor on swimming-, and migration speed in the experimental streams.

Sea entry and adult return rates (nominal variables; 0 or 1) where evaluated with nominal logistic regression and odds ratio was used to evaluate significant differences. Contingency tables and Fisher's exact test were used to evaluate differences in return rates and life history among fish groups, and unless otherwise indicated p-values are given for Fisher's two-tailed test. The data were analysed using JMP Pro statistical software (12.2.0, 2015 SAS Institute Inc.). The variation in body size and condition factor within groups was large.

Therefore the individual data were used to evaluate the effect of smolt body size and condition factor on the probability of sea entry and adult return from the sea in hatchery-reared fish.

Nominal logistic regression was used to evaluate the effect of smolt body length (l) and condition factor (K) on sea entry. Data from fish from the large scale hatchery experiment were included, whereas data from fish from the research laboratory experiment and from wild fish were excluded. Year (y) was included as a factor and to further consider differences among years, the interaction terms length*year and condition factor*year were included. The best model was found using Akaike's information criteria (AIC) and the best model was then used to graphically illustrate the effect of body length and condition factor on probability of sea entry for the different years. The data were analysed using JMP Pro statistical software (12.2.0, 2015 SAS Institute Inc.)

A generalized linear model (GLM) was used to model the adult return rate as an effect of smolt body length and condition factor at the time of release. Data from two year old smolts released in 2011 and 2012 were used. "Return" was treated as a binomial distributed response and a logit-link function was used. Smolt body length and condition factor were used as main effects and year was included as a two-lever factor. I hypothesized that length would have a non-linear relationship with return rate and the relationship between the main effect "length" and the response variable was therefore modelled with a linear, a second, and a third polynomial. The interaction terms year*length and year*condition factor were also included. To derive the most parsimonious model (best model) using the above model as the full model, an information theoretical approach was used based on AIC. The model selection was performed in R using the package MuMIn (Barton, 2017). The best model was used to graphically find the body length and condition factor of a two year old smolt released in 2011 or 2012 with the highest probability of return.

A GLM was also used to model the probability of return as grilse as an effect of smolt body length. Length was included with both a linear and a second polynomial. Data from two year old smolts released between 2011 and 2013 were used. The model was used to graphically evaluate the relation between body length and the probability of return as grilse. The data were analysed in R (R core team 2016). For more detailed description of the analyses, please see respective paper.

3 Results

Here I present the most important results from the experiments and start with the effects of the feed treatments on the physiology and welfare of the fish, then present the effects on smolt migration; in experimental streams and in the river, and finish with the effects on adult return rates and life history. For more detailed results, please see the respective paper. Unless otherwise indicated, ANOVA has been used for statistical test of effects on physiological measures.

3.1.1 Calculated feed rations

In the hatchery, the estimated feed rations ranged between 2 and 3 % of body weight day^{-1} for control fish (table 1). At feed rations exceeding 2 % of body weight day^{-1} no additional growth occurred, which indicated feed waste at higher rations (figure 5a). Feed rations had to be around 1.5 % of body weight day^{-1} to result in a true feed restriction that reduced the size of the fish compared to control fish. In the hatchery, this was only achieved during the last two years of the experiment (figure 5a). In the research laboratory, the fish were strongly feed restricted and the feed rations ranged between approximately 0.3 and 0.7 % of body weight day^{-1} in the first experiment and between 0.6 and 0.9 % of body weight day^{-1} in the second experiment (figure 5a). For comparison, the unrestricted feed ration would have been about 2 % of body weight day^{-1} according to the feed manufacturer (BioMar: www.biomar.com).

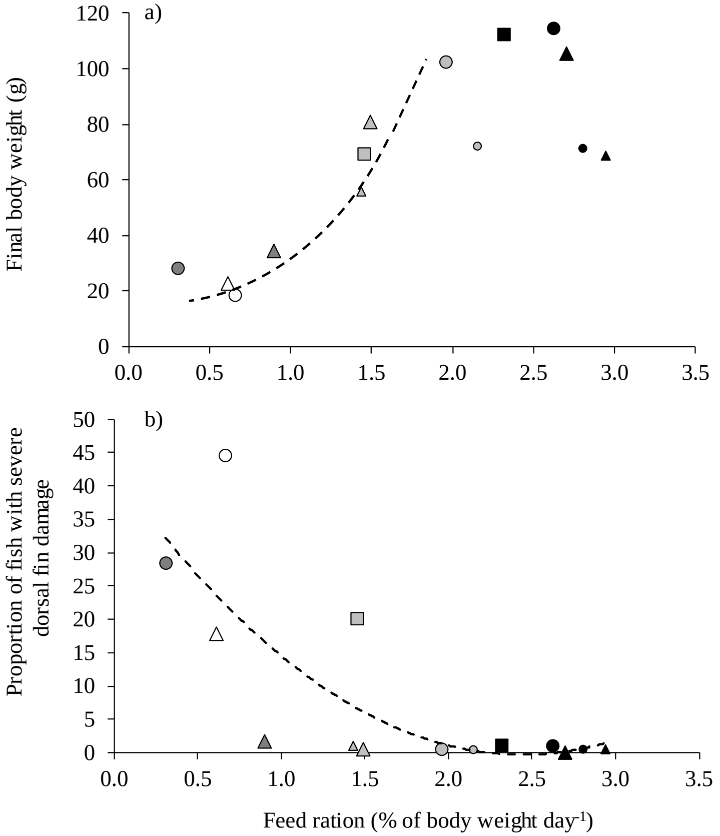

Figure 5. Relation between feed ration and a) final body weight of the fish and b) proportion of fish with severe dorsal fin damage (score 3) at the end of the growth season in hatchery-reared Atlantic salmon juveniles between 2010 and 2012. Circles denote experimental year 2010, triangles 2011, and squares 2012. White symbols denote feed restricted fish and dark grey symbols denote control fish in the research laboratory (regardless of shelter and dietary lipid treatment), and light grey symbols denote feed restricted fish and black symbols denote control fish in the hatchery. Smaller symbols denote fish graded as small in the hatchery compared with fish graded as medium in the hatchery.

Table 1. *Average length, weight, and condition factor (K, based on fork length) (± 1 SD)*[1] *after the growth season and the following spring for treatment groups in the hatchery and in the research laboratory. Data from wild fish at the time of smolt migration are also included. Grading as small or medium before the start of the experiment, feed treatment (control/restricted) and correction factor is given for fish in the hatchery. Feed treatment and additional treatment: shelter/no shelter in 2011, dietary lipid content (high 15 %, low 9 %) 2012, is given for fish in the research laboratory. Starvation applied during winter and spring after the growth season 2012 in the research laboratory is indicated by Yes or No. Feed ration indicate the actual feed ration (% of body weight day*$^{-1}$*) calculated based on the final weight after the growth season. Fish groups used for evaluation of performance are indicated by respective paper; migration in experimental streams (II), river migration (III), and return rates (IV).*

Year/ Facility	Grading	Feed treatment	Feed ration (%)	Oct length (mm)	Oct weight (g)	Oct K	Starvation	May length (mm)	May weight (g)	May K	Paper
Hatch.											
2010	Medium	Control 1.2	2.6	221	115	1.25		225	110	1.12	III, IV
2010	Medium	Restricted 0.7	2.0	219	109	1.21		223	106	1.12	
2010	Small	Control 1.2	2.8	196	76	1.17		200	75	1.10	
2010	Small	Restricted 0.7	2.2	202	83	1.18		199	78	1.15	IV
2011	Medium	Control 1.2	2.7	211±1	104±4	1.28±0.01		221±1	105±2	1.11±0.01	III, IV
2011	Medium	Restricted 0.7	1.5	188±5	78±3	1.29±0.01		202±7	82±7	1.12±0.01	
2011	Small	Control 1.2	2.9	183±1	67±1	1.24±0.01		190±9	68±11	1.07±0.02	
2011	Small	Restricted 0.7	1.4	171±10	54±9	1.25±0.02		184±4	58±5	1.08±0.01	III, IV
2012	Medium	Control 1.2	2.3	221±3	119±1	1.30±0.01		229±5	113±5	1.09±0.03	III, IV
2012	Medium	Restricted 0.6	1.5	188±0	72±1	1.23±0.01		193±1	65±1	1.05±0.00	III, IV
Lab.											
2011		Control	0.7	138±1	28±1	1.06±0.02		140±3	26±1	0.94±0.02	III
2011		Control, shelter	0.7	135±2	27±2	1.06±0.02		142±3	27±2	0.95±0.02	III
2011		Restricted	0.3	122±2	18±1	0.97±0.01		132±3	22±2	0.93±0.02	

Year/ Facility	Grading	Feed treatment	Feed ration (%)	Oct length (mm)	Oct weight (g)	Oct K	Starvation	May length (mm)	May weight (g)	May K	Paper
2011		Restricted, shelter	0.3	122±1	18±1	0.96±0.02		131±3	21±1	0.92±0.03	
2012		Control, high lipid	0.9	147±6	34±4	1.06±0.01	No	146±3	29±2	0.90±0.02	II
							Yes	149±8	27±6	0.79±0.04	II
2012		Control, low lipid	0.9	148±5	34±3	1.05±0.00	No	147±6	29±4	0.90±0.01	II
							Yes	149±1	27±1	0.80±0.01	II
2012		Restricted, high lipid	0.6	130±3	23±2	1.03±0.02	No	134±2	21±0	0.87±0.02	II
							Yes	130±1	16±1	0.71±0.02	II
2012		Restricted, low lipid	0.6	129±3	22±2	1.01±0.01	No	132±4	20±2	0.85±0.00	II
							Yes	130±3	16±1	0.72±0.01	II
Wild											
2011								147±14	27±7	0.76±0.07	III, IV
2012								145±16	24±8	0.72±0.06	IV
2013								142±17	20±7	0.68±0.05	IV

[1] In 2010 there were no replicate tanks due to lack of fish of similar initial grading, hence no standard deviation.

3.1.2 Effects on growth

In the large scale feeding experiment the specific growth rate was lower for the feed restricted groups compared to control groups in 2011 and 2012 but not in 2010 (feed treatment: $F_{1,13} = 15.5$, $p = 0.002$, year: $F_{2,13} = 22.2$, $p < 0.001$, paper IV). There was no effect of the interaction between feed treatment and year. The difference in SGR was largest the last year and the resulting average weight was 72 g for the feed restricted fish and 120 g for the control fish after the growth season. Restricted feed rations negatively affected the growth of fish in the research laboratory and the weight and condition factor were lower for fish that had received the lower feed rations compared to fish that had received the higher feed rations (2011; weight: $F_{3,12} = 275.7$, $p < 0.001$, K: $F_{3,12} = 115.9$, $p < 0.001$, paper I, 2012; weight: $F_{1,12,} = 68.0$, $p <0.001$, K: $F_{1,12,} = 38.6$, $p <0.001$, paper II, table 1).

3.1.3 Effects on fin damage

Fin damage was most frequent on the dorsal fin and problems with severe dorsal fin damage started to occur at feed rations between 1 and 1.5 % of body weight day^{-1} (figure 5b). In the hatchery, fin damage was generally moderate across groups and the summed fin damage scores (fin index) ranged between 3.3 and 6.0 after the growth season. There was no effect of feed treatment on the fin index in the hatchery but the amount of damage varied among years (feed treatment; $F_{1,12} = 2.7$, $p = 0.129$, year; $F_{2,12} = 271.5$, $p < 0.001$, paper IV). The average proportion of fish with severe dorsal fin damage (2011; score 4 and 5 combined, 2012; score 3) in the research laboratory ranged between 46 and 76 % in the first experiment, and between 10 and 42 % in the second experiment. During the first experiment in 2011, the negative change in fin status was evaluated and the lower feed ration increased the proportion of fish with a negative change on the dorsal fin over the growth season ($F_{3,12} = 5.1$, $p = 0.043$, paper I), but see the section 3.1.7 *Effect of shelter* for possible influence of the interaction with shelter. During the second experiment in 2012, the lower feed ration increased the proportion of fish with severe dorsal fin damage ($F_{1,12} = 8.3$, $p = 0.014$, paper II).

3.1.4 Effects on mortality

The mortality in the hatchery was low and ranged between 1.4 and 3.7 % regardless of treatment. In the research laboratory the average mortality ranged between 2.5 and 13.5 % in the first experiment and it appeared as if the lower feed ration increased mortality ($F_{3,12} = 4.2$, $p = 0.064$, paper I). During the second experiment the mortality ranged between 4.7 and 11.3 % and was higher for groups fed the lower feed ration ($F_{1,12} = 6.2$, $p = 0.028$, paper II).

3.1.5 Condition factor

The condition factor of the fish in the hatchery decreased over winter. For fish released as two year old smolts, the condition factor was approximately 1.09 for feed restricted fish and 1.14 for control fish in March, and the condition factor did not change notably until the time of release in the end of May (figure 6). At approximately the same time the condition factor of fish from the research laboratory experiments ranged between on average 0.68 for starved fish to about 0.90 for fish that had been fed. For the fish released as one year old smolts the condition factor increased from approximately 1.03 in March to 1.20 by the end of June (figure 6).

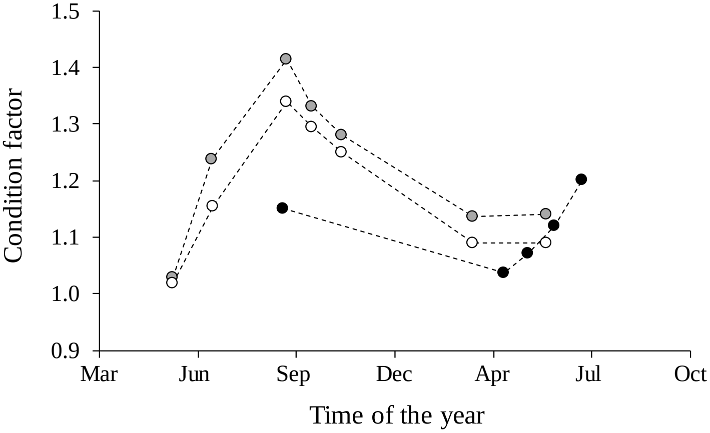

Figure 6. The change in condition factor between May 2011 and July 2012 in two year old fish with control feed ration (grey) and restricted feed ration (white), and one year old fish (black). Fork length was used to calculate the condition factor.

3.1.6 Energetic state

In the large scale feeding experiment the body lipids ranged between 6.7 and 8.1 % of body weight for control fish and between 6.6 and 7.5 % for feed restricted fish in the spring. Along the condition factor range covered by fish from the different experiments, the condition factor was positively related with the energetic state of the fish (linear regression, $F_{1,238} = 683.0$, $p < 0.001$; $R^2 = 0.74$; energetic state = -2.42 + 7.95 * K, figure 7).

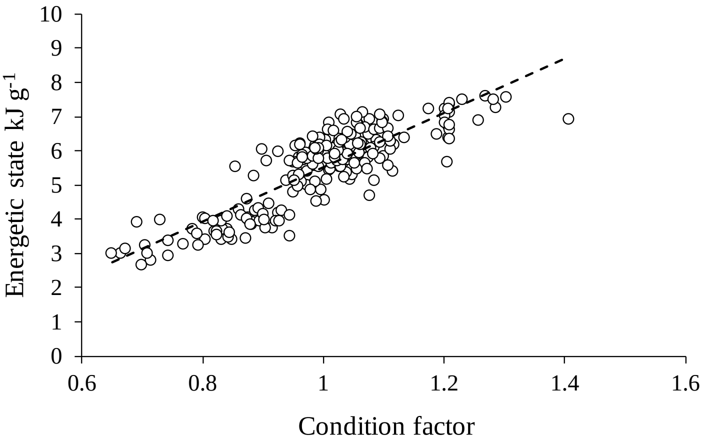

Figure 7. Relation between condition factor and energetic state in juvenile Atlantic salmon.

3.1.7 Effect of shelter (paper I)

The effect of shelter on the negative change in dorsal fin status was complex. Although not significant, it appeared as if the shelter increased the proportion of fish with severe dorsal fin damage at the 0.3 % feed ration whereas shelter decreased the proportion of fish with severe dorsal fin damage at the 0.7 % feed ration (ration*shelter: $F_{3,12} = 3.7$, $p = 0.080$). A pairwise test showed no significant differences in the proportion of fish experiencing a negative change in dorsal fin status between the feed ration levels in tanks without shelter (Students t-test, $t_6 = 0.20$, $p = 0.845$), whereas a significantly higher proportion of fish experienced a negative change in the 0.3 % feed ration treatment with shelter compared to fish in the 0.7 % feed ration with shelter (Students t-test, $t_6 = 4.04$, $p = 0.021$).

3.1.8 Effect of dietary lipid content (paper II)

There was no effect of dietary lipid content on the final weight or condition factor of the fish. Neither did the dietary lipid content affect the welfare of the fish. The dietary lipid content of the feed affected the amount of body lipids in the fish and high dietary lipid content resulted in fish with higher body lipids after the growth season compared to fish fed feed with lower dietary lipid content ($F_{1,12} = 24.8$, $p < 0.001$). Both feed ration and dietary lipid content affected the amount of proteins and subsequently the amount of energy in the fish after the growth season (ration: $F_{1,12} = 13.8$, dietary lipid: $p = 0.01$, $F_{1,12} = 10.9$, $p = 0.01$); in a descending order where fish fed high ration and high dietary lipid feed had the highest amount of energy, and the fish fed low ration and low dietary lipid feed had the lowest amount of energy.

3.1.9 Effect of starvation (paper II)

During the winter and early spring 2013, the starvation treatment pushed the fish further down the energetic scale with enhanced welfare problems as a consequence. Starved fish lost relatively more weight and dropped relatively more in condition factor compared to fish that had been fed (body weight: $t_{14} = 9.6$, $p < 0.001$, K: $t_{14} = 9.0$, $p < 0.001$). The average weight ranged between 16 and 30 g and the condition factor of the starved fish ranged between 0.71 and 0.80 compared to 0.85 and 0.90 for fish that had been fed. The weight and condition factor of the fish were in the range of wild fish that had an average weight of 20 g and a condition factor that ranged between 0.68 and 1.04 in 2013 (table 1).

3.1.10 Metabolic shift (paper II)

In November, the energetic state of the fish was positively related to the body lipids of the fish but not to the body proteins. In May, the energetic state was lower and the relation with body lipids weakened and there was a positive relation to body proteins that indicated a metabolic shift (figure 8).

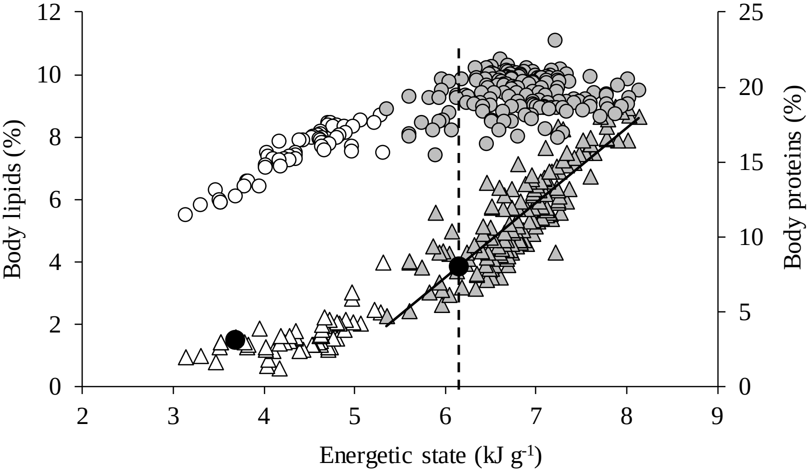

Figure 8. The relation between the energetic state of juvenile Atlantic salmon and body lipids (triangles) and body proteins (circles). Grey circles denote November 2012 values and white circles denote May 2013 values. Black circles indicate the breakpoints for logistic regression.

To illustrate the shift in metabolism from body lipids to body proteins two breakpoints were identified (figure 8). Above body lipid levels of 3.5 % (upper breakpoint), the metabolism was primarily based on body lipids. Below body lipids of 1.5 % (lower breakpoint) the metabolism was primarily based on body proteins. Logistic regression derived the shape of the metabolic shift between using body lipids and using body proteins. The resulting curve was steep and indicated that the shift was almost like a switch (figure 9).

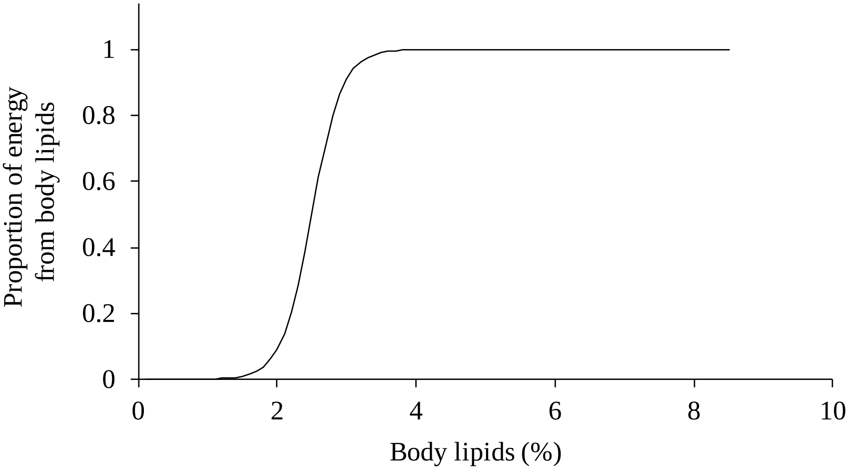

Figure 9. The proportion of body lipids used for metabolism in relation to amount of body lipids in juvenile Atlantic salmon.

3.1.11 Migration in experimental streams (paper II)

Phenotypically wild-like fish in terms of size and energetic state from the second experiment in the research laboratory were used in the study on smolt migration in experimental streams in 2013. Fish that had been fed swam faster than starved fish ($F_{1,39} = 19.8$, $p < 0.001$), but in contrast, starved fish migrated faster (i.e. further) compared to fish that had been fed ($F_{1,39} = 5.5$, $p = 0.02$). The condition factor was positively related to swimming speed measured in body length s^{-1} ($R^2 = 0.51$, $F_{1,43} = 10.0$, $p = 0.003$, figure 10a) but negatively related to migration speed measured as km day^{-1} ($R^2 = 0.44$, $F_{1,43} = 10.8$, $p = 0.002$, figure 10b).

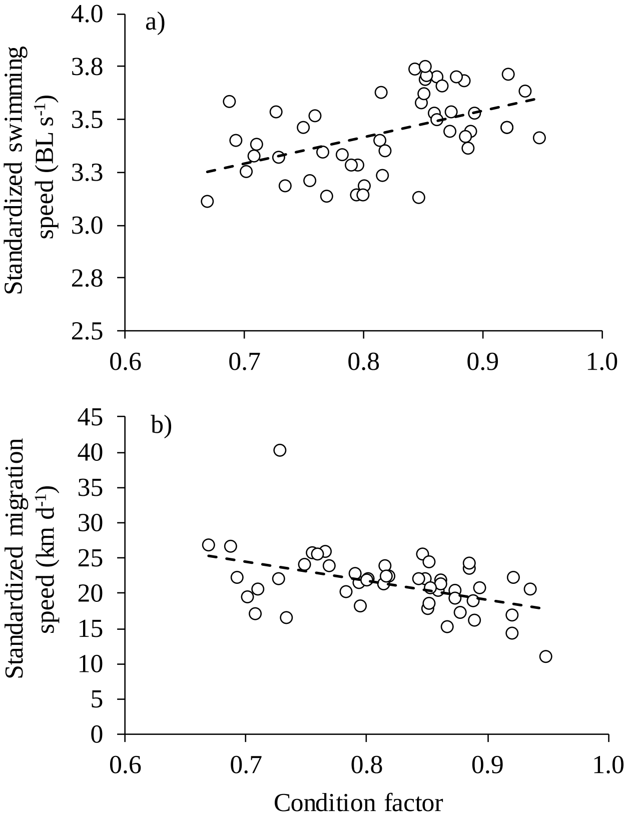

Figure 10. The relation between condition factor and a) swimming speed and b) migration speed in Atlantic salmon smolts in May 2013. For illustration the values for swimming and migration speed were standardized since there were differences between experimental streams and among rounds that were treated as random factors in the statistical analyses. Values were standardized as follows: individual speed minus the average speed in each experimental round and experimental stream, plus the average speed for all rounds and streams.

3.1.12 River migration (paper III)

Fish from the large scale feeding experiment in the hatchery and one group of fish form the first feeding experiment in the laboratory 2011, as well as one group of wild fish, were used in the study on smolt migration in the river. In 2011, the medium group had lower sea entry rate compared to the other groups (nominal logistic regression, χ^2 = 6.9, p = 0.032, small group; odds ratio confidence limits: 1.4 – 20.4, p = 0.014, wild group; odds ratio confidence limits: 1.2 – 14.1, p = 0.027). There were no differences in sea entry rate among groups in 2012 and 2013, and no effect of feed treatment on the sea entry rate (control vs restricted 2012 and 2013; nominal logistic regression, χ^2 = 0.4, p = 0.542).

3.1.13 Effects of water discharge (paper III)

The discharge situation in the bypass channel differed among years and affected how fast the fish migrated through the bypass channel. In 2011 and 2012, the discharge was 10 m^3 s^{-1} at the time of release and only a few fish reached the confluence area (about 8 km downstream the release site) within five days (figure 11a and b).

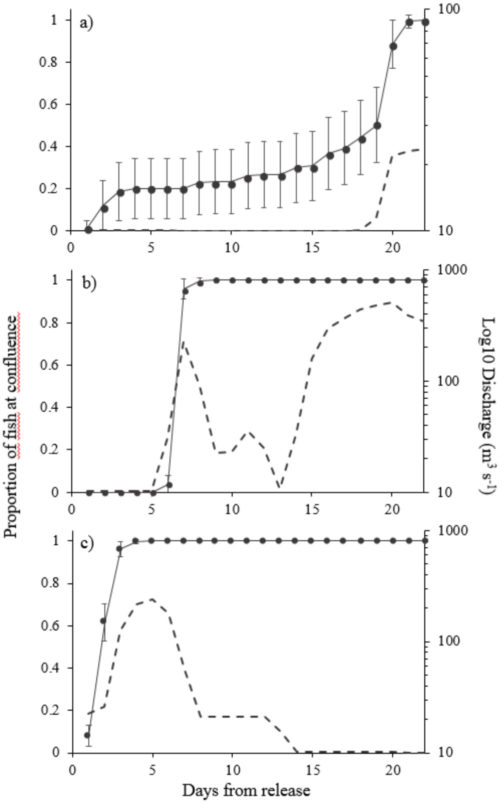

Figure 11. Time to reach the confluence area in relation to discharge in the bypass channel in a) 2011, b) 2012, and c) 2013. Markers denote proportion of fish at the confluence area (calculated CI) and dashed lines denote the flow after x number of days after release (note the Log10 scale on the secondary y-axis). Only fish that were registered at the confluence area were used in the analysis (2011 n = 30, 2012 n = 63, 2013 n = 120).

When the discharge was 23 m^3 s^{-1} at the time of release in 2013, about 60 % of the fish reached the confluence area within two days (figure 11c). In 2011 and 2012, fish that remained in the bypass channel responded rapidly to increased discharge and reached the confluence area shortly after the discharge increase (figure 11a and b). In 2013, most fish had already reached the confluence area when the discharge increased after two days (figure 11c).

3.1.14 Smolt characteristics and sea entry (paper III)

On an individual basis, the sea entry rate of hatchery-reared fish was modelled and the model that included year, length, and condition factor, without interaction terms was found to best explain the probability of sea entry (figure 12). Fish were more likely to enter the sea in 2012 and 2013 compared to in 2011, and there was a positive effect of length and a negative effect of condition factor (figure 12).

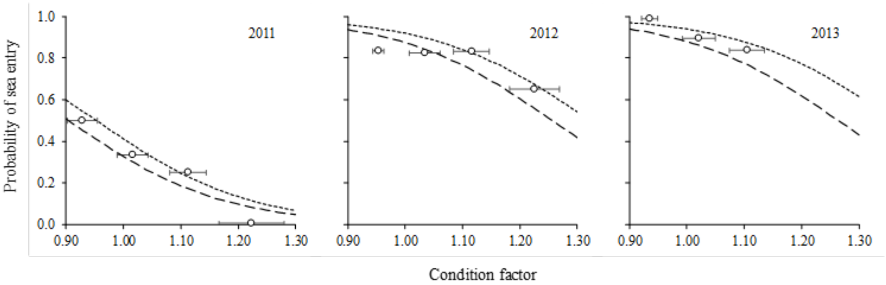

Figure 12. The probability of sea entry as an effect of condition factor in hatchery-reared Atlantic salmon smolts. For illustration, fish were grouped based on their condition factor and the white circles denote observed sea entry rate at the average condition factor (± 1 SD) for each of these groups. The dashed line represents the result of the best model at the lowest average length of the different condition factor groups and the dotted line represents the result of the best model at the highest average length of the different condition factor groups. The difference between the dashed and the dotted lines illustrates the effect of length on probability of sea entry and the difference among graphs represent the difference among years on the probability of sea entry.

3.1.15 Return rate and life history (paper IV)

Fish from the large scale feeding experiment in the hatchery were used to evaluate effects of feed restrictions on return rates and life history in terms of sea age at maturity. Something appeared to have happened in the sea affecting all fish that had not returned by 2014. From the 2013 tagging groups (including wild fish) only 27 fish returned as multi-sea-winter fish whereas from the 2011 tagging groups 130 fish returned as multi-sea-winter fish. This indicated that the majority of multi-sea-winter fish after 2014 were “missing”, since approximately the same number of fish were tagged in 2011 and 2013. Due to missing data, I used data from fish that were tagged in 2011 to compare adult return rates and life history among groups. This was unfortunate since the last release year (2013) was the only release year that included feed restricted and control fish that were from the same initial grading size but differed in smolt size. Hence, true effects of feed treatment on the adult return rates and the life history could not be evaluated. Instead I analysed effects of smolt size; due in part to treatment but mainly due to grading of 0+ fish. In analyses of effects of treatment and grading on adult return rates; as well as in analyses of effects of individual smolt characteristics on adult return rates, data from fish released as two year old smolts in both 2011 and 2012 were used since the effect of "missing fish" was thought to be small for these groups. In the analysis of individual smolt length and the probability to return after only one sea winter data from all releases were included.

3.1.16 Return rates from the sea (paper IV)

There was no effect of feed treatment and grading on the total return rates from the sea (grilse and multi-sea-winter fish). The total return rate of wild fish tagged in 2011 was 5.6 % and that was higher compared to hatchery-reared fish released as two year old smolts in 2011 that had a total return rate from the sea of 1.2 % (Fisher's exact test $p < 0.001$). Fish released as two year old smolts in 2011 had a slightly higher probability of return compared to fish released as one year old smolts that had a total return rate of 0.8 % (Fisher's exact test one tailed $p = 0.032$, two tailed; $p = 0.064$).

The model that best explained the probability of return based on individual smolt characteristics included the following variables: length, length^2, condition factor, year, length*year, and condition factor*year. The result of the model illustrated that it was a quadratic relation between smolt length and the probability of return from the sea where the intermediate sized smolts had the highest probability of return. The optimal smolt length was approximately 235 mm in 2011 and approximately 185 mm in 2012 (figure 13). The condition factor of the smolt with the highest probability of return differed between years; in 2011 the larger smolts had higher probability of return if they had lower condition factor compared to in 2012 when the opposite relation was observed and the smaller smolt had a higher probability of return if they had a higher condition factor (table 2).

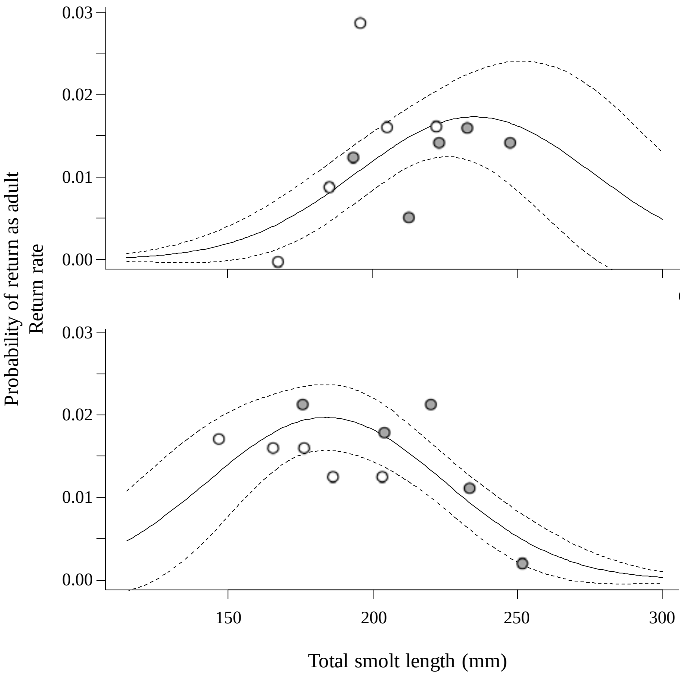

Figure 13. Probability of return from the sea in relation to total smolt length (black line) modelled at the average smolt condition factor of hatchery-reared Atlantic salmon released as two year old smolts in a) 2011 and in b) 2012. Dashed lines indicate confidence intervals (95 %). Circles denote observed return rate from the sea of fish graded as small and given restricted feed rations (white) and of fish graded as medium and given control feed rations (grey). The number of fish in each group was ca 560 in 2011 and ca 870 in 2012. The black arrows indicate the average total length of wild smolts tagged in 2011 (147 ± 14 mm) and 2012 (145 ± 16).

Table 2. *Proportion of fish that returned within each quadrant of data (length and condition factor were split in half) for fish released as immature two year old smolts in 2011 and 2012.*

		Shorter half	Longer half
2011	Lower half K	1.43	1.64
	Upper half K	1.05	1.14
2012	Lower half K	1.32	1.17
	Upper half K	2.07	1.44

3.1.17 Life history (paper IV)

The medium graded fish fed control feed rations had lower sea age at maturity compared to wild fish (Fisher’s exact test, p = 0.009), but there was no difference in sea age at maturity between wild fish and the small graded fish fed restricted feed rations (Fisher's exact test, p = 0.870). The probability of return as grilse was modelled using individual data and main effect length as both a linear-, and a second polynomial. The model illustrated that up to a length of approximately 225 mm there was a positive relation between length and the probability of return as grilse, whereas above this length the probability decreased (figure 14).

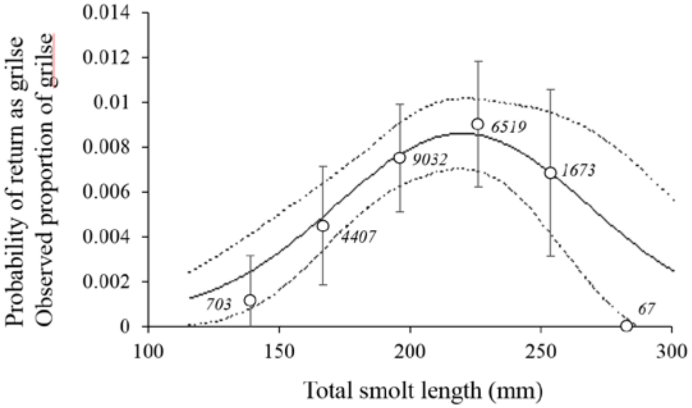

Figure 14. The probability of return as grilse as a function of smolt length in hatchery-reared Atlantic salmon released as two year old smolts between 2011 and 2013 (black line). White circles denote observed proportion of fish that returned as grilse ± 1 SD within a certain length class. Error bars represent annual variation. Numbers in italics indicate total number of fish in each length class.

4 Discussion

Globally, hatchery-release programs have been largely guided by production of high number of hatchery-reared fish rather than the quality of the fish (Paquet *et al.*, 2011; Brown & Day, 2002). In the Baltic Sea area the decreasing trend in recapture rates of hatchery-reared salmon after the year 2000 (Koljonen, 2006) resulted in that the power companies, where Energiforsk took the lead, called for a review of the current knowledge about the hatchery-reared smolts. The resulting review by people at the Swedish University of Agricultural Sciences (Eriksson *et al.*, 2008) and a corresponding workshop gave rise to the project: *"Functional methods for rearing of smolts adapted to the wild"* (Elforsk). During the same time period another project *"Sustainable smolt production – an integrated approach"* (SMOLTPRO) was funded. My role in those projects was to improve the rearing methods so that a higher quality and a phenotypically more wild-like smolt could be produced. My thesis comprises the results of some of the work done in these two projects. The energetic state and the body size of the fish need to be reduced in order to achieve a phenotypically more wild-like smolt. In this thesis, I have focused on how a lower energetic state and a smaller body size can be attained and how these phenotypic traits affect smolt performances and adult return rates.

It was difficult to adjust the feeding regimes in the large scale hatchery experiment to the desired feed rations, thus, in the first year there was no effect of treatment. However, due to different initial size of treatment groups because of different grading as 0+ fish, the average smolt weight of the different treatment groups differed. The last year the difference in specific growth rate was the largest between feed restricted and control fish (conventionally fed) and the average weight was lower for feed restricted fish compared to control fish (paper IV). However, the average weight of the feed restricted fish in the spring at the time of smolt migration was still about double the weight of the equivalent wild smolts from River Vindelälven, and the condition factors indicated large differences in energetic states as well (table 1). This is similar to other studies where moderately feed restricted fish have been larger and have had higher condition factors compared to wild fish at the time of release (Norrgård *et al.*, 2014b; Vainikka *et al.*, 2012; Lans *et al.*, 2011). Feed with lower dietary lipid content can be used to decrease the energetic state of hatchery-reared fish (paper II, Norrgård *et al.*, 2014a), but in order to produce a phenotypically wild-like smolt strong feed restrictions are necessary, as shown by my feeding experiments in the research laboratory (paper I and II). However, the strong feed restrictions used in the research laboratory compromised the welfare of the fish whereas the moderate feed restrictions used in the large scale hatchery experiment did not. In the research laboratory, high amount of severe dorsal fin damage (more than 50 % eroded) was observed and the mortality was higher for feed restricted as well as for starved fish (paper I and II). Similar negative effects of restricted feed rations were observed by Vainikka *et al*. (2012), but the mortality rates and the amount of severe fin damage were lower than in my studies. The results indicated that it is possible to produce a smolt with equivalent body size and condition factor as wild smolts but at a cost of severely compromised welfare (paper I and II).

Fin damage in juvenile Atlantic salmon is often related to aggression (Canon Jones *et al.*, 2011; Latremouille, 2003), and likely associated with competition for feed (Norrgård *et al.*, 2014a). In the research laboratory, the use of shelter mitigated the amount of severe dorsal fin damage at feed restrictions of 0.7 % of body weight day^{-1} but seemed to enhance the problems at strong feed restrictions of 0.3 % of body weight day^{-1} (paper I). The enhanced problems indicate increased competition connected to the shelter in addition to the competition for feed. Due to the design of the shelter and the location of the feeder, the feed was distributed right above the entrance of the shelter in the centre of the tank. A different design with openings around the edges may have prevented increased competition at strongly restricted feed rations. Different types of enrichment in the hatchery environment have decreased fin erosion in both Atlantic salmon (Näslund *et al.*, 2013) and in other species of salmonids (Berejikian & Tezak, 2005; Bosakowski & Wagner, 1995). Other positive effects of enrichment in the rearing environment are reduced stress levels and improved shelter seeking behaviour (Näslund *et al.*, 2013). Additionally, Alanärä (1992) suggested that feeding should be focused to two more intense feeding periods in the morning and the evening to reduce energy loss from swimming activity and that would probably also reduce aggressive interactions. It is likely that the morning-evening feeding schedule in the hatchery; combined with the spreading of the feed across a large part of the water surface, helped to prevent severe dorsal fin damage (paper IV), which is not uncommon in hatchery-reared populations of salmonids (Bosakowski & Wagner, 1994).

Starvation has been used to lower the condition factor of hatchery-reared trout to levels of wild trout smolts (Larsson *et al.*, 2012). In my second feeding experiment in the research laboratory, a period of winter and spring starvation was induced for half of the treatment groups after the growth season. Starvation resulted in low body weights and condition factors of the fish in the spring that were within the range of wild smolts, but starvation enhanced previously described welfare problems with severe dorsal fin damage and increased mortality (paper II). During periods of feed shortage and at body lipid levels below 3.5 %, fish appeared to switch to use more protein as energy source and thereby conserved their body lipid levels (paper II). However, increased use of protein may compromise vital tissue functions, finally leading to death (Castellini & Rea, 1992). The condition factor of the fish was positively correlated to the energetic state of the fish in terms of total energy from both body lipids and body proteins (paper II). Thus, the condition factor can be used as a proxy for the energetic state of Atlantic salmon juveniles.

The condition factor was positively related to swimming speed but negatively related to migration speed. This was found when phenotypically wild-like smolts from the second laboratory experiment were tested in experimental streams in the spring at the time of smolt migration (paper II). The lower swimming speed of starved fish, which had the lowest condition factors, was possibly related to the occurrence of severe fin damage that may reduce the manoeuvring capability (Noble *et al.*, 2012). Despite that, starved fish migrated further during the time of the experiment (paper II). Positive effects of feed restriction on smolt migration has been reported previously (Norrgård *et al.*, 2014b; Vainikka *et al.*, 2012; Lans *et al.*, 2011). Although the fish here were substantially smaller and had much lower condition factor compared to previous studies, the effects on migration were similar. Fish at a lower energetic state appeared to have a stronger drive to switch habitat to the more productive sea (paper II).

There was also a positive effect of lower energetic state on sea entry in the river migration study (paper III), which to some extent verified the findings in the experimental streams (paper II), and was in line with previous studies on feed restrictions and the effects on smolt migration (Norrgård *et al.*, 2014b; Vainikka *et al.*, 2012; Lans *et al.*, 2011). There was also a small positive effect of smolt length on the sea entry (paper III) and smolt length has been found to be positively related to swimming speed during downstream river migration in hatchery-reared steelhead (*Oncorhynchus mykiss*) (Johnson *et al.*, 2010). Overall, the discharge in the bypass channel in the River Umeälven was important for the sea entry rate of the fish. When the discharge was low for an extended period of time after release, the proportion of fish that entered the sea was lower compared to when the discharge was higher at the time of release or a river spate occurred within a few days after release (paper III). The positive effects of increased water discharge on migration have been attributed to higher migration speed and increased turbidity that together decrease the risk of being predated (Karppinen *et al.*, 2014; Knudsen *et al.*, 2000). Other positive effects of higher discharge have also been reported, such as lower energetic cost of migration (Jonsson, 1991) and increased willingness to migrate (Norrgård *et al.*, 2013).

There was a small positive effect of smolt length on the probability of sea entry (paper III), but the probability of return from the sea as an adult was highest for intermediate sized smolts (paper IV). In previous studies based on Carlin-tags, a positive more linear relation between smolt size and adult return or recapture rates has been reported (Jonsson & Jonsson, 2014; Kallio-Nyberg *et al.*, 2004; Lundqvist *et al.*, 1988). However, previous observations may have been size biased in favour of large fish since Carlin-tags are known to increase mortality, and especially in small smolts (Hansen, 1988). Consequently, the positive linear relation with size observed previously may not has been as strong as suggested. Additionally, the difference in survival between large hatchery-reared and small wild fish may have been underestimated. The quadratic relation between smolt size and adult return rate observed using PIT-tags was thought to be free of size bias since salmon parr from about 60 mm have been tagged with 12 mm PIT-tags without any effects on survival and without any tag shedding (Riley *et al.*, 2003). Another advantage with PIT-tags is that they are fishery independent (Huusko *et al.*, 2016) and therefore not influenced by the willingness of fishers to report tags or fluctuations in fishing intensity. The difference between the pattern observed in the data from the 1980-1990s (Carlin tags), and the pattern observed in the data from after 2010 (PIT-tags), was likely influenced by the different tags used. It is also possible that the environmental conditions have changed over time in a way that has decreased the positive effect of a large smolt size (Kallio-Nyberg *et al.*, 2009).

The effect of smolt condition factor on adult return rates of fish released as two year old smolts varied between years. It appeared as if larger smolts suffered from larger energy reserves in 2011, whereas smaller smolts benefited from larger energy reserves in 2012 (paper IV). There is a possibility that a high energetic state of large sized hatchery-reared fish increases the tendency for them to stay resident in the river (discussed by Thorstad *et al.*, 2012; Thorstad *et al.*, 2011), and Lans *et al.* (2011) observed reduced migration tendency in Atlantic salmon with high condition factor compared to feed restricted fish with lower condition factor. This may partly explain why large smolts with higher condition factor in my study had lower probability of return compared to large smolts with lower condition factor (paper IV).

Wild fish had a higher adult return rate compared to hatchery-reared fish (paper IV) and that has been reported several times before and is similar in different areas of the world and for various species of salmonids (Evans *et al.*, 2014; Araki & Schmid, 2010; Jokikokko *et al.*, 2006; Jonsson *et al.*, 2003; Maynard *et al.*, 1995). The return rate of hatchery-reared fish may have been underestimated since hatchery-reared fish were released below the entrance to the fish ladder and therefore might have had less incentive to enter the fish ladder compared to wild fish. That would have resulted in fewer registrations of adult fish upon return since the PIT-tag antennas were installed in the fish ladder. Additionally, the amount of males that had previously been sexually mature was likely higher in hatchery-reared fish compared to wild fish, and since the return rate was lower for fish that had been sexually mature as parr, this also contributed to lower return rates of hatchery-reared fish. Although potentially overestimated due to the described factors, the difference between wild and hatchery-reared fish was 4.5 times in favour of wild fish (paper IV), and that was of the same magnitude as reported by Siira *et al.* (2006).

Adult return rates of fish released as two year old smolts were not affected by treatment but the fish graded as small and given restricted feed rations had a life history similar to wild fish whereas fish graded as medium and given control feed rations had lower sea age at maturity (paper IV). Lower sea age at maturity in hatchery-reared fish compared to wild fish has been reported both from the Baltic Sea area (Kallio-Nyberg *et al.*, 2015; Jutila *et al.*, 2003) and the Atlantic Ocean area (Jensen *et al.*, 2016). There was a positive relation between smolt size and probability of return as grilse up to a smolt length of about 225 mm. Thereafter the probability seemed to decrease but was likely related to the overall lower return rate of larger smolts. Large smolts of Neva salmon yielded proportionately more grilse than small smolts and the marine growth in the Gulf of Finland and the Bothnian Sea was positively related to the grilse fraction (Salminen, 1997). Thorpe *et al.* (1998) suggested that the fish assess their lipid reserves and the rate of change of those reserves against a genetic maturation threshold the year before reproduction. If the fish reach the threshold the maturation switch is activated (Thorpe *et al.*, 1998). It has been suggested that larger post-smolts can switch to piscivory faster than smaller post-smolts and therefore utilize the feeding opportunities in the Bothnian Sea more efficiently (Salminen *et al.*, 2001). That would result in higher marine growth rate in larger post-smolts, which potentially could activate the maturation switch. Contrasting, high early growth rate in the Atlantic Ocean results in higher sea age at maturity (Jonsson & Jonsson, 2007). Jonsson and Jonsson (2007) speculated that fast-growing fish will attain maturity a) early when later growth is constrained and b) late when high growth rate is retained also later in life. It is possible that the opposite patterns result from differences in fishing pressure that has constrained growth later in life for salmon in the Baltic Sea to a larger extent than in the Atlantic Ocean. The fishing pressure in the Baltic Sea has been substantial (Eriksson & Eriksson, 1993) and has targeted larger (older) fish (McKinnell, 1997), which may have contributed to selection for lower sea age at maturity in fast growing fish in the Baltic Sea.

Fish released as one year old smolts in 2011 had low return rates (paper IV). One explanation may be the late release of one year old smolts that occurred when the wild smolt migration in the River Vindelälven had ceased (paper IV). Hatchery-reared fish that are retained in freshwater after the corresponding wild smolt migration will start to lose their motivation to migrate and their salinity tolerance (McCormick *et al.*, 1998). Additionally, it is possible that not all fish had reached the growth and energetic threshold the previous fall that would have activated the smoltification process as described by Thorpe *et al.* (1998). Hence, some of the fish may not have smoltified before they were released. Partly due to that and the late release, some of the fish released as one year old smolts may have stayed in the river. Kesler *et al.* (2013), speculated that competition with wild conspecifics in the river as well as prolonged exposure to predators could have contributed to the higher mortality of fish released as one year old compared to fish released as two year old observed in their study.

Fish released as one year old smolts also had different growth patterns during the spring before release compared to fish released as two year old smolts. One year old smolts grew substantially and their energetic state increased a lot between the tagging and the release, whereas two year old smolts had approximately the same size throughout the spring and the energetic state rather dropped slightly, which is common for fish during smoltification (McCormick *et al.*, 1998). Since a high energetic state has a negative impact on smolt migration in two year old smolts (Norrgård *et al.*, 2014b; Lans *et al.*, 2011), it is possible that the high energetic state of one year old smolts negatively affected their downstream migration in the river. Another explanation for the low adult return rates may be that the fish released as one year old smolts were the once that grew rapidly during their first year in the hatchery. Fish that prosper in the hatchery environment may not be the once that are fit to survive after release and rapid growth in the hatchery could indicate poor performance in the wild (Saikkonen *et al.*, 2011).

The proportion of fish released as one year old smolts has increased substantially since the 1990s (ICES, 2017). The low return rates as adults of fish released as one year old smolts in my study are therefore somewhat worrying. More knowledge is urgently needed about how the adult return rates of fish released as one year old smolts are affected by the timing of release, the physical smolt characteristics, and the post-release behaviour.

As described earlier for the large scale feeding experiment in the hatchery, it was only in the spring 2013 that the average smolt size differed between treatment groups solely due to feed restrictions. Unfortunately I could not use the data from the 2013 release groups due to the lack of fish returning as multi-sea-winter fish after 2014. Therefore it was not possible to evaluate the effects of feed treatment on adult return rates and life history. The lack of returning multi-sea-winter fish after 2014 indicated unusually high adult mortality for fish that remained in the sea (paper IV). The lack of multi-sea-winter fish highlights the value of long term studies as well as the vulnerability to unforeseen events when working with natural systems. In addition to the unusually high adult mortality in the sea, there has also been observations of unhealthy spawners in several rivers entering the Baltic Sea since the summer of 2014, but the underlying mechanism/disease has not been fully identified (SVA, 2017). A widespread thiamine deficiency in wildlife in the Northern Hemisphere has been reported (Balk *et al.*, 2016), but how - and if - that is related to the lack of returning adults after 2014 and the presence of unhealthy spawners in the rivers remains unknown.

4.1.1 Conclusion

The smallest two-year old hatchery-reared smolts that were most similar to wild smolts in terms of body size, had lower return rates compared to intermediate sized smolts (paper IV). When hatchery-reared fish are released they often show large deficits in foraging behaviour and substantial weight loss (Brown & Day, 2002) and the first period in the sea is associated with high mortality (Friedland *et al.*, 2009). I therefore suggest, that hatchery-reared smolts need to be slightly larger and have larger energy reserves compared to wild smolts (IV), and that the strive for a phenotypically wild-like smolt in terms of body size, does not seem to be ideal. This means that strong feed restrictions in the hatchery are not necessary. However, I believe that moderate feed restrictions should be used for the larger two year old fish to lower their size and condition factor. That would improve smolt migration (paper II and III, Norrgård *et al.*, 2014b; Vainikka *et al.*, 2012; Lans *et al.*, 2011); produce a fish with a life history similar to wild fish (paper IV); and potentially increase adult return rates as indicated by the quadratic relation between smolt length and probability of return (paper IV). Lower use of feed in the hatchery would also generally decrease the environmental impact of the hatchery operations (Naylor *et al.*, 2000).

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Popular science summary

Hydropower developments have had negative impacts on Atlantic salmon populations through the degradation of river habitats. The hydropower dams have also cut off the salmon migration routes from the sea to their spawning and juvenile rearing areas in the rivers; and complicated the subsequent downstream migration to the sea. In Sweden, hydropower companies have been sentenced to compensate the fisheries for lost natural salmon production. This is done by rearing salmon in fish farms and releasing juveniles into the wild. The survival of released salmon has been lower compared to that of wild fish and the difference appears to have increased since the middle 1990s. This may be due to the body size and energy reserves of farmed fish that have increased over time and that differs very much from the wild fish.

In this thesis I present the results of my efforts to produce a more wild-like salmon by reducing the amount of food in the fish farm. I evaluate effects of different amounts of food on the seaward migration in salmon juveniles and the subsequent adult return rates to the river from the sea. I conclude that it is possible to produce a salmon juvenile of the same size as a wild salmon juvenile, but in order to do so, very small portions of food are necessary. Fish given very small portions of food suffered from increased fin damage due to aggressive interactions among fish and higher mortality. If the fish were given the opportunity to hide under a shelter that mitigated some of the negative effects on fin status but only at moderately reduced food portions.

Salmon juveniles with small energy reserves were more motivated to migrate to the sea. It varied between years if a small energy reserve was positive or negative for the survival in the sea and the probability that the salmon returned to the river as an adult. The size of the juvenile salmon at the time of release affected if it survived and returned as an adult from the sea. The intermediate sized juveniles had the highest return rates. That indicated that farmed fish should not be too large but that they likely need to be slightly larger than wild fish to be able to cope with the unfamiliar environment in the river and the sea where no regular meals are provided and predators are present. The larger juveniles returned to the river as adults after only one year in the sea to a larger extent than the smaller juveniles did. After only one year at sea the average weight of the fish is about 1.8 kg when it returns to the river. The smaller juveniles behaved more similar to wild fish that often stayed in the sea more than one year before they returned as adults. After at least two years in the sea the average weight of the fish is about 5.2 kg when it returns to the river.

My summarized conclusions are that it is possible to use moderately reduced food portions in the fish farm without getting negative effects such as increased frequency of fin damage and higher mortality. Moderately reduced food portions for the larger juveniles in the fish farm, are enough to achieve positive effects on seaward migration and prolong the time the fish spend in the sea and increase their corresponding size at return. In addition, it is also likely that moderately reduced food portions, which reduce the size of the larger juveniles in the fish farm, could increase their adult return rates. However, the return rates of wild salmon continue to be higher than the return rates of farmed salmon.

Populärvetenskaplig sammanfattning

Laxen har påverkats negativt av vattenkraftsutbyggnad som dels förstört lekområden och dels gjort det svårt för laxen att vandra mellan havet och kvarvarande reproduktions-, och uppväxtmiljöer i sötvatten. För att kompensera fisket för den minskade naturliga laxproduktionen, har vattenkraftsbolagen blivit ålagda att föda upp och sätta ut laxungar. Flera miljoner av dessa sätts ut varje år i Östersjöområdet. Överlevnaden hos den odlade laxen efter utsättningen är sämre än för den vilda och tycks ha försämrats ytterligare sedan mitten av 1990-talet. En anledning tros vara att de odlade laxungarna har blivit större och fetare över tid och avviker mycket i jämförelse med vilda laxungar.

I avhandlingen redovisar jag de försök jag bedrivit med målet att producera en mer vildlik laxunge genom att begränsa mängden mat i odlingen. Jag har sedan testat hur effekterna av mina behandlingar påverkat dels laxungens vandring till havet och dels hur stor andel av laxungarna som kommer tillbaka från havet som vuxna. Resultaten visar att det går att producera en laxunge som är lika liten som en vild laxunge men när maten är begränsad ökar aggressiviteten hos laxungarna och de får problem med fenskador och dödligheten ökar. När laxungarna fick tillgång till skydd att gömma sig under och foderbegränsningen inte var alltför stor, kunde skyddet motverka uppkomsten av allvarliga fenskador.

Laxungar med mindre fett var mer angelägna att vandra ut i havet vilket var en positiv effekt av foderbegränsningarna. Hur det sedan gick när de mindre feta laxungarna kom ut i havet varierade mellan år. Små odlade laxungar verkar behöva extra energireserver i form av fett jämfört med större odlade laxungar för att klara sig i havet. Generellt behöver nog en odlad laxunge vara lite större än en vild laxunge för att klara sig i en naturlig miljö där de måste akta sig för att bli uppätna och lära sig att hitta och fånga byten. Det är alltså inte bra att vara för liten. Det verkar inte heller vara bra att vara för stor eftersom de mellanstora laxungarna var de som i störst utsträckning återvände från havet som vuxna. Dessutom kom de stora odlade laxungar i större utsträckning tillbaka efter bara ett år i havet och vägde då ca 1.8 kg. De laxungar som var mindre när de sattes ut betedde sig mer som vild fisk och kom i större utsträckning tillbaka efter fler än ett år i havet. Då var de betydligt större och vägde ca 5.2 kg eller mer beroende på hur länge de stannat i havet.

Mina slutsatser blir att lagom foderbegränsning i odlingen för de större laxungarna inte innebär ökade problem med fenskador eller dödlighet. Lagom foderbegränsning för de större fiskarna kan ha positiva effekter på vandring till havet och på den tid fisken stannar i havet innan den återvänder som vuxen till hemälven. Det är också troligt att lagom foderbegränsning för de större fiskarna kan öka andelen fisk som återvänder från havet som vuxna. De mellanstora laxungarna hade störst chans att återvända från havet som vuxna men andelen som återvände var ändå lägre jämfört med andelen av de vilda laxarna som återvände från havet till hemälven som vuxna.

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