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Swedish University of Agricultural Sciences

Department of Wildlife, Fish, and Environmental Studies

Effects of Body Condition on Facultative Anadromy in Brown Trout (Salmo trutta)

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Master´s thesis • 60 credits
Management of Fish and Wildlife Populations
Examensarbete/Master's thesis, 2018:12
Department of Wildlife, Fish, and Environmental Studies
Umeå 2018

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Credits: 60 credits
Level: Second cycle, A2E
Course title: Master degree thesis in Biology at the department of Wildlife, Fish, and Environmental Studies
Course code: EX0595
Programme/education: Management of Fish and Wildlife Populations

Place of publication: Umeå
Year of publication: 2018
Cover picture: Gustav Hellström
Title of series: Examensarbete/Master's thesis
Part number: 2018:12
Online publication: https://stud.epsilon.slu.se

Keywords: brown trout, migration, condition factor, facultative anadromy

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Abstract

Fish behavior and life history is influenced by factors such as the environment, genetics, and their physiological state. One key life history stage in brown trout is decision to migrate to the sea or reside in the river. The energy status and body condition of the fish is thought to play a role in the timing and duration of migration to the sea. In this study, I examined the role of body condition in the initiation of this life history stage and determined the importance of feeding regimes in the physiological trade-off between migration and residency. I used four different feeding regimes in age one and age two cohorts of hatchery-reared brown trout to observe if starvation or feeding saturation induce behavioral changes in migration both in a controlled environment as well as a natural river system. I used both passive integrative transponder tags (PIT) as well as acoustic telemetry tags to analyze migration. I was successfully able to manipulate body condition using variable feeding regimes in both cohorts and I found that migration initiation and behavior was influenced by feeding regime. Feeding increased migration in both cohorts in the laboratory setting, but not in the natural setting. Laboratory migration in the age two cohort was primarily independent of feeding treatments as almost all age two fish migrated, but migration intensity was found to be greater with fed treatment groups. In contrast, age one fish were highly influenced by feeding regime, with fewer starved fish migrating and at a slower rate. Downstream migration in the wild was extremely low for both cohorts independent of feeding treatment. Overall, the findings indicate that age at release and feeding condition prior to release can impact migration initiation and duration. The results contribute to a better understanding of this complex life history stage and the mechanisms involved in the initiation, behavior, and survival of migrating brown trout.

Keywords: brown trout, migration, condition factor, facultative anadromy

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1 Introduction

Brown trout (Salmo trutta) can exhibit high variability in life history strategies and can adapt to differing stream types (Elliott 1994, Jonsson et al. 2001, Lobon-Cervia & Sanz 2017). The continuum of their migratory life history strategies includes: sea migration (anadromy), river to lake migration (adfluvial potamodromy), river to river migration (fluvial potamodromy), river resident, and lake resident (Eliott 1994, Klemetsen et al. 2003, Cucherousset et al. 2005 Ferguson 2006). Anadromous brown trout (sea trout) developed the ability to migrate great distances across salinity and temperature gradients for benefits such as reaching better feeding locations, growing larger, and increasing fecundity, but at a cost of delaying maturity and possibly lowering survival (Thorpe 1994, Gross et al. 1988, Thorpe et al. 1998, Alerstam et al. 2003, Fleming & Reynolds 2004, Jonsson & Jonsson 2006, Sloat et al 2014).

There have been major declines in Baltic sea trout populations over the years due to overexploitation, river modification (hydropower), habitat modification (lumber floating), disease (M74), and pollutants (Romakkaniemi et al. 2003, Jutila et al. 2006, Lundqvist et al 2006, Milner et al. 2007, Scruton et al. 2007, Casini 2017). Most of the concern for the Baltic fisheries has been concentrated on rebuilding Atlantic salmon populations, with minor attention given to sea trout populations, even though in some cases in the Northern Baltic, sea trout stocks are exhausted worse than salmon stocks (Kallio-Nyberg et al. 2002, Rivinoja 2004). There is an urgent need to understand Baltic sea trout populations and their declining stocks (Milner et al. 2007).

To promote the recovery of these populations, one solution has been to supplement the population with hatchery-reared smolts. Hatchery-compensatory releases have had low efficiency, with few fish migrating, possibly due to diffing environmental conditions, such as energy status and feeding regimes in the hatch-

ery setting (Eriksson et al. 2008). In the hydro power regulated Ume-Vindel River system a compensatory hatchery release program has stocked genetically integrated brown trout smolts since the 1950's, with the intent of supplementing the wild, anadromous population due to wild production loss caused by damming (Degerman et al. 2012). The effect of compensatory releases is dependent on hatchery-stocked individuals migrating and returning to spawn to sustain anadromous life history strategies (Brown & Laland 2001, Davidsen et al. 2014).

Anadromy is highly variable, with some populations exhibiting partial migration (facultative anadromy), where the cue to migrate is at the individual level, leading to migration in a proportion of the population (Dellefors & Faremo 1988, Jonsson & Jonsson 1993, Cucherousset et al. 2005). Previous research suggests that cues for migration come from the environment, individual physiological energy status, and genetics, and a balance between these factors influences migration or residency (Kendall et al. 2014, Ferguson 2017). Age structure at migration is usually associated with size and can vary based on latitude (Jonsson & L'Abee-Lund 1993, Klemetsen et al. 2003, Salminen et al. 2007). Prior to the onset of migration, smoltification usually occurs as a response to environmental cues and leads to physiological and biochemical changes in preparation for the marine habitat (McCormick et al. 1998, Dann et al. 2003, Jensen et al. 2012). Measures such as metabolic rate, growth rate, weight, lipid levels, and length are all indications of an individual's physiological state or body condition, and have been shown to influence the decision to migrate (Jonsson 1985, Theriault & Dodson 2003). In some systems, cohorts may migrate over successive years, delaying migration because of poor body condition (i.e. size and growth rate) (Metcalfe et al. 1990, Thorpe et al. 1992, Theriault et al. 2007).

Condition factor is a good, non-invasive proxy for energetic state (Persson et al. 2018), calculated based on the length and weight of an individual, and body condition has been shown to affect the decision to migrate (Neff & Cargnelli 2004). Energy limitations have been suggested as the incentive to migrate, with individuals remaining residents until growth rate slows due to food limitations (Jonsson & Jonsson 1993, Cucherousset et al. 2005). A decrease in individual condition factor has been a characteristic associated with the initiation of smoltification and migratory behavior in salmonids (Cunjak et al. 1990, McCormick and Bjornsson 1994, McCormick et al. 1985, Reis-Henriques et al. 1996, Sigholt et al. 1998, Aarestrup et al. 2000, Wysujack et al. 2009). For example, lower condition factor has been associated with higher migration rates in steelhead (Oncorhynchus mykiss) (Hecht et al. 2015). An environmentally-cued genetic condition threshold model proposed by Tompkin & Hazel (2007) describes genetic limits at which

individuals decide to migrate or not based on the influence of environmental factors and their own condition. If an individual's condition is high enough (above the threshold) it will stay in the river and mature (i.e., resident), but if falls below this threshold window, it will migrate and delay maturation to reach better feeding/growth conditions (i.e., migrant). These competitive alternative life history strategies have evolved to maximize reproductive success and has led to population resilience in variable environmental conditions. There could also be multiple decision windows over time when an individual decides to either migrate, mature as a resident, or wait till the following decision window (Satterthwaite et al. 2009, McCormick 2009, Dodson et al. 2013). A state-dependent migration strategy could be influenced directly by immediate feeding status (i.e. hunger) (Brodersen et al. 2008, Poulsen et al. 2010). Reaching a specific condition threshold for individuals may be a significant factor in their decision to migrate or reside, and resource availability (food) may cause an individual to reach a specific condition (Nordeng 1983, Olsson et al. 2006, Boel et al. 2014). As such, food limitation has been found to induce a higher proportion of migrants in salmonids (Olsson et al 2006, Wysujack et al. 2009, O'Neal & Stanford 2011, Lans et al. 2011). Overall, the influence of low body condition on migration has been shown to induce two possible strategies, either migrate to reach better feeding conditions, or delay migration until a certain body condition threshold has been reached.

Fish seek to maintain and increase their energy status by increasing consumption and decreasing energy expenditure, but starvation effects both immediate energy (causing hunger from low glycogen levels) and energy reserves (lipid storage). Smoltification and migration has been shown to increase catabolism of body lipids, depleting energy reserves (Fessler and Wagner 1969, Ota and Yamada 1971, Sheridan 1989), lower glycogen levels (Wendt and Saunders 1973), and increase standard metabolic rate (Baraduc and Fontaine 1955). The difference in food availability over time may impact both immediate energy status and secondary energy reserves, and variation in either may induce migratory behavior. Most starvation studies to date that have investigated the link between energy status and migration (Olsson et al. 2006, Wysujack et al. 2009, Persson et al. 2018) have not addressed the specific effect of short term vs. long term starvation on migration decision and behavior. In this study, I manipulated starvation time to try to induce four energy state levels: one with depleted immediate energy (low glycogen levels, high lipid storage), one with depleted energy reserves (high glycogen levels, low lipid storage) one with depleted immediate energy and energy reserves (low glycogen levels, low lipid storage), and one un-starved control (high glycogen levels, high lipid storage). I expected to observe the highest degree of variation in the

long-term starvation and long-term feeding groups, with a migration response possibly affected by these extreme conditions.

In this study, I manipulated feeding regimes to induce variation in hatchery-reared sea trout condition factor, which I then tested as a migration cue and its effects on migration behavior. I used four different feeding treatments to induce a spectrum of energy states (as stated above) in hatchery-reared sea trout for both age one and age two cohorts. I then assessed migration behavior across three spatial scales: using controlled laboratory migration pools, in the field across a small spatial scale in a creek, and across a large spatial scale in the Ume River. I hypothesize that there will be a positive relationship between body condition and feeding, with longer durations of feeding leading to higher body condition. I then expect starvation to induce a migratory response, increasing the decision to migrate and the migration intensity behavior. I expect this to occur in both age cohorts, dependent mainly on low relative condition rather than age. I also expect to observe the highest degree of variation in the long-term starvation and long-term feeding groups, with a migration response possibly affected the most by these extremes.

2 Methods & Materials

2.1 Fish Source and Husbandry

The study took place at Norrfors research laboratory within Norrfors fish hatchery (63°52'N 20°01'E), outside Umeå, Sweden. Fish were produced at Norrfors fish hatchery using brood stock of returning wild and hatchery origin S.trutta spawners. The fish were hatched and raised under standard hatchery procedures until the start of the experiment. Sea trout are annually released from the hatchery at both age one and age two. The hatchery and research laboratory use a flow through circulation system from the adjacent river, causing water temperature to vary based on river conditions. The laboratory had numerous windows allowing for semi-natural circadian light rhythms (63° N). The study period lasted from February 23, 2017 – July 18, 2017. A random sample (N=1269) from two cohorts, age one (N = 599) and age two (N = 670) respectively, were used in three segments of the project (Table 1). The first segment assessed migration in the laboratory using experimental migration pools and two passive integrated transponder tag (PIT tag) antennas. The second segment assessed migration across a small spatial scale in the wild using PIT tag antennas and tagged individuals in a small creek. The third segment assessed large scale migration in the wild using acoustic telemetry transmitter tagged individuals and RFID-telemetry in the Ume River.

Study Segments	Timeline					
	February	March	April	May	June	July
Laboratory Study	Tagging		Begin Feeding Treatments		Migration Study	Migration Study
Small-scale Migration	Tagging		Begin Feeding Treatments			Release
Large-scale Migration				Tagging & Begin Feeding Treatments	Release	

Table 1. A timeline of when each study segment was carried out during the spring/summer of 2017. Each study segment had specific dates when tagging, feeding treatments began, and when data was collected.

2.2 Fish Tagging & Feeding Treatments

All segments of the study tested the effect of different feeding treatments on migration. Before placing fish in a feeding treatment, I tagged them using PIT and/or acoustic transmitters for later identification. On February 23, a random subsample of N = 1209 individuals from two cohorts (age one N = 599, age two N = 610) were tagged with 12 mm PIT-tags (Biomark HPT12), and baseline morphological data was recorded. Individuals were anaesthetized using diluted tricaine methanesulfonate (MS-222), tagged using scalpel incision (tag placed in gastrical cavity), and measurements of total length (mm) and body mass (g) were recorded.

Fish were then placed in 24 separate flow through tanks based on cohort and feeding treatment immediately following tagging on February 23, 2017. Tanks were dark green with a diameter of 1 m and water depth of 40 cm. Age one individuals were placed in tanks with N = 75 per tank. Age two individuals were placed in tanks with N = 38 per tank. Because of water temperature conditions being too cold to induce feeding, fish were not administered their feeding treatments until April 1st and were then fed till the start of the laboratory migration tests or field measures of migration (further details below). Feed was distributed using automatic feeders (TDrum 2000 feeders from Arvo-Tec; www.arvotec.fi) regulated with timer control (Sterner Fish Tech AS; www.fishtech.no). Age one

cohort were given 1.1 mm sinking pellets, whereas age two cohort were given 2 mm floating pellets (Inicio plus and Inicio 917, BioMar; www.biomar.se). Both cohorts were given daily standard portions of 45g (April 1-June 16) and 55g (June 16-end of study), which was sufficient for saturation, based on procedures from Alanärä et al. (2014); Persson et al. (2018). Fish were separated by age cohorts and divided into four feeding treatment groups. The first treatment group comprised of individuals that were starved for the entire duration of the study (SS). The second treatment group were starved until the 72 hours before the behavioral measures commenced, at which point they were fed standard daily portions (SF). The third treatment group were fed standard daily portions until the 72 hours before the behavioral measures commenced, at which point they were starved (FS). The fourth treatment group were fed standard daily portions for the entire duration of the study (FF). After undergoing 10 weeks within the four treatment groups, the initial migration trial commenced.

2.3 Laboratory Migration

A random subsample from the initial tagging of (N = 611, age one N = 303, age two N = 308) were used in the experimental migration pools. I measured migratory behavior in the laboratory using two identical circular concrete rearing pools (diameter: 11 m) that were made into experimental streams following previous methods (Hellström et al. 2016, Persson et al. 2018; Fig 1). Briefly, the boundaries were constructed from transparent Plexiglas® sheets and weighted by concrete blocks to form a stream course along the outer edge of the pool. Water entering the pools was forced into this outside boundary to form the flow through stream course. For each pool, a portion of the stream concaved and became an inlet, forming flatwater. The inlets included a shelter structures (40-cm polyvinyl chloride (PVC) pipe cut lengthwise). The stream channel measured 30.1 m in length, 1.5 m wide, and had a water depth of approximately 33 cm. Two pass-through PIT-tag antennas (Biomark Inc.; www.biomark.com) with accompanying HPR plus tag readers (Biomark Inc.; www.biomark.com) were placed within each stream, approximately 6 m apart. Stream flow was counter-clockwise throughout the study and kept at a constant velocity for the duration of the study (~ 0.17 m/s, electromagnetic flow meter, Valeport Model 801).

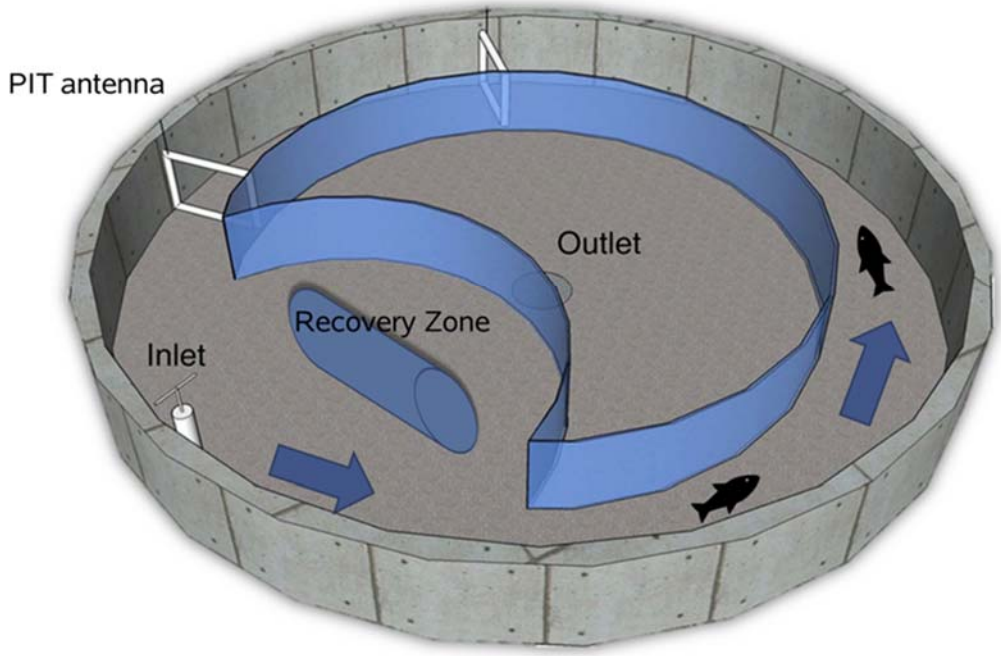

Fig 1. Illustration of migration pool set up for laboratory migration study. Water flows in a counter-clockwise direction, with fish migrating along the outside parameter of the tank. Illustration adapted from Hellström et al. (2016).

Three migration pool trials were conducted in total, with each trial consisting of two replicate pools, resulting in six replicate groups. Within a trial, 20 individuals from each treatment group were randomly selected from each cohort and released into each replicate pool, resulting in approximately 160 fish per pool, per trial. Each trial lasted for 72-hours and fish migratory behavior was continuously measured using PIT-tag antenna detections.

After the 72-hour period, individuals were removed and euthanized (via cerebral concussion). I collected baseline morphological data again: total length (mm), body mass (g), as well as additional morphological measures: smolt stage (coloration index, details below), sex, male maturity (increased visual gonadal growth), and fin condition (visual damage index). Smolt stage was assessed using an established coloration index (Johnston and Eales 1967; Birt and Green 1986; Persson et al. 2018). Individuals were categorized (0-3) depending on factors such as parr-mark visibility, silvering coloration, body elongation, and dark fin margins. Smolt

stage scores began with 0 (parr markings, residents) and continued to 3 (silver coloration, smolts). I used a similar style of index to assess fin condition following Hoyle et al. (2007). An individual's fin condition was determined by visual inspection of the dorsal, pectoral, and caudal fins compared to a photographic identification key, then ranked on a scale (0-5). A fin damage score of 0 indicates intact fins, whereas a fin damage score of 5 indicates severe fin damage.

2.4 Small-scale field migration

On July 7, a random subsample of N = 322 from all treatment groups and both cohorts were released into a natural creek habitat (Table 2). Individuals were anesthetized (MS-222) before release to re-measure total length (mm) and body mass (g), and additionally recorded smolt stage (coloration index), and fin condition (visual damage index).

Treatment	Age One	Age Two	Total
FF	51	24	75
FS	50	25	75
SF	47	37	84
SS	47	41	88

Table 2. Number of individuals released during small-scale field migration. Divided by cohort (age) and treatment group (feed entirely: FF, feed, then 3 day starve: FS, starved, then 3 day feed: SF, starved entirely: SS).

The creek is approximately 240 m in length, with the release site located at the origin (fig 2). Within this creek, two PIT-tag antennas and accompanying HPR plus tag readers were installed to track fish downstream migration. The first antenna was located approximately 110 m downstream from the release site, whilst the second antenna was located approximately 87 m downstream from the first antenna. Both antennas were run continuously for 10 days after release to record all migratory behavior.

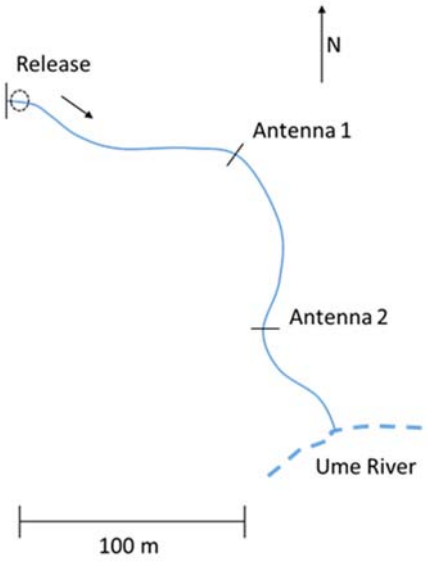

Fig 2. Illustration of creek antenna set-up for the small-scale migration study. Individuals released upstream and detected on two PIT-tag antennas with downstream migration.

2.5 Large-scale field migration

On May 3, a random sample (N=60) from the age two cohort were anesthetized (MS-222) and tagged with both PIT (12 mm) and acoustic v5-180 khz (Vemco ©; www.vemco.com) tags (delay time HR 0.7 sec, PPM 33 sec). Morphological data (total length (mm) and body mass (g)) was recorded. These individuals were divided into the same four treatment groups as the migration pool individuals, using the same classifications (SS, SF, FS, FF).

After approximately five weeks (37 days), individuals were anesthetized (MS-222) and reassessed for the same morphological parameters measured previously. A 24-hour recuperation time was given and then all individuals were released into the same natural creek habitat used during the small-scale field migration.

The creek and antenna set-up were identical to what was described in the small-scale field migration, however; for this study, both antennas were run continuously for three days after release to record all migratory behavior.

The creek flows directly into the undammed portion of the Ume River, allowing for a free-flowing river from the creek to the Gulf of Bothnia, approximately 30km from the release site. The river flow is controlled by the dam above and is adjusted daily to try and replicate natural flow variation (flow ranges from 15 m3/s – 50 m3/s). Within this stretch of river, 14 acoustic 180 khz receivers (VR2W and HR2, Vemco ©; www.vemco.com) were located at seven locations, dispersed throughout the river. Receivers were placed in centralized locations within the river and submerged approximately one meter off the riverbed using an anchor/buoy system (fig 3). Receivers detected individual passage continuously from release till approximately 15 weeks afterwards when receivers were removed from the river.

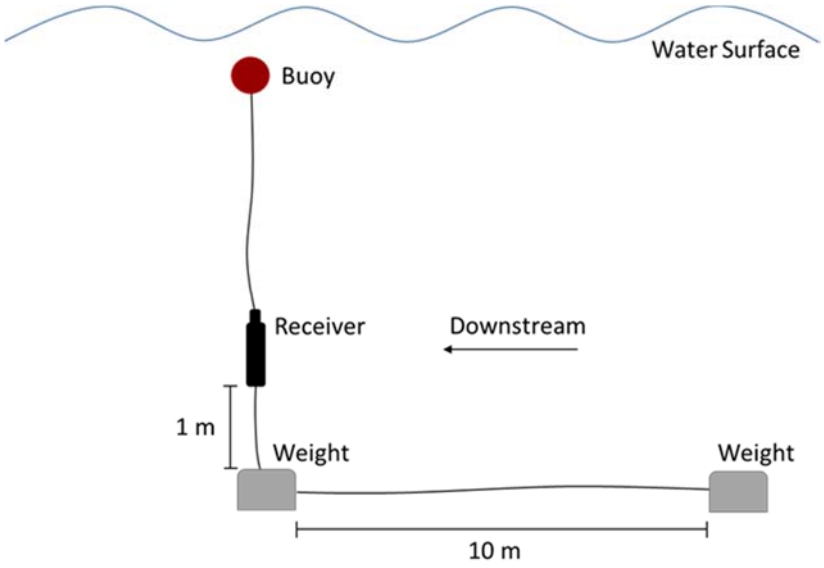

Fig 3. Illustration of receiver set-up for hydro-acoustic receivers for the large-scale field migration study. A double-weight drag line secured the receiver to the bottom and the buoy kept it in a vertical position.

2.6 Laboratory Migration Analysis

All analyses were carried out in R (R core team 2017, version: 3.4.0). In all analyses, I tested model assumptions of normality and homogeneity of variance using visual inspection of diagnostic plots, Shapiro-Wilk, and Breusch-Pagan tests. I

used mixed models to meet independence assumptions and test for the effect of feeding treatment on all endpoints, including treatment as a fixed factor, and random effects of housing tank and trial replicate. I tested for the overall effect of feeding treatment using a likelihood ratio test, followed by Tukey's post-hoc-analyses. In all analyses, I analyzed each age cohort separately. A critical value of $\alpha = 0.05$ was used and means are reported ± 1SE unless specified otherwise. Analysis in the age one cohort consisted of the four treatment groups (FF, FS, SF, SS). Within the age two cohort, I was unable to analyze the four feeding treatment groups separately because of origin confusion and were condensed to two treatment groups (fed and starved).

Initial total length and body mass were compared to final total length and body mass to determine the change in relative condition factor over the study period (Le Cren 1951). I calculated relative condition factor at baseline and final sampling following Equation 1. It takes the length-weight relationship of the sampled population using a least-squares regression. From the regression, the slope and intercept are used to calculate a unique relative condition factor per individual for the population, which gives a more precise value of condition for the specific population of study.

$$K_n = \mathrm{W}/aTL^n$$

Equation 1. Calculation of the relative condition factor Kn. Body mass (g) is denoted by W and total length (mm) is denoted by TL. The exponential intercept n and slope a are derived from a least-square regression.

I calculated relative condition factor for each age cohort separately. I used a linear mixed effects model (LMM, lme4 package) to test for the effect of feeding treatment on change in relative condition factor, using a power transformation to meet model assumptions (Fox and Weisberg 2011). Ordinal mixed model regressions (ordinal package, Christensen 2015) were used to compare treatment effects on smolt stage and fin condition. I assessed sex using visual confirmation from dissection of reproductive organs (gonads, ovaries) and the extent of gonadal growth as an indication of male maturity.

All PIT detections included the unique PIT identification code and time stamp. Analysis of detections was carried out using detections from only one antenna per pool. I found that both antennas had similar detection rates, and the number of detects per individuals was highly correlated (Pearson correlation, mean lap, N =

560, R = 0.68, P = <0.0001, number of detects, N = 560, R = 0.94, P = <0.0001). I therefore chose the antenna with the highest performance (number of detections) for further migration behavior analyses. Both antennas were only used to analyze migration direction. Individuals were assigned as either a “migrator” if they obtained at least 10 detections on both antennas at identical time splits, or “non-migrator” if they had less than 10 detections. In most individuals a clear pattern of either “migrator” or ”non-migrator” was observed, with most migrators ranging in number of detections over 200 at certain time frames. For migrators, I determined migration direction based on elapsed detection time between antennas. Individuals were assigned as either downstream or upstream migrators. Overall, 66% migrated downstream, 33% were non-migrators, and only 1% migrated upstream. I excluded the upstream migrators from further analysis. To determine the effect of treatment on whether or not a fish migrated, I used a binomial generalized linear mixed effects model (GLMM).

To analyze migratory behavior, only assigned downstream migrating individuals were used to calculate individual lap times and the number of detections. Individual lap times were calculated by taking the difference in time between detections on the same antenna. Because some individuals lingered in the antenna detection range, a minimal lap time of 10 seconds was enacted to reduce detection noise. I calculated the mean lap time per individual from all lap times detected and compared across treatment groups. Because individuals did not migrate the entire time, there was high variation across individuals, but I did find peak times of detection that were common, indicating lap times. I therefore made a cut off time of 90 seconds, based on a common time when the first trough between peek detection times occurred, and examined variation across lap times during active migration. I labelled these mean lap times separately, one being mean “all laps” time (including laps before and after 90 seconds) and mean “real laps” time (laps occurring between 10-90 seconds). I used a linear mixed model (LMM) with power transformation to meet model assumptions, a chi-squared test, and Tukey post-hoc analysis to determine the effect of treatment on mean lap time. I analyzed the number of individual detects per one antenna using a negative binomial GLMM appropriate for over-dispersed data (glmmTMB package, Magnusson et al. 2017). Mean lap time was analyzed to investigate speed of migration and number of detections were analyzed to investigate the persistence of migration.

2.7 Small-Scale Field Migration Analysis

As previously, I calculated relative condition factor for all individuals in each cohort and compared between treatment groups. Cohorts were separated, but subject to the same statistical analyses. Because of large heteroskedasticity between feeding treatment groups in age one fish, I used a generalized least squares (GLS) model (nlme package, Pinheiro J et al. 2017) to assess the effect of treatment on power-transformed change in condition factor. I included the random effect of tank in the GLS model. The variances between treatment groups were separately weighted in the GLS model. I followed this analysis with a likelihood ratio test and combined with Tukey post-hoc testing.

To measure short-distance migration, I calculated the difference in time between first PIT detection on each antenna per individual. I power transformed data to meet model assumptions and analyzed the effect of treatment on migration speed using a LMM with a random effect of housing tank. Again, I used a likelihood ratio test followed by Tukey post-hoc testing.

2.8 Large-Scale Field Migration Analysis

As previously, relative condition factor was calculated for all individuals and was compared between treatment groups using the same statistical analysis.

The effect of treatment on migration time between PIT antennas followed the previously described analysis procedure. I calculated difference in time between first detection on each antenna per individual and analyzed the difference in emigration time between treatment groups.

To measure long-distance migration, distance between acoustic receivers and the release site were calculated using the GPS locations of the receivers. Migration success (detection from one receiver to the next) of the released individuals was performed using an interval-censored survival analysis (interval package, Therneau 2015). Each receiver acted as intervals and time of unique last detection for each receiver was used to determine an individual's last interval of survival. I tested for the effect of feeding treatment on migration success using a non-parametric maximum likelihood (NPMLE) permutation test suitable for interval-censored data with small sample sizes.

3 Results

3.1 Laboratory Migration

3.1.1 Relative Condition Factor

I found that relative condition factor differed between feeding treatment groups within cohorts. Within the age one cohort, (LMM N = 237, $\chi 2$ = 12.3, P = 0.006, Fig 4A) the main differences occurred between the FF treatment and the SF and SS treatments (SF-FF Z = -3.19, P = 0.008, SS-FF, Z = -3.41, P = 0.004). High variation in FS treatment group was caused by high housing tank variation. For age two fish, the fed treatment group had higher change in condition factor when compared to the starved treatment group (N = 255, $\chi 2$ = 361, P = <0.0001, Fig 4B).

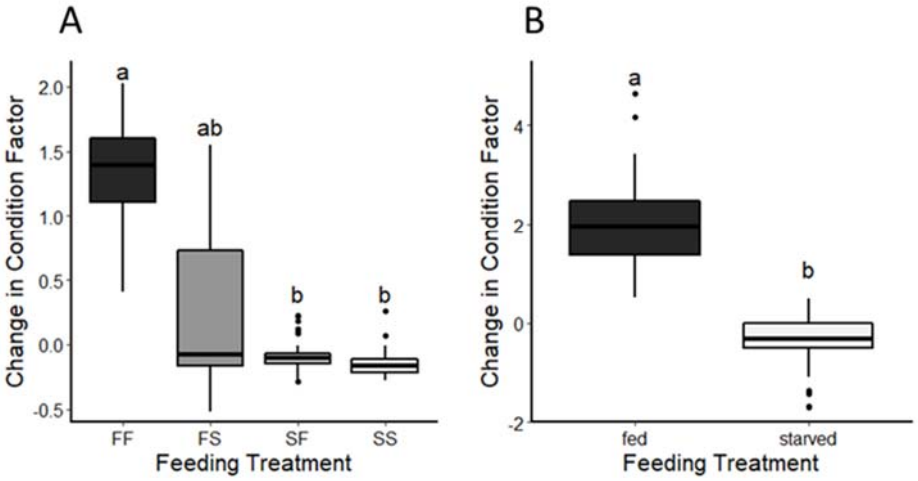

Fig 4. Change in condition factor plotted by treatment groups and two cohorts during the laboratory migration study. A) represents age one cohort, B) represents age two cohort. Significant differences following Tukey post-hoc testing denoted by lettering. Where lettering is the same, there is no significant difference. Differing letters indicate significance.

3.1.2 Smolt Stage

I observed no significant differences in smolt stage score between treatment groups in age one fish (ordinal mixed model, N = 237, LR = 4.27, P = 0.23, Fig 5A). Most age-one individuals were scored as smolt stage one (light, but visible parr-marks, faint indication of smoltification). With age two fish, individuals that were fed exhibited a lower smolt stage score compared to starved individuals (ordinal mixed model N = 255, Z = 1.92, P = 0.055, Fig 5B). A low smolt stage score indicates visible parr-marks and little to no smoltification. Most age-two individuals were scored as smolt stage two (little to no visible parr-marks, some silver coloration visible).

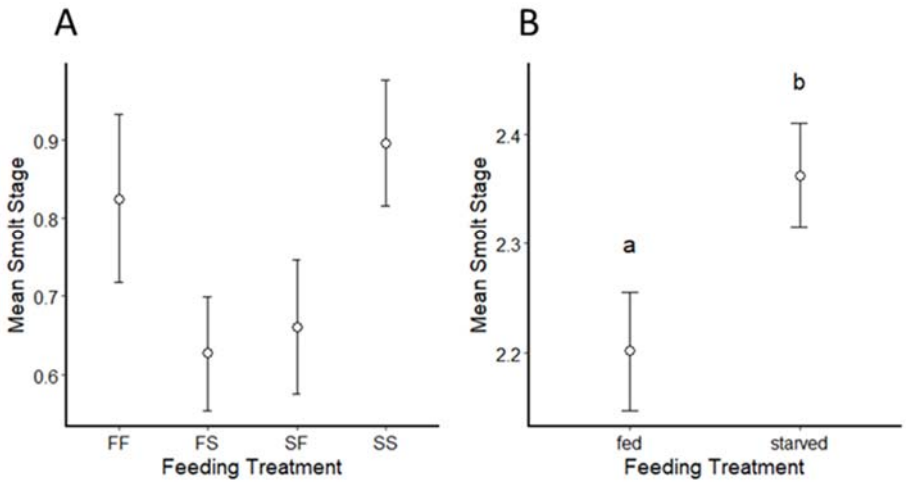

Fig 5. Mean smolt stage score based on treatment groups for the laboratory migration study. A higher smolt score indicates visual smoltification coloration. A) represents age one cohort (finding not significant), B) represents age two cohort (significant differences denoted by lettering). Error bars represent ± 1 standard error.

3.1.3 Sexual Maturity

Sex ratios across all treatment groups and cohorts were split equally. Within the age one cohort, I had 109 females, 126 males, with 3 of these males reaching maturity. The three males reaching maturity were from the treatment group FF. Within the age two cohort, I had 125 females, 129 males, with 51 of these males reaching maturity. The 51 mature males were evenly split between the fed and starved treatment groups. I found that male maturity was not dependent on feeding treatment, with 26 mature males found in the fed treatments, and 25 in the starved treatments (binomial mixed model, N = 51, LRT = 0.67, $\chi 2 = 0.41$).

3.1.4 Fin Damage

Differences in fin damage between treatment groups were significant for all fins in both cohorts (Fig 6). In the age one cohort (Fig 6A), the FF treatment group scored lower in all fin scores, indicating lower levels of fin damage. The overall caudal fin score approached statistical significance (ordinal mixed model, N = 237, $\chi 2 = 7.33$, P = 0.06), and in the post-hoc analysis the FF treatment group scored lower than the SF and SS groups (FF-SF Z = -3.02, P = 0.01, FF-SS Z = -3.43, P = 0.003). The overall effect of treatment was significant for both the dorsal fin score ($\chi 2 = 8.7$, P = 0.03) and pectoral fin score ($\chi 2 = 13.1$, P = 0.005). For both fins, the FF group had lower scores than the three remaining treatment groups (dorsal: FF-FS Z = -2.57, P = 0.05, FF-SF Z = -3.53, P = 0.002, FF-SS Z = -3.42, P = 0.004, pectoral: FF-FS Z = -2.85, P = 0.02, FF-SF Z = -4.57, P = <0.0001, FF-SS Z = -4.91, P = <0.0001). Across all fins in the age one cohort, I found a pattern of increasing fin damage scores with decreasing feed treatments.

In the age two cohort (Fig 6B), a similar pattern was observed in two of the three fin scores. In the caudal fin score, fed fish had higher find damage scores than starved fish (ordinal mixed model N = 255, $\chi 2 = 6.43$, P = 0.01, Z = -2.52, P = 0.01). For the dorsal fin and pectoral fin, fed groups had lower fin damage than starved groups (Dorsal: $\chi 2 = 11.1$, P = 0.001, Z = 3.3, P = 0.001; Pectoral: $\chi 2 = 34$, P = <0.0001, Z = 5.76, P = <0.0001). From decreasing feed, I found higher fin damage in both cohorts with the dorsal and pectoral fins.

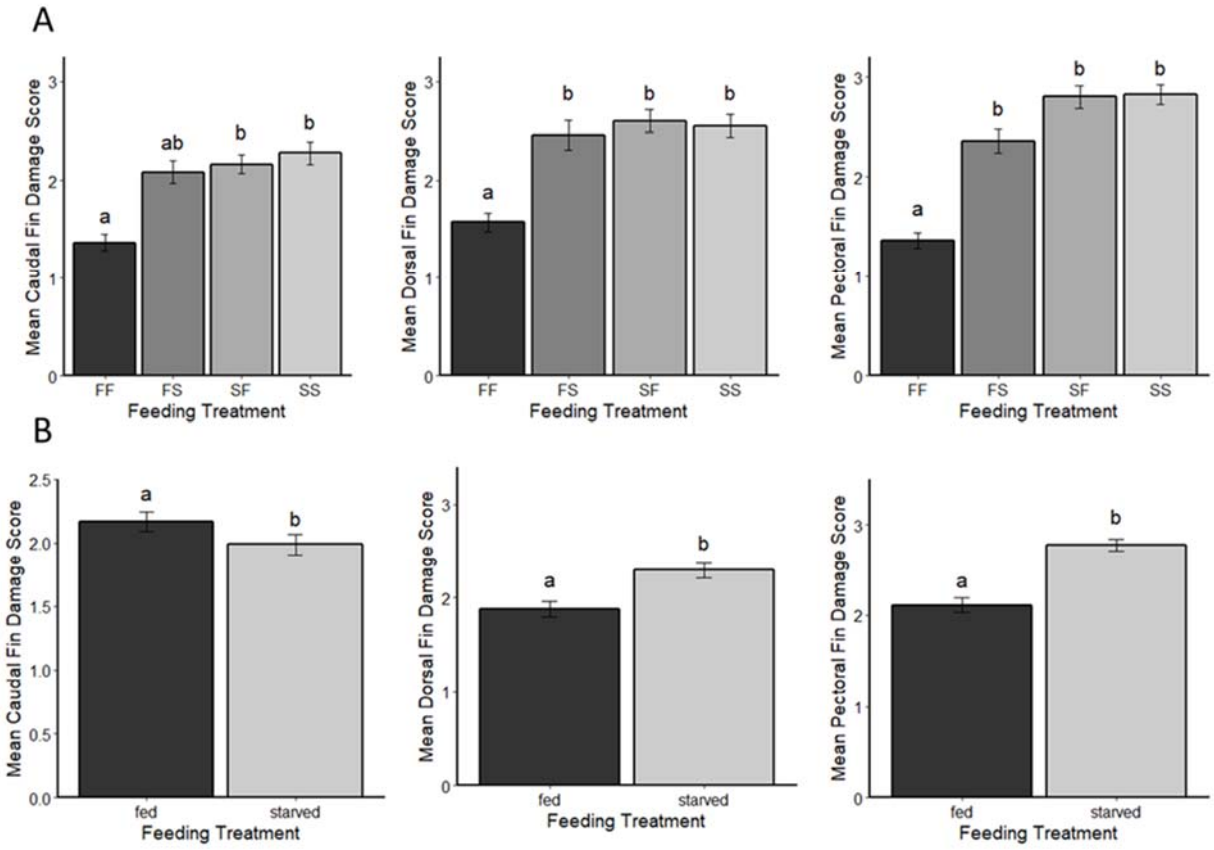

Fig 6. Mean fin damage scores for each treatment group and cohort during the laboratory migration study. High scores indicate more visible fin damage. From left to right: Caudal fin, Dorsal fin, Pectoral fin. A) represents age one cohort, B) represents age two cohort. Error bars represent ±1 standard error. Significant differences indicated by lettering.

3.1.5 Migration Decision

The age one cohort had varying levels of migration (Binomial GLMM N = 237, $\chi 2$ = 11.7, P = 0.009, Fig 7A) with more FF individuals migrating compared to other groups (FS-FF Z = 2.78, P = 0.03, SF-FF Z = 3.94, P = <0.001, SS-FF Z = 4.09, P = <0.001). The proportion of age one fish initiating migration was relatively low (39%) compared to the age two cohort (94%). In the age two cohort (Fig 7B), the initiation of migration occurred in almost all individuals with no significant differences between feeding treatments (GLMM, N = 255, LRT = 0.86, P = 0.35).

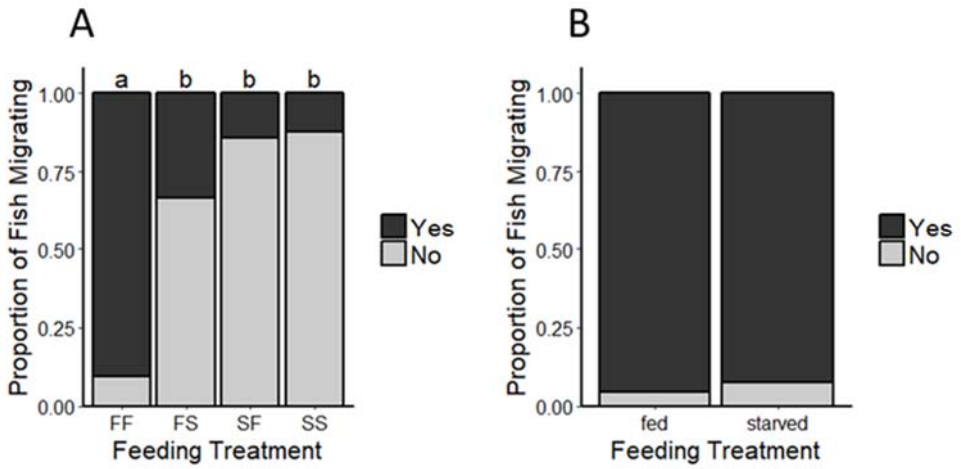

Fig 7. Proportion of fish migrating for each treatment group and cohort during the laboratory migration study. Black represents the proportion of fish initiating migration, whereas gray represents the proportion of fish labelled as non-migrators. A) represents age one cohort (significant differences denoted by lettering), B) represents age two cohort (finding not significant)

3.1.6 Mean Lap Time

When all detection times spent migrating were include in mean lap time calculations ("all lap" times), there were no significant differences between treatment groups within each cohort (age one LMM, N = 92, LRT = 3.69, P = 0.3, age two LMM, N = 255, LRT = 2.83, P = 0.092). However, when I investigated only the time fish spent actively migrating ("Real lap" times), there were effects of feeding treatment within each age cohorts (Fig 8). For age one fish (LMM N = 92, $\chi 2$ = 14.8, P = 0.002, Fig 8A), the FF treatment group was found to have significantly faster lap times than both the starved treatments (SF-FF Z = 4.89, P = <0.001, SS-FF Z = 2.81, P = 0.02, SF-FS Z = 3.39, P = 0.004). In the age two cohort (LMM N = 255 T = 2.26, P = 0.03, Fig 8B), the fed treatment group had faster lap times than the starved group.

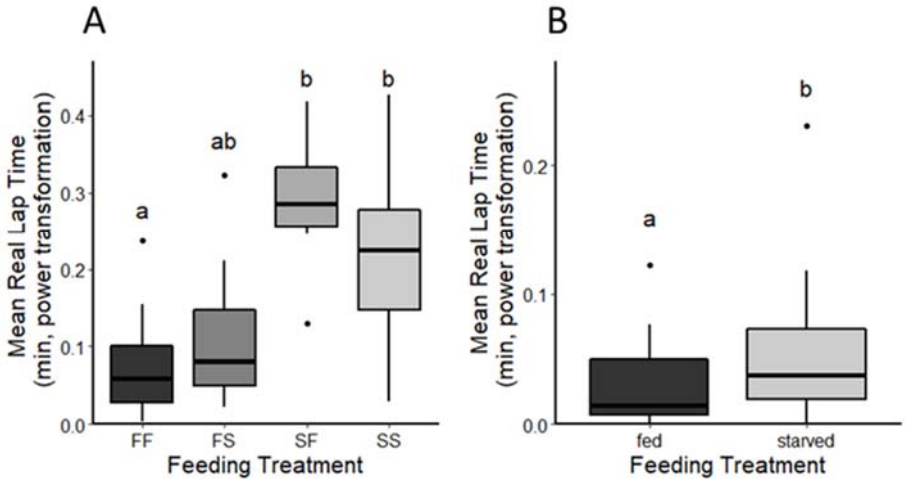

Fig 8. Mean "real lap" times for each feeding treatment and cohort during the laboratory migration study. A power transformation was used for both cohorts. A) represents age one cohort, B) represents age two cohort. Significant differences denoted by lettering.

3.1.7 Number of Detections

Detections between treatment groups varied within cohort (Fig 9). In the age one cohort (Fig 9A), I did not find a significant effect of feeding treatment (Negative Binomial GLMM, N = 92, LRT = 4.02, P = 0.26). The fed treatment groups had high variation, with some individuals having much higher detections than starved individuals. In the age two cohort (Negative Binomial GLMM N = 255, Z = -2.0, P = 0.046, Fig 9B), the fed treatment group had more detections than the starved treatment group, indicating increased migratory behavior.

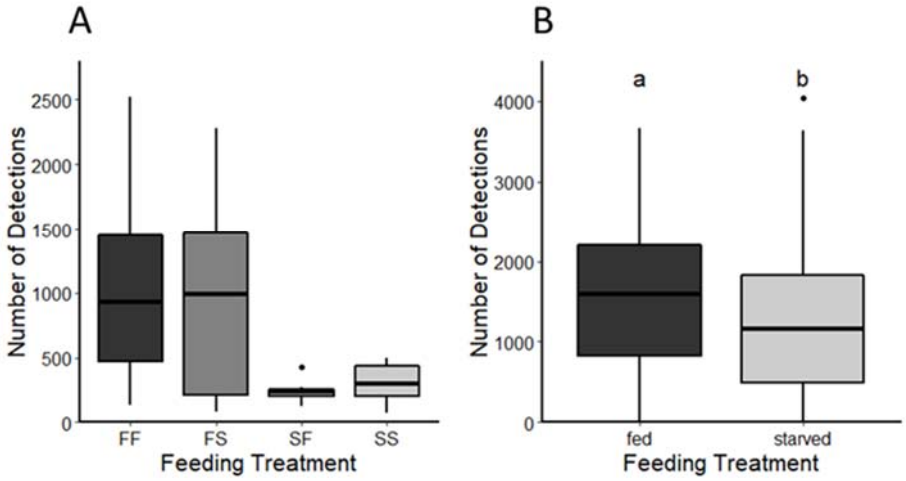

Fig 9. The number of detections compared between feeding treatments and cohorts during the laboratory migration study. A) represents age one cohort (finding not significant), B) represents age two cohort (significant differences denoted by lettering).

3.2 Small-Scale Field Migration

3.2.1 Relative Condition Factor

Variation in condition factor across treatment groups and within cohorts mirrored laboratory migration results (Fig 10), with a positive condition factor found in the fed treatment groups when compared to the starved treatment groups. In the age one fish, both fed treatment groups had a more positive change in condition factor than the starved groups (GLS, N = 194, $\chi 2$ = 172, P = <0.0001, Fig 10A; FF-SF T = 12.4, P = <0.0001, FF-SS T = 14.9, P = <0.0001, FS-SF T = 9.8, P = <0.0001, FS-SS T = 12.0, P = <0.0001, SF-SS T = 5.9, P = <0.0001). In the age two cohort, fed treatment groups again exhibit positive change in condition factor (GLS, N = 127, $\chi 2$ = 134, P = <0.0001, Fig 10B; FF-FS T = 2.8, P = 0.03, FF-SF T = 20.0, P = <0.0001, FF-SS T = 19.3, P = <0.0001, FS-SF T = 11.6, P = <0.0001, FS-SS T = 12.2, P = <0.0001). For both cohorts, change in condition factor deteriorates with decreased feed.

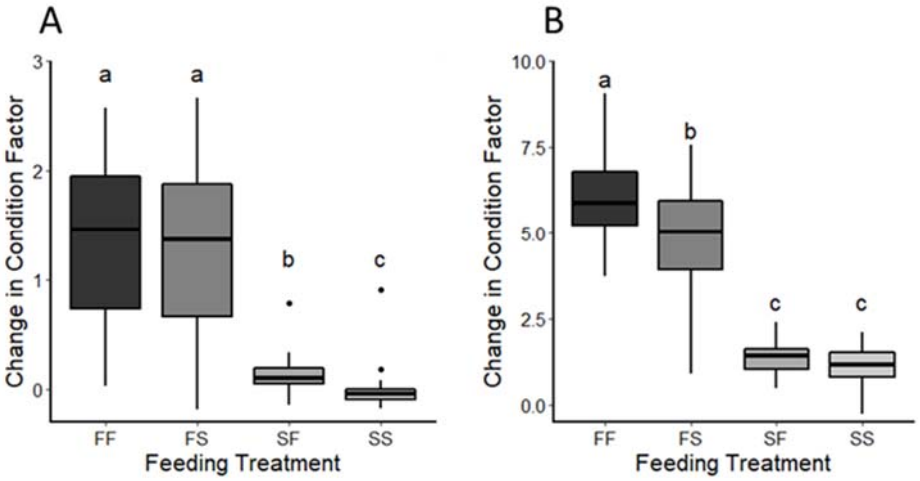

Fig 10. Change in relative condition factor for each treatment group and cohort during the small-scale field migration study. A) represents age one cohort, B) represents age two cohort. Significant differences denoted by lettering.

3.2.2 Smolt Stage

I found variation in mean smolt stage score between treatment groups within cohorts (Fig 11). For the age one cohort (ordinal-mixed model regression, LR = 17.5, P = 0.001, Fig 11A), smolt stage score was lower for FS treatment compared to SF treatment, with FF and SS treatment groups intermediate (FS-SF Z = -4.0, P = 0.0003). Most age one fish were scored as smolt stage zero (visible parr-marks, no visual indication of smoltification). In the age two cohort (Fig 11B), the effect of feeding treatment was not significant (ordinal ANOVA N = 127, LRT = 0.51, P = 0.92). Most age two fish were scored as smolt stage two (little to no visible parr-marks, some silver coloration visible).

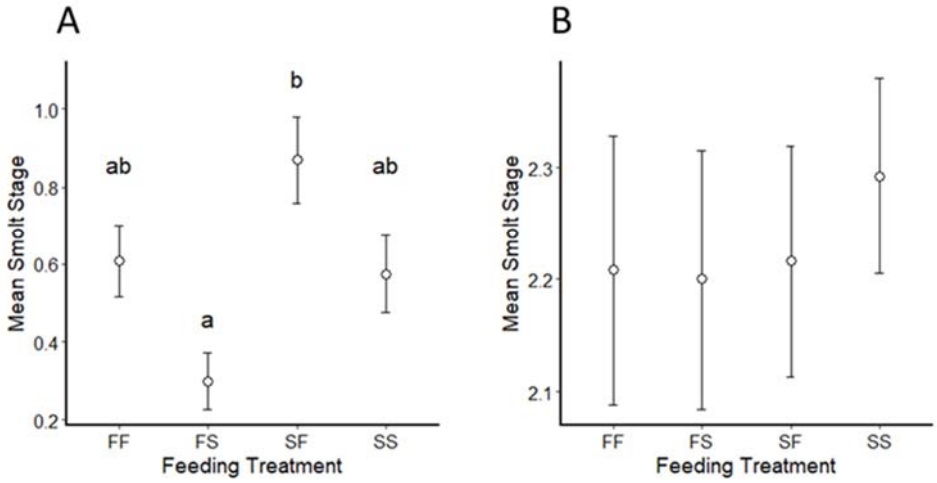

Fig 11. Mean smolt stage score for each treatment group and cohort during the small-scale field migration study. A) represents age one cohort (significant differences denoted by lettering), B) represents age two cohort (finding not significant). Error bars represent ± 1 standard error.

3.2.3 Fin Damage

Findings for fin damage across treatment groups and cohorts were similar to laboratory migration results, with fed treatment groups exhibiting overall lower fin damage in the dorsal and pectoral fins (Fig 12.). The age one cohort (Fig 12A) caudal fin was borderline significant with no significant post-hoc relationships (Ordinal CLM, N = 194, LR = 7.59, P = 0.055). Dorsal fins had significantly lower fin damage in the fed groups compared to the starved groups (Ordinal CLM, LR = 35, P = <0.0001; FF-SF Z = -2.9, P = 0.02, FF-SS Z = -4.6, P = <0.0001, FS-SF Z = -3.4, P = 0.005, FS-SS Z = -5.0, P = <0.0001). Pectoral fins also had significantly lower fin damage within the fed treatment groups compared to the starved groups (Ordinal CLM, LR = 62.4, P = <0.0001; FF-SF Z = -4.8, P = <0.0001, FF-SS Z = -5.9, P = <0.0001, FS-SF Z = -4.8, P = <0.0001, FS-SS Z = -5.9, P = <0.0001).

The age two cohort (Fig 12B) had no significant effect of treatment group on caudal fin damage (Ordinal CLM, N = 127, LRT = 2.82, P = 0.42). Dorsal fins had significantly lower fin damage in the fed group when compared to the starved group (Ordinal CLM LR = 47.4, P = <0.0001; Tukey, FF-SF Z = -3.2, P = 0.007,

FF-SS Z = -4.5, P = 0.0001, FS-SF Z = -4.7, P = <0.0001, FS-SS Z = -5.8, P = <0.0001). Pectoral fins also exhibited lower fin damage scores in fed treatment groups than in starved treatment groups (Ordinal CLM, LR = 23.9, P = <0.0001; Tukey, FF-SF Z = -3.2, P = 0.007, FF-SS Z = -4.5, P = 0.0001, FS-SF Z = -4.7, P = <0.0001, FS-SS Z = -5.8, P = <0.0001).

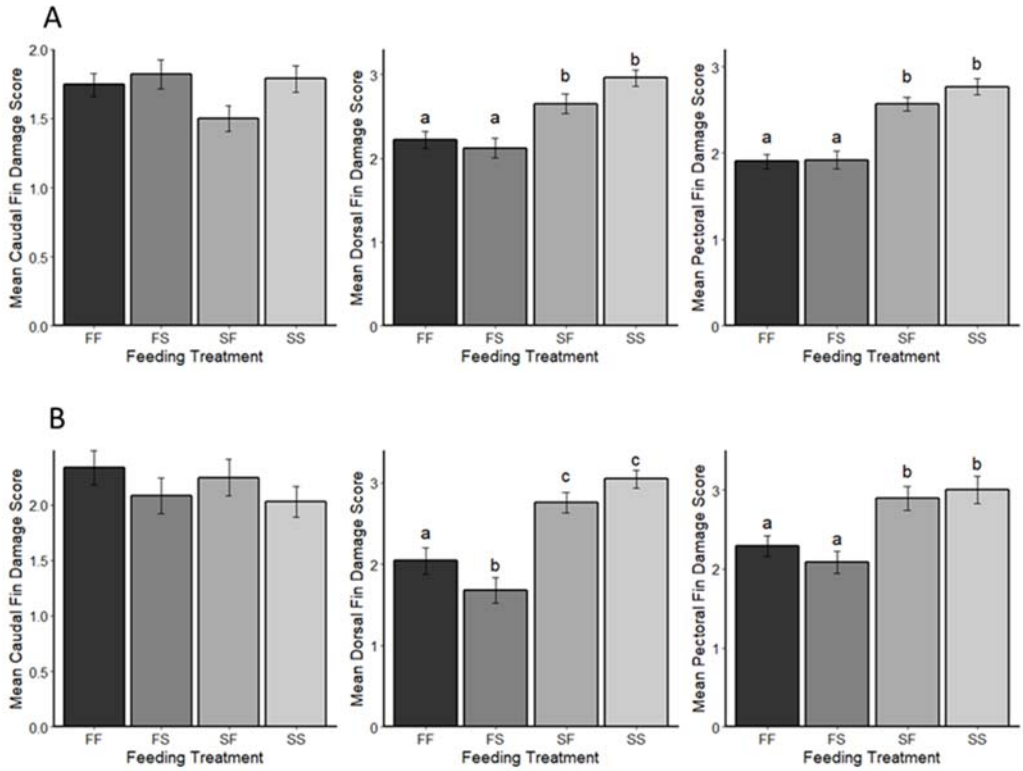

Fig 12. Mean fin damage scores for each treatment group and cohort during the small-scale field migration study. From left to right: caudal fin, dorsal fin, pectoral fin. A) represents age one cohort, B) represents age two cohort. Error bars represent ±1 standard error. Significant differences following Tukey post-hoc testing indicated by lettering.

3.2.4 Migration Decision

The proportion of fish migrating downstream in the creek was not significantly affected by feeding treatment for either age cohort (Fig 13). For the age one cohort (Fig 13A), only eight fish (4%) migrated (Binomial GLM, N = 195, LRT = 6.39, P

= 0.094). For the age two cohort (Fig 13B), 92 fish (72%) migrated (Binomial GLM N = 127, LRT = 3.89, P = 0.27).

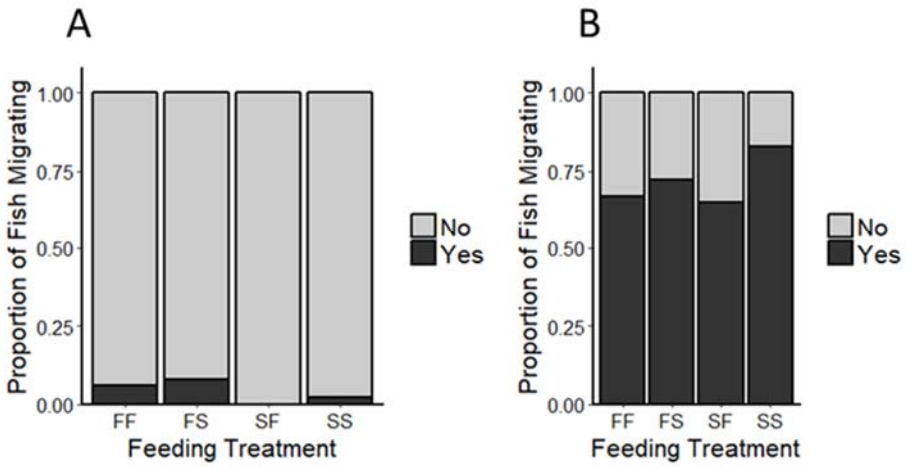

Fig 13. Proportion of fish migrating for each treatment group and cohort during the small-scale field migration study. Black represents the proportion of fish initiating migration, whereas gray represents the proportion of fish labelled as non-migrators. A) represents age one cohort, B) represents age two cohort. Findings not significant.

3.2.5 Creek Migration Time

In the age one cohort, a low sample size of eight individuals was not sufficient to run statistical testing (N = 8, Fig 14A). In the age two cohort, both fed treatment groups tended to have faster migration times than both the starved treatment groups (LMM, N = 92, $\chi 2 = 98.4$, P = 0.0003, Fig 14B; SF-FF T = 2.6, P = 0.05, SS-FF T = 3.7, P = 0.002, SS-FS T = 3.5, P = 0.005).

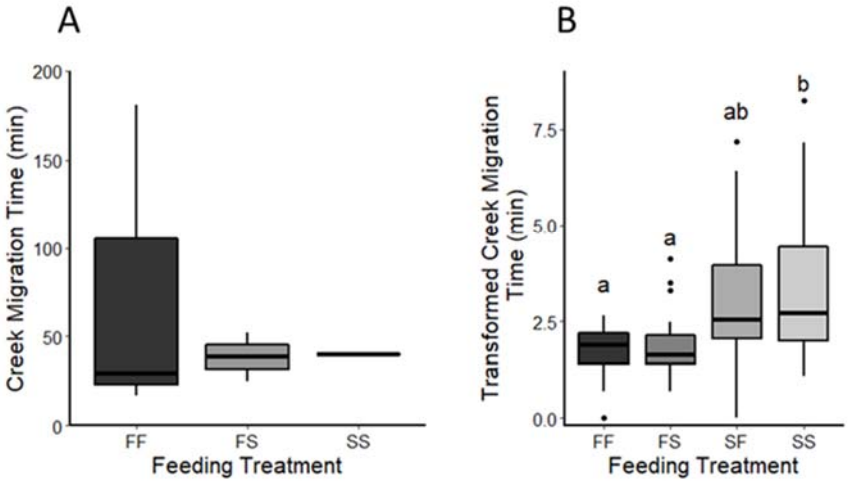

Fig 14. Creek migration time (min) for each treatment group and age cohort during the small-scale field migration study. A) indicates age one cohort, B) represents a transformed age two cohort (significant differences following Tukey post-hoc testing denoted by lettering).

3.3 Large-Scale Field Migration

3.3.1 Relative Condition Factor

Feeding treatments significantly affected relative condition (GLS, N = 42, $\chi 2$ = 42.6, P = <0.0001, Fig 15), with change in condition factor declining with less feed (FF-SF T = 4.2, P = 0.001, FF-SS T = 12.0, P = <0.0001, FS-SF T = 2.7, P = 0.05, FS-SS T = 8.0, P = <0.0001, SF-SS T = 3.1, P = 0.02).

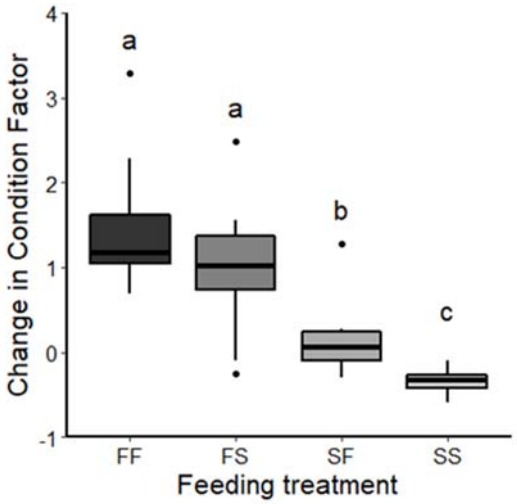

Fig 15. Change in relative condition factor across feeding treatment groups during the large-scale migration study. Significant differences denoted by lettering.

3.3.2 Creek Migration Time

Within the creek equipped with PIT antennas, 40 fish (77%) were detected on both antennas. Elapsed time between detections ranged from 2 minutes to 21 hours. Migration time between antennas was not affect by feeding treatment (ANOVA N = 32, F(3,28) = 0.31, P = 0.82, Fig 16), and I found high variation in migration time within the FF and SS treatment groups.

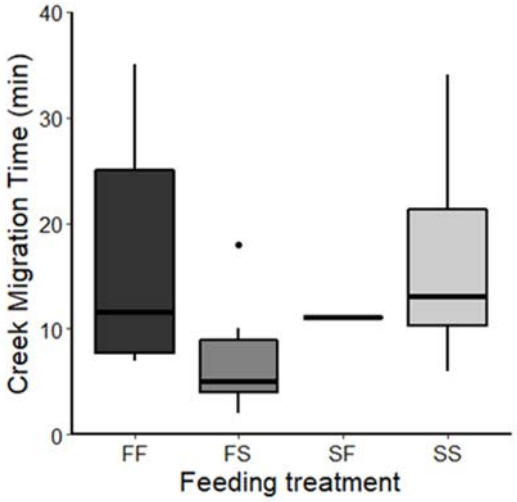

Fig 16. Creek migration time (min) for all treatment groups during the large-scale migration study. Finding is not significant.

3.3.3 Survival Analysis

Migration success of the 52 fish declined rapidly after release and leveled off with four unique detections at the furthest detection point (NPMLE permutation test, N = 52, $\chi 2 = 6.84$, P = 0.07, Fig. 17). After release, 41 fish were detected leaving the creek and entering the river between 1- 48 hours later. Once in the river, detection numbers dropped to 14 unique individuals (27%) around 0.8 km from release site. By 8 km downstream from release site, only four unique individuals were detected and these four continued to the river delta 29 km downstream. It took between 5 – 17 days for these four fish to migrate out of the river system (Fig 18). Three of the four out migrating fish were from the treatment group FF, while one was from treatment group SS.

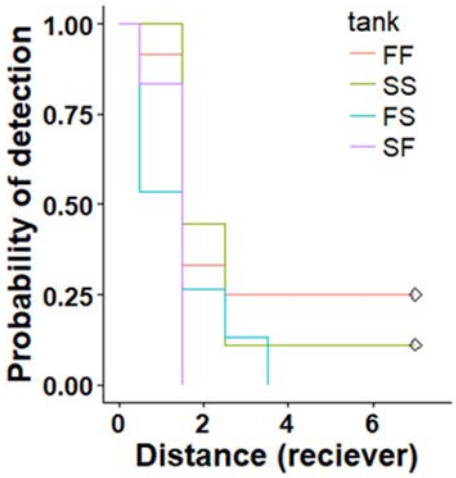

Fig 17. Survival analysis for each treatment group in the age two cohort during the large-scale field migration study. Treatment groups are colored coordinated, FF (orange), FS (turquoise), SF (purple), SS (green). Diamonds indicate fish were still present in that group after the last detection point.

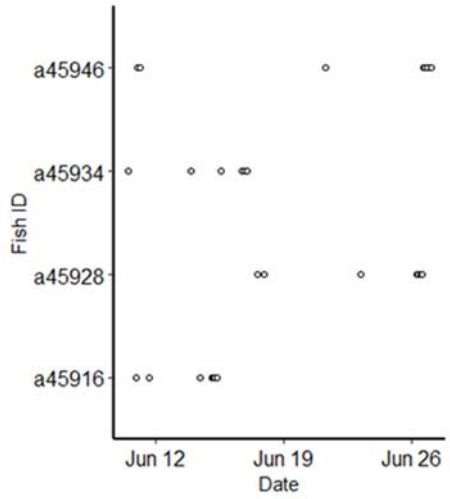

Fig 18. Migration first detection times on the seven receivers for the four unique individuals emigrating out of the river system during the large-scale migration study.

Migration success could only be calculated for downstream swimming individuals, but I did observe some upstream migratory behavior as well. Five of the 52 fish were detected 1.3 km upstream from release site in the reservoir above Stornorrfors hydropower dam. These five fish swam up the fish ladder (300 m long) and into the reservoir above. The fish were detected in the above dam reservoir between 1 – 6 days after release. Of these five fish, two came from the treatment group SS, two came from the treatment group FS, and one came from the treatment group FF.

4 Discussion

4.1 Condition Factor and Morphological Metrics

In all three study segments, I observed significantly different relative condition factors between feeding treatment groups, even when the duration of treatment was as little as five weeks. I found a positive relationship between feeding and condition factor, with fed treatment groups exhibiting the highest relative condition, similar to previous studies (Wysujack et al. 2009, Lans et al. 2011).

Smolt stage scores indicated that primarily the age two cohort was smolting, with a slight increase in smoltification for the starved treatment groups. Withholding food may hence have initiated the smoltification in some fish of the age two cohort, a result in line with other feed manipulation studies (Wysujack et al. 2009, Davidsen et al. 2014). External sign of smoltification in the age one cohort was not observed in any of the treatment groups, indicating cohort differences. This result indicated smoltification in the age one cohort is not occurring, an important factor to consider when evaluating the effect of releasing age one smolts for compensating the natural population. Smolt stage scores may have been affected by our method of observed coloration post-mortem. Morphological metrics were collected immediately after euthanasia, but detailed coloration and markings could have been lost due to processing time. For future studies, it is advised to evaluate smolt stage before euthanizing to ensure accurate observations.

Decreased feed rations increased fin damage in almost all fins within both cohorts similar to findings by Persson et al. (2018) who manipulated feeding regimes in Atlantic salmon. Most fin damage occurred on the dorsal and pectoral fins, with the highest fin damage in the starved feeding treatment. Starvation treatments may

have increased competition and aggression in the rearing tanks (Storebakken & Austreng 1987, Brännäs & Alanärä 1994). Our rearing densities were selected based on previous food manipulation and starvation studies to minimize excessive aggression-related mortality (Persson & Alanärä 2014, Persson et al. 2018. Rearing densities must be taken into account if starvation treatments are used, since aggression may lead to lower survival (Petersson et al. 2013, Persson & Alanärä 2014). Fin damage is also of importance to hatchery rearing practices because hatchery smolts have to undergo inspection before release; these fish must be produced at a high quality to meet national regulations.

I also found male maturity occurred in the age two cohort independent of feeding treatment, indicating an obligate physiological transition. There may be low energetic costs in male maturation, and individuals may not be constrained from maturing because of low energy status (Jonsson and Jonsson et al. 2012, Sloat & Reeves 2014). Other factors such as temperature, photoperiods, and age may be more influential to maturation than condition (McMillan et al. 2012, Sloat & Reeves 2014). It would be of great interest in future studies to follow these precocious males post release and observe if these fish return early as "jacks". It is also noteworthy that no females showed indications of maturation, perhaps due to higher energetic costs of producing eggs compared to males.

Overall, our treatment groups successfully differentiated individuals into the four energy statuses I envisioned, with significant variability between treatment groups for each cohort. The highest contrast for most of the study aspects occurred between the long-term starvation treatment and the un-starved control treatment. The short-term starvation and feed treatment groups did show some variation, but individuals tended to have higher variation in these groups. Intense starvation over a long duration depleted both immediate and secondary energy reserves, and led a general trend of lower condition factor, higher fin damage, slower migration speeds, and lower migration intensity.

4.2 Migration Decision and Behavior

In the laboratory setting, I found the decision to migrate was dependent on feeding treatment in the age one cohort, but not in the age two cohort. For the age one fish, the proportion of fish migrating increased with increasing feed. This suggests an increase in hatchery feeding can lead to an increase in migration initiation, indicat-

ing nutritional status may predict migration or residency in this younger cohort (Boel et al. 2014). This result is opposite to other studies, who have found that nutritional restriction can increase migration response (Wysujack et al. 2009, Davidsen et al. 2014). I hypothesized that low energy status would induce a higher migratory response, but the opposite occurred. This could be an alternative strategy, where individuals delay migration until energy status has reached a certain threshold (Metcalfe et al. 1990, Thorpe et al. 1992, Theriault et al. 2007). Delayed age one migrators may require another summer feeding season to reach an adequate energy status to initiate migration. Fed individuals may have reached this migration threshold and had the energy reserves and immediate status to undertake migration. These differences may also be due somewhat to local adaptations, the laboratory setting, and/or hatchery rearing differences. In the age two fish, the majority of fish initiated migration, independent of treatment group. With little effect of treatment groups, this could indicate the decision to migrate may have already been taken before the study began, perhaps in previous fall, based on growth and nutritional status from the summer months (Metcalfe 1998; Martin-Smith et al. 2004). However, a lower overwintering condition factor of pre-migratory individuals should have been observed if the migration decision was taken in the previous fall, as this form of physiological preparation for migration has been shown in past studies (Amstutz et al. 2006, Giger et al. 2008). To capture how migration decisions are linked to the previous season's energetic status, future studies should measure initial condition during the summer and fall before potential migration (Boel et al. 2014).

In the natural creek setting, I found contrasting results in the age one cohort, with almost no fish initiating migration. This could be due to differences in the hatchery vs. wild environments, such as risk of predation, water flow, hiding structures, etc. Once the age one cohort was released, perhaps ample food within the creek setting met the energy requirements for them to stay or delay migration for another year (Forseth et al. 1999). Those that did migrate from the age one cohort were primarily from the fed treatment groups, perhaps indicating energetic limitations for starved treatment groups (Olsson et al. 2006, Wysujack et al. 2009). It would also be of interest in future studies to continue the study duration for the age one cohort into the following year, and see if feeding treatment variation at age will affect the migration at age two. Quantifying available food resources in the natural creek setting would also be beneficial to understand if residency occurs where ample food is available. In the age two cohort, I found a high proportion of fish initiating migration, similar to the laboratory study, again indicating cohort differences in migration. I did observe a slight increase in the proportion initiating migration in the starved treatment groups in the age two cohort, though this was

not statistically significant. This finding coincides with similar studies that found higher propensity of migration in starved individuals (Larsson et al. 2011, Davidsen et al. 2014).

Together, my results can be incorporated into an environmentally-cued genetic condition threshold model (Aubin-Horth & Dodson 2004, Tompkin & Hazel 2007) and can be adapted to each cohort separately. I found that fish age is one of the primary factors for migration initiation and is dependent on the setting. The decision window to migrate for age one fish may be energy-state dependent, and occur over a matter of weeks before migration initiation. In age two fish, the decision window to migrate may occur in the fall before migration, indicative of growth and energy reserves at that stage. The decision to mature might occur simultaneously, with individuals focusing energy towards differing life history strategies, smoltification (migration) or maturation (residency).

My measures of migration behavior indicate that increased feeding can have a positive effect on the speed and intensity of migration. In the laboratory setting, I found mean "real lap" time decreased with higher feed rations in both cohorts. I also found the highest number of detections was in the fed treatment groups in both cohorts, indicating a higher intensity of migration. In the field study, I find similar results, observing faster migration times between our creek antennas from the fed treatment groups in the age two cohort. These results mimic Persson et al. (2018) where increased feeding was beneficial for migration intensity in Atlantic salmon. In the age one cohort, I found an increase in feed can induce faster migration in the laboratory setting, but in a natural setting, the effect is lost due to most age one individuals not initiating migration. In the age two cohort, feed increased migration speed and intensity, indicating feeding was beneficial to migration behavior. Decreasing time spent migrating in the river has been shown to benefit fish energy status and survival (Thorpe and Morgan 1978, Peake and McKinley 1998, Aarestrup et al. 2005, Salminene et al. 2007). Even if the decision to migrate was not affected in the age two cohort, I did affect migration intensity with feeding treatments. Applying this result to the hatchery release may increase speed and duration of age two smolt migration.

4.3 Large-scale Migration

Migration success was very low, with only four (8 %) individuals making it to the coast in the large-scale migration study. It is known that smolt survival is low, and can vary based on environmental factors and distance of travel (Aarestrup & Koed 2003, Thorstad et al. 2007, Davidson et al. 2014). Migration speeds can vary greatly between studies, with usually high mortality the first few days, and a negative correlation between time and survival in the river (Thorpe and Morgan 1978, Peake and McKinley 1998, Aarestrup et al. 2005, Salminene et al. 2007). I found survival was not dependent on feeding treatment, though sample size was relatively low. Of the four individuals that made it to the coast three of the four were from the fed treatment group, possibly indicating that increased feed was beneficial for survival to the coast. Similar large-scale survival studies have indicated distance and duration of migration may be positively correlated to energy state and condition factor (Brodersen et al. 2008, Poulsen et al. 2010, Boel et al. 2014). Since, sea trout in the Baltic Sea rarely migrate further than 20 km from their natal river (Carlin 1969), energy state and lipid levels may not be as vital as for Atlantic salmon, which migrate hundreds of kilometers.

Migration speed and duration in the main river channel could have been influenced by flow rate, temperature, predation risk, and timing of release. Previous studies have observed a positive correlation between flow rate and migration speed (Hansen et al. 1985, Moore et al. 2012). For the day of release, flow within the river was measured at 15 m3 per second, relatively low compared to typical flow periods in this river that can be measured at 23-50 m3 per second. A slower flow rate may have been detrimental, leading to increased predation and increased energy expenditure to migrate, which could have both reduced fish survival in our study. Water temperature can also be an influential factor in the decision to migrate (Brannon et al. 2004, Sogard et al. 2012, Sloat & Reeves 2014). McMillan et al. (2012) found an inverse relationship between individual condition and water temperature, with greater growth in warmer water, but increased lipid storage in colder water. Higher water temperatures may also impede maturation even with high individual growth rates (Sloat & Reeves 2014). The temperature profile during this study was similar to previous years and reflected typical seasonal values for this river, with temperatures ranging from 11° C in May to 16° C in July. I did not analyze the effect of temperature in this study, and could be another factor to control for in future studies. However, all treatments experienced similar temperatures during our study. Timing of release has also been shown to be an important factor to migration (Peterson 1973, Bilton et al. 1984, Lundqvist et al. 1994, McKinnell 1998). In the Vindel River system, hatchery fish are released at the end of May annually (Peterson 1973), with both age one and age two cohorts released. Natural salmon smolt runs in the vicinity of Vindel river peak between mid-May

to mid-June (Österdahl 1969). Our fish were released June 10th, so timing of release was similar to both hatchery practice and natural migration. Most individuals were detected moving downstream, but I did observe five individuals moving upstream, past the dam, and into the reservoir above, indicating migratory behavior, but not anadromy. These individuals are likely to become residents, but there is no clear indication whether this migratory decision was influenced by feeding treatments, since these fish came from varying treatment groups.

4.4 Hatchery effect during natural release

Hatchery stocking has also been shown to affect the decision to migrate because of the contrasting differences in hatchery/wild environments, and could be a possible cause for variation between my laboratory and natural migration responses. Ruzzante et al. (2004) found high mortality at sea of hatchery-reared smolts, however, Hansen et al. (2000) found stocked hatchery trout that became residents could breed successfully, possibly increasing the proportion of residents in the population, genetically selecting against anadromous behavior. Even though fish used in this study came from genetically diverse brood stock (supportive breeding), hatchery-rearing may alter fish condition and physiology, possibly affecting their migration decision (Davidsen et al. 2014).

Hatchery-reared smolts can have a lower survival rate than wild smolts in the wild (Jonsson et al. 2003, Saloniemi et al. 2004, Serrano et al. 2009, Larsson et al. 2011). Increasing the energetic status of hatchery-reared and wild smolts has been shown to increase their survival in the wild (Henderson and Cass 1991, Lundqvist et al. 1994, Saloniemi et al. 2004). However, an overabundance of feed in the hatcheries can also have the opposite effect by reducing anadromous behavior, since energetic status and lipid levels are so high (Bergström 1989, Poole et al. 2003, Serrano et al. 2009). With high energy status from overfeeding, individuals are more likely to mature, inhibiting smoltification, and becoming residents (Poliscansky 1983, Thorpe 1986, Jonsson et al. 1995, Ugedal et al. 1998). I did observe a proportion of age two males did mature, and I did have some age two fish that did not migrate, but I cannot identify the sex and or maturity of these individuals. Release time and size-at-release of hatchery-reared salmonids have been shown to affect migration propensity (Peterson 1973, Bilton et al. 1984, Lundqvist et al. 1994, McKinnell 1998), but as it has been shown in this study, fish condition and energy status should also be evaluated before release to benefit

increased migration initiation and higher migration intensity, hopefully leading to higher survival of returning mature adults.

4.5 Conclusions

I have shown how proximate factors such as fish condition and age can influence the decision to migrate as well as migratory behavior, emphasizing the importance of timing of release for migration propensity. The timing of release in this study may have influenced the age one cohort significantly, with energy state-dependence inhibiting migration, but I may have missed the decision window for the age two cohort. Even if migration initiation occurred independently of feeding regime, I may have altered their migration behavior (speed and duration) with our feeding treatments, with fed treatment groups migrating faster and further. Maturity also occurred independent of feeding treatment, which may be an obligatory process for certain individuals. I have shown the importance of the study environment, and how migration can vary between laboratory and natural settings. Almost no age one fish migrated in the natural environment, which could indicate a release at age one is inefficient at producing migrating sea trout. In all treatment groups, smolt survival to sea was very low, indicating other factors of migration inhibition, such as mortality from predation or residency. Migration survival is critical for future sea trout generations. If migrating fish have reduced migration survival, this can reduce or inhibit the decision to migrate over generations through selection, given that the trait is heritable (Sandlund & Jonsson 2016). It is critical that we sustain both anadromous and residency morphs to ensure population life history diversity.

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Acknowledgements

I would like to thank first and foremost my advisors, Gustav, Erin, and Anders. Without their guidance, experience, and support this project would not have been possible. I want to thank everyone assisting with the project in the Department of Wildlife, Fish, and Environmental Sciences. I also want to thank everyone at Norrfors Fish Hatchery for their generous time, help, and use of facilities. Thank you Sofie for your never-ending support and love throughout this adventure.

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