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Density effect on growth rate of juvenile Atlantic salmon *(Salmo salar) in manipulated large rivers*

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Contents

Abstract

Growth rate of young-of-the-year (YOY) Atlantic salmon (*Salmo salar*) in low-density rivers was substantial better relative to YOY captured in normal density rivers. Mean growth index ± SD for YOY in low-density rivers was 1.10 ± 0.36 while the corresponding value in normal density rivers was 0.60 ± 0.22. The YOY originated from eight different rivers located in the middle and Northern Norway. Rivers were classified into two types, low-density rivers and normal density rivers. Rivers under restoring after rotenone treatment were used as low-density rivers. Regular rivers, which have not been treated with rotenone, were used to represent normal density rivers. Growth rate (temperature adjusted) comparisons were done by comparing predicted mean body mass of YOY with observed mean body mass of YOY in each river.

Keywords: Density dependent • Salmonid • Young-of-the-year • Competition • Growth Index

Sammendrag

Vekst hos 0-årig yngel innen arten Atlantisk laks (*Salmo salar*) som lever i elver med lav populasjonstetthet er påvist å være vesentlig bedre sammenlignet med 0-årig lakseyngel i elver med normal populasjonstetthet. Vekstindeksen ± SD i lavtetthetselver ble funnet til å være 1.10 ± 0.36, mens den i elver med normal tetthet var 0.60 ± 0.22. Sammenligning av vekstrate hos lakseyngel ble utført i 8 elver lokalisert i Midt-og Nord-Norge. 4 elver hadde lav populasjonstetthet mens de resterende 4 hadde normal populasjonstetthet. Elver som var i gjenoppretningsfasen etter rotenon-behandling ble brukt som lav-tetthetselver mens ubehandlede elver representerer normal tetthet. Ved å sammenligne lakseyngelens gjennomsnittlige predikerte masse med den gjennomsnittlig observerte massen i hver elv, ble det opprettet en vekst-indeks som gjorde sammenligning på tvers av behandling (lav/normal tetthet) mulig.

Introduction

Growth is defined as a change in size of an individual and is usually measured in the units of length, body mass or energy. For fish species, growth is a life-history trait linked to population regulation and is mainly affected by temperature, competition and nutrients (Wootton, 1990). Several studies support the hypothesis suggesting that larger or faster growing members of a cohort gain a survival advantage over smaller conspecifics via enhanced resistance to starvation, decreased vulnerability to predators, and better tolerance of environmental extremes (Sogard, 1997).

Temperature is the most important environmental factor determining the growth rate of teleost fish (Amin *et al.*, 2014). Teleost fish are ectothermic organisms, which means they adjust their body temperature with the environmental temperatures (Molles and Tibbets, 1999). Water-temperature dictates how consumed nutrients are allocated to either basal metabolic processes or additional tissue growth (Weber *et al.*, 2014). Fish consume to meet their energy requirement. With increasing water-temperatures, fish need to consume more in order to meet their metabolic demand until appetite is inhibited (Kaushik and Medale, 1994; Jobling, 1997). Optimum water-temperature, for fish growth, is dependent on food availability. Water-temperatures below the optimum, gives a positive correlation to fish-growth. Water-temperatures higher than the optimum gives a negative correlation to fish growth (Wootton, 1990). This is also according to findings in Atlantic salmon (*Salmo salar*) (Forseth *et al.*, 2001; Jonsson *et al.*, 2001)

A simple growth model, which is based on achieved size, provides a description of an observation. To get information about causal processes that generates the growth pattern, components that is related to the rate of food consumption and metabolism, e.g. temperature, must be included (Wootton, 1990). Bioenergetics models are based on metabolic equations that quantify functional relationships between water temperature, digestion, metabolic, kinetic, and growth processes in fish based on energy as a common unit (Elliott, 1976; Hayes *et al.*, 2000). A major assumption when estimating growth based on bioenergetics is that fishes are able to locate and consume prey at a constant proportion of their maximum physiological rate (Weber *et al.*, 2014).

Ratkowsky (1983) came up with a growth model for bacterial cultures. This growth model was highly dependent on temperatures and could be applied over the whole temperature range. It was easy to fit and contained desirable statistical properties. For fish-growth, Elliott *et al.* (1995) came up with a generic growth model later refereed to as the Elliot model. The Elliot model contained solid biologically interpretable parameters. Ratkowskys growth model was re-parameterized in order to make a temperature dependent growth model for Atlantic salmon parr (Forseth *et al.*, 2001). The original parameters were replaced by the same parameters as in the Elliot model. In that way the meaningful parameters from the Elliot model were incorporated into the new Ratkowsky model (hereafter modified Ratkowsky model). According to comparisons with predicted growth from the more known growth model for Atlantic salmon parr made by Elliott and Hurley (1997), the modified Ratkowsky model was very applicable and performed well for thermal responses (Forseth *et al.*, 2001; Jonsson *et al.*, 2001). Hence, it was well suited for modeling salmon growth under known water-temperature conditions in the river.

Competition and population-density affects growth in freshwater fishes (Deverill *et al.*, 1999; Jenkins *et al.*, 1999; Bohlin *et al.*, 2002; Sundstrom *et al.*, 2004). Competition is defined as an interaction between two individuals from the same or different species that reduce the fitness of the involved individuals (Molles and Tibbets, 1999). Competitive effects on growth occur when behavioral interactions between fish species cause an unequal distribution of a resource leading to a skewed size distribution (Wootton, 1990; Ohlberger *et al.*, 2013). Dispersion from nursery area comes with an energetically cost due to limited dispersal abilities for the young-of-the-year (YOY). Hence YOY tend to stay close to their nursery area during their first summer (Einum *et al.*, 2012). Atlantic salmon may reside as juveniles for up to 8 years before migrating to sea (Thorstad *et al.*, 2011). This leads to an increase of coexisting cohorts and population density in the rivers.

Thus different types of competition events are more likely to happen. Growth tends to decline for stream dwelling salmons due to exploitative and interference competition (Grant and Imre, 2005; Ward *et al.*, 2007; Imre *et al.*, 2010). Studies performed by Nordwall *et al.* (2001); Imre *et al.* (2005); Kaspersson and Hojesjo (2009); Kaspersson *et al.* (2012) shows that increased density of older cohorts affects the growth of YOY cohorts. Einum and Kvingedal (2011) suggest that these findings are due to a niche overlap between overyearlings and YOY, which has a negative effect on YOY growth.

Nutrient abundance is documented to have an effect on growth (Bacon *et al.*, 2005; Rosenfeld *et al.*, 2005; Martinussen *et al.*, 2011). When a teleost fish consume food, the fate of the energy extracted from the food is divided into two trajectories. (1) It could leave the body as waste products or heat (energetic cost of work) or (2) it could be incorporated as new tissue, as in protein, skeleton or fat (Wootton, 1990). For YOY Atlantic Salmon in lotic populations, increased densities of conspecies and inter species leads to a change in diet from smaller to bigger invertebrate prey. Thus the rivers delivery-rate of optimal sized prey for YOY seems to decrease with increased density (Martinussen *et al.*, 2011). According to Wankowski and Thorpe (1979) there is an optimal prey size in which yield maximum growth. Consumption of prey larger than the optimum prey size comes with an energetic cost, which results in reduced growth. Overlapping niches between and within cohorts leads to intra and inter cohort competition (Einum and Kvingedal, 2011). Thus, competition is also related to nutrient abundance and it can be hard to separate the effect of them and look at the effects isolated from each other. Nutrient abundance is reported to vary within a season. Therefore, YOY responds to the same temperatures in different ways at different time of the season (Bacon *et al.*, 2005).

The goal of this thesis was to explore the effect of density on growth rate of juvenile Atlantic salmon YOY. YOY living in natural rivers with normal population density were compared with YOY living in rivers with assumed low population density. Former rotenone treated rivers under restoring were used to represent rivers with low population density. Such rivers are expected to contain less dense populations of YOY, inter cohorts and interspecies because gill-breathing organisms dies after treatment. Therefore the biotic environment for YOY should differ from regular rivers with normal population densities. This enables a unique opportunity to test for density-dependent growth of YOY in whole rivers. Earlier studies of density-dependent growth have been conducted under limited spatial extent, or have considered natural variation in density. In this study, the entire rivers are manipulated. Thus density-dependency is tested between river-types: low-density rivers and normal density rivers. Due to our assumption regarding different densities of overyearlings and inter species in rotenone treated vs. regular rivers, different growth patterns are expected to be found. The null hypothesis is that the growth rate of YOY in rivers with low population density is similar to the growth rate in rivers with normal population density. The alternative hypothesis is that the growth rate of YOY in the two river-types deviates in different ways from the modified Ratkowsky model.

Material and Methods

Material

The data used in comparing density-effect on growth consist of measures of body mass of young-of-the-year (YOY) Atlantic salmon along with water-temperatures. Total sample size N was 195 YOY captured in eight different rivers. Four of the rivers (128 YOY) were manipulated and represented low-density populations while the other four (67 YOY) were natural rivers and represented normal density populations (Table 1).

Table 1: Rivers under investigation with belonging: number of YOY sampled in each river, density level and sampling year.

River	n	Density	Sampling year
Vefsna	13	Low	2014
Fusta	54	Low	2014
Figga	34	Low	2011
Røssåga	27	Low	2009
Gaula	22	Normal	2006
Humla	9	Normal	2006
Surna	20	Normal	2006
Stjørdalselva	16	Normal	1997

Sampling

In river Figga and river Røssåga, the Norwegian Veterinary Institute sampled YOY. These samples contained only length measurements. In the rivers Gaula, Humla, Surna and Stjørdalselva sampling was performed by Berg *et al.* (2009) and included both measurements on body mass and length. YOY in river Vefsna and river Fusta was sampled by us, using the same method as Berg *et al.* (2009). In the latter two rivers, sampling was performed at stations made by NINA (The Norwegian Institute for Nature Research). Each station covered at least 100 m^2 (typically 4 m x 25 m). Some stations were located in fast flowing riffles and some in more slow flowing pools. All fish were sampled with a 12 V backpack electroshocker (Bohlin *et al.*, 1989). Each fish was killed with a quick blow to the head.

Weighing

After sampling, both total length (mm) and body mass (g) was determined. Body mass was measured as fresh body mass using a precision balance (type NJW-50, precision: ± 0.005 g; Universal Weight Enterprise; www.labeling-uwe.com). To standardize the water content of the fish at weighing, each individual was taken from the water bucket with a pair of tweezers, allowed to drain for 2 seconds. The head of the fish was then held downward for 2 seconds in contact with blotting paper before weighing.

Age Determination

To avoid any overyearlings in our dataset, fish were age-determined. Fish derived from the Norwegian Veterinary institute and the study of Berg et al. (2009) was already age-determined to YOY. By making a frequency-diagram, based on fish-body length, any fish of an upper length was further investigated by counting growth-periods in the scales. In that way we ensured that our dataset only contained YOY Atlantic salmon.

Condition-Factor

In order to obtain data on body mass of YOY in river Figga and river Røssåga, Fulton's conditions factor (hereafter K-factor) were used (Equation 1). In these rivers only measurements of length were available.

$$K = \frac{W \times 100}{L^3} \quad (1)$$

The unit of body mass (W) is gram while the unit of length (L) is centimeters. When knowing the K-factor, it is possible to estimate the body mass corresponding to a given length. The K-factor represents the condition of the fish and can be used to compare the fatness or well being of fishes (Wootton, 1990). During a season, the fatness of Atlantic salmon varies. Thus, measurements from fish used in establishing the K-factor should be from the same time of the season as the fish which body mass is estimated (Froese, 2006). According to Imholt *et al.* (2011), ration does have a substantial effect on the K-factor. Therefore, rivers with low population density were expected to show a greater K-factor than regular rivers due to our assumption of more food per capita. The fish used in estimating the K-factor involves only YOY Atlantic salmon and derives from the 14 rivers in Berg *et al.* (2009) study. These rivers has not been treated with rotenone, thus population density is expected to be normal. To reduce noise in the data, which was used to establish the K-factor, length was plotted against body mass to detect possible outliers (Figure 1). The rivers were located in three areas of Norway: northern, middle and south (south-west). This explains the broad size distribution in Figure 1. In order to check the assumption regarding a greater K-factor for YOY living in rivers with low population density, body mass of YOY in both river Vefsna and river Fusta were estimated based on the K-factor established from Berg *et al.* (2009). In river Vefsna and river Fusta, sampled data of YOY contained measurements on body mass. Hence, by comparing estimated body masses, based on Fulton's condition factor, with observed body mass in river Vefsna and river Fusta, our assumption could be tested, see discussion.

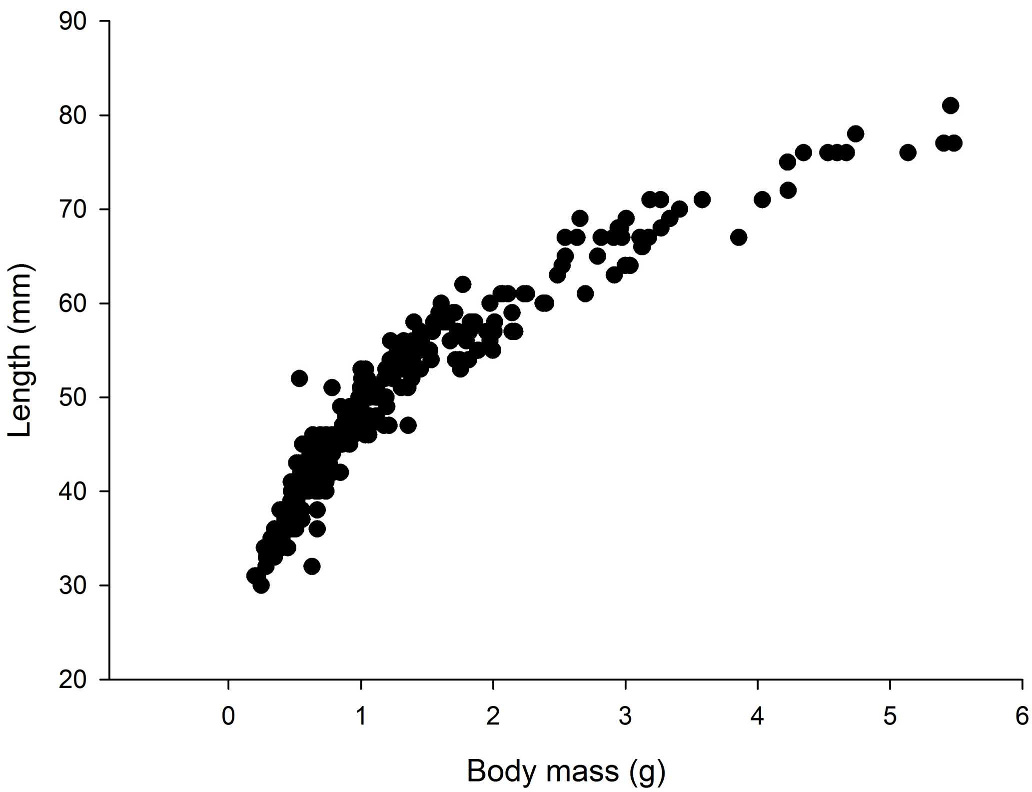

Figure 1: Length-mass relationship of the YOY used to establish the K-factor.

Temperature

Water-temperatures of the rivers; Gaula, Humla, Surna and Stjørdalselva originates from NVE (Norwegian Water Resource and Energy Directorate) while the rivers; Vefsna, Fusta, Figga and Røssåga originates from the Norwegian Veterinary institute. For each river, there were several measurements of water-temperatures per day. According to Imholt *et al.* (2011) mean daily water-temperatures are adequate enough when modeling fish in the wild. Hence, that's what is used in the modified Ratkowsky model. In river Stjørdalselva (1997) and river Figga (2011), there were a lack of data on water-temperatures due to high flow of water and strong current. In order to get data on water-temperatures in these rivers, a correlation-study based on similar nearby rivers had to be performed. This had to be done at a year where temperature-loggers in both rivers still were active. In river Stjørdalselva, river Forra was chosen as correlation-river. For river Figga, river Stjørdalselva was used. Temperatures of the two rivers were plotted pairwise against each other (Figure 2) and a linear regression analysis was performed. This enabled us to see how well one river represented the water-temperature of the other. The correlation between river Stjørdalselva and river Forra was very strong with R^2=0.99. In river Stjørdalselva and river Figga the corresponding value for R^2=0.84. As a supplement to the regression analysis, mean water-temperatures ± standard deviation (hereafter SD) of the correlated rivers were calculated over a period where temperature-loggers still were active. Water-temperatures of river Stjørdalselva (1997) and river Forra (1997) were respectively 9.4 ± 4.6^{0}C and 9.3 ± 5.3^{0}C. In 2013, river Stjørdalselva and river Figga had water-temperatures 11.4 ± 3.7^{0}C and 11.2 ± 4.0^{0}C.

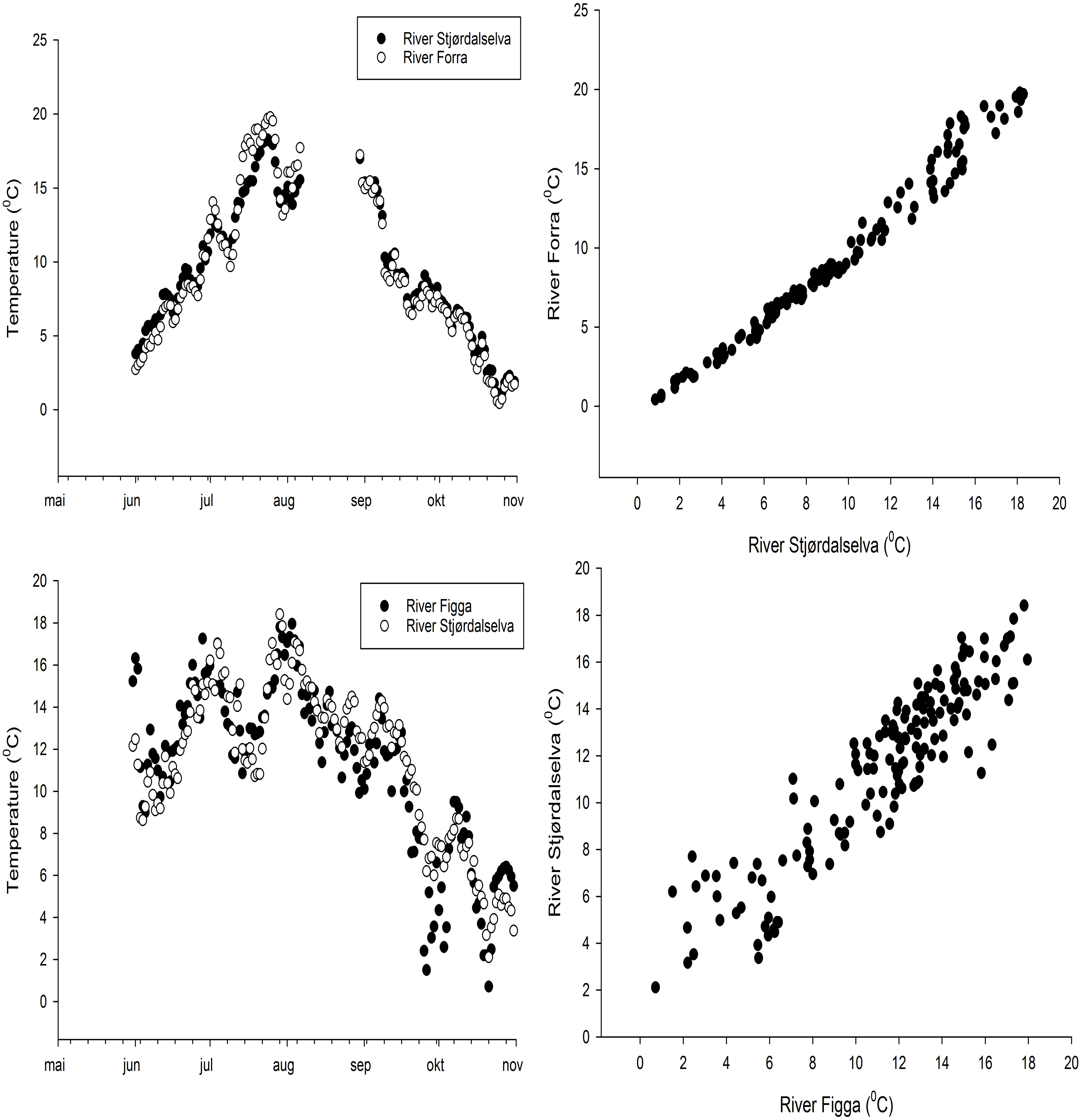

Figure 2: Temperatures and temperature-correlations. Upper-left corner: Temperature of river Stjørdalselva and river Forra from estimated swim-up until sampling-date. Upper-right: Correlation in temperature between river Forra and river Stjørdalselva. Lower-left corner: Temperature of river Stjørdalselva and river Figga from swim-up until sampling date. Lower-right corner: Correlation in temperature between river Figga and river Stjørdalselva.

Swim up

Most of the rivers lacked information regarding the YOY´s emergence from the gravel and initiated external feeding (hereafter swim-up). Only river Røssåga contained information on the date of swim-up. It was estimated, based on Crisp (1988), to occur (D.M.Y) 07.07.2009 (Norwegian Veterinary Institute reports). From fertilization to hatching, the development time is mainly dependent on water-temperature and river flow. According to Jensen *et al.* (1989), the development time decreases with increasing water-temperature, and there are two different strategies for swim-up; (1) before spring-flow and (2) after spring-flow. An estimation of swim-up for Atlantic salmon in 10 Norwegian rivers done by Jensen *et al.* (1991), shows that swim up don't occur until water-temperature reaches approximately 8^0C. Thus, due to a lack in information about hatching time, swim-up date was set to be the date when mean daily water-temperature reached 8^0C in the rivers (Table 3).

Growth model

Growth predictions of YOY Atlantic salmon was done with the modified Ratkowsky model by Forseth *et al.* (2001) (Equation 2). The modified Ratkowsky model describes fish growth as a function of water-temperature when nutrient availability is unlimited and assumes that the fish consume at a maximum rate. M_0 represents the initial body-mass while M_t represents the body-mass of the fish after t-days. The initial body mass, body mass of YOY right after swim-up, does not vary much between rivers, hence it was set to be 0.15 g (Einum, 2003). The estimated parameter-values used, T_L, T_U, d, b and g, originate from Jonsson *et al.* (2001) study from five Norwegian rivers (Table 4). The coefficient b is the exponent that leads to linear growth with time. Due to small size differences in Juvenile Atlantic salmons, it is difficult to estimate b (Forseth *et al.*, 2001). Hence b is fixed and set to be 0.31 according to Elliott *et al.* (1997).

$$M_t = (M_0^b + (b(td(T - T_L)(1 - e^{g(T-T_U)}))/100))^{\frac{1}{b}} \qquad (2)$$

For computation, two conditions were set based on the lower and upper temperature limit for growth rate: If $T_n < T_L$, then $M_n = M_{n-1}$ and if $T_n > T_U$, then $M_n = M_{n-1}$. In that way the model accounts for the days were temperatures was too low or too high for the fish to perform any growth.

Analysis

To illustrate potential differences in growth rate between YOY living in rivers with normal-density populations and rivers with low-density populations, an index value for growth was made (hereafter GI, growth index). The GI was based on the relationship between observations of mean body mass and predicted (temperature adjusted) body mass. For each river (*j*), the mean observed body mass (i) were divided by the mean of its respective prediction from the modified Ratkowsky model (Equation 3). In that way comparison of growth performance of YOY relative to its respective prediction, in each river, were enabled. A GI equal to 1 means that the predicted body mass is the same as the observed body mass at sampling date. A GI bigger than 1 means that the observed body mass is higher than the predicted body mass. When GI is less than 1 predicted body mass is greater than observed body mass.

$$GI_{i,j} = \frac{obs_i}{pred_j} \qquad (3)$$

Statistics

All statistical analysis was conducted from the statistical software R, v. 3.1.1. (R Development Core Team 2009). GI was modeled as a function of treatment. Treatment 1 represented low-density populations, and treatment 2 normal-density populations. To test for river-effects, two models with and without river-effect as random factors were compared. In order to do so the models had to be implemented using the mixed effect models *lme* and general linear least squares function *gls* in the linear and nonlinear mixed effect models package *nlme* (Pinheiro *et al.*, 2007). In these models a likelihood ratio test is used which is calculated based on REML. To compare the two different models, an ANOVA comparison was performed. The contrast showed a significant river-effect (Log likelihood contrast, P=0.016). Thus, to isolate the effect of treatment from river-effect on growth, further analyses were done using the *lme* model. Residuals were normally distributed, but the variance differed between the rivers. Hence the varIdent-function had to be implemented. This function allows for differences in variance and explicitly models different variance in each river (Pinheiro *et al.*, 2007). According to the ANOVA comparison, this was a significant improvement of the *lme* model (log likelihood contrast, $P < 0.0001$). Effects of treatment on GI were then tested. This was done by comparing two models, one model with treatment as a predictor variable and one without. The ANOVA-comparison showed that the *lme* model containing treatment as a predictor was the best (log likelihood contrast, $P = 0.001$). The *lme* model was then fitted with ML in order to compare the effect-size on growth between the two treatments.

Results

River Figga and river Røssåga showed the lowest mean water-temperatures with 11.6^{0}C and 11.8^{0}C. River Fusta and river Vefsna showed the highest mean water-temperatures with respectively 14.98^{0}C and 14.11^{0}C (Table 3). Most of the YOY was sampled in October. According to the prediction regarding date of swim-up, YOY in river Vefsna had the shortest period of growth with less than three months. YOY in river Figga had the longest predicted growth period of approximately 5 months.

Table 3: Density level, swim-up date, sample date, growth period, mean temperature and mean percentage-growth (%ΔBM/day) relative to YOY body mass in each river of the study.

River	Density	”Swim-up” date	Sample date	Growth-period (days)	Mean Temperature (^{0}C)	%ΔBM/day
Vefsna	Low	23.06.2014	12.09.2014	81	14.1	1.16
Fusta	Low	03.06.2014	13.09.2014	110	14.9	1.11
Figga	Low	01.06.2011	28.10.2011	150	11.6	0.53
Røssåga	Low	08.06.2009	03.10.2009	119	11.8	0.87
Gaula	High	08.06.2006	10.10.2006	124	13.9	0.61
Humla	High	07.05.2006	29.09.2006	145	13.6	0.39
Surna	High	26.05.2006	13.10.2006	141	14.0	0.78
Stjørdalselva	High	19.06.1997	07.10.1997	111	12.7	0.47

Mean observed body mass ± SD of YOY in rivers with assumed low population-density were found to be 1.18 ± 0.38g. In rivers with normal population density mean observed body mass was 0.89 ± 0.32g, (Figure 3). This constitutes to a difference in 25% in mean body mass between treatments. The exceptions of this observed pattern were the rivers Røssåga and Surna. River Røssåga contains YOY with body mass less than both river

Gaula and river Surna. It also shows the lowest variation in body mass. River Surna on the other hand, which is a river with normal population density, contain YOY with mean body mass heavier than both river Røssåga and river Vefsna (Figure 3), indicating good growth conditions. Same pattern were found for the SD between treatments. However, the latter finding was not significant (P=0.48).

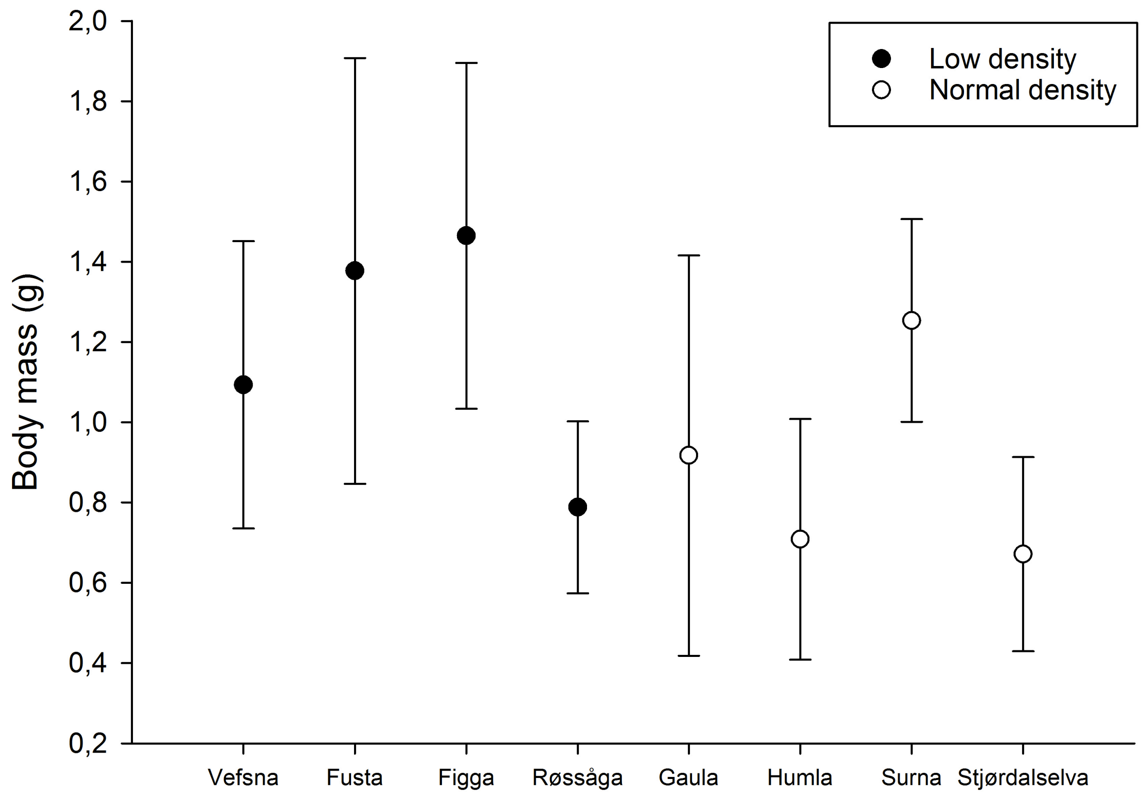

Figure 3: Mean observed body mass (*g*) ± Standard deviation (SD) in the low-density rivers: Vefsna, Fusta, Figga, Røssåga and normal-density rivers: Gaula, Humla, Surna and Stjørdalselva.

As mentioned in the introduction, bioenergetics models assumes maximum food intake. This is not very likely. For the modified Ratkowsky model, Jonsson *et al.* (2001) parameterized three stages of growth with respect to the fish's food intake (Table 4). The fast growing fish is feeding at maximum rate, the moderate fast growing fish is feeding at 80% of maximum while the slow growing fish is feeding at 60% of maximum. YOY in the rivers of this study were found to feed at 80% of its maximum. Hence parameters for the moderate fast growing fish were used in the modified Ratkowsky model to predict growth.

Mean GI ± SD of YOY living in rivers with assumed low-density populations was generally higher, 1.10 ± 0.36, than YOY living in rivers with normal population density, 0.60 ± 0.22, (Figure 4). This constitutes to a difference of 46% in growth between the two treatments. According to the *lme* model, this difference was highly significant (P=0.03). GI of YOY in rivers with assumed low-density populations was found to be bigger than 1 while for rivers with YOY living in normal-density populations GI was less than 1. This means that growth of YOY in the two treatments deviates in opposite directions from the modified Ratkowsky model. Mean percentage daily growth relative to total mean body mass when captured was for YOY in rivers with assumed low-density populations found to be 0.92% while for YOY in normal-density populations 0.56% (Table 3). Thus, mean gain in body mass per day for YOY in low-density populations was 0.011g, while for YOY in normal-density populations it were 0.005g. In addition, SD was bigger in normal density rivers compared to low-density rivers. This indicates bigger variance in growth in rivers with assumed low-density populations (P=1.264e-05). This is also according to the likelihood ratio test. The *lme* model that explicitly modeled different variance in the different rivers was the best fit of our data (log likelihood contrast, P<0.001). Only river Gaula of the normal density rivers displayed similar variation in growth.

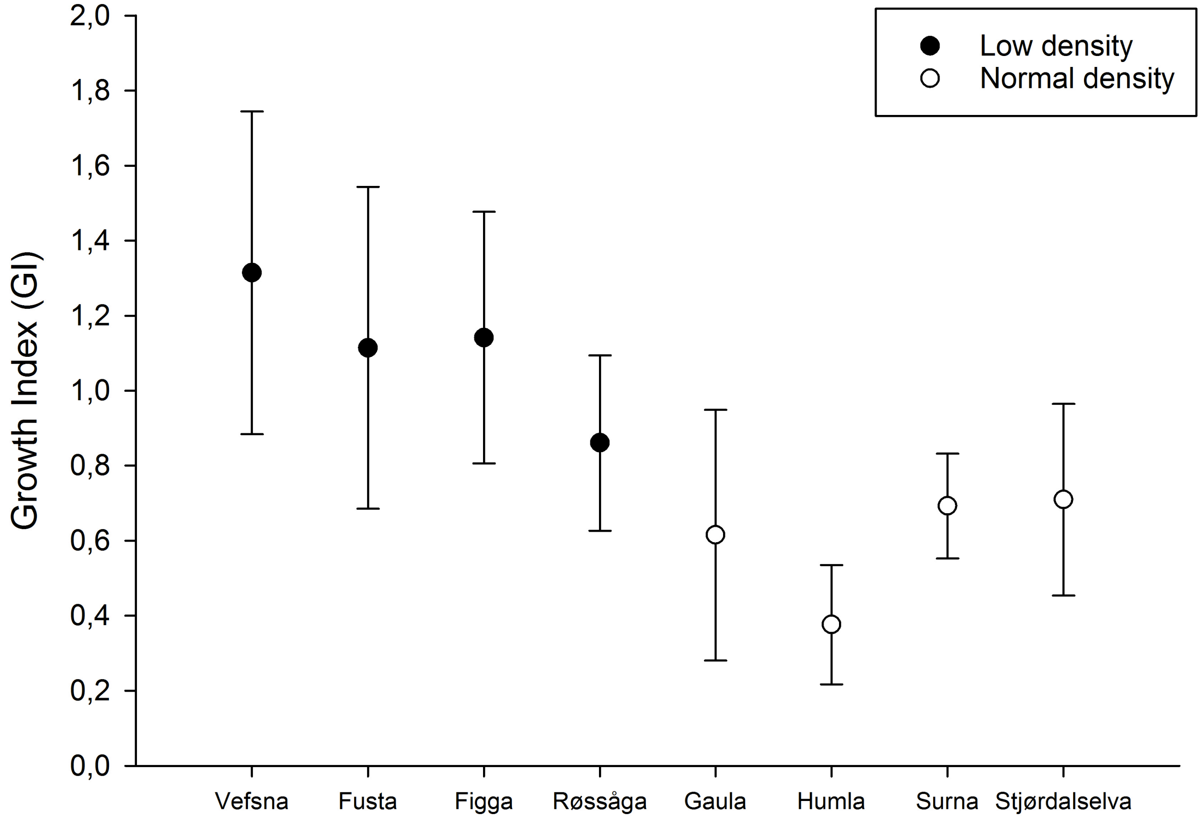

Figure 4: Mean GI (growth index) ± SD in the low-density rivers Vefsna, Fusta, Figga and Røsskåga and the normal-density rivers, Gaula, Humla, Surna and Stjørdalselva

Table 4: Estimated values of the model-parameters (±SE) for thermal relationships in growth of Atlantic salmon for three groups of fish (Fast, mod and slow-growing) from five different Norwegian populations. T_L and T_U represent the critical temperature limits for growth, while d and g are constants that determine the optimal temperature for growth T_M. The coefficient b represents the allometric relationship between growth-rate and fish mass (Jonsson *et al.*, 2001).

Population	Group	d	g	b	T_L	T_M	T_U	R^2
Alta	Fast	0.371 (0.029)	0.248 (0.164)	0.310	6.0 (0.3)	20.0 (0.5)	26*	0.74
	Mod.fast	0.256 (0.075)	0.260 (0.658)	0.310	8.0 (0.2)	19.6 (0.5)	25.0 (0.5)	0.82
	Slow	0.152 (0.490)	0.400 (0.227)	0.310	10.7 (0.6)	20.0 (0.5)	23.9 (0.9)	0.69
Stryn	Fast	0.530 (0.043)	0.208 (0.032)	0.310	6.0 (0.3)	18.4 (0.2)	24.5 (0.2)	0.82
	Mod.fast	0.374 (0.047)	0.201 (0.044)	0.310	6.9 (0.3)	18.4 (0.3)	24.3 (0.2)	0.84
	Slow	0.259 (0.040)	0.232 (0.079)	0.310	7.7 (0.4)	18.7 (0.5)	24.2 (0.3)	0.82
Suldal	Fast	0.973 (15.3)	0.030 (0.274)	0.310	4.9 (0.2)	16.3 (0.6)	26.1 (2.4)	0.72
	Mod.fast	0.260 (3.31)	0.092 (0.054)	0.310	6.4 (0.2)	16.3 (0.7)	23.3 (0.8)	0.67
	Slow	-	-	-	-	-	-	
Lone	Fast	0.476 (0.21)	0.132 (0.079)	0.310	6.0 (0.3)	17.9 (0.6)	25.1 (0.7)	0.56
	Mod.fast	0.260 (1.750)	0.120 (0.147)	0.310	7.9 (0.7)	17.9 (0.9)	24.5 (0.7)	0.51
	Slow	-	-	-	-	-	-	
Imsa	Fast	0.390 (0.168)	0.134 (0.056)	0.310	4.9 (0.4)	18.1 (0.5)	26.7 (0.5)	0.74
	Mod.fast	0.270 (0.113)	0.200 (0.073)	0.310	6.7 (0.4)	19.1 (0.3)	25.4 (0.4)	0.87
	Slow	0.190 (0.055)	0.250 (0.888)	0.310	8.6 (0.5)	19.8 (0.7)	25.1 (1.3)	0.79

*Fixed parameter

Discussion

Growth rate of Atlantic salmon YOY, in low-density populations, were substantially better than the growth displayed in the normal-density populations. However, it is important to notice that parts of the material used in this thesis are based on assumptions and estimates. Thus, the reliability of the results has to be discussed.

In river Røssåga and river Figga there was a lack of measurements of body mass for the YOY. Fulton's condition factor, K, was estimated based on YOY sampled by Berg *et al.* (2009). Observed body mass of YOY caught in river Vefsna and river Fusta were used to verify the estimated K-factor. Food ration affects the K-factor of a fish (Imholt *et al.*, 2011). River Vefsna and river Fusta were both treated with rotenone and assumed to be low-density rivers. Thus, rotenone treated rivers were expected to display better rations of food per individual and contain YOY with a K-factor equal to or bigger than normal-density rivers. Observed body mass of YOY in river Fusta was just below the estimated body mass based on K=0.908. In river Vefsna the observed body-mass of YOY was higher than the estimated body mass (Figure 5 in appendix). Normally, growth tends to decline with a latitudinal gradient due to shorter growth season. River Vefsna and river Fusta both lie in northern Norway. Thus, a K-factor established based on YOY mostly originating from rivers in the middle and south of Norway, was expected to overestimate the body mass of YOY in river Vefsna and river Fusta. However, this was not the case. Probably, due to less dense populations in river Vefsna and river Fusta, estimated body mass of YOY were well represented based on K=0.908 (Figure 5 in appendix). Since river Røssåga is located just north to river Vefsna and river Fusta, estimated body mass based on K=0.908 are not likely to lead to overestimation of body mass of YOY in river Røssåga and river Figga.

Temperatures predicted in river Figga (2011) and river Stjørdalselva (1997), were based on the correlation study described in the method section. In river Stjørdalselva, where only two weeks of water-temperatures were missing, river Forra was used as correlation-river. River Forra is drained into river Stjørdalselva. Therefore water-temperatures between these rivers should not deviate too much. Mean water-temperature, over a period where temperature loggers in both rivers still were active, showed a difference in just 0.1 ^{0}C (Figure 2). With R^2 found to be 0.96, the regressed model explained 96% of the variation between the observed water-temperatures. It is therefore reasonable to assume that the predicted water-temperatures give a good representation of the water-temperatures in river Stjørdalselva. In river Figga, river Stjørdalselva was used as a correlation-river. The observed correlation pattern between these two rivers was not that similar compared to river Stjørdalselva and river Forra (Figure 2). Still R^2 were found to be 0.88, meaning that 88% of the variation between the two rivers were explained. The average temperature between (D.M.Y) 31.05.2013 and 31.10.2013 were 11.45^{0}C in river Stjørdalselva and 11.22^{0}C in river Figga. Predicted body mass of YOY based on these water-temperatures between 31.05.2013 and 31.10.2013 gave a difference in 0.06g. Thus estimated body mass of YOY in river Figga based on water-temperatures from river Stjørdalselva gave a relatively good accuracy.

The last assumption made in this study was the date of swim-up. Only river Røssåga contained information on swim-up. It was estimated to occur at 07.07.2009 (Norwegian veterinary institute report). All other rivers lacked this kind of information. Therefore predicted dates on swim-up were based on Jensen *et al.* (1991) findings and suggested to occur when mean daily water-temperature was 8^{0}C. River Røssåga reached 8^{0}C 08.06.2009. The difference in time between estimated and predicted date of swim-up was 1-month. It made a substantial impact on the estimates of body mass of YOY. Estimated mean body mass of YOY with swim-up at 08.06.2009 were 0.6g while for YOY with swim-up 07.07.2009 mean body mass were estimated to be 0.9g. Obviously such a difference will affect the accuracy and credibility of our study. However, by assuming swim-up to happen when temperature reaches 8^{0}C, it is not likely that it happens before (Jensen *et al.*, 1991). Thus, overestimations of growth indices are avoided. In addition same assumptions were done for all the rivers. Therefore the errors are probably more or less the same in each river.

When looking at the mean body mass of the YOY in each river, together with its predicted growth period, it is clear that the rivers with assumed low-density populations differ from the rivers with assumed normal-density populations (Figure 3 and Table 3). For river Vefsna, only river Surna of the normal-density-rivers displayed heavier YOY. This is not surprising considering that YOY in river Surna lived 60 days longer than in river Vefsna. However, by looking at the heaviest YOY individuals in these two rivers, the biggest YOY in river Vefsna has approximately the same body mass as the biggest YOY in river Surna (upper limit SD, Figure 3). Hence, growth rate of YOY in river Vefsna should bee higher than in river Surna. Water-temperature is the only factor affecting growth in the modified Ratkowsky model, and nutrient availability is assumed to be unlimited (Forseth *et al.*, 2001). Mean water-temperature during the growth period in river Vefsna was 14.11 ^{0}C while in river Surna it was 14.05^{0}C. Therefore, according to the modified Ratkowsky model, growth conditions should be similar, and YOY should display similar growth. However, this was not the case. Mean GI of YOY in river Vefsna was 1.3 while the corresponding value in river Surna was 0.7 (Figure 4). This means that GI for YOY in river Vefsna was 47% higher than in river Surna. According to the daily percentage growth of YOY relative to total mean body mass in each river, YOY in river Vefsna grew substantial better compared to YOY in river Surna (Table 3). Thus, growth of YOY in river Vefsna, which is a low-density river, was demonstrated to be substantial better compared to river Surna.

In river Røssåga the observed mean body mass of YOY were almost as low as the YOY living in river Humla and river Stjørdalselva. Both rivers, Gaula and Surna contained heavier YOY than river Røssåga (Figure 3). Mean water-temperature was clearly lower in river Røssåga compared to the rivers Gaula, Stjørdalselva and Surna (Table 3). Thus, growth conditions, based on water-temperatures, should be poorer in river Røssåga. However, our results suggest the opposite. Mean GI of YOY in river Røssåga was estimated to be 0.86. In the rivers Gaula, Stjørdalselva and Surna mean GI was respectively estimated to be 0.61, 0.71 and 0.69. This means that the GI of YOY in river

Røssåga was 29% higher than in river Gaula, 17% higher than in river Stjørdalselva and 20 % higher than in river Surna. Mean percentage-daily-growth in all of these rivers (Table 3) supports the statement drawn based on the GI.

Variation in GI between treatments was also found to be different. Rivers with low-density populations seemed to contain YOY with bigger variance in GI relative to rivers with normal density populations (Figure 4). This was also observed for the body mass, although not that convenient (Figure 3). However, a substantial difference in sample-size between the two treatments makes this a less trustable observation. In river Vefsna 54 YOY was sampled. In river Humla, only 9 YOY was sampled. Thus, chances are that with a greater amount of samples, the SD increases.

A plausible explanation to the observed differences in growth could be differences in competition-level due to different densities of interspecies and coexisting cohorts in low-density rivers compared to normal density rivers. Growth is reported to be density dependent for juvenile Atlantic salmon (Grant and Imre, 2005; Ward *et al.*, 2007; Imre *et al.*, 2010). Both rivers, Vefsna and Røssåga, as discussed above, along with river Fusta and river Figga are rivers expected to contain low densities of fish due to rotenone treatment. River Gaula, river Humla, river Surna and river Stjørdalselva have never been treated with rotenone. Therefore, these rivers are expected to contain higher densities of fish. When population-density increases, niches are more likely to overlap. Thus inter and intra cohort competition is likely to occur. Size is often related to competitive ability. Hence the density of older or larger individuals within or between cohorts affects the growth of newly emerged YOY in a negative way (Nordwall *et al.*, 2001; Einum and Kvingedal, 2011; Kvingedal and Einum, 2011; Kaspersson *et al.*, 2012). In addition, the normal density rivers in this study also contained other species than Atlantic salmon. Thus, the reduced growth observed in the normal density rivers could be due to interspecific competition (Harwood *et al.*, 2001).

Nutrient availability is also reported to affect the growth in salmonieds (Rosenfeld *et al.*, 2005; Martinussen *et al.*, 2011). Parameters from the moderate fast growing fish gave the most accurate estimates when predicting body mass in YOY. Thus, for further estimations of body mass, fish were assumed to be feeding at 80% of its maximum consumption rate. A GI equal to 1 would then mean that the YOY consumed according to the assumption. Bacon *et al.* (2005) found that nutrient abundance varies within a season. Thus, feeding at a constant rate through the growth season is not very likely. Weber *et al.* (2014) support this statement and conclude that temperature-driven growth models are unrealistic because they ignore components such as food availability. However, same assumption regarding consumption rate was made for all rivers. Mean GI in the low-density rivers was found to be 1.109, while mean GI in high-density rivers was 0.598 (Figure 4). Even though the modified Ratkowsky model does not account for differences in food availability, the GI illustrates a substantial difference (46%) in growth between treatments. Therefore, an additional explanation to the difference in growth between normal density rivers and low-density rivers could be different availabilities of nutrients. YOY living in low-density rivers seems to consume food at a higher rate than YOY living in low-density rivers.

In conclusion, growth of YOY in assumed low-density rivers is observed to be substantial better compared to high-density rivers. Thus, the assumption regarding different densities of fish between rotenone treated rivers relative to regular rivers seems to be correct. Density affects both competition level and nutrient availability and based on our results it can be difficult to separate the effect of them. Therefore, the reason for the observed difference in growth can be a combination of less competition and better food availability per capita in low-density rivers relative to normal density rivers.

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References

Amin, M. N., Barnes, R. K. & Adams, L. R. (2014). Effect of temperature and varying level of carbohydrate and lipid on growth, feed efficiency and nutrient digestibility of brook trout, Salvelinus fontinalis (Mitchill, 1814). *Animal Feed Science and Technology* **193**, 111-123.

Bacon, P. J., Gurney, W. S. C., Jones, W., Mclaren, I. S. & Youngson, A. F. (2005). Seasonal growth patterns of wild juvenile fish: partitioning variation among explanatory variables, based on individual growth trajectories of Atlantic salmon (Salmo salar) parr. *Journal of Animal Ecology* **74**, 1-11.

Berg, O. K., Finstad, A. G., Solem, O., Ugedal, O., Forseth, T., Niemela, E., Arnekleiv, J. V., Lohrmann, A. & Naesje, T. F. (2009). Pre-winter lipid stores in young-of-year Atlantic salmon along a north-south gradient. *Journal of Fish Biology* **74**, 1383-1393.

Bohlin, T., Hamrin, S., Heggberget, T. G., Rasmussen, G. & Saltveit, S. J. (1989). Electrofishing—theory and practice with special emphasis on salmonids. *Hydrobiologia* **173**, 9-43.

Bohlin, T., Sundstrom, L. F., Johnsson, J. I., Hojesjo, J. & Pettersson, J. (2002). Density-dependent growth in brown trout: effects of introducing wild and hatchery fish. *Journal of Animal Ecology* **71**, 683-692.

Crisp, D. T. (1988). Prediction, from Temperature, of Eyeing, Hatching and Swim-up Times for Salmonid Embryos. *Freshwater biology* **19**, 41-48.

Deverill, J. I., Adams, C. E. & Bean, C. W. (1999). Prior residence, aggression and territory acquisition in hatchery-reared and wild brown trout. *Journal of Fish Biology* **55**, 868-875.

Einum, S. (2003). Atlantic salmon growth in strongly food-limited environments: Effects of egg size and paternal phenotype? *Environmental Biology of Fishes* **67**, 263-268.

Einum, S., Finstad, A. G., Robertsen, G., Nislow, K. H., McKelvey, S. & Armstrong, J. D. (2012). Natal movement in juvenile Atlantic salmon: a body size-dependent strategy? *Population Ecology* **54**, 285-294.

Einum, S. & Kvingedal, E. (2011). Relative importance of size-based competitive ability and degree of niche overlap in inter-cohort competition of Atlantic salmon (*Salmo salar*) juveniles. *Canadian Journal of Fisheries and Aquatic Sciences* **68**, 969-976.

Elliott, J. M. (1976). The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta L.*) in relation to body weight, water temperature and ration size. *Journal of Animal Ecology* **45**, 923-948.

Elliott, J. M. & Hurley, M. A. (1997). A functional model for maximum growth of Atlantic Salmon parr, *Salmo salar*, from two populations in northwest England. *Functional Ecology* **11**, 592-603.

Elliott, J. M., Hurley, M. A. & Elliott, J. A. (1997). Variable effects of droughts on the density of a sea-trout (*Salmo trutta*) population over 30 years. *Journal of Applied Ecology*, 1229-1238.

Elliott, J. M., Hurley, M. A. & Fryer, R. J. (1995). A new, improved growth model for brown trout, *Salmo trutta*. *Functional Ecology*, 290-298.

Forseth, T., Hurley, M. A., Jensen, A. J. & Elliott, J. M. (2001). Functional models for growth and food consumption of Atlantic salmon parr, *Salmo salar*, from a Norwegian river. *Freshwater biology* **46**, 173-186.

Froese, R. (2006). Cube law, condition factor and weight–length relationships: history, meta‐analysis and recommendations. *Journal of Applied Ichthyology* **22**, 241-253.

Grant, J. W. A. & Imre, I. (2005). Patterns of density-dependent growth in juvenile stream-dwelling salmonids. *Journal of Fish Biology* **67**, 100-110.

Harwood, A. J., Metcalfe, N. B., Armstrong, J. D. & Griffiths, S. W. (2001). Spatial and temporal effects of interspecific competition between Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in winter. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 1133-1140.

Hayes, J. W., Stark, J. D. & Shearer, K. A. (2000). Development and test of a whole-lifetime foraging and bioenergetics growth model for drift-feeding brown trout. *Transactions of the American Fisheries Society* **129**, 315-332.

Imholt, C., Malcolm, I. A., Bacon, P. J., Gibbins, C. N., Soulsby, C., Miles, M. & Fryer, R. J. (2011). Does diurnal temperature variability affect growth in juvenile Atlantic salmon (*Salmo salar*)? *Journal of Fish Biology* **78**, 436-448.

Imre, I., Grant, J. W. A. & Cunjak, R. A. (2005). Density-dependent growth of young-of-the-year atlantic salmon (*Salmo salar*) in Catamaran Brook, New Brunswick. *Journal of Animal Ecology* **74**, 508-516.

Imre, I., Grant, J. W. A. & Cunjak, R. A. (2010). Density-dependent growth of young-of-the-year Atlantic salmon (*Salmo salar)* revisited. *Ecology of Freshwater Fish* **19**, 1-6.

Jenkins, T. M., Diehl, S., Kratz, K. W. & Cooper, S. D. (1999). Effects of population density on individual growth of brown trout in streams. *Ecology* **80**, 941-956.

Jensen, A. J., Johnsen, B. O. & Heggberget, T. G. (1991). Initial feeding time of Atlantic salmon, *Salmo-Salar*, alevins compared to river flow and water temperature in Norwegian streams. *Environmental Biology of Fishes* **30**, 379-385.

Jensen, A. J., Johnsen, B. O. & Saksgard, L. (1989). Temperature requirements in Atlantic salmon (*Salmo-salar*), brown trout (*Salmo-trutta*), and Arctic char (*Salvelinus-alpinus*) from hatching to initial feeding compared with geographic-distribution. *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 786-789.

Jobling, M. (1997). Temperature and growth: modulation of growth rate via temperature change. In *Seminar series-society for experimental biology*, pp. 225-254: Cambridge University Press.

Jonsson, B., Forseth, T., Jensen, A. J. & Naesje, T. F. (2001). Thermal performance of juvenile Atlantic Salmon, *Salmo salar L*. *Functional Ecology* **15**, 701-711.

Kaspersson, R. & Hojesjo, J. (2009). Density-dependent growth rate in an age-structured population: a field study on stream-dwelling brown trout (*Salmo trutta*). *Journal of Fish Biology* **74**, 2196-2215.

Kaspersson, R., Hojesjo, J. & Bohlin, T. (2012). Habitat exclusion and reduced growth: a field experiment on the effects of inter-cohort competition in young-of-the-year brown trout. *Oecologia* **169**, 733-742.

Kaushik, S. J. & Medale, F. (1994). Energy-Requirements, Utilization and Dietary Supply to Salmonids. *Aquaculture* **124**, 81-97.

Kvingedal, E. & Einum, S. (2011). Intracohort and intercohort spatial density dependence in juvenile brown trout (*Salmo trutta)*. *Canadian Journal of Fisheries and Aquatic Sciences* **68**, 115-121.

Martinussen, P. A., Robertsen, G. & Einum, S. (2011). Density-dependent diet composition of juvenile Atlantic salmon (*Salmo salar*). *Ecology of Freshwater Fish* **20**, 384-392.

Molles, M. C. & Tibbets, T. (1999). *Ecology: concepts and applications*: WCB/McGraw-Hill Dubuque, IA.

Nordwall, F., Naslund, I. & Degerman, E. (2001). Intercohort competition effects on survival, movement, and growth of brown trout (*Salmo trutta*) in Swedish streams. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 2298-2308.

Ohlberger, J., Otero, J., Edeline, E., Winfield, I. J., Stenseth, N. C. & Vollestad, L. A. (2013). Biotic and abiotic effects on cohort size distributions in fish. *Oikos* **122**, 835-844.

Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. (2007). Linear and nonlinear mixed effects models. *R package version* **3**, 57.

Ratkowsky, D. A. (1983). *Nonlinear regression modeling: a unified practical approach*. New York: Dekker.

R Development Core Team (2009) R: A Language and Environment for Statisti- cal Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org [Accessed 01 Dec 2011]

Rosenfeld, J. S., Leiter, T., Lindner, G. & Rothman, L. (2005). Food abundance and fish density alters habitat selection, growth, and habitat suitability curves for juvenile coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 1691-1701.

Sogard, S. M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: A review. *Bulletin of Marine Science* **60**, 1129-1157.

Sundstrom, L. F., Bohlin, T. & Johnsson, J. I. (2004). Density-dependent growth in hatchery-reared brown trout released into a natural stream. *Journal of Fish Biology* **65**, 1385-1391.

Thorstad, E. B., Whoriskey, F., Rikardsen, A. H. & Aarestrup, K. (2011). Aquatic nomads: the life and migrations of the Atlantic salmon. *Atlantic salmon ecology*, 1-32.

Wankowski, J. W. J. & Thorpe, J. E. (1979). Role of food particle-size in the growth of juvenile Atlantic Salmon (*Salmo-Salar L*). *Journal of Fish Biology* **14**, 351-370.

Ward, D. M., Nislow, K. H., Armstrong, J. D., Einum, S. & Folt, C. L. (2007). Is the shape of the density-growth relationship for stream salmonids evidence for exploitative rather than interference competition? *Journal of Animal Ecology* **76**, 135-138.

Weber, N., Bouwes, N. & Jordan, C. E. (2014). Estimation of salmonid habitat growth potential through measurements of invertebrate food abundance and temperature. *Canadian Journal of Fisheries and Aquatic Sciences* **71**, 1158-1170.

Wootton, R. J. (1990). *Ecology of teleost fishes*: Chapman and Hall.

Appendix

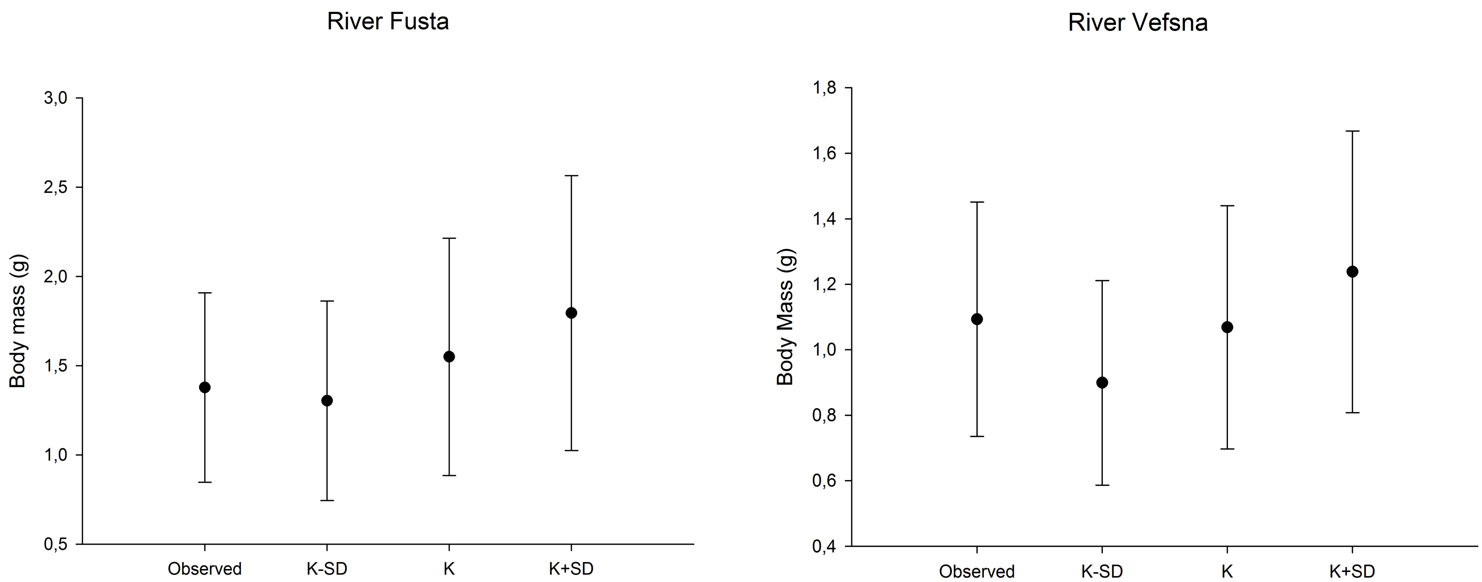

Figure 5: Comparison of mean observed body mass ± standard deviation with mean estimated body mass ± Standard deviation based on; mean condition factor – Standard deviation (K-SD), mean condition factor (K) and mean condition factor + Standard deviation (K+SD). The left figure represents YOY in river Fusta while the figure to the right represents YOY in river Vefsna.