The Importance of Temperature in Farmed Salmon Growth: Regional Growth Functions for Norwegian Farmed Salmon

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by

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Abstract

A reliable growth function is a vital part of deriving the optimal harvesting strategy and production plan for any aquaculture operation. The range of environmental and biological conditions along the Norwegian coast suggests that the growth of farmed salmon will differ from one region to another. We estimate an aggregated regional growth function for three different regions in Norway using monthly data from 2005 to 2011. There is currently some variation for the grow-out period, and Atlantic salmon is raised between 16 – 24 months to reach weights of 2 – 8 kg. These results indicate that an increase in sea temperature positively affects the growth in the regions of Northern and Central Norway, while an increase in sea temperatures negatively affect the growth in the Southern region.

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Introduction

Since the introduction of salmon aquaculture in the early 1980s, the global supply of farmed salmon, including Atlantic salmon, coho and salmon trout, has increased from a few thousand tons in 1980 to over 2.4 million tons in 2011 (Asche et al., 2013). Atlantic salmon is the dominant specie, accounting for almost 77 percent of the worldwide output in 2006, and Norway is the world's leading producer of farmed salmon, accounting for 51 percent of global production in 2009 (Larsen & Asche, 2011). The main reasons for this tremendous growth in salmon production are dramatic increases in both productivity and demand (Asche, 2008).

However, as in most food producing industries, the grow-out phase is affected by external factors over which the producers have little control. The variations in biophysical conditions along the Norwegian coast as well as the variation in biophysical conditions over the years affect the production of Norwegian farmed salmon, which can affect prices and the profitability for the industry. For a salmon farmer, the production process begins when juvenile salmon weighing less than 250 g are released into the sea pens and grown until reaching marketable size. The grow-out period can vary, and Atlantic salmon can be raised between 16 – 24 months to reach a marketable size. Today, 80 percent of slaughtered Norwegian salmon weigh between 3 – 6 kg. Lorentzen (2008) shows that the grow-out period differs between northern and southern part of Norway, using experimental data from two different fish plants. He finds that the optimal rotation period for base projections are 17 months in the south and 19 months in the north. Hermansen and Heen (2012) show in a scenario of a linear temperature increase of 1° Celsius from 2008 to 2030, ignoring the effect of technology, would the productivity increase in the north and decrease in the south, while there will be more or less status quo in the central region of Norway.

To analyze the production of farmed salmon, a reliable salmon growth function must be obtained. Existing studies on salmon growth mainly rely on experimental data or data from only a single or several fish farms (e.g., Bjørndal, 1988; Forsberg, 1999; Halachmi et al.,2005; Lorentzen, 2008). This study models salmon growth with a logistic function using aggregated data from three different regions of Norway estimated for five different generations, or year classes, of farmed salmon. The purpose of this study is to determine how the varying biophysical conditions along the Norwegian coast affect the production of farmed salmon. Using aggregated regional production data from three different Norwegian regions with three different temperature regimes, we are able to determine how the variation in biophysical conditions affects the growth from year to year as well as from region to region.

As the production of farmed salmon takes a significant period of time, changes in biophysical conditions have a large influence of production of salmon since there is a close relationship between productivity and sea temperature (Hermansen & Heen, 2012). The industry has experienced a productivity growth for several decades which have lowered the production costs and the cost reductions are mainly due to technological progress which in turn have increased the control over the production process (Roll, 2012). This has further led to an improvement of the technical efficiency for salmon farmers over time and the inefficiency that is still present is mainly due to temporary shocks (Asche & Roll, 2013). Still, since 2005 productivity have slowed down and it seems that demand is now outpacing productivity (Asche et al., 2013; Vassdal & Sørensen Holst, 2011). Shocks in biophysical conditions also increase the production risk and lead to considerable variations in industry profit levels (Tveterås, 1999). Further, price volatility in the salmon market have been increasing and salmon prices are considered to be highly volatile (Oglend & Sikveland, 2008; Oglend, 2013; Solibakke, 2012), short-run supply of farmed salmon is considered to be highly inelastic (Aasheim et al., 2011; Andersen et al., 2008), and a contribution to this development is the use of fixed-price contracts (Larsen & Asche, 2011). These effects can in part be explained by changes in biophysical conditions which may lead to over and under supply of salmon which will cause fluctuating prices and variations in profit levels.

Determining growth on an aggregate level has captured little attention among academics. To my knowledge, only two other studies have examined the development of biomass on an aggregate level. Asheim et al. (2011) study how biomass development affects short run supply using aggregated time series data, while Løland et al. (2011) have established a model to predict biomass in Norwegian fish farms using data from individual farmers that they have aggregated to regional data. The latter study computes the number of fish growing into the next weight class (0-1 kg, 1-2 kg, …, 10 kg). None of those studies examined how variations in biophysical factors affect growth from year to year. This situation means that we have limited knowledge of how variations in biophysical conditions affect the production process in the industry as a whole.

This paper begins with a discussion of the various factors that affect the growth of farmed salmon. Then, the growth model is presented, followed by the data set and the specified growth model. After the model is solved, the empirical results are reported and discussed, and the conclusions of this work are summarized.

Production Process

Many factors influence salmon growth. The endogenous factors that are controlled by the manager at the fish plant include the stocking density, the number of juveniles released into the sea pens, the feeding pattern, and the type of feed. However, the variation in the grow-out period mainly results from the effects of exogenous biophysical factors on salmon production such as sea temperature, sea current, waves, disease outbreaks, and daylight hours (Lorentzen, 2008).

Fish are highly reliant on temperature (Boeuf & Le Bail, 1999), and the variation in sea temperature is considered to be the most important biophysical factor that influences salmon growth. Efficient salmon growth was previously believed to be best promoted at water temperatures between 13 – 17 degrees Celsius (Wallace, 1993). However, recent studies show that growth is better achieved at colder temperatures. In controlled experiments in which salmon were fed at temperatures of 13, 15, 17, and 19 degrees Celsius over 45 days, the experiment showed that the most efficient growth was achieved at a water temperature of 13 degrees Celsius (Ernst M Hevrøy et al., 2013). Furthermore, salmon that lived at temperatures of 15 and 17 degrees Celsius grew efficiently in the first two weeks but exhibited reduced feed intake and growth over the remainder of the study period. Additional research is necessary to determine whether the optimal temperature is lower than 13 degrees Celsius. This finding indicates that the best temperature interval, or the comfort zone for the salmon, should be somewhere around or below 13 degrees Celsius. However, when the temperature is below this range, the fish consume less feed because fish appetites depend on sea temperature (Austreng et al. 1987). Interestingly, wild salmon often will not feed at all during the winter months (Asche & Bjørndal, 2011). Sea temperatures above this range lead to more serious problems because high sea temperatures lead to increased densities of algae and parasites in the water as well as a lower level of oxygen, and these factors increase fish mortality. Salmon living at 19 degrees Celsius reduce their feed intake by 50 percent compared to salmon living at 14 degrees Celsius (Hevrøy et al., 2012). Thus, sea temperature above the threshold of 17 degrees Celsius has a significantly negative effect on growth, with growth between 18 and 19 degrees Celsius occurring at the same rate as observed for 3 degrees Celsius, and with a sea temperature above 20 degrees Celsius leading to physiological breakdown (Lorentzen, 2008). This observation implies that sea temperatures above 17 - 18 degrees Celsius will lead to significant decreases in growth.

In contrast to wild salmon, who find their nutrition from the sea, farmed salmon are fed at the fish plant, and feeding obviously enhances growth. However, when the food supply is not limited, the specific growth rate increases with increasing sea temperature, while at any sea temperature, the specific growth rate decreases with increasing body weight (Talbot, 1993). This observation indicates that any feeding regime will increase the feed conversion ratio (i.e., the feed quantity per kilogram of growth) and that little variation will be observed in feeding patterns after controlling for climatic and environmental variables (Asche & Bjørndal, 2011).

The growth of salmon is also affected by the number of daylight hours (Boeuf & Le Bail, 1999). Because of Norway's geographic location and its high latitude, there are large seasonal variations in the number of daylight hours. In the northern part of Norway (above the Arctic Circle), there are 24 hours of daylight (midnight sun) from late May to late July, while the rest of the country experiences approximately 20 hours of daylight. From late November to late January, there are no daylight hours (polar nights) in the northern part of the country, while the daylight hours are very short in the rest of the country. However, the salmon industry uses additional artificial light during the winter and spring to compensate for the lack of natural light, and the use of artificial light in fish pens has reduced the proportion of fish that undergo sexual maturation and enhanced the growth of Atlantic salmon (Oppedal et al. 2001).

Growth Model

The biomass stock of the salmon of a year class at time *t* is dependent on the number of fish and the weight of the individual fish

$$B_t = w_t N_t \qquad (1)$$

where B_t is the biomass stock of the salmon at time *t*, w_t is the average weight of the fish at time *t*, and N_t is the number of fish at time *t*. For an individual farmer with only one release of juvenile salmon and a single harvesting time, the biological process can be described with an adapted Beverton-Holt model for a single year class (Bjørndal, 1988), where:

$$N_0 = R \tag{2}$$

$$\dot{N}_t \equiv \frac{dN}{dt} = -m_t N_t, \qquad 0 \leq t \leq T \tag{3}$$

$$N_t = Re^{-\int_0^t m(u)du} \tag{4}$$

in which *t* represents the time from the release of the fish, $\dot{N}_t$ denotes the rate of change in the number of fish, and *R* is the number of juveniles that are released at the outset, *t* = 0. m_t is the mortality rate, which can vary over time, and the number of fish changes over time due to natural mortality.

If we assume the mortality rate to be constant over time, i.e., $m_t = m$, then equations (3) and (4) can be rewritten as follows:

$$\dot{N}_t \equiv \frac{dN}{dt} = -mN_t, \qquad 0 \leq t \leq T \tag{5}$$

$$N_t = Re^{-m_t} \tag{6}$$

The average weight of the fish at time *t* is represented by w_t. The change in the weight over time, i.e., the growth, will then be $\dot{w}_t \equiv dw/dt$. A general growth function can then be expressed as follows:

$$\dot{w}_t = g\left(X_{i,t}\right) \tag{7}$$

Growth can be expressed as a function of different variables such as time (age), sea temperature, number of fish (density), feed quantity, and daylight hours.

The change in biomass over time can then be given by

$$\dot{B}_t = \dot{w}_t N_t + w_t \dot{N}_t = \left[\frac{\dot{w}_t}{w_t} - m\right] B_t \qquad (8)$$

in which the relative growth rate, $\dot{w}_t/w_t$, is the derivative of the weight function with respect to *t* divided by the weight function itself. As long as the relative growth rate is greater than the mortality rate, $\dot{w}_t/w_t > m$, the biomass increases, and when the relative growth rate equals the mortality rate, $\dot{w}_t/w_t = m$, the biomass reaches its maximum.

This study uses aggregated data, meaning that juveniles for a given year class are released throughout the first year, with harvest occurring at several points in time. Thus, the number of fish in the pens at time *t* can be defined as:

$$N_t = (1 - m_t - s_t + r_t)N_{t-1} \qquad (9)$$

where s_t is the harvest rate at time *t*, r_t is the rate of juveniles released at time *t*, N_{t-1} is the number of fish at time *t-1*, and N_t and m_t are defined as the number of fish at time *t* and the mortality rate at time *t*, respectively. Using the same notation as in equation (3), the change in the number of fish in the pens at time *t* can be defined as:

$$\dot{N}_t \equiv \frac{dN}{dt} = (-m_t - s_t + r_t)N_t \qquad (10)$$

The data used in this paper will be discussed later, but a short overview is presented here. As seen in table 1, the data follow each year class over three years, and the nature of the aggregated data means that *N* changes from one month to another due to harvest, the release of juveniles and the loss of fish (escape and death by other causes than harvest). This pattern means that the number of fish will increase or decrease depending on the life cycle stage of the generation of interest. The number will increase during the first year, year 0, because at that time, the juveniles are released into the pens, and will decrease in years 1 and 2 because of harvest and loss[i].

To simplify, we assume that the mortality rate, the slaughter rate, and the rate of juvenile release are constant over time, i.e., $m_t = m, s_t = s, r_t = r$, enabling equation (9) to be written as follows

$$\dot{N}_t \equiv \frac{dN}{dt} = (-m - s + r)N_t \qquad (11)$$

$$m > 0, s > 0, r > 0$$

Changes in biomass over time can then be given by

$$\dot{B}_t = \dot{w}_t N_t + w_t \dot{N}_t = \left[\frac{\dot{w}_t}{w_t} - m - s + r\right] B_t \qquad (12)$$

And the relative growth rate, f_t, will then be:

$$f_t = \frac{\dot{w}_t}{w_t} \qquad (13)$$

As long as the relative growth rate is greater than the sum of the mortality rate, the slaughter rate, and the rate of juvenile release, $\dot{w}_t / w_t > \sum m + s - r$, the biomass increases, and when the relative growth rate equals the sum of the mortality rate $\dot{w}_t / w_t = \sum m + s - r$, the biomass reaches its maximum.

As shown, the biomass will eventually reach a maximum point where no further growth is possible. Any population of fish has a saturation level, a carrying capacity, which sets bounds on the population's growth potential (Tsoularis & Wallace, 2002). Let us denote B_{MAX} as the finite upper bound to which the population can grow. Then, we can use a simple logistic function to determine the stock growth, so

$$\dot{B} \equiv \frac{dB}{dt} = r\left(1 - \frac{B}{B_{MAX}}\right)B \qquad (14)$$

The individual fish, however, seem to continue growing for as long as they live, although the growth rate decreases with increasing body weight (Talbot, 1993). However, a fish farmer does not normally let fish grow unhindered to large sizes for at least two reasons. First, the sexual maturity of the salmon limits the length of time a farmer can keep a fish in a pen (Asche & Guttormsen, 2002). An Atlantic salmon can become sexually mature several times during its lifetime; a sexually mature fish is visibly identifiable, and its flesh deteriorates. These fish are not appropriate for human consumption, making the value of a sexually mature fish close to zero. Sexual maturity can be controlled to some extent, but most fish become sexually mature when they reach a weight between 5 to 7 kg and the water temperature is relatively high. Second, when the fish grows, the feed conversion ratio will increase, consequently increasing the cost. This phenomenon means that at some point, it will become unprofitable for the fish farmer to continue to grow the fish, with the result that individual fish have a saturation level, an asymptotic maximum weight, which forms a numerical upper bound for the fish.

Several different growth functions for fish exist in the literature; Tian et al. (1993) estimate seven different growth functions to examine what function best describes the development in the weight of farmed shrimp and conclude that the von Bertalanffy and Gompertz functions describe growth best. Lorentzen (2008) tests three different growth functions; von Bertalanffy, one exponential, and one logistic growth function, and finds that a logistic function describes the data best. Bjørndal (1988) uses a polynomial model to describe the growth. In this study, we have found that the logistic growth function best describes the growth. Other functions, such as von Bertalanffy and the Gompertz, are tested and rejected due to unrealistically high asymptotic values or problems with the convergence of the model. Here, we use the Tian et al. (1993) version of a logistic growth function, where

$$w_t = \frac{w_\infty}{\left[1+e^{-k(t-t_i)}\right]} \qquad (15)$$

$$w_\infty > 0$$

in which w_t is the weight at time *t*, w_∞ is the asymptotic maximum weight, *t* is time, t_i is the inflection point, and *k* is a constant. The logistic function is a sigmoid-shaped curve where the fish grows to the limited value w_∞, and the parameter *k* affects the steepness of the curve. Another important characteristic is the shape, with the inflection point t_i the point where the curve changes from concave up to concave down. The logistic model has mostly been used in wild fisheries to explain the growth of non-migratory species at a particular location, which obviously fits well for farmed salmon.

Procedure and Data

The increase in the growth of the fish is mainly determined by feeding intensity and temperature (Aasheim et al., 2011). However, because feeding patterns exhibit little variation, only temperature is used as an explanatory variable in the model. Thus, the specific model that is estimated for each region *i* and cohort *c* at month *t* is:

$$w_{i,c,t} = \frac{\alpha}{\left[1+e^{-\left(\beta T_{i,t}\right)(t-\mu)}\right]} \tag{16}$$

in which $w_{i,c,t}$ is the average weight of the fish in region *i* in cohort *c* at month *t*, and $T_{i,t}$ is temperature in region *i* in month *t*. $\alpha, \beta, and\ \mu$ are parameters to be estimated; α is the asymptotic maximum weight, β is the slope coefficient, and μ is the inflection point.

The relative growth rate for each region *i* and cohort *c* at month *t* is then defined as:

$$f_{i,c,t} \equiv \frac{\dot{w}_{i,c,t}}{w_{i,c,t}} = \frac{\beta T_{i,t}}{1+e^{(\beta T_{i,t})(t-\mu)}} \tag{17}$$

At a constant temperature, the relative growth rate decreases over time. However, the temperature varies seasonally, which means that the relative growth rate will also vary seasonally, although the relative growth rate will decline over time.

As Norway is the only salmon-producing country where data are systematically gathered, practically all studies of farmed salmon have used Norwegian data. For a long time, it was only possible to obtain annual observations of Norwegian salmon farms' production and profitability. However, in 2009, the Norwegian Directorate of Fisheries began to report the "Biomass Statistics of Norwegian Farmed Salmon" with monthly observations dating back to January 2005 from the nine salmon-producing counties in Norway. Here, we have aggregated the three northernmost counties as one region called Northern Norway, the three southernmost counties as Southern Norway and the three in the middle as Central Norway.

The regions contribute approximately equal shares to the total production, with the North and South producing an average of 34 percent each, while Central Norway accounts for 32 percent of the total production over the time span studied here. The data are arranged in generations, with each generation lasting approximately three years, as shown in table 1. The average weight data, $w_{i,c,t}$, are retrieved from the Norwegian Directorate of Fisheries. The temperature data, $T_{i,t}$, are retrieved from the Norwegian Seafood Federation and represent temperature measurements at a depth of 3 meters.

$$w_{i,c,t} = \frac{\sum B_{j,c,t}}{\sum N_{j,c,t}} \tag{18}$$

$$T_{i,t} = \frac{\sum T_{j,t}}{\sum j} \tag{19}$$

Equation (18) and (19) shows how the weight variable and the temperature have been generated. The weight variable in region *i* is generated by the sum of the biomass in counties *j* divided with the sum of number of fish in counties *j*. Temperature in region *i* is the sum of the temperature in counties *j* divided with the sum of counties. Temperature could also be aggregated by using weighted average depended on each county's contribution to the weight variable but, by doing it this way, there is a bigger variation in the temperature variable.

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Table 1 around here

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Note that these data are not error free. The publically available data are aggregated based on monthly reports from each fish farmer in Norway. The data contain two types of errors; i) farmers fail to report data, and ii) farmers report incorrect numbers (measurement error). The first error is impossible to observe in the dataset but is documented by Løland et al. (2011), who have access to the individual farmers' data, while the second error can be observed to some extent. At the beginning and end of the data series for each county when few fish are present in the pens, some strange observations are reported. As few juveniles are released before April in year 0 (see figure 1) and most of the harvest occurs before September in year 2 (see figure 2), the observations prior to April in year 0 and after August in year 2 are deleted from the dataset. Thus, the observations begin in April of year 0 and end in August of year 2, leaving 29 observations for each estimated growth curve. However, the 2006 generation in the South region only include 28 observations due to an outlier in the end of the time frame.

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Figures 1 and 2 around here

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Results

The model was estimated for each region and generation separately on the data from 2005 to 2011. As shown in table 2, all models achieved very good fits, with R-squared values above 0.95, and all coefficients were statistically significant at a 0.01 significance level. The estimated weight curves are presented in figure 3. The weight curves are fairly similar for each generation, and the growth rate is higher in months with higher sea temperatures compared to months with lower sea temperatures.

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Table 2 and figure 3 around here

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Figure 4 shows the average relative growth rate together with the average sea temperature for the three regions for the whole time span. The figure clearly shows that the growth rate exhibits seasonal variation and that the relative growth rate is higher in the months when the sea temperature is higher. Table 3 shows the average growth rate for each generation.

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Figure 4 and table 3 around here

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Growth curves can be compared using a variety of different methods. Francis (1996) introduces six different methods to compare growth curves between different species of fish. Wang and Milton (2000) state that all six methods seem to be valid when comparing growth curves within the same species, which is relevant in this case. Francis' preferred method is to compare growth curves using the slope coefficient, the β value from equation (13), with larger β values indicating faster growth. However, Wang and Milton (2000) suggest that only using β can be misleading and that comparing the actual growth rates at a particular age or length could sometimes be more appropriate to determine what fish will reach a marketable size first. Another suggestion made by Francis is to determine the age at which a fish reaches

90 percent of the asymptotic maximum weight, α in equation (13). For those reasons, we measure how much time it takes for a salmon to reach 3 kg (the marketable size) using average sea temperatures, the specific growth rate to reach 3 kg, and the time to reach 90 percent of the asymptotic maximum weight at average sea temperature. To calculate the specific growth rate (SGR), we use the following equation:

$$SGR = \left(\frac{\ln w_2 - \ln w_1}{m}\right) \times 100\% \qquad (20)$$

in which w_2 and w_1 are the final (3 kg) and initial weights in kg, and m represents the number of months it takes to reach 3 kg.

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Table 4 around here

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The results in table 4 indicate that increasing the temperature leads to faster growth in the North and Central regions but leads to slower growth in the South region. This result is in line with the findings of Lorentzen (2008), who shows that a temperature increase will have a positive effect on productivity but that the southern part of Norway has a smaller safety margin because of the higher sea temperature in this region. Still, variations occur in the growth parameters for generations with fairly similar average sea temperatures. The 2007 and 2008 generations in the South region have similar average sea temperatures for the time period under study here. The 2007 generation has a higher slope coefficient and takes less time to reach 90 percent of the asymptotic maximum weight, but the 2008 generation has a higher specific growth rate to reach marketable size.

Observant readers may have noticed that the South region apparently takes a longer time to reach 3 kg compared with the North and Central regions, while the North region requires a shorter time to reach 90 percent of the asymptotic maximum weight than the Central and South regions. These results contradict the finding of Lorentzen (2008), who finds that the grow-out period is shorter in the southern part of Norway compared to the northern part. One reason for this difference is that the temperature used by Lorentzen is based on the water column between 1 to 50 meters, while the temperatures used in this study are measured at a depth of 3 meters, and surface temperatures will be higher in the summer and colder in the winter. As farming takes place at the surface, Lorentzen expect that lower growth and higher mortality would show up earlier than indicated by his simulations, which is with the case for the findings of our study. However, it is not accurate to assume that these regions are equivalent. As seen in figure 1, the South region releases half of the juveniles in the spring release and the other half in the autumn, while the North and Central regions release most of their juveniles in the spring release. This behavior will affect the average weight, as smaller fish are released later in the year in the South compared to the two other regions. These differences in juvenile release also affect the rate of harvest, and the North and Central regions harvest a larger share of their fish in year 1 than the South region, as seen in figure 2. In addition, the coefficient for the asymptotic maximum weight, α, is smaller for the North region than the for the Central and South regions, indicating that the North produces smaller fish than the Central and South regions. Thus, comparing regions with each other might be less desirable than following an individual fish over time, and further research is necessary to verify whether these findings would hold for individual fish.

Concluding Remarks

In this paper, a logistic growth function was estimated for three different regions in Norway to determine how temperature affects the growth of farmed salmon. Although the growth rates of an individual salmon depend on several factors, such as the amount of feed, light conditions and sea temperature (Løland et al., 2011), we have chosen to focus only on sea temperature to explain growth. As feeding patterns exhibit little variation when sea temperature is controlled and as the industry's use of artificial lights prevents different light conditions from affecting salmon growth, sea temperature is left as the most important factor to explain growth. The results of the growth model developed here suggest that temperature is a critical factor affecting the growth of farmed salmon. Periods with higher sea temperatures lead to faster growth of farmed salmon in the North and Central regions, while leading to slower growth in the South region. The opposite occurs in periods with relatively low sea temperatures, leading to faster growth of farmed salmon in the South region and slower growth in the North and Central regions.

Prior to January 2013, the maximum allowable juvenile weight was 250 g. In January 2013, this value was changed to 1 kg, increasing the flexibility of the production process. This alteration means that juvenile salmon will spend a greater part of their lives in a controlled environment. The tremendous growth in salmon farming is to a large extent due to increased control in the production process. Further increasing the control of the production process would possibly mean that the industry will experience a further productivity growth. Still, it will be interesting to see whether the change in maximum juvenile weight will diminish the generational difference currently observed in salmon growth.

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Table 1

Data scheme.

	2005	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**
Year 0	A	B	C	D	E		
Year 1		A	B	C	D	E	
Year 2			A	B	C	D	E

A is essentially the 2005 generation, B is the 2006 generation, C is the 2007 generation, and so forth.

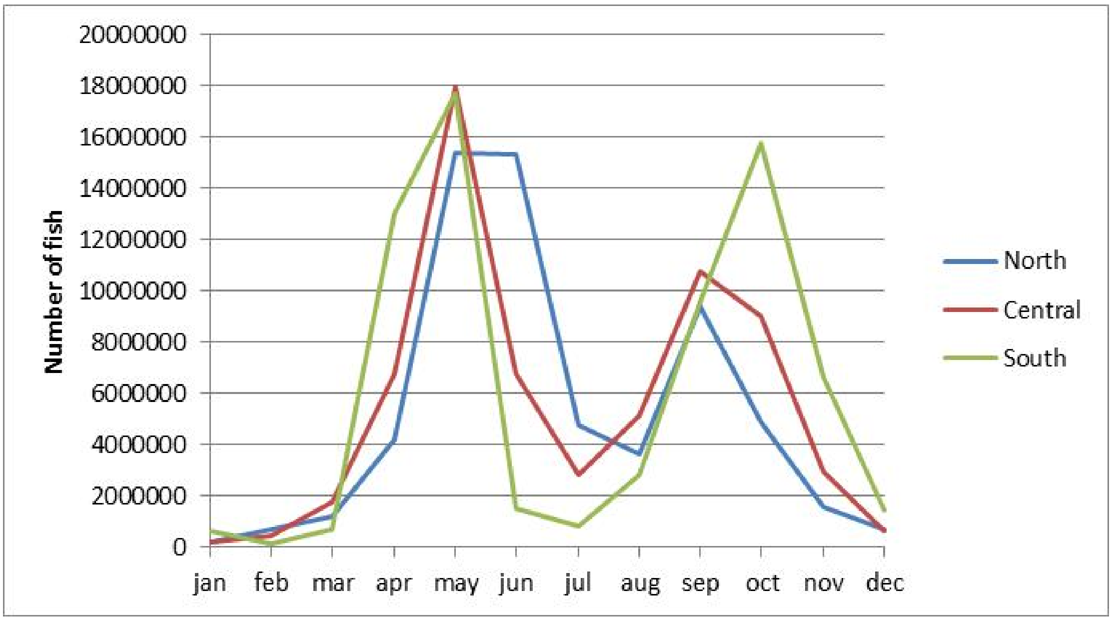

Figure 1. Average release of juveniles between 2005 and 2009.

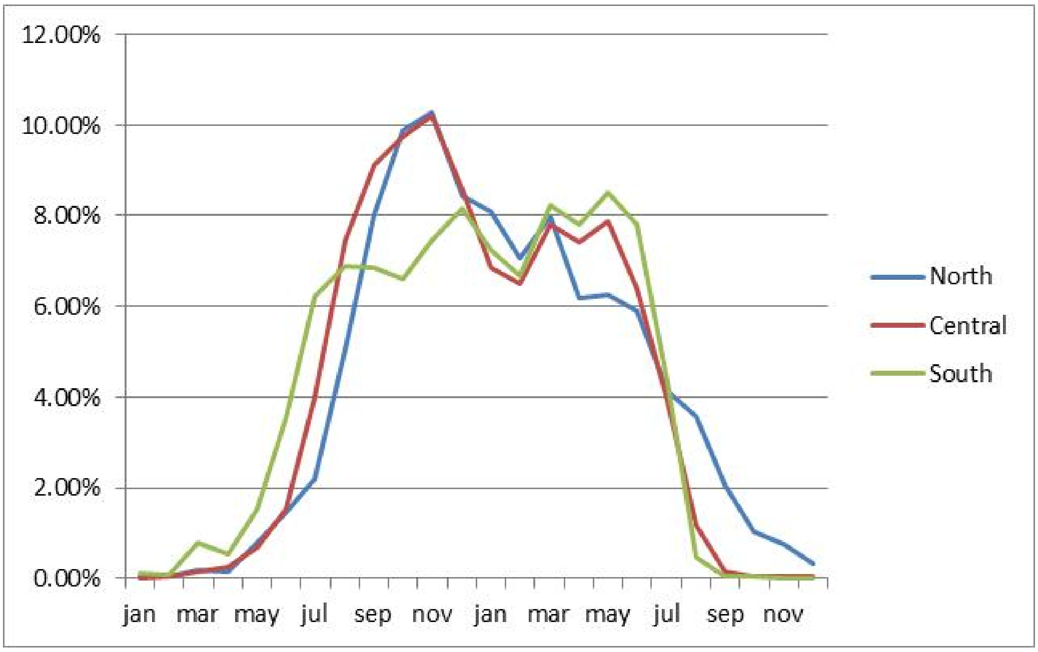

Figure 2. Average harvest rates in year 1 and year 2 between 2005 and 2009.

Table 2

Estimated Models

Gen	North				Central				South			
	α	β	μ	R^2	α	β	μ	R^2	α	β	μ	R^2
2005	4.327	.074	14.483	.952	4.829	.039	15.408	.981	5.926	.026	17.833	.985
	(.257)	(.020)	(.641)		(.196)	(.005)	(.420)		(.225)	(.003)	(.399)	
2006	4.815	.052	15.353	.987	5.655	.030	16.422	.994	5.553	.028	17.187	.990*
	(.160)	(.006)	(.337)		(.144)	(.002)	(.295)		(.186)	(.002)	(.358)	
2007	4.424	.049	15.624	.989	4.898	.034	16.314	.992	4.826	.031	16.669	.978
	(.136)	(.005)	(.331)		(.132)	(.003)	(.285)		(.205)	(.004)	(.430)	
2008	4.612	.051	16.300	.989	5.746	.034	16.913	.989	5.591	.029	16.974	.985
	(.136)	(.005)	(.275)		(.179)	(.003)	(.320)		(.229)	(.003)	(.403)	
2009	4.972	.055	16.079	.986	5.701	.037	17.037	.990	4.839	.040	16.110	.952
	(.166)	(.006)	(.323)		(.184)	(.003)	(.309)		(.314)	(.008)	(.610)	

Standard errors in parentheses. All regression include 29 observations, except for the regression marked with a *, which has 28 observations.

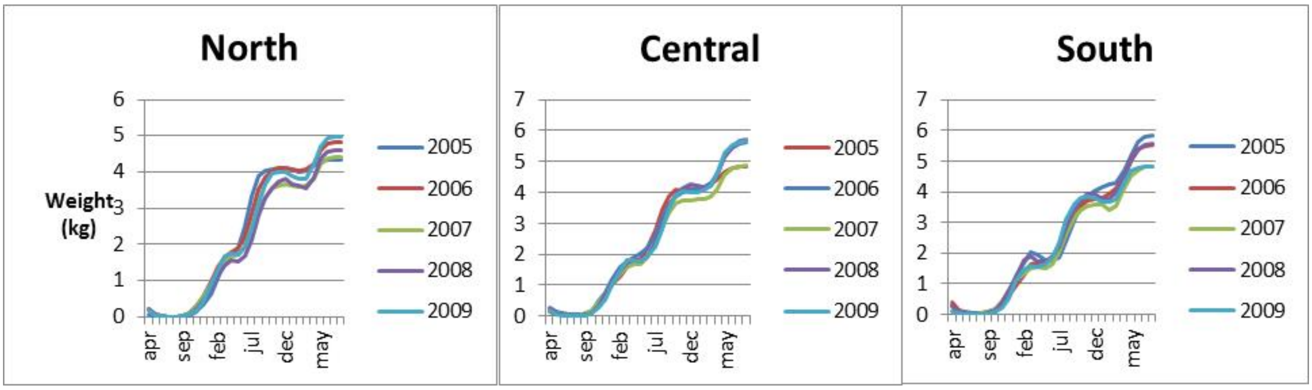

Figure 3. Estimated growth curves for each generation and region

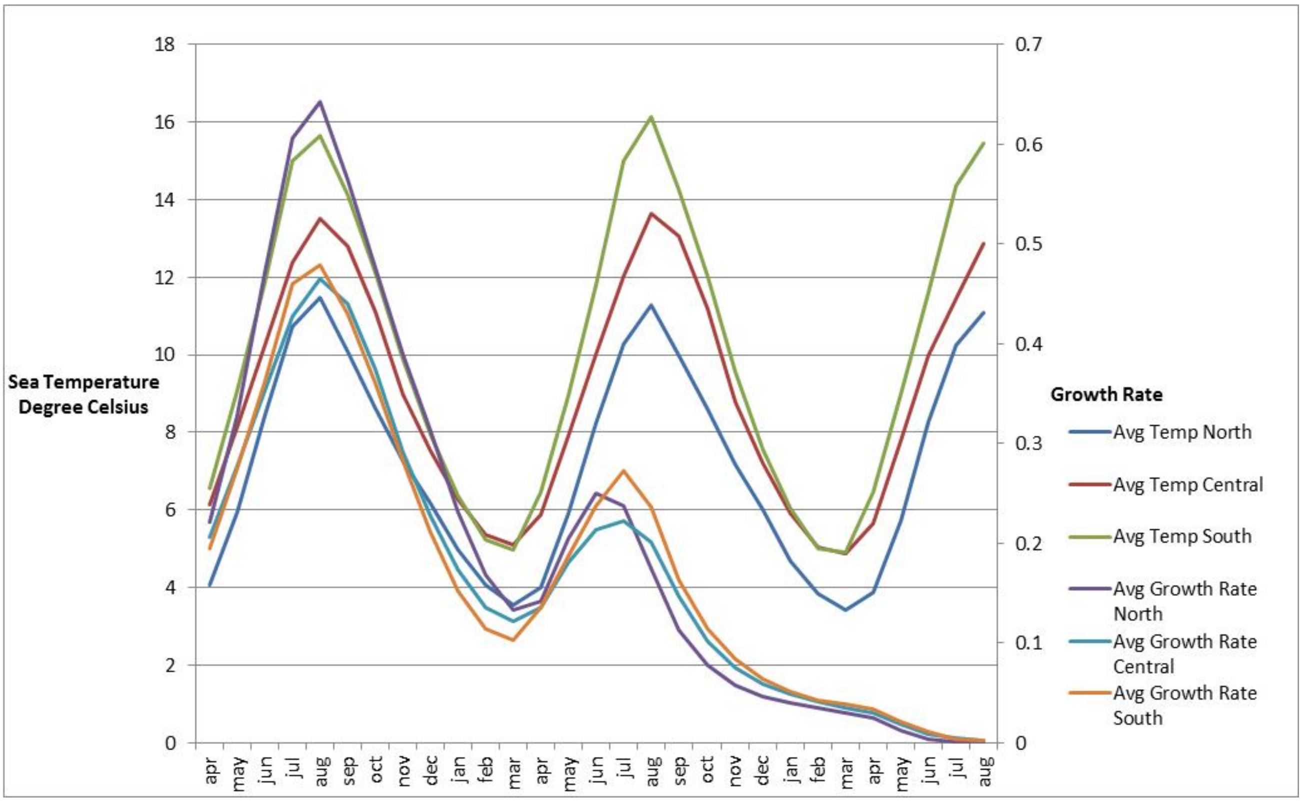

Figure 4. Average relative growth rate and sea temperature.

Table 3

The average relative growth rate for each generation.

Generation / **Region**	**2005**	**2006**	**2007**	**2008**	**2009**
North	25.39 %	19.26 %	18.48 %	19.52 %	20.70 %
Central	18.10 %	16.02 %	16.46 %	17.68 %	18.35 %
South	15.87 %	17.48 %	17.06 %	17.15 %	20.79 %

Table 4

The results of different methods of comparing growth curves and average temperatures for all generations and regions.

North Region

Gen	Months to reach 90 % of α	Months to reach 3 kg	SGR	β (slope coefficient)	Average temperature
2005	18.484	15.969	19.51%	0.074	7.438 (2.812)
2006	21.180	16.686	16.83%	0.052	7.288 (2.699)
2007	21.872	17.744	17.15%	0.049	7.199 (2.662)
2008	22.393	18.022	16.05%	0.051	7.013 (2.618)
2009	21.903	17.192	16.59%	0.055	6.927 (2.816)

Central Region

Gen	Months to reach 90 % of α	Months to reach 3 kg	SGR	β (slope coefficient)	Average temperature
2005	21.441	16.767	18.96%	0.039	9.354 (2.889)
2006	24.235	16.857	18.16%	0.030	9.243

					(3.014)
2007	23.479	17.807	16.43%	0.034	8.995 (2.925)
2008	24.191	17.206	18.37%	0.034	8.931 (3.078)
2009	24.117	17.375	16.71%	0.037	8.460 (3.074)
South Region					
Gen	**Months to reach 90 % of α**	**Months to reach 3 kg**	**SGR**	**β (slope coefficient)**	**Average temperature**
2005	25.910	17.909	15.98%	0.026	10.466 (3.704)
2006	24.687	18.520	16.98%	0.028	10.301 (3.846)
2007	23.754	18.788	13.85%	0.031	10.066 (3.765)
2008	24.494	18.696	17.02%	0.029	10.000 (4.041)
2009	21.911	17.222	17.80%	0.040	9.555 (3.958)

Standard errors in parentheses.

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[i] The mortality rate increases as the fish becomes older. The first year that the fish is in the pen, year 0, the mortality rate is only approximately 0.5 percent per month, while at the end of the second year, year 1, the mortality rate is as high as 12 percent. See Asche & Bjørndal (2011, p. 191) for more details.