UiT The Arctic University of Norway

Faculty of Biosciences, Fisheries and Economics

Marine growth of introduced pink salmon (*Oncorhynchus gorbuscha*) caught in northern and central Norway

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Summary

The introduction of pink salmon in the White Sea area during the second half of the 20th century has resulted in the establishment of a self-sustaining population of pink salmon in rivers draining to the Barents Sea and North Atlantic Ocean. The size and abundance of pink salmon is dependent on survival during the marine phase, where they acquire more than 95% of their body weight. Investigating marine growth of pink salmon caught in Norwegian rivers is important to understand population dynamics, and their geographical expansion and variation in abundance and size over time.

The aim of this study was to investigate how early marine growth affect adult size of pink salmon caught in Norwegian rivers prior to spawning. Scales from pink salmon caught in the river Skallelva in Finnmark county in 2019 and 2021, and scales from pink salmon caught in Central Norway in 2021, were used in scale analyses to compare annual, seasonal and regional growth characteristics.

Scale analyses of pink salmon in this study showed that fish entering Norwegian rivers in 2021 seemed to have had better growth conditions from sea entry to the winter, compared to fish entering rivers in 2019, despite large individual variation. The growth pattern showed a short period of reduced growth during summer and early autumn that was characteristic in fish caught in both Skallelva in 2019, Skallelva in 2021 and Central Norway in 2021. This seems a typical trait of growth in pink salmon when they are believed to stay in coastal areas and has been described for pink salmon native to the Pacific Ocean. During autumn the growth increased and stabilized before a pronounced period of reduced growth during winter. The autumn and winter growth had more effect on fish size at river entry than the first period of marine growth.

This study is the first to provide detailed information about scale growth in pink salmon between years and regions. The results from this work is important in understanding early growth in pink salmon and what may affect their size as adults entering Norwegian rivers to spawn.

1 Introduction

Invasive species are well documented as major drivers of loss in global biodiversity, outcompeting native species, degrading habitats and altering community structures and functions (Mainka & Howard, 2010). The social and economic impacts from invasive species on human activities may include reduced economic gain from fisheries, aquaculture or tourism, and a decrease in employment or quality of environmental surroundings, though also having a potential for positive effects like new industry (Bax et al., 2003).

Salmonid species have since prehistoric times been important sources of economic and social development of human populations (Criddle & Shimizu, 2014; Newell, 1994). Both the Pacific and Atlantic Ocean salmonids are important in commercial and subsistence fisheries, valuable to sports fishing, and important species in healthy food webs. Pink salmon (*Oncorhynchus gorbuscha*) is the most abundant of the seven salmonid species in the Pacific Ocean, genus *Oncorhynchus*. Of the three most numerous pacific salmonid species, pink salmon, chum salmon (*O. keta*) and sockeye salmon (*O. nerka*), pink salmon accounted for 67% of adult abundance and 48% of adult biomass from 1990 to 2015 (Ruggerone & Irvine, 2018). Pink salmon has a strict two-year life cycle, resulting in grouping of odd and even year spawners (Heard, 1991). Short-lived species, like the pink salmon, have the ability to adapt quickly to changing conditions (Pethon & Nyström, 1998), making pink salmon an invasive species with high plasticity to their surrounding environment.

Pink salmon was first introduced to the North Atlantic Ocean and Barents Sea in the 1950s, as the Soviet government started transplanting pink salmon eggs from the Pacific Ocean to the White Sea basin with the goal of establishing a new fishery resource (Alekseev et al., 2019). The transplant program to the White Sea resulted in high numbers of returning odd year spawners and lower returns of even year spawners (Gordeeva & Salmenkova, 2011), and the first pink salmon in Norway were registered as early as in 1960 in north-east Finnmark (Berg, 1961). Norwegian catches were low from 1960 to 2000 and increased to moderate catches from 2001 to 2016 (Sandlund et al., 2019; VKM et al., 2020). Catches in 2017 and 2019 peaked, and river catches from 2021 indicate the highest abundance of pink salmon ever recorded in rivers draining to the Barents and Norwegian seas (Berntsen et al., 2020; Berntsen et al., 2018; Statistics Norway, 2022). Catches have been highest in Troms and Finnmark county, with an expansion to rivers further west and south from 2017 to 2021, and also reaching beyond Norway (Pettit, 2017; VKM et al., 2020).

The impact of pink salmon on native species in Barents and North Atlantic ecosystems are not well known, though a recent risk assessment identified several areas of concern (VKM et al., 2020). Abundant numbers of pink salmon in rivers may compete with native species for space and food during the early juvenile stage, compete for space before and during spawning, impact angling opportunities, have a negative impact on marine ecosystems, and spread pathogens that impact both river ecosystems and aquaculture (VKM et al., 2020). Further, pink salmon carcasses, eggs and juveniles transfer marine derived nutrients to aquatic and terrestrial environments that may alter local ecosystems and biodiversity (Dunlop, Eloranta, et al., 2021; Dunlop, Wipfli, et al., 2021; VKM et al., 2020).

Number of pink salmon migrating to rivers to spawn is dependent on marine growth and survival (Beamish, 2012). In the Pacific Ocean, marine feeding accounts for more than 95% of growth of pink salmon, and the marine phase is a key factor for survival (Beamish, 2012; Heard, 1991; Kaev & Irvine, 2016). Little is known about growth and survival of pink salmon in the Barents Sea and North Atlantic Ocean, but warming ocean temperatures were positively correlated with the increase in pink salmon catches over the past years in Norwegian rivers, indicating that the conditions for pink salmon at sea has improved with climate change (VKM et al., 2020).

The marine growth period from sea entry in spring to winter, referred to as early marine growth, was correlated with survival of pink salmon in the Pacific Ocean, especially referring to the first weeks at sea as a “critical period” for growth (Beamish & Mahnken, 2001; Murphy et al., 1998; Parker, 1968). Some authors also refer to autumn and winter growth as a second “critical period” (Beamish & Mahnken, 2001). Kaev and Irvine (2016) found that the early marine period of pink salmon in the Pacific Ocean may determine abundance of returning fish, while size of adults returning may be impacted by environmental conditions in the later marine period when they stay further off coast. Hence, studying growth in the early marine period of pink salmon in the Northern Atlantic Ocean and Barents Sea may indicate critical periods of growth and what factors may influence them.

A common way of studying growth in salmonids is by scale reading, as scales form sclerites (hereafter mentioned as circuli) at regular time intervals, and the width between circuli reflect growth rate (Courtney et al., 2000; Gilbert, 1913). During the winter season with low temperatures at sea and less favorable feeding conditions, the scales form circuli with narrow distances referred to as the winter zone. During spring and summer, with increasing temperature and feeding conditions, the distance becomes wider (Myers, 1994). Scales of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) are commonly used to determine age and growth by counting winter zones and measuring scale size between summer and winter zones, but detailed studies based on circuli spacing have not been common (Dahl, 1911; Todd et al., 2014). Scale analyses of circuli spacing in pink salmon in the Pacific Ocean have been used in several studies of growth (Cross et al., 2009; Kaev, 2015b). Using circuli spacing as a measure of growth is a time-consuming method but provides detailed information about the growth rates in different periods. To my knowledge, there is only one study of growth in scales of introduced pink salmon in the Barents Sea area (Paulsen et al., 2021).

The main objective of this study was to investigate early marine growth in scales of pink salmon caught in Norwegian rivers prior to spawning. The specific aims were to 1) compare growth of pink salmon caught in Northern Norway between 2019 and 2021, 2) compare growth between pink salmon caught in Northern Norway and Central Norway in 2021, 3) describe seasonal variation in marine growth during summer, autumn and winter, and 4) examine how marine growth in the different seasons may affect adult fish size at spawning.

2 Method

2.1 Study area

The material for this study was collected in river Skallelva in Northern Norway and 19 rivers in Central Norway in the summer of 2021 (*Figure 1*). There were few pink salmon caught in rivers in Central and Southern Norway in 2021, so aggregated samples from several rivers represented the geographic region south of river Skallelva, termed Central Norway (*Appendix 1*). In addition, samples from the study of Paulsen et al. (2021) of pink salmon in Skallelva in 2019 were included for comparison between years.

River Skallelva (70.11 °N, 30.20 °E) flows into Varangerfjorden in Vadsø municipality in Troms and Finnmark county and has a mean annual water discharge of 5.5 $m^3 sec^{-1}$, draining a catchment area of 259 km^2 (Sandlund et al., 2019). The catchment area has a mean annual precipitation of 503 mm over the past 40 years, and a mean annual air temperature of 1.3 °C (Norwegian Centre for Climate Services, 2022). Rivers in Central Norway, represented by the locations furthest north and south, has a mean annual air temperature of 5.78 °C in Namsos and 6.86 °C in Ørsta-Volda over the last five years, and a mean annual precipitation of 1505 mm in Namsos and 1656 mm in Ørsta-Volda (Norwegian Centre for Climate Services, 2022).

Figure 1 Map showing locations where pink salmon were caught and sampled for scales. Skallelva in Northern Norway was sampled in 2019 and 2021, and rivers in Central Norway were sampled in 2021. Map: Geodata AS

2.2 Sampling

In Skallelva 2021, pink salmon were captured through targeted removal fishing with gill nets (mesh size 50-63 mm knot-to-knot) from 4 July to 13 August 2021. In Skallelva 2019, pink salmon were captured by using gill nets (mesh size 65 mm knot-to-knot) in August (Paulsen et al., 2021). Pink salmon from Central Norway were captured by angling, harpooning and seine nets (*Appendix 1*).

Scale samples were taken from the area above the lateral line posterior to the dorsal fin (Major et al., 1972). In a minor part of the fish captured close to spawning, the skin was leathery and tough, making the collection of scales difficult. In these cases, a slice of skin with scales was cut off and frozen until scales could be sampled in the laboratory. All samples were eventually frozen or dried until further analysis. For all fish, total length was measured to the nearest 0.5 cm and sex were recorded (*Table 1*). Sex was determined by opening the fish.

Table 1 Overview of years and numbers of sampling, sex, mean, standard deviation (SD) and range for total body length (mm) for pink salmon in Norway. Data are presented for sampling in river Skallelva in 2019 and 2021, and sampling from rivers in Central Norway in 2021. Data for Skallelva 2019 are from Paulsen et al. (2021) and included for comparisons.

			Total body length (mm)		
Region/Year	**Sex**	**N**	**Mean**	**SD (±)**	**Range**
2019 Skallelva	Female	20	459	27	405-495
	Male	28	510	52	400-610
	Total	48	489	50	400-610
2021					
Skallelva	Female	76	493	29	415-545
	Male	129	530	52	380-715
	Total	205	517	48	380-715
2021					
Central Norway	Female	79	460	31	402-540
	Male	110	502	46	400-610
	Total	189	484	45	400-610
Total	Female	175	474	34	402-545
	Male	267	517	51	380-715
	Total	**442**	**500**	**50**	**380-715**

Scale analyses were carried out by selecting 3-4 readable scales from each sample through a Wild Heerbrugg M8 stereo microscope (type MDG13, Leica Geosystems, Heerbrugg, Switzerland). Scales were placed on a plastic strip and run through a printing press, copying the structure of the scale. The printed plastic strips were then controlled in an Indus COM reader (class 4601 model 1, Indus International, Wisconsin, USA).

The scale with the highest quality print of the selected 3-4 readable scales was photographed through a Leica Z6 AP0 (model MSV266, Leica Geosystems, Wetzlar, Germany) with a NIKON Digital Sight DS-Ri1 camera (Nikon, Tokyo, Japan) with x40 magnification and NIS-Elements F imaging software (Nikon, Melville NY, USA). Images were analyzed using Image-Pro Plus software (Media Cybernetics, Silver Spring MD, USA). The center of the focus area on the scale was visually determined, as was the last circulus in the winter zone (*Figure 2, left*). The last circulus in the winter zone was defined as the second circulus in a pair of two circuli forming the shortest circuli spacing (Todd et al., 2014). Length from the center of the focus area to the last circulus (mm) in the winter zone, and distance between each circulus (mm) from the focus area to the last circulus in the winter zone, were recorded following the method of Fisheries Research Board of Canada, & Station, P. B. (1972) and Bugaev (2004). The software identified each circulus between the focus area and the last circulus, but manual control and adjustments of circuli were required. The software occasionally recorded double circuli, and also this was manually adjusted (*Figure 2, right*). Pink salmon scales were often eroded from the edge towards the center, and measurements of scale circuli from the winter zone to the date of capture were not possible.

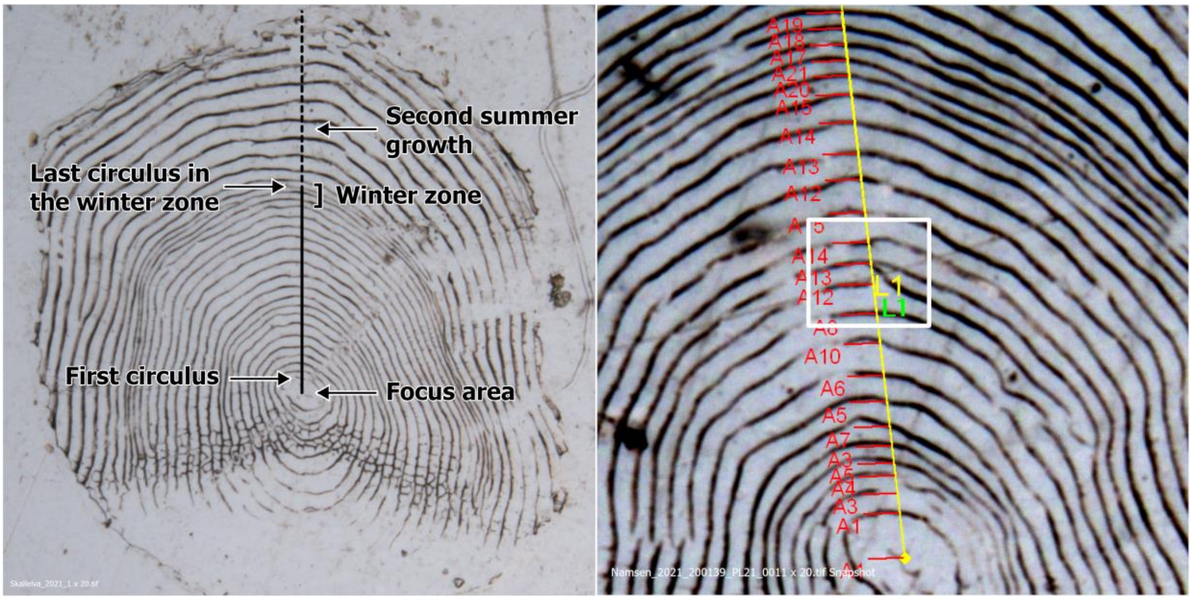

Figure 2 Left: illustration of scale annotation. Right: illustration of two circuli having a connecting line between them. Image-Pro Plus software (Media Cybernetics, Silver Spring MD, USA) recorded it as three circuli and manual control was in such cases necessary to correct the lines.

2.3 Data analyses

Data on scale length (mm), referring to the distance from the focus area to the last circulus in the winter zone, and circulus spacing, referring to the distance between two consecutive circuli (mm), were exported from Image-Pro Plus to Excel (Microsoft Excel version 2109, Microsoft Corporation, Redmond, Washington, USA). RStudio (version 2022.02.1, RStudio PBC, Boston, USA) was used for statistical analyses. Number of fish sampled was 544, but due to eroded scales the number of fish with readable scales was 442.

2.3.1 Comparing growth between pink salmon caught in 2019 and 2021

Mean total body length, number of circuli, scale length and circuli spacing were compared between males and females caught in Skallelva in 2019 and 2021, and in rivers in Central Norway and river Skallelva in 2021 using one-way ANOVA with "lm" function in R Studio (R Core Team, n.d.). The test assumes independence of observations and no outliers, distribution of normality, and homogeneity of variance. The assumption of independence of observations was met as all data are from different groups. There were no outliers in either variable within each group, as determined by visually inspections of the data using the "geom_histogram" and "stat_qq + stat_qq_line" functions in ggplot package in "ggpubr" in R (Wickham, 2016). Using "geom_histogram" function, total body length, number of circuli and scale length in males and females caught in Skallelva 2019 had a non-normal skewed distribution, while all other variables were normally distributed within groups.

Distribution of normality was tested using Shapiro-Wilk “shapiro.test” function in “stats” package in R (R Core Team, n.d.). Scale length and mean circuli spacing in all groups were normally distributed. Total body length in females caught in Central Norway 2021 and number of circuli in females caught in Skallelva 2019, males caught in Skallelva 2021 and males and females caught in Central Norway 2021 were not normally distributed.

Assumption of homogeneity of variance was tested with “homog.test” function in “onewaytests” package (Dag, 2018). Length between males and females in Skallelva 2019, Skallelva 2021 and Central Norway 2021 were not homogenous. Length in males between Skallelva 2019, Skallelva 2021 and Central Norway 2021 were homogenous. Also, length in females between Skallelva 2019, Skallelva 2021 and Central Norway 2021 were homogenous. Mean circuli spacing in all groups were homogenous. Number of circuli and scale length between males and females in Skallelva 2019 were not homogenous, also, scale length between males in Skallelva 2019, Skallelva 2021 and Central Norway 2021 were not homogenous. Number of circuli and scale length in all other groups were homogenous.

As some variables in different groups did not meet the assumptions of a one-way ANOVA test, the groups were compared by using non-parametric tests. Groups with non-normal distribution were tested using the pairwise comparisons Wilcoxon rank sum test with continuity correction, “pairwise.wilcox.test” in R (R Core Team, n.d.). Groups with heterogeneity of variance were tested using Welch one-way test with “games_howell_test” function in “rstatix” package in R (Alboukadel, 2022). Use of non-parametric tests is indicated in the test reports in the result chapter. In all other cases, the parametric test one-way ANOVA with “lm” function was used (R Core Team, n.d.). All model residuals from the one-way ANOVA were normally distributed using “hist(resid)” and “plot” functions.

2.3.2 Marine growth pattern

There was large variation in number of circuli in scales from pink salmon caught in both Skallelva 2019, Skallelva 2021 and Central Norway 2021 (min = 15, max = 27; *Appendix 2*). To visually inspect the growth pattern, total number of circuli for each individual was standardized in 10 periods, and mean circuli spacing was calculated for each period. This prevented that the winter zone of fish with few circuli interfered with the interpretation of autumn and winter growth of all individuals, as illustrated in *Appendix 3*.

Total body length as response variable was tested for correlation with number of circuli from first circulus at the focus area to last circulus in the winter zone, scale length from the focus area and including the winter zone, and mean length between circuli, as predictor variables. Test of correlation was done using simple linear regression model with “lm” function in R (R Core Team, n.d.). Response and predictor variables were tested within the groups males and females, and Skallelva 2019, Skallelva 2021 and Central Norway 2021. All model residuals met assumptions of normal distribution and homoscedasticity using “hist(resid)” and “plot” functions, together with the Breusch-Pegan test using “bptest” function in “lmtest” package and “gvlma” function in “gvlma” package in R (Pena & Slate, 2019; R Core Team, n.d.; Zeileis & Hothorn, 2002).

2.3.3 Growth during summer, autumn and winter

When investigating three periods of growth, the total number of circuli from focus to the last circulus in the winter zone was divided in three periods. Period 1 likely covers the first growth phase during spring/summer after the fish migrated to sea. The scales are formed in the period when fish migrate from freshwater to sea, so no freshwater growth is recorded in the scales. Period 2 likely covers late summer and early autumn, and period 3 late autumn and winter (Paulsen et al., 2021). The summarized circuli spacing for each period as predictor variable was fitted in a linear regression model with total body length as response variable. The relationship between each of the three periods and total body length was tested using “lm” function in R (R Core Team, n.d.). Response and predictor variables were tested within the groups males and females, and Skallelva 2019, Skallelva 2021 and Central Norway 2021. All model residuals met assumptions of normal distribution and homoscedasticity using “hist(resid)” and “plot” functions, together with the Breusch-Pegan test using “bptest” function in “lmtest” package and “gvlma” function in “gvlma” package in R (Pena & Slate, 2019; R Core Team, n.d.; Zeileis & Hothorn, 2002).

3 Results

3.1 Comparing growth between pink salmon caught in 2019 and 2021

Total body length (mm) of fish caught in Skallelva 2019, Skallelva 2021 and Central Norway 2021 varied among individuals and groups (*Figure 3*). Overall, males had larger total body length than females (males: mean 517 mm; females: mean 474 mm; P-value < 0.001; *Table 1*). In 2021, males and females caught in Central Norway had smaller body length than males and females caught in Skallelva (males P-values < 0.001; females P-value < 0.001; *Appendix 4*). Females caught in Skallelva 2021 was larger than females caught in Skallelva 2019 (P-values < 0.001; *Appendix 4*). Males caught in Skallelva 2021 did not differ in body length from males caught in Skallelva 2019 (P-values > 0.05; *Appendix 4*).

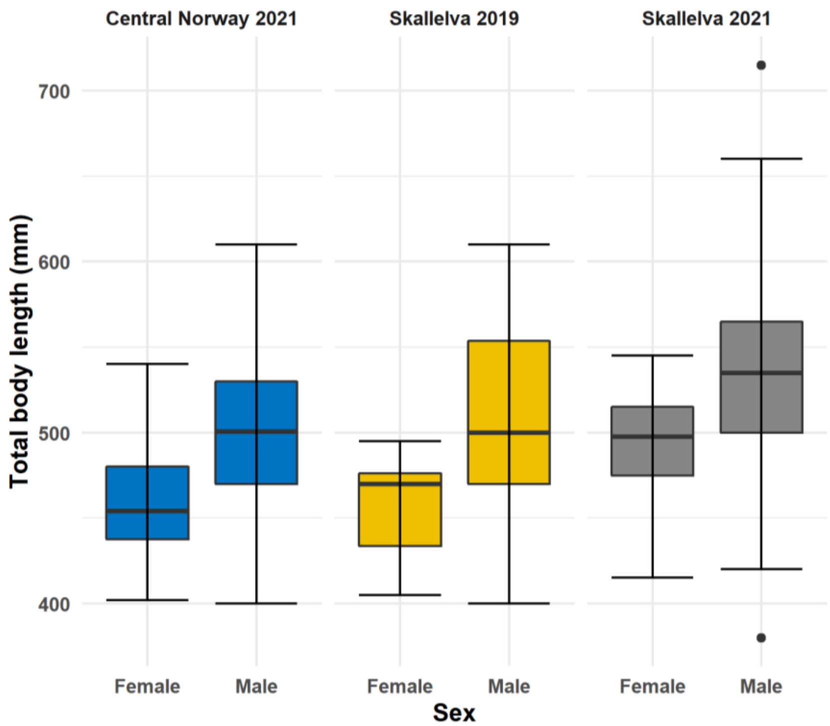

Figure 3 Total body length of males and females caught in Central Norway 2021, Skallelva 2019 and Skallelva 2021. Boxplots show interquartile range with minimum and maximum values as whiskers, the box with 1st and 3rd quartile, and median as interior line within the box. Outliers are shown as single dots. Data for Skallelva 2019 are from Paulsen et al. (2021) and included for comparisons.

Mean number of circuli for all fish was 20, but with a large variation among individuals (SD 2, range 15-27, N = 442; *Figure 4, Appendix 2*). There was no difference in number of circuli between males and females in any region or year (P-values > 0.1; *Appendix 4*). Females caught in Skallelva 2021 had more circuli than females caught in Skallelva 2019, while males in Skallelva did not differ in number of circuli between 2019 and 2021 (females P-value < 0.01; males P-value > 0.1; *Appendix 4*). Males caught in Central Norway 2021 had more circuli than males caught in Skallelva 2021, while females in Central Norway 2021 and Skallelva 2021 did not differ in number of circuli (males P-value < 0.01; females P-value > 0.1; *Appendix 4*).

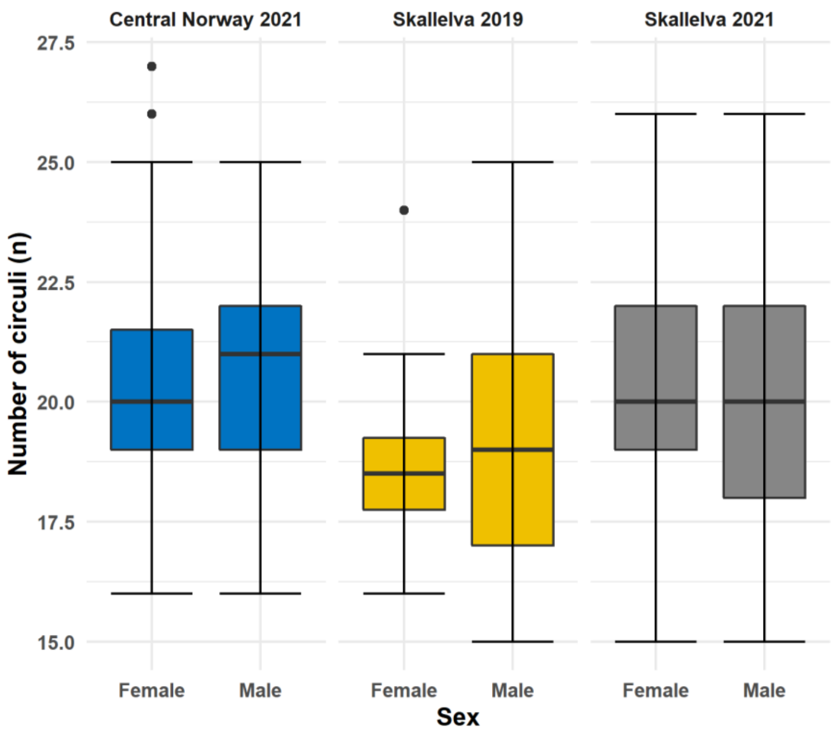

Figure 4 Number of circuli in scales from males and females caught in Central Norway 2021, Skallelva 2019 and Skallelva 2021. Boxplots show interquartile range with minimum and maximum values as whiskers, the box with 1st and 3rd quartile, and median as interior line within the box. Outliers are shown as single dots. Data for Skallelva 2019 are from Paulsen et al. (2021) and included for comparisons.

Distance from the focus area up to and including the last circulus in the winter zone, termed scale length, was on average 0.78 mm (SD 0.108mm, range 0.505-1.166 mm, N = 442; *Figure 5*, *Appendix 2*). Scale length did not differ between males and females in any region or year (all P-values > 0.1; *Appendix 4*). Scale length in females caught in Skallelva 2019 was smaller than in females caught in Skallelva 2021 (P-value < 0.05; *Appendix 4*). There was no difference in scale length in females caught in Skallelva 2021 and Central Norway 2021 (P-value > 0.1; *Appendix 4*). Scale length in males caught in Skallelva 2019 did not differ from males caught in Skallelva 2021 (P-value > 0.1; *Appendix 4*), while males caught in Central Norway 2021 had larger scale length than males caught in Skallelva 2021 (P-value < 0.01; *Appendix 4*).

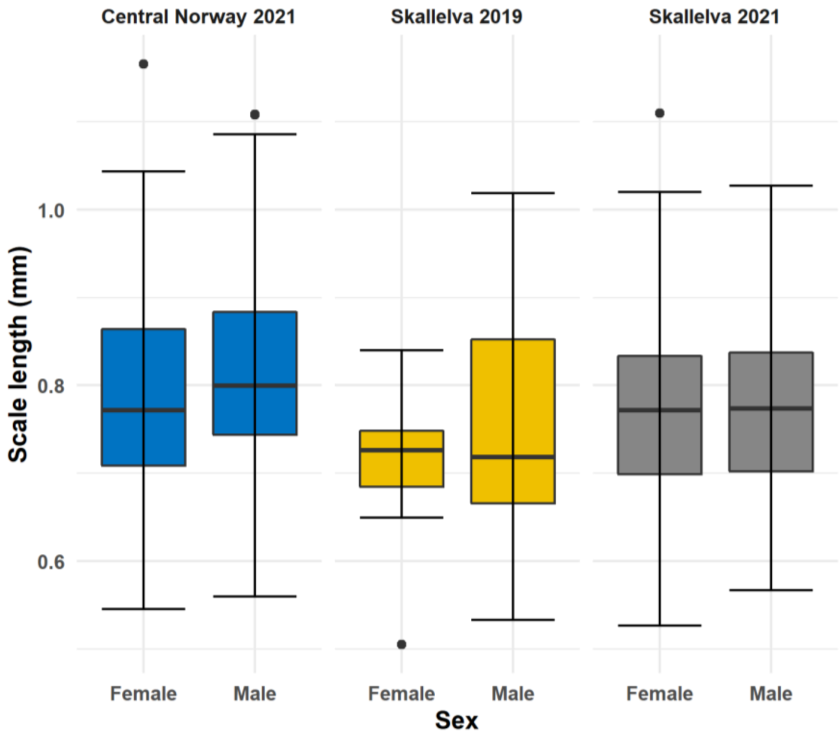

Figure 5 Scale length (mm) in males and females caught in Central Norway 2021, Skallelva 2019 and Skallelva 2021. Boxplots show interquartile range with minimum and maximum values as whiskers, the box with 1st and 3rd quartile, and median as interior line within the box. Outliers are shown as single dots. Data for Skallelva 2019 are from Paulsen et al. (2021) and included for comparisons.

Mean circuli spacing for all fish was 0.036 mm (SD 0.009 mm, range 0.010-0.07 mm, N = 442; *Figure 6*, *Appendix 2*). There was no difference in mean circuli spacing between males and females caught in Skallelva in 2021 and 2019 (all P-values > 0.05; *Appendix 4*). Also, there was no difference in mean circuli spacing between males and females caught in 2021 in Central Norway and Skallelva (all P-values > 0.05; *Appendix 4*).

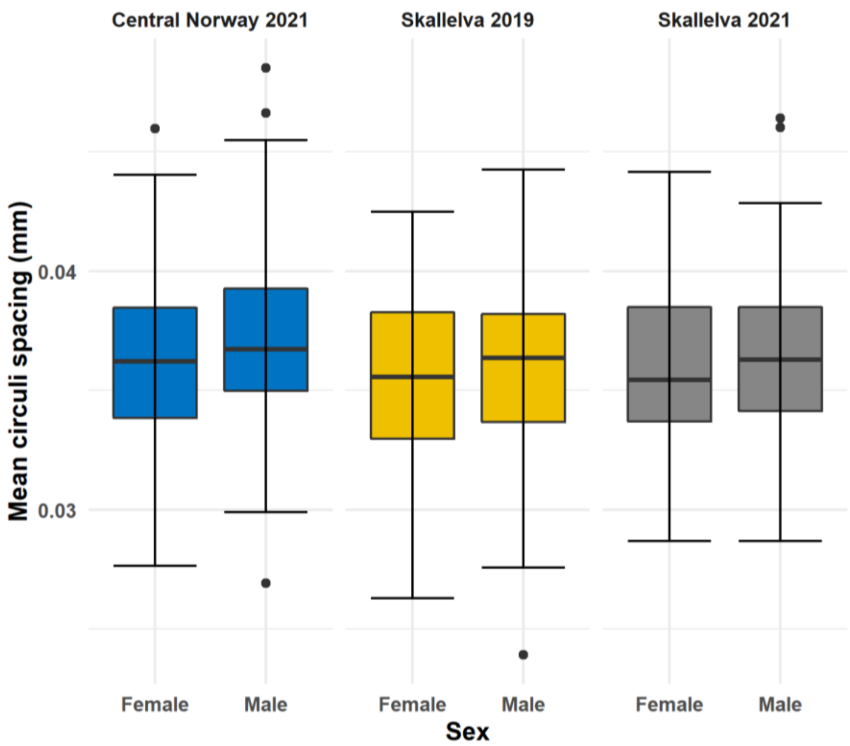

Figure 6 Mean circuli spacing (mm) in males and females caught in Central Norway 2021, Skallelva 2019 and Skallelva 2021. Boxplots show interquartile range with minimum and maximum values as whiskers, the box with 1st and 3rd quartile, and median as interior line within the box. Outliers are shown as single dots. Data for Skallelva 2019 are from Paulsen et al. (2021) and included for comparisons.

3.2 Marine growth pattern

The growth rate varied from first circulus to last circulus in the winter zone (*Figure 7*). Scale growth declined over the first 5-6 circuli (standardized into C1-C3 in *Figure 7*), followed by an increase towards circuli 10-11 (C4-C5). From circuli 10-11 (C6-C8), growth stabilized before approaching the winter zone (C9-C10). The period from C1 to C3 is interpreted as the summer and early autumn growth, C4 to C7 as autumn growth and C8 to C10 as late autumn and winter growth.

Growth during summer and early autumn of fish caught in Skallelva 2019 indicates a longer period of decline than fish caught in Skallelva 2021 and Central Norway 2021. Fish caught in Skallelva 2021 seem to have a less pronounced decline over the same period, while fish caught in Central Norway 2021 seem to increase in growth earlier than fish caught in Skallelva 2019 and 2021. Growth from autumn to winter (C6-C10) give the impression of being more similar between Skallelva 2019, Skallelva 2021 and Central Norway 2021.

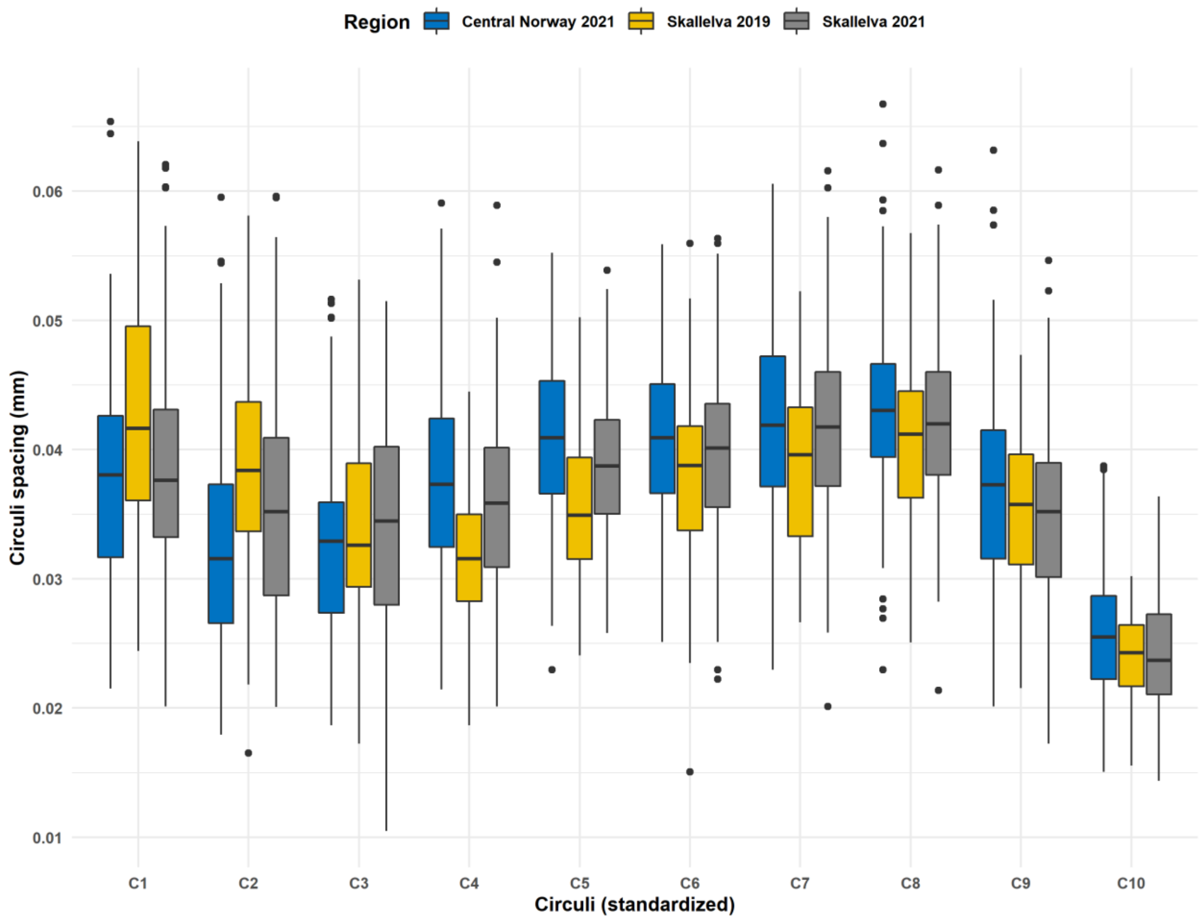

Figure 7 Circulus spacing from the first circulus (C1) up to and including the winter zone (C10). Number of circuli are standardized in 10 periods, and circuli spacing is the calculated mean length in each period. Boxplots are shown for Skallelva in 2019 and 2021, and Central Norway in 2021. Circuli spacing in males and females are not shown as no difference between them was found. Boxplots show interquartile range with minimum and maximum values as whiskers, the box with 1st and 3rd quartile, and median as interior line within the box. Outliers are shown as single dots. Data for Skallelva 2019 are from Paulsen et al. (2021) and included for comparisons.

Number of circuli and scale length increased with increasing total body length in males and females caught in Skallelva 2019, Skallelva 2021 and Central Norway 2021 (*Table*), except in females caught in Skallelva 2019 (*Table*). Number of circuli and scale length explained only 7% and 8% of the variation in total body length in males caught in Central Norway 2021, while number of circuli and scale length explained 46% and 35% of the variation in total body length in males caught in Skallelva 2019. The explanatory power of number of circuli and scale length for both males and females caught in Skallelva 2021 were 12-20% (*Table*).

Females caught in Central Norway 2021 had positively correlating total body length and mean circuli spacing, though the explanatory power was only 7%, contrary to males and females caught in Skallelva 2019, Skallelva 2021, and males caught in Central Norway 2021 which has no correlation between total body length and mean circuli spacing (*Table*).

*Table 2 Linear regression analysis of total body length (mm) as response variable, and number of circuli (n), scale length (mm) and mean circuli spacing (mm) as predictor variables. Table show p-value, adjusted r^2 representing how much of the variation in total body length was explained by the predictor variables, and regression equation of significant correlations. Significance codes: < 0.001 = ***, < 0.01 = **, < 0.05 = *, < 0.1 = .. Data for Skallelva 2019 are from Paulsen et al. (2021) and included for comparisons.*

Response variable:	**Total body length**				
Group		**p-value**		**r^2**	**Regression equation**
Predictor variable:	**Number of circuli**				
Skallelva 2019	Males	< 0.001	***	0.46	y = 251.25 + 13.36x
	Females	0.13		0.07	
Skallelva 2021	Males	< 0.001	***	0.19	y = 340.32 + 9.65x
	Females	< 0.01	**	0.12	y = 401.31 + 4.56x
Central Norway 2021	Males	< 0.01	**	0.07	y = 369.72 + 6.4x
	Females	< 0.001	***	0.12	y = 348.41 + 5.47x
Predictor variable:	**Scale length**				
Skallelva 2019	Males	< 0.001	***	0.35	y = 338.61 + 228.83x
	Females	0.69		-0.05	
Skallelva 2021	Males	< 0.001	***	0.2	y = 336.75 + 251.15x
	Females	< 0.01	**	0.12	y = 415.05 + 100.85x
Central Norway 2021	Males	< 0.01	**	0.08	y = 400.78 + 124.77x
	Females	< 0.001	***	0.18	y = 366.31 + 119.08x
Predictor variable:	**Circuli spacing**				
Skallelva 2019	Males	0.31		0.002	
	Females	0.47		-0.02	
Skallelva 2021	Males	0.49		-0.004	
	Females	0.28		0.002	
Central Norway 2021	Males	0.11		0.01	
	Females	< 0.05	*	0.07	y = 373.2 + 2395.2x

3.3 Growth during summer, autumn and winter

There was no relationship between mean circuli spacing over all circuli (from the first circulus to the last in the winter zone) and total body length, except in females caught in Central Norway 2021 (*Table*). Cumulative circuli spacing in three periods of growth shows a stronger correlation with fish growth (*Figure 8*).

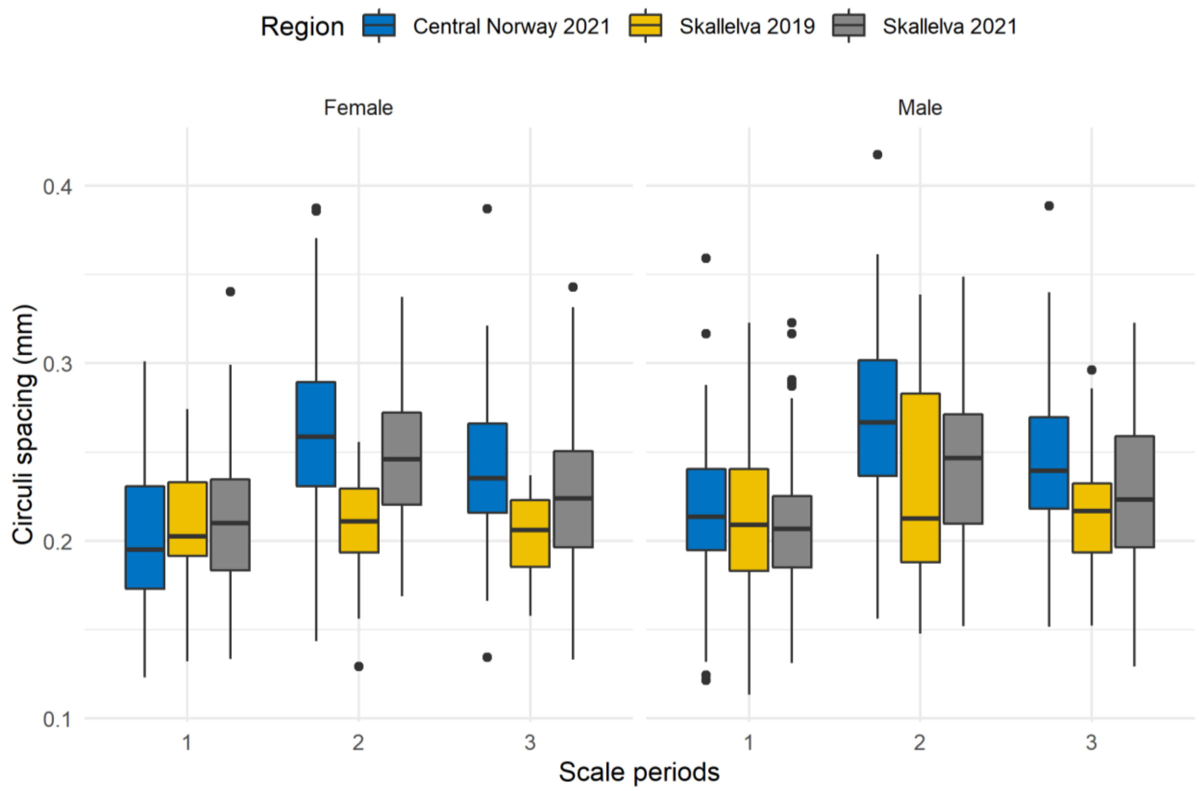

Figure 8 Cumulated circuli spacing in period 1, 2 and 3 divided by males and females. Boxplots are shown for Skallelva in 2019 and 2021, and Central Norway in 2021. Boxplot shows interquartile range with minimum and maximum values as whiskers, the box with 1st and 3rd quartile, and median as interior line within the box. Outliers are shown as single dots. Data for Skallelva 2019 are from Paulsen et al. (2021) and included for comparisons.

Cumulative circuli spacing in period 1 was positively correlated with total body length in males caught in Skallelva 2019, and males and females caught in Central Norway 2021 (*Table 3*). The explanatory power was 16 % for males caught in Skallelva 2019, and 5-6 % for males and females caught in Central Norway 2021. Total body length for females caught in Skallelva 2019, and males and females caught in Skallelva 2021 was not explained by circuli spacing in period 1.

Cumulative circuli spacing in period 2 was positively correlated with total body length in males caught in Skallelva 2019, males and females caught in Skallelva 2021, and females caught in Central Norway 2021 (*Table 3*). The explanatory power was 57% for males caught in Skallelva 2019 and 12-19% for females caught in Central Norway 2021, and males and females caught in Skallelva 2021. Total body length in females caught in Skallelva 2019 and males caught in Central Norway 2021 was not explained by circuli spacing in period 2.

Circuli spacing in period 3 was positively correlated with total body length in all groups, except for females caught in Skallelva 2019 (*Table 3*). Circuli spacing in period 3 explained 23% of total body length in males caught in Skallelva 2019 and Skallelva 2021, while the explanatory power of circuli spacing in period 3 on total body length in females caught in Skallelva 2021 and males caught in Central Norway 2021 was 11%.

*Table 3 Linear regression analysis of total body length (mm) as response variable, and period 1, 2 and 3 as predictor variables. Table shows p-values, adjusted r^2 representing how much of the variation in total body length was explained by the predictor variables, and regression equation of significant correlations. Significance codes: < 0.001 = ***, < 0.01 = **, < 0.05 = *, < 0.1 = .. Data for Skallelva 2019 are from Paulsen et al. (2021) and included for comparisons.*

Response variable:	**Total body length**	**p**		**r^2**	**Regression equation**
Predictor variable:	**Period 1**				
Skallelva 2019	Males	< 0.05	*	0.16	y = 418.31 + 432.12x
	Females	0.72		-0.05	
Skallelva 2021	Males	0.05	.	0.02	
	Females	0.06	.	0.04	
Central Norway 2021	Males	< 0.01	**	0.06	y = 435.51 + 307.9x
	Females	< 0.05	*	0.05	y = 422.97 + 183.07x
Predictor variable:	**Period 2**				
Skallelva 2019	Males	< 0.001	***	0.57	y = 346.14 + 729.56x
	Females	0.56		-0.04	
Skallelva 2021	Males	< 0.001	***	0.12	y = 424.91 + 430.03x
	Females	< 0.001	***	0.14	y = 418.14 + 302.9x
Central Norway 2021	Males	0.12		0.01	
	Females	< 0.001	***	0.19	y = 380.52 + 304.22x
Predictor variable:	**Period 3**				
Skallelva 2019	Males	< 0.01	**	0.23	y = 365.29 + 664.71x
	Females	0.53		-0.03	
Skallelva 2021	Males	< 0.001	***	0.23	y = 401.58 + 573.95x
	Females	< 0.01	**	0.11	y = 441.2 + 229.21x
Central Norway 2021	Males	< 0.001	***	0.11	y = 408.71 + 382.41x
	Females	< 0.001	***	0.17	y = 384.16 + 315.96x

4 Discussion

Scale analyses of pink salmon in this study showed that fish who entered Norwegian rivers in 2021 seemed to have had better growth conditions from sea entry to the winter, compared to fish entering rivers in 2019, despite large individual variation and the exception of some groups of fish. This was particularly evident for females caught in Skallelva. Growth rate was generally high during summer to autumn, and low during winter, as expected this was similar to other studies of salmonids (Jensen et al., 2018; Kaev, 2015a; Todd et al., 2014). A short period of reduction in growth during summer and early autumn was characteristic in both males and females caught in Skallelva 2019, Skallelva 2021 and Central Norway 2021. This seems a typical trait of growth in pink salmon that is not seen in Atlantic salmon (McCarthy et al., 2008; Todd et al., 2014). The three periods of growth during summer, autumn and winter seems to have different impact on length of fish at river entry.

Overall, males had larger body length than females. Body size at spawning is important for both sexes, but for different reasons; larger males may outcompete smaller males, and larger females produce more eggs than smaller females. Males may invest their energy in growth and grow longer, and development of the jaw also add to them having larger body length than females. In Skallelva, females caught in 2021 had larger total body length, higher number of circuli and larger scale length than in 2019, while there was no difference in total body length, number of circuli or scale length of males between 2019 and 2021. Weight was no used as a variable in this study due to frozen samples from Central Norway that may have biased the weight measurements.

The difference in annual comparison of total body length, number of circuli and scale length between males and females was surprising and difficult to explain. Total body length at spawning is important for both sexes. It has been shown that males and females of Atlantic salmon have different strategies in how they respond in growth to different growth conditions at sea (Tréhin et al., 2021), but sexual dimorphism in marine growth of Atlantic salmon and pink salmon is not directly comparable, since Atlantic salmon is more flexible regarding how many years they spend at sea before spawning. Spidle et al. (1998) found that males and females of coho salmon (*O. kisutch*) in the Pacific Ocean had different strategies of growth related to survival. The growth strategy of females in their study benefitted larger size but higher mortality, while in males the strategy benefitted smaller size but greater survival. The results above indicate that there are both individual, regional and annual differences in growth features of pink salmon. This was evident in the present study where comparison between fish caught in 2021 show that fish caught in Central Norway were smaller than fish caught in Skallelva, and there was large individual variation in number of circuli and scale length. Catch method may have influenced the sample selection as angling and harpooning are more selective to aggressive fish, and seine nets are selective in that smaller sized fish may have escaped. Catch period throughout the spawning season may also have had an effect on the sample selection, as length in males increase when they develop the jaw.

The growth pattern from sea entry to winter in fish caught in Skallelva 2021 and Central Norway 2021 did not differ from the pattern seen in Skallelva 2019, as first described in Paulsen et al. (2021), and seen in studies of growth pattern in the Pacific Ocean Kaev (2015a, 2015b). The first period of growth was characterized by declining circuli spacing. Several studies of pink salmon in the Pacific Ocean refer to this period as the coastal period, where pink salmon stay in shallow water to avoid predation and feed on smaller prey (Beamish, 2012; Walker et al., 1998). This period of reduced growth may be a transition to other habitats, or the growth may be limited by type of prey present in the habitat where they stay.

The second period of growth was characterized by an increase in growth that stabilized at approximately the same circuli spacing as the first couple of circuli. The shift from declining to increasing circuli spacing may be related to a shift in prey size and type, to more energy efficient food items. As pink salmon migrate from shallow waters to open ocean, their prey size increase with increasing body size (Radchenko et al., 2018). This shift is by many authors referred to as the “critical period” of growth (Beamish & Mahnken, 2001; Murphy et al., 1998; Parker, 1968). Kaev and Irvine (2016) argued that this period of growth may determine abundance of returning pink salmon.

The third period of growth was characterized by stable growth in what we assume was autumn to winter, resulting in declining growth during winter. The circuli spacing was at its lowest in the winter zone, forming a narrow band of circuli. Variation in circuli spacing between fish caught in Skallelva 2019, Skallelva 2021 and Central Norway 2021 seem to be lower in this period than the summer and autumn growth. Growth beyond the winter zone was not included in this study, as the outer edges of scales were eroded due to capture close to spawning. As the early period of marine growth is important for survival and abundance, this period is often studied, but it does not exclude the importance of growth from winter to river entry. Further studies of growth in scales of pink salmon in the North Atlantic Ocean and

Barents Sea should aim to include the late marine growth period, but scales would have to be collected at an earlier stage prior to spawning before they start eroding.

The difference in growth between Skallelva 2019, Skallelva 2021 and Central Norway 2021 seemed to be smaller during winter than in the earlier marine periods. This may indicate that pink salmon in the different groups experienced similar growth conditions in this period. Constraints in feeding ratio and digestion rate during dark and cold conditions may for instance generally restrict the growth during the winter period. Individual variation in growth during winter seemed smaller than in other periods. Variation in growth between Skallelva 2019, Skallelva 2021 and Central Norway 2021 before the winter zone seemed larger, but more studies are needed to determine if pink salmon returning to different areas and rivers in the North Atlantic Ocean and Barents Sea have different migrating routes during their marine life stage.

Overall, number of circuli and scale length to the end of the winter zone were positively correlated with total body length. The relationship between total body length and number of circuli is still being debated, as there are uncertainties about the exact rate of circulus formation (Kaev, 2015a). Courtney et al. (2000) found that the average time between each circuli formation was 7.4 days. The range of number of circuli in pink salmon caught in Norwegian rivers were 15-27. With a circuli formation every 7.4 days, the period of growth from sea entry to winter would be 111-200 days, or 3-7 months. Assuming that the first circuli was formed at sea entry in late spring or early summer, and the winter zone was formed in January (Bilton & Ludwig, 1966; Muladal, 2018; Pearson, 1966), closer to 7 months was consistent with the period of early marine growth in the present material.

Total body length of females caught in Skallelva 2019 had no correlation with number of circuli or scale length. This may be explained by a lack of observations, as the data only consisted of 20 females caught in Skallelva 2019. Number of circuli in females from Skallelva 2019 was lower than females caught in Skallelva 2021 and Central Norway 2021.

Overall, the first period at sea explained some part of fish size at river entry, while the second and third period, from fall to winter, explained a larger part of fish size at river entry. Growth during autumn was most important for size at river entry of fish caught in Skallelva 2019, which differed from fish caught in Skallelva in 2021 and Central Norway in 2021 who relied more on both autumn and winter growth. It may be that the growth conditions at sea differed between the two years, resulting in winter growth having more effect on size at river entry for fish caught in 2021. The present study was of surviving fish that entered rivers to spawn, fish with poorer growth in periods who died were not represented in the material.

Several studies have found that winter growth was most important for adult fish size (Beamish & Mahnken, 2001; Myers, 1994; Rogers, 1984). This corresponds well with the result in the present study. Growth during the first few weeks at sea may not be as important for adult fish size, rather this period may determine mortality and thereby abundance of returning pink salmon (Beamish & Mahnken, 2001; Mortensen et al., 2000; Murphy et al., 1998; Parker, 1968). Growth pattern in pink salmon from the Pacific Ocean must be carefully interpreted to reflect growth in pink salmon residing in the North Atlantic Ocean and Barents Sea, as environmental differences may affect how an introduced population respond compared to a donor population (Kennedy et al., 2005; Whitney & Gabler, 2008). Studying growth in the marine period of pink salmon in the Northern Atlantic Ocean and Barents Sea may indicate critical periods of growth and what factors may influence them.

5 Conclusion

The results of this study show that growth conditions for pink salmon at sea varied between the years, and individual variation was large. The growth pattern shows reduced growth over the first period at sea when pink salmon is believed to stay in coastal areas, followed by increased growth towards autumn and another growth period of reduced growth during winter. The autumn and winter growth had more effect on fish size at river entry than the first period of marine growth.

Further studies should aim to include data on biotic and abiotic factors at sea and spatial distribution of pink salmon through seasons together with time series of growth. This may contribute to the understanding of how variation in the marine environment influence the pink salmon population in the Barents Sea and Atlantic Ocean.

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Appendix

Appendix 1 Data samples

Table 1 Captured pink salmon in Norwegian rivers summer of 2019 and 2021. Data for Skallelva 2019 are from Paulsen et al. (2021) and included for comparisons.

County	River	Date	Equipment	N
Troms and Finnmark	Skallelva	14.08 – 19.08 2019	Seine net and angling	48
	Skallelva	18.07 - 29.08 2021	Seine net, angling and harpoon	260
Nordland	Storelva Tosbotn	09.08 - 29.08 2021	Angling and harpoon	32
Trøndelag	Gaula	05.08.2021	Angling	1
	Namsen[1]	03.06 - 21.08 2021	Seine net, angling and harpoon	27
	Nidelva in Trondheim	22.07 - 29.08 2021	Angling	12
	Nordalselva	18.07.2021	Angling	1
	Orkla	18.07 - 31.08 2021	Angling	4
	Skauga	23.07 - 19.08 2021	Angling and harpoon	14
	Stjørdalselva	08.09.2021		2
	Stordalselva in Åfjord	18.08 - 19.08 2021		17
	Verdalselva	21.07.2021		1
Møre and Romsdal	Eira	15.07 - 08.08 2021	Angling and harpoon	8
	Oselva (Osenvassdraget) in Molde	03.07 - 30.07 2021	Harpoon	15
	Stordalselva	10.07 - 31.07 2021	Angling and harpoon	7
	Storelva in Årestdalen (Søre Vartdal) in Ørsta			10
	Sylte-/Moaelva	16.08.2021	Harpoon	8
	Tressa	12.07 - 29.08 2021	Harpoon	19
	Vatnevassdraget	09.08.2021	Harpoon	5
	Vikelva	07.07 - 18.09 2021	Angling	17
	Ørstaelva (Storelva)	08.07 - 26.08 2021	Angling and harpoon	32

[1] 18 of the observations in Namsen were caught with seine net close to the river mouth

Appendix 2 Data summary

Table 2 Number of circuli, length of scale (mm) from center of focus to end of winter zone and average of circuli spacing (mm) given as mean ± SD and range. Pink salmon was sampled in Skallelva 2019, Skallelva 2021 and Central Norway 2021. Data for Skallelva 2019 are from Paulsen et al. (2021) and included for comparisons.

			Number of circuli (n)			**Scale length (mm)**			**Mean circuli spacing (mm)**		
Region/Year	**Sex**	**N**	**Mean**	**SD (±)**	**Range (min-max)**	**Mean**	**SD (±)**	**Range (min-max)**	**Mean**	**SD (±)**	**Range (min-max)**
Skallelva 2019	Female	20	19	2	16-24	0.715	0.07	0.505-0.84	0.035	0.009	0.014-0.064
	Male	28	19	3	15-25	0.751	0.139	0.533-1.019	0.036	0.009	0.014-0.069
	Total	48	19	2	15-25	0.736	0.116	0.505-1.019	0.035	0.009	0.014-0.069
Skallelva 2021	Female	76	20	2	15-26	0.776	0.106	0.526-1.11	0.036	0.009	0.001-0.067
	Male	129	20	2	15-26	0.77	0.093	0.567-1.027	0.036	0.009	0.007-0.064
	Total	205	20	2	15-26	0.773	0.098	0.527-1.11	0.036	0.009	0.001-0.067
Central Norway 2021	Female	79	20	2	16-27	0.786	0.114	0.545-1.166	0.036	0.009	0.013-0.064
	Male	110	21	2	16-25	0.812	0.11	0.559-1.109	0.037	0.01	0.013-0.07
	Total	189	21	2	16-27	0.801	0.112	0.545-1.166	0.037	0.01	0.013-0.07
Total		**442**	**20**	**2**	**15-27**	**0.78**	**0.108**	**0.505-1.166**	**0.036**	**0.009**	**0.001-0.07**

Appendix 3 Growth pattern

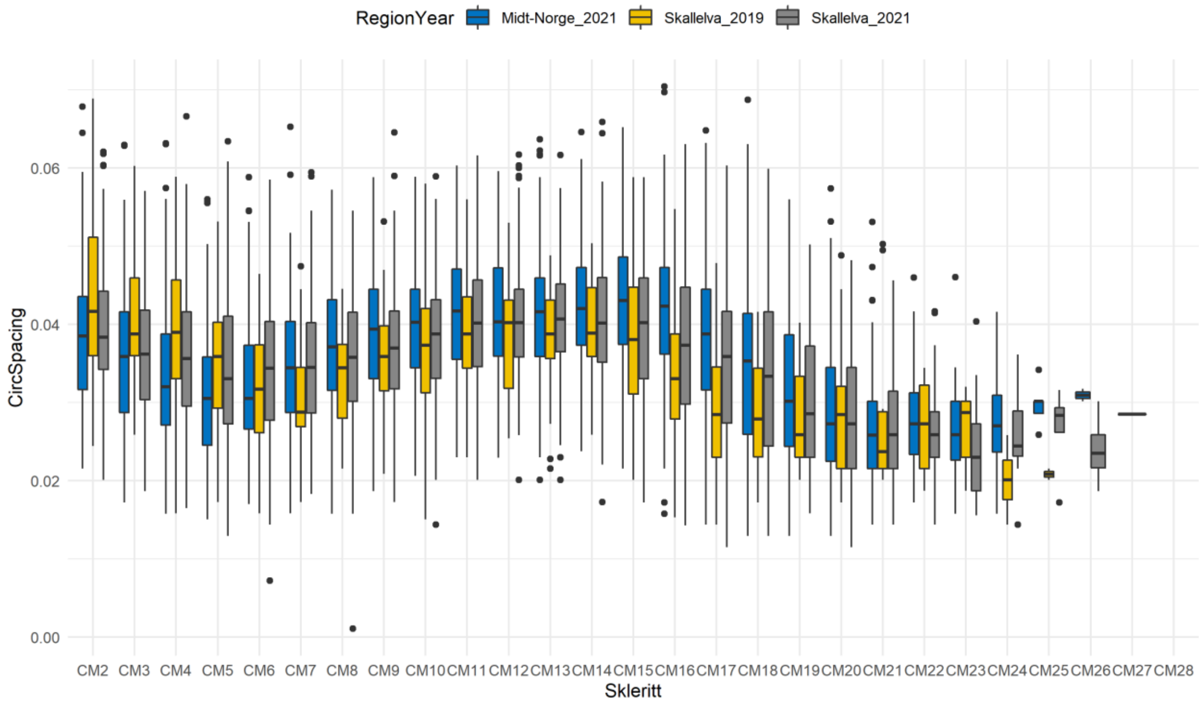

Figure 1 Growth rate of individual circulus shown for Skallelva 2019, Skallelva 2021 and Central Norway 2021. Data for Skallelva 2019 are from Paulsen et al. (2021) and included for comparisons.

Appendix 4 Comparison of means

*Table 3 Test statistics of comparison of means of total body length (mm), number of circuli (n), scale length (mm) and mean circuli spacing (mm) in variables within males and females caught in Skallelva 2019, Skallelva 2021 and Central Norway 2021. Significance codes: < 0.001 = ***, < 0.01 = **, < 0.05 = *, < 0.1 = .. Data for Skallelva 2019 are from (Paulsen et al., 2021) and included for comparisons.*

1 = pairwise.wilcox.test
2 = games_howell_test

Variable	Group	(intercept)		p	Level of significance	Test
Total body length (mm)	**Females**	Skallelva 2021	Central Norway 2021	< 0.001	***	1
		Skallelva 2021	Skallelva 2019	< 0.001	***	1
	Males	Skallelva 2021	Central Norway 2021	< 0.001	***	1
		Skallelva 2021	Skallelva 2019	0.09	.	1
	Skallelva 2019	Females	Males	< 0.001	***	2
	Skallelva 2021	Females	Males	< 0.001	***	2
	Central Norway 2021	Females	Males	< 0.001	***	1, 2
Number of circuli	**Females**	Skallelva 2021	Central Norway 2021	0.67		1
		Skallelva 2021	Skallelva 2019	0.01	**	1
	Males	Skallelva 2021	Central Norway 2021	< 0.01	**	1
		Skallelva 2021	Skallelva 2019	0.42		1
	Skallelva 2019	Females	Males	> 0.1		1, 2
	Skallelva 2021	Females	Males	0.18		1
	Central Norway 2021	Females	Males	0.3		1
Scale length	**Females**	Skallelva 2019	Skallelva 2021	< 0.05	*	
		Skallelva 2021	Central Norway 2021	0.57		
	Males	Central Norway 2021	Skallelva 2021	< 0.01	**	2
		Skallelva 2019	Skallelva 2021	0.75		2
	Skallelva 2019	Females	Males	0.26		2
	Skallelva 2021	Females	Males	0.66		

	Central Norway 2021	Females	Males	0.11
Circuli spacing	**Females**	Skallelva 2019	Skallelva 2021	0.45
		Skallelva 2021	Central Norway 2021	0.58
	Males	Skallelva 2019	Skallelva 2021	0.29
		Skallelva 2021	Central Norway 2021	0.19
	Skallelva 2019	Females	Males	0.72
	Skallelva 2021	Females	Males	0.26
	Central Norway 2021	Females	Males	0.13