





Growth of invasive pink salmon (*Oncorhynchus gorbuscha*) at sea assessed by scale analysis

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Abstract

Invasive pink salmon (*Oncorhynchus gorbuscha*) has been present in variable, but low, numbers in Norwegian waters since c. 1960, but beginning in 2017 their numbers have exploded in rivers in northern Norway, with considerable numbers also recorded in rivers in southern Norway and other countries bordering the North Atlantic. Analysis of pink salmon scales from two rivers draining to the western Barents Sea showed declining growth during the first weeks after entering the sea, and some individuals even showed a pronounced growth arrest, based on detailed scale circulus analyses. This was followed by a period of growth increase and stability during late summer and autumn, which may reflect a transition to better food sources, as the fish migrate from coastal waters to the open ocean, and as they grow larger and can eat larger and more energy efficient food items. Growth declined to a minimum during winter. Fish body size at spawning was positively correlated with the distance from scale focus to the last winter circulus, as well as with the number of circuli. When dividing scale growth into three periods, better growth during the first period at sea was related to increased fish body length at spawning, but this early growth explained only a minor part (6%) of the variation in final body length. The reason for this may be large individual variation in growth combined with large mortality during the first weeks at sea. If mortality is selective, removing fish with poor growth may reduce a correlation between early growth and body size at spawning. Scale growth during late summer and early autumn explained more of the variation in fish length at spawning (27%). Hence, late summer and early autumn was likely an important period for marine growth and survival in the invasive pink salmon.

KEYWORDS

Barents Sea, invasive species, North Atlantic Ocean, pink salmon, scale analysis, sea growth

1 | INTRODUCTION

Invasive alien species are among the most prominent threats to native biodiversity and ecosystems (Pejchar & Mooney, 2009; Rahel, 2002).

Their impact on native biodiversity is associated with predation, competition, hybridization, energy transfer and transfer of parasites and diseases. Pink salmon (*Oncorhynchus gorbuscha*) is an anadromous salmonid originating in the North Pacific. With an aim to establish a

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fishery resource, it was purposely introduced to rivers in the White Sea area in north-west Russia, which has resulted in the establishment of self-sustaining populations (Sandlund *et al.*, 2019). A secondary spread has resulted in regular spawning of pink salmon in rivers close to the Russian border in northern Norway in recent years (Berntsen *et al.*, 2020; Niemelä, 2016; Sandlund *et al.*, 2019).

From 2017, the abundance and distribution of invasive pink salmon in Norway increased dramatically (Sandlund *et al.*, 2019; Berntsen *et al.*, 2020, NINA, unpublished data), while also spreading to numerous rivers in other countries draining into the North Atlantic Ocean, including Sweden, Denmark, the United Kingdom, Ireland, Iceland, Germany, France, the Faroe Islands and Greenland (*e.g.* Armstrong *et al.*, 2018; Millane *et al.*, 2019; Nielsen *et al.*, 2020).

There are serious concerns that the establishment of invasive pink salmon will have considerable impacts on native salmonids and the ecosystems (Copp, 2017; Dunlop *et al.*, 2020; Hindar *et al.*, 2020). In its native range, pink salmon is known to be a species that can be very abundant and greatly impact freshwater, marine and terrestrial ecosystems (*e.g.* Ruggerone & Nielsen, 2004; Willson & Halupka, 1995). Invasive pink salmon has shown that ability to occur in large numbers, with several thousand pink salmon occurring in some small catchments in northern Norway (Berntsen *et al.*, 2020, NINA, unpublished data). Information on life history, population dynamics, survival bottlenecks and potential impacts of invasive pink salmon in and around the North Atlantic Ocean and Barents Sea is scarce.

The reasons for the sudden increase in invasive pink salmon from 2017 are not known. However, in a variety of examples from many taxonomic groups, introduced species may experience a substantial lag time until there is an explosion in abundance (Crooks & Soulé, 1999), as we have seen in pink salmon. Pink salmon originating from a southern river in Sakhalin were released in north-west Russia from the 1950s, but no self-sustaining populations were established in nature until stocking material was taken from a more northern population on the Russian Pacific, beginning in 1985 (Sandlund *et al.*, 2019). Since 2000, no stocking has occurred. Another reason for the increased abundance in recent years might be climate change and a warmer ocean in the northern areas. Abundant returns of pink salmon are correlated with ocean surface temperatures in the North Atlantic Ocean and Barents Sea, and the current increasing trends in sea-surface temperatures and reduced ice cover seem to benefit the sea survival of pink salmon in this area (Hindar *et al.*, 2020). Hence, marine conditions impacting pink salmon growth and survival may be key to understanding variation in population abundance. Studies of the growth patterns of pink salmon during the ocean phase to identify important growth periods and variation during the season may be important for disentangling potential reasons for their increase in the region.

Pink salmon typically have a strict 2-year life cycle. After spawning in rivers in August–September, all spawners die and the eggs hatch the following spring. The emerged juveniles are saltwater tolerant smolts that migrate downriver to the estuary and coastal waters, usually only a few days or weeks after hatching (Heard, 1991; Quinn, 2005). After 1 year in the ocean, the fish mature and return to rivers to spawn. Consequently, fish originating from eggs spawned in odd years will spawn in odd years, whereas even-year spawning gives

rise to even-year spawners. Odd-year pink salmon are by far the most numerous in rivers that drain into the North Atlantic Ocean and Barents Sea (Gordeeva & Salmenkova, 2011; Sandlund *et al.*, 2019; Zubchenko *et al.*, 2004).

Despite being the Pacific salmon species with the smallest body size at spawning, pink salmon have the highest growth rates at sea within this group of species. More than 95% of their adult body weight is gained in the marine phase (Heard, 1991). Growth rates at sea are important for survival during several stages. In the estuary and coastal waters, the small-sized smolts depend on rapid growth to reduce predation (Parker, 1968). Kaev (2015a) and Farley Jr. *et al.* (2020) showed that survival was positively correlated with growth rates in the early marine phase. Salmon that have reached sufficient size and energy reserves during summer and autumn may have higher survival rates during the subsequent winter at sea (Beamish & Mahnken, 2001). Thus, survival at sea is linked to marine ecosystem conditions, particularly water temperatures optimal for growth, and the quantity and quality of available prey (Moss *et al.*, 2005; Radchenko *et al.*, 2018). Studies of marine growth and survival have been performed in the native range in the Pacific Ocean (Kaev, 2015a, 2015b; Myers, 1994; Radchenko *et al.*, 2018). Studies from the north Pacific Ocean may not be representative for the descendants of introduced pink salmon that migrate to the Barents Sea and North Atlantic Ocean, where environmental conditions are different.

Growth in salmonids, including pink salmon, can be recorded by analysing their scales (Dahl, 1910). The distance between circuli in the scale reflects the growth rate of the fish (Courtney *et al.*, 2000). Kaev (2015b) found a positive correlation between pink salmon size and the scale circuli spacing. Thus, analysing the distance between circuli in pink salmon scales can reveal the growth rate during the various life stages. Here, we used scale analyses to assess the growth patterns of invasive pink salmon in north-eastern Norway up to and including the winter period at sea. The aim was to describe the marine growth patterns of pink salmon during this period and to investigate how the detected growth pattern in scales was correlated to the body size of the returning spawners. As is the case in their native waters, we hypothesised that the body size of returning pink salmon spawners would be positively associated with growth patterns, as observed in their scales.

2 | MATERIALS AND METHODS

Pink salmon were collected with gill nets (mesh size 65 mm knot-to-knot) in August 2019 in the rivers Skallelva and Vesterelva, in eastern Finnmark, northern Norway (Figure 1). Skallelva (70.11°N, 30.20°E) drains a catchment area of 259 km² and has a mean annual water discharge of 5.5 m³ s⁻¹. Vesterelva (70.09°N, 28.30°E) drains 277 km² and has a mean annual water discharge of 2.5 m³ s⁻¹ (Sandlund *et al.*, 2019).

Scale samples were collected from 132 fish in Skallelva and 60 fish in Vesterelva. Scale samples were taken near the lateral line posterior to the dorsal fin (Bilton, 1985; Major *et al.*, 1972). All fish were weighed to the nearest 0.05 kg, measured in length to the nearest cm and the sex

FIGURE 1 The location of the rivers Vesterelva (outlet coordinates 70°09'N, 28°34'E) and Skallelva (outlet coordinates 70°11'N, 30°20'E) in north-eastern Norway, where pink salmon (*Oncorhynchus gorbuscha*) spawners were sampled



was determined. A large proportion of the sampled fish was relatively small; 38 fish (21%) were below 1.00 kg and five of these fish were at 0.5 kg or less. Sex and gonad development stage were determined by opening the fish, and 3% (six fish) had gonads under development, 68% (131 fish) were ready for spawning and 29% (56 fish) had spawned. As the presence or absence of mature gonads impacts the body weight of the fish, the analyses in this paper were mainly based on the body length of the fish. Scale samples were obtained by dissecting pieces of skin, which were stored frozen until analysed.

For analysis, eight to 12 readable scales from each fish were selected and placed in microscope glue (Kaiser's Glycerol Gelatine, Karlsruhe, Germany) on a microscope slide under a stereo microscope (Leica M60, Wetzlar, Germany). Scales from only 87 of the total 182 fish were in a condition that allowed reliable analysis (Table 1). The reason for the many discarded samples was the advanced stage of erosion of scales, likely because the samples were collected immediately before, during or shortly after spawning. The scale erosion appeared to start at the outer scale edge, but continued to affect the entire scale area, eventually making it difficult to identify reliably the central area laid down when the scale was first formed on the juvenile fish (focal area) and the first circulus. The mean length and weight of fish with scales that could be analysed ($n = 87$) were 48.8 cm and 1.1 kg, whereas for the remaining fish ($n = 94$) the corresponding values were 47.9 cm and 1.0 kg. The two groups were not significantly different in length (independent-samples t -test $t = 1.5$, $P = 0.14$), but the omitted fish had significantly lower weight than the fish that could be analysed ($t = 2.2$, $P = 0.03$). The difference in

weight was small, however, and could probably be due to the fact that fish with heavily eroded scales (*i.e.*, those omitted) were closer to spawning and therefore could have lost more weight than the fish with less eroded scales.

The scales were photographed under a stereo microscope (Leica Z6 APO, Wetzlar, Germany) with a NIKON Digital Sight DS-Ri1 camera (Nikon, Tokyo, Japan) and NIS-Elements F imaging software (Nikon, Melville, NY, USA), and analysed with Image-Pro Plus software (Media Cybernetics, Silver Spring, MD, USA). All pictures were taken at $\times 40$ magnification. The distance from the visually determined centre of the focus area to the last circulus in the winter zone (defined as the section with the shortest circuli spacing; Todd *et al.*, 2014) was defined as the total scale diameter (mm) used in the analysis (Figure 2). The number of circuli was counted from the focus area up to and including the winter zone. The first circuli spacing was measured (mm) from the first circulus bordering the focus area to the next circulus, *etc.* (Figure 2), following the protocol of Bugaev (2004) and Bilton (1972).

The relationship between fish length and weight as response variables, and total scale diameter, number of circuli within this distance and mean circuli spacing as explanatory variables was assessed with linear regression analyses. We used univariate regression analysis, in which we fitted each response variable to the explanatory variable in separate models. We used $\alpha = 0.05$ as a threshold for statistical significance.

The relationship between the different growth periods and the adult body size of the fish at capture during the spawning season was

Locality	Sex	n	Length (cm)		Weight (kg)	
			Mean \pm s.d.	Range	Mean \pm s.d.	Range
Skallelva	Male	28	51 \pm 5.2	40–61	1.3 \pm 0.5	0.55–2.7
	Female	20	46 \pm 2.7	41–50	0.9 \pm 0.2	0.55–1.3
	Total	48	49 \pm 5.0	40–61	1.1 \pm 0.5	0.55–2.7
Vesterelva	Male	15	51 \pm 4.8	43–59	1.3 \pm 0.5	0.35–2.3
	Female	24	48 \pm 2.4	44–52	1.0 \pm 0.4	0.35–1.7
	Total	39	49 \pm 3.7	43–59	1.1 \pm 0.5	0.35–2.3
Total		87	49 \pm 4.4	40–61	1.1 \pm 0.5	0.35–2.7

Note: n, sample size in terms of number of fish with readable/valid scale samples; s.d., standard deviation. Range is given as minimum–maximum values.

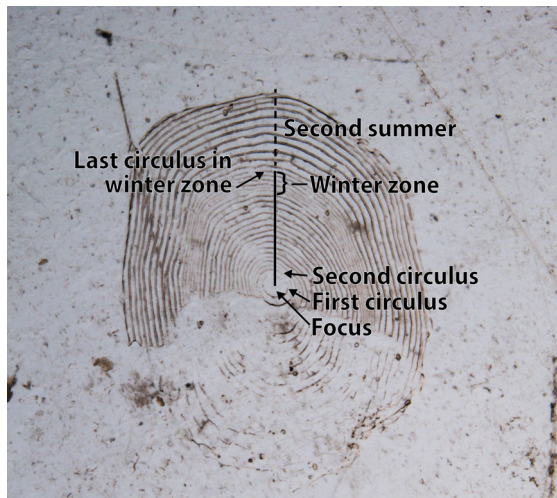


FIGURE 2 Pink salmon (*Oncorhynchus gorbuscha*) scale with radii used for measurements indicated. The first circuli spacing (cf. Figures 3 and 4) is from the first circulus at the edge of the focus area to the second circulus. The winter zone is the group of the most tightly spaced circuli. In the total material, the mean distance (\pm s.d.) from the first circulus up to and including the winter zone was 0.652 \pm 0.102 mm (cf. Table 2)

investigated by dividing the total number of circuli from the focus area up to and including the winter zone by three. Period 1 is the distance across one-third of the circuli counted from the focus area, period 2 is the distance over the central third of the circuli and period 3 is the distance over the last third of the circuli up to and including the winter zone. The relationship between each of these distances and the body size of the fish was assessed using linear regression as described above.

2.1 | Ethical statement

Samples were taken from invasive pink salmon, which were captured to be destroyed with permission from the County Governor of Troms and Finnmark (in letter dated 13 June 2019,

TABLE 1 Overview of pink salmon (*Oncorhynchus gorbuscha*) sampled for scale analyses in the rivers Skallelva and Vesterelva, north Norway, in 2019

ref. 2019/6126) to protect native salmonids spawning in these rivers.

3 | RESULTS

When pooling data from all individual fish, the distance from the focus up to and including the winter zone of the scales was on average 0.653 mm (range 0.427–0.942 mm, s.d. 0.104; Table 2). The mean number of circuli in this area was 18 (range 14–26, s.d. 2, median 18) and the mean circuli spacing was 0.036 (range 0.014–0.069 mm, s.d. 0.009). There were no significant differences between rivers or between males and females, or interactions between river and sex in any of these parameters (ANOVAs: distance from focus to winter zone $F = 1.18$, $P = 0.32$, $r^2 = 0.041$; number of circuli $F = 0.55$, $P = 0.65$, $r^2 = 0.019$; mean circuli spacing $F = 0.35$, $P = 0.79$, $r^2 = 0.013$).

The growth rate, as indicated by circuli spacing, varied from the point of scale formation until the end of the winter (Figure 3). The mean distance from the scale focus to the first circulus was 0.043 mm, whereas the mean spacing between circuli 5 and 6, which represents the first narrow circuli spacing, was reduced to 0.032 mm. There was large individual variation in growth rates at this early stage, and the spacing between circuli 5 and 6 varied from 0.015802 to 0.062123 mm. The minimum values might be interpreted as a growth arrest. There was a subsequent increase in circuli spacing to 0.039 mm until circulus 11 (Figure 3). Further, circuli spacing remained stable from 11 to 13 before declining towards the winter (Figure 3). Because not all scales had more than 15 circuli, the development of scale growth between circuli 16 and 26 is based on declining sample sizes, and the last circuli spacings, representing winter growth, are based on scales from very few fish (one to three individuals) (Figure 3).

The varying number of circuli among fish is an analytical challenge. We therefore analysed separately the first 10 and the last 10 circuli in each scale sample within the area from scale formation until the end of the winter (Figure 4). The first 10 circuli spacings represent marine growth from scale formation through summer, while the last 10 circuli spacings likely represent the marine growth in autumn and winter. The last four circuli spacings represent winter,

TABLE 2 Total scale diameter, number of circuli and circuli spacing of pink salmon (*Oncorhynchus gorbuscha*) scales from Skallelva and Vesterelva, north Norway

	<i>n</i>	Total scale diameter (mm)		Number of circuli		Circuli spacing (mm)	
		Mean ± s.d.	Range	Mean ± s.d.	Range	Mean ± s.d.	Range
Skallelva							
Males	28	0.656 ± 0.129	0.441–0.908	18 ± 3	14–24	0.036 ± 0.009	0.014–0.069
Females	20	0.621 ± 0.067	0.427–0.738	18 ± 2	15–23	0.035 ± 0.009	0.014–0.064
Total	48	0.642 ± 0.108	0.427–0.908	18 ± 2	14–24	0.035 ± 0.009	0.014–0.069
Vesterelva							
Males	15	0.673 ± 0.056	0.553–0.768	19 ± 2	16–23	0.036 ± 0.009	0.017–0.057
Females	24	0.663 ± 0.118	0.470–0.942	18 ± 3	15–26	0.036 ± 0.009	0.014–0.062
Total	39	0.667 ± 0.098	0.470–0.942	18 ± 2	15–26	0.036 ± 0.009	0.014–0.062
Total	87	0.653 ± 0.104	0.427–0.942	18 ± 2	14–26	0.036 ± 0.009	0.014–0.069

Note: *n*, sample size in terms of number of fish with readable/valid scale samples; s.d., standard deviation.

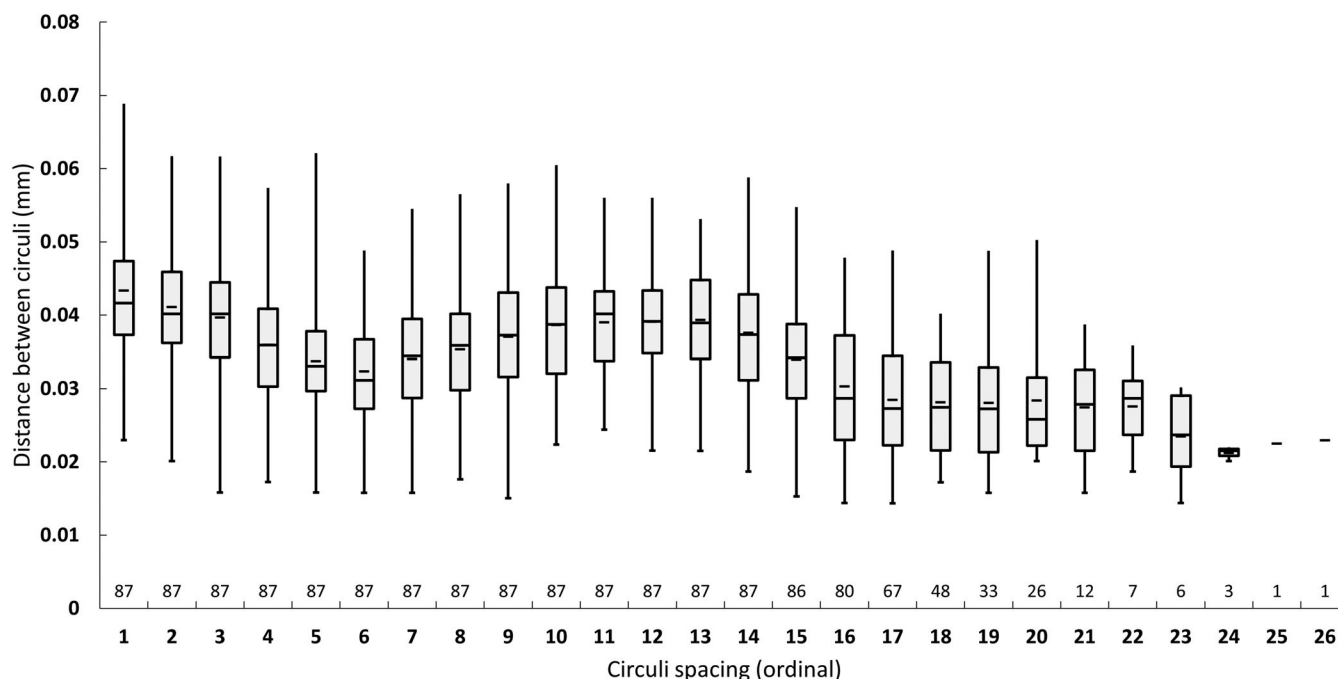


FIGURE 3 Box plot of the circuli spacing from the first circulus at the focus area up to and including the winter zone in pink salmon scales. Circulus spacing 1 is the distance between the first and the second circulus, circulus spacing 2 is the distance between the second and third circulus, and so on. The box area is between the first and third quartile, the horizontal bar is the median value, the hyphen is the mean value and the vertical lines indicate minimum and maximum values. Note that due to the varying number of circuli among fish, the number of measurements declines from circulus 15

with a substantial decline in growth rate. Overall, the average values for the six circuli spacings during autumn were stable at 0.037–0.039 mm. In contrast, the last circuli spacing in winter was on average 0.023 mm.

There were slight differences in scale growth between males and females, and between the two rivers (Figure 4). The mean distance from the first to the second circulus (circuli spacing I1 in Figure 4a–d) varied, being 0.045 mm in males in Skallelva, 0.043 mm in females in Skallelva, 0.042 mm in males in Vesterelva and 0.043 mm in females in Vesterelva. Variation in this parameter was greatest in males from

Skallelva (between 0.037 and 0.055 mm from the first to the third quartile; Figure 4a, circuli I1).

Separate analyses of data from males and females from the two rivers revealed only slight differences between groups (Figure 4a–d). The development in circuli spacing between the first 10 circuli in all four groups mirrors the total material, with declining distances from circuli spacing I1 to I6 or I7. However, the rate of change was somewhat different among groups. In males from Skallelva (Figure 4a), mean circuli spacing declined from 0.045 (circulus I1) to 0.029 (circulus I6). In females from Skallelva and both sexes from Vesterelva,

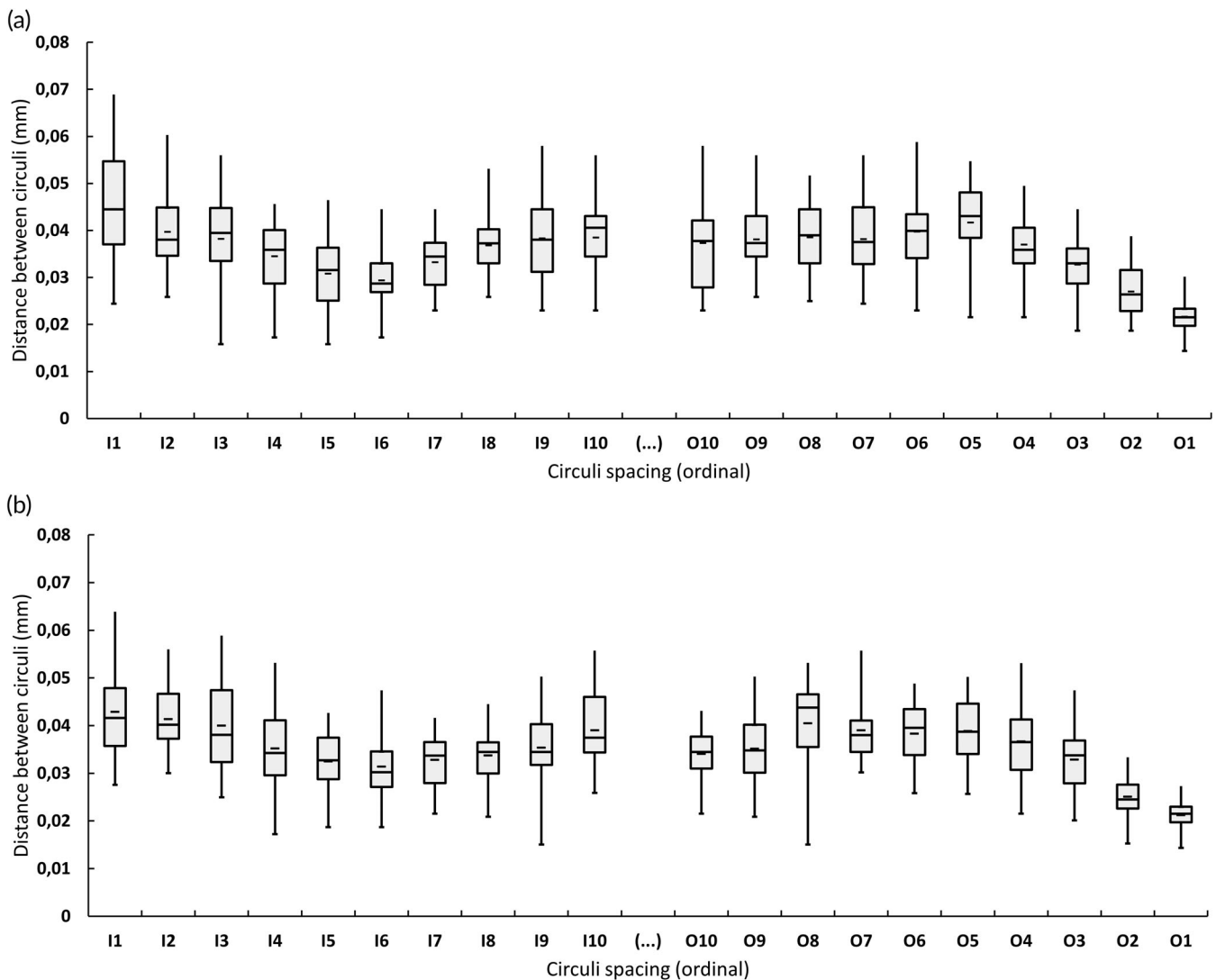


FIGURE 4 Box plot of the circuli spacing from the focus up to and including circulus 10 (named I1 to I10, left-hand part of graphs) and circuli spacing for the last 10 circuli up to and including the last winter circuli of the same pink salmon scale samples (named O10 to O1, right-hand part of graphs). (a) Skallelva males; (b) Skalleva females; (c) Vesterelva males; (d) Vesterelva females. Circulus spacing I1 is the distance between the first and second circulus from the focus area, circulus spacing I2 is between the second and third circulus, and so on. Circulus spacing O1 is the distance between the last and the second to last circulus in the winter zone, and so on counting backwards to circuli spacing O10. The box area is between the first and third quartiles, the horizontal bar is the median value, the hyphen is the mean value and the vertical lines indicate minimum and maximum values

this decline was less pronounced. There was a slight subsequent increase in circuli spacing up to circulus I10 (Figure 4a–d).

When examining the last 10 circuli up to and including the last winter circulus, all four groups exhibited declining growth through the last four or five circuli spacings (O5 to O1 in the right-hand section of Figure 4a–d). Before this development, there was generally a relatively stable scale growth judged from circuli spacings O10–O6.

The distance from the first circulus on the focus area to the last winter circulus and the number of circuli over this distance were significantly and positively correlated with the body length and weight of the fish when caught in the rivers (all P values <0.001 ; Table 3). However, only 19%–24% of the variation in body length was explained by these scale characters, and the explanatory power for body weight

was even poorer (16%–18%). The mean distance between circuli was not significantly correlated to fish size.

The growth pattern in scales (Figures 3 and 4) indicates that there are three periods (Figure 3) with different development in growth characteristics in the marine life of pink salmon, from the scale formation early in their life until the end of the winter. The first period indicates declining growth during the first part of marine life. During the second period, scale growth indicates stable or increasing fish growth, while the third period indicates declining growth when the fish live through autumn and winter. The body size of the fish at spawning was particularly well correlated to scale growth (cumulative circuli spacing) during the second period (fish length: $R^2 = 0.27$, $P < 0.001$; Figure 5b). Scale growth during the third period was somewhat less

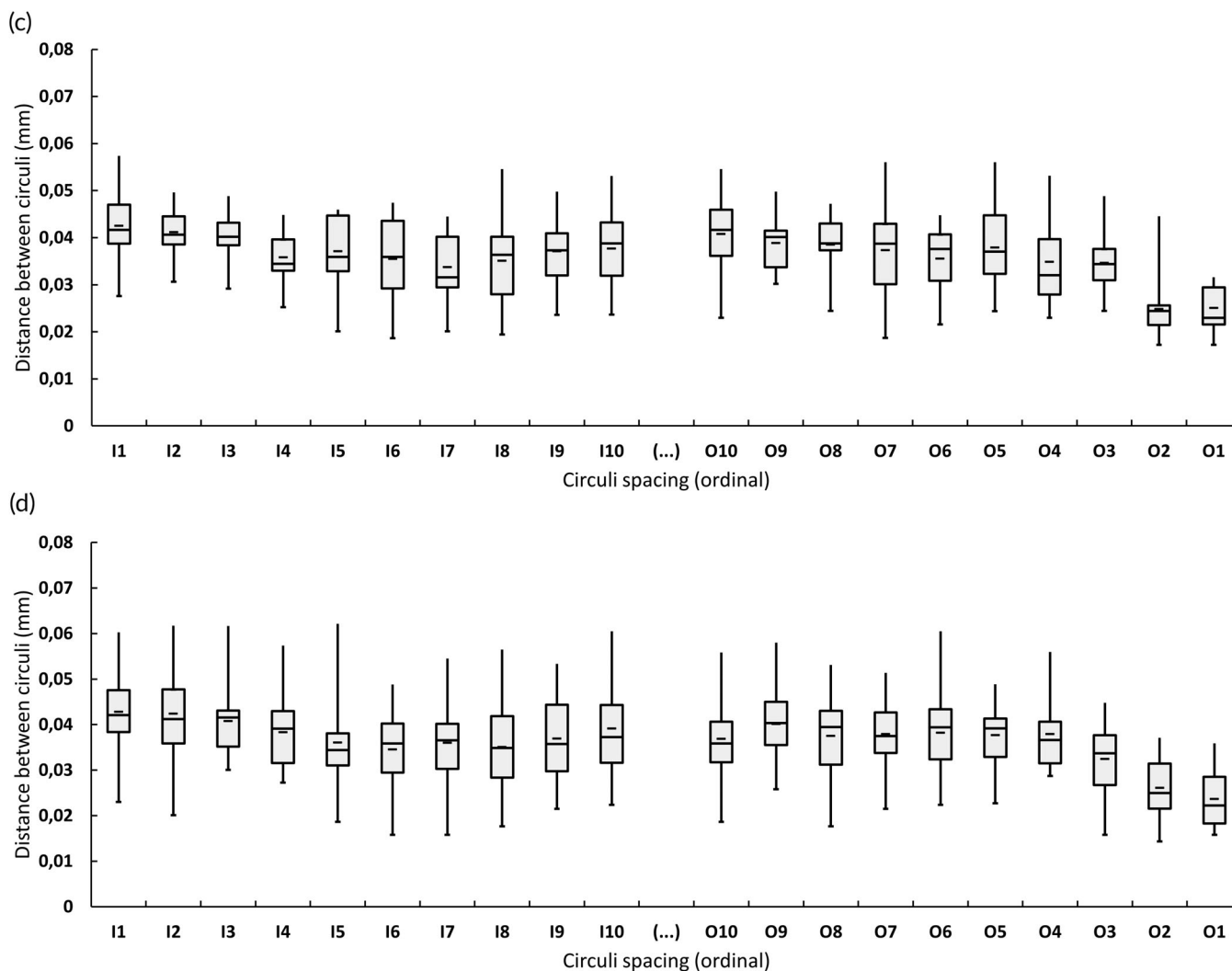


FIGURE 4 (Continued)

TABLE 3 Pearson correlation coefficients for distance from the first circulus at the focus area to the last winter circulus, the number of circuli within this area and the mean circuli spacing, correlated to pink salmon (*Oncorhynchus gorbuscha*) body length and body weight ($n = 87$)

	Focus area to winter zone		Number of circuli		Mean circuli spacing	
	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>
Length	<0.001	0.41	<0.001	0.49	0.639	0.05
Weight	<0.001	0.36	<0.001	0.43	0.451	0.08

well correlated to fish size (length: $R^2 = 0.13$, $P < 0.001$; Figure 5c), while scale growth during the first period was only weakly correlated to fish size (length: $R^2 = 0.06$, $P < 0.05$; Figure 5a). The correlation of scale growth to fish weight at spawning exhibited slightly lower correlation coefficients (Table 4).

4 | DISCUSSION

The present study demonstrates that introduced pink salmon migrating into the Barents Sea varied in their growth over time during the

first months at sea and until the end of the subsequent winter. According to the scale patterns, this period may consist of three stages: (a) declining growth, (b) stable or increasing growth and (c) declining growth. Analysis of pink salmon scales from their native area in the north-western Pacific indicates a similar temporal pattern (Kaev, 2015a, 2015b). The scale growth patterns indicated a declining growth during the first few weeks of marine life. Some individuals in the present study also showed a more pronounced growth reduction at this early stage, which might be interpreted as a growth arrest. A similar period of reduced growth after sea entry has not been documented in Atlantic salmon (e.g., Peyronnet *et al.*, 2015), but Atlantic

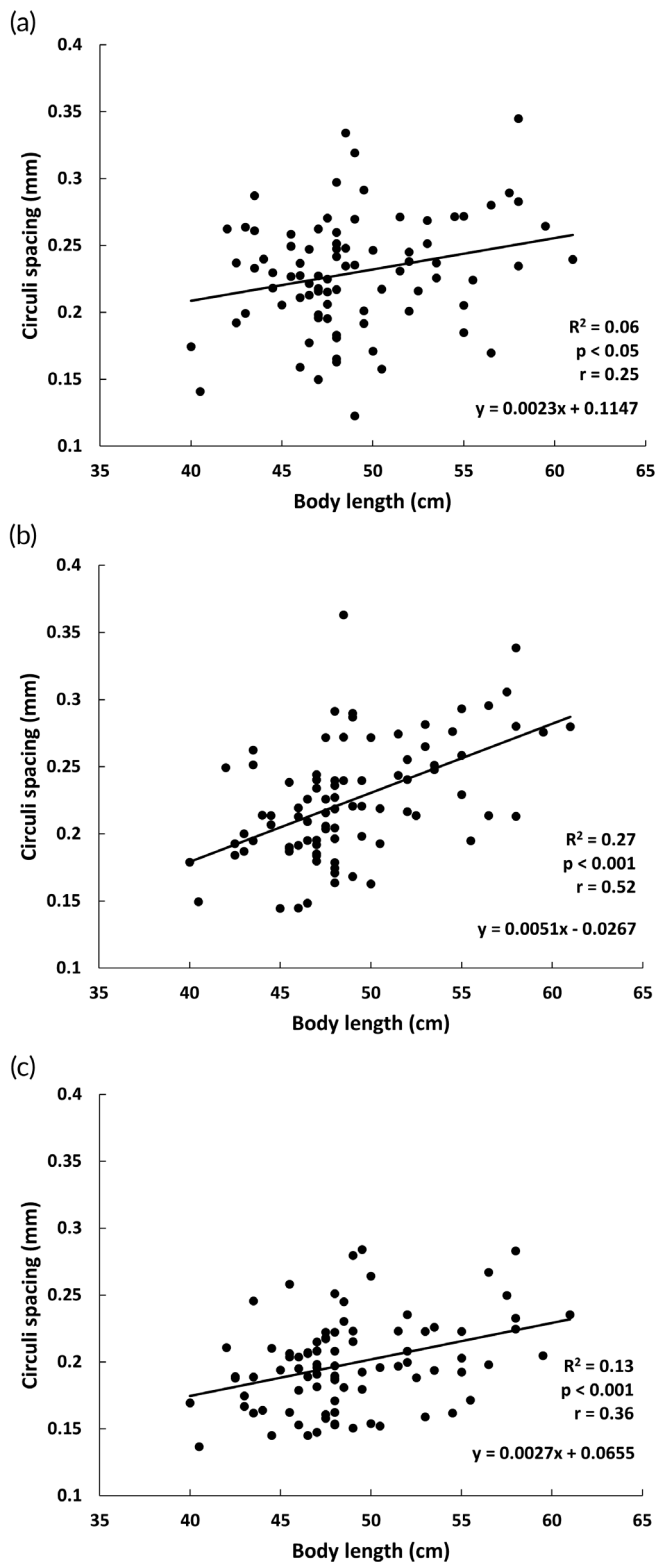


FIGURE 5 Correlation between pink salmon body length at spawning and the cumulative circuli spacing of three different periods from scale formation until the end of the winter. Period 1 is from focus over the first third of circuli, period 2 is over the second third of circuli and period 3 is the last third of circuli including the last winter circulus

TABLE 4 Correlations between pink salmon (*Oncorhynchus gorbuscha*) body weight at spawning (y) and the cumulative circuli spacing (x) of three different periods from scale formation until the end of the winter

Period	Regression line	r	P
1	$y = 0.022x + 2.205$	0.24	<0.05
2	$y = 0.043x + 0.177$	0.45	<0.001
3	$y = 0.024x + 0.172$	0.33	<0.05

Note: Periods are described in the text and in Figure 5.

salmon have a much larger body size than pink salmon when they move into saltwater, and they may stay for a shorter time period in river mouths, fjords and near-coastal areas than pink salmon. They are therefore able to utilize a wider array of prey than pink salmon smolts. After the initial decline, the scale growth of pink salmon indicated a period of stable or increasing fish growth, which likely occurred during late summer and early autumn. We suggest that this growth pattern reflects a transition to better food sources, as the fish migrate from the estuaries and coastal areas to the open ocean. As the fish grow larger, they may be able to eat larger and more energy-efficient food items. As winter approached, fish growth again decreased. This was an expected consequence of decreasing ocean temperatures and reduced feeding. A similarly reduced growth is seen in native Atlantic salmon during this time period of their marine life (Dahl, 1910; Peyronnet *et al.*, 2015). The second period, when growth was increasing, was the period when scale growth showed the highest correlation with the final body size of the pink salmon at spawning. Hence, this is likely an important period for growth, and perhaps also for survival.

The number of circuli up to and including the last winter circuli in the pink salmon scales in this study (14–26 circuli, mean 18 circuli) was similar to the results of Myers (1994) and Kaev (2015b). However, there appears to be regional and temporal variation, as Kaev (2015b) found a higher mean number of circuli ($n = 23$) in the north-western Pacific in 1997 and 2011. We are not aware of earlier studies than this in the introduced pink salmon stocks in the Barents Sea and North Atlantic Ocean.

Pink salmon smolts in Finnmark leave the rivers in May, at a body length of 30–40 mm (Muladal, 2018). Smolt size is similar in rivers in north-west Russia, although in recent years it has been documented that in some Russian rivers smolts migrate later than usual and with a larger body size (Veselov *et al.*, 2016). According to Pearson (1966), pink salmon smolts commence scale formation at a body length of ~60 mm. This would indicate that the first scale circulus was formed in late spring or early summer shortly after entering the marine environment, *i.e.*, while the fish are still in coastal waters. According to Bilton and Ludwig (1966) and Pearson (1966), the winter zone in pink salmon scales in the Pacific is formed in January. If we assume that scales of pink salmon originating in the Barents region had been growing from June to January, this would include 7–8 months or 210–240 days. Courtney *et al.* (2000) reported that formation of a

new circulus in pink salmon scales occurred every 4–8 days. If we assume the same rate of circuli formation in the present material, a growth period forming 14 circuli (the minimum number of circuli in the present study) would have lasted 56–112 days, while 26 circuli (the maximum number of circuli in the present study) would have been formed over a period of 104–208 days. This suggests that there is a quite extensive variation in the rate of circuli formation. In Atlantic salmon, the numbers and spacing of marine circuli during their first months at sea have been interpreted as indicators of variation in growth, with possible linkages to changes in size-related mortality at sea (e.g., Friedland *et al.*, 2009; Hogan & Friedland, 2010; McCarthy *et al.*, 2008; Peyronnet *et al.*, 2015). However, it has not been shown for pink salmon that circuli spacing truly reflects length increment (Kaev, 2015b). It is not known whether circuli are formed at fixed time intervals, which would imply that scale growth reflects growth in length through the full growth period, as suggested by Courtney *et al.* (2000). This warrants careful interpretation of our results.

The circuli spacing varied through the season, with a mean width of 0.036 mm. The distance from the first circulus at scale formation to the last winter circulus was 0.635 mm. This is considerably smaller than the measurements on pink salmon collected in the southern Bering Sea in 1959–1967 and 1983–1995, where the distance from the first circulus to the last winter circulus was at 0.945 and 0.942 mm, respectively (Walker *et al.*, 1998). This may partly be explained by the relatively small size of pink salmon spawners in the present study. The mean circuli spacing in the Bering Sea data was 0.044 mm (Walker *et al.*, 1998), which is more similar to our results. The smaller scale size at the end of the winter does indicate a lower growth rate during the first marine year in the Barents than in the Bering Sea.

Within the scale section with declining growth rate over the first six circuli spacings, some fish had a few very small circuli spacings, somewhat similar to the winter zone. Heard (1991) showed that this zone emerges between July and September, when the fish are about 10–18 cm long. This declining growth is probably associated with changes in environment or diet, as the fish move from coastal areas to the open sea (Myers, 1994). Todd *et al.* (2014) argues that such changes in Atlantic salmon growth are so swift that they must be caused by rapid diet shifts rather than changes in temperature, which normally happens more slowly. The growth arrest in the present data varied among individuals, being prominent in some fish and absent in others. This may indicate individual differences in migration patterns and/or diet. Differences in body size when habitat shifts occur may also have an impact on the ability to utilize food resources in a new environment.

One aim of this project was to investigate whether the body size of pink salmon spawners correlated to the various stages in the growth pattern of their scales. Both scale radius and the number of circuli from scale formation to the end of the winter zone were significantly correlated to the body size of the spawners. Thus, the growth during the first months at sea and until the end of the winter zone had an impact on the adult size of pink salmon in the investigated rivers. This differs from the results of Kaev (2015b), who did not find

any correlation between the number of circuli and the body length of the adult fish.

There was no significant correlation between mean circuli spacing and adult fish size in our data. This differs from the results of both Courtney *et al.* (2000) and Kaev (2015a), who found a strong correlation between circuli spacings and adult fish length. This comparison must, however, be treated with care, as there are some differences in the analytical methods applied. Kaev (2015b), for example, used circuli spacing as a percentage of the cumulative distance from focus to the last winter circulus. The relationship between scale circuli formation and fish growth is not entirely clear in pink salmon. For subadult fish caught in the ocean, Courtney *et al.* (2000) found better correlation between the latest circuli spacings and fish length at capture.

The correlation between cumulative circuli spacing during the first period at sea and fish body length was significant but explained only 6% of the variation. The reason for this may be large individual variation in growth combined with large mortality during the first weeks at sea. If mortality is selective, removing fish with poor growth, this may cause a poorer correlation between early growth and body size at spawning. Some fish had a pronounced decline in growth with very small circuli spacing, whereas others did not exhibit this. Bilton and Ricker (1965) claimed that approximately 30% of pink salmon from various regions in the Pacific had this extra zone of poor scale growth, somewhat similar to a winter zone. In our data set, a visual inspection of the scales may indicate a similar proportion of individuals with such retardation of growth.

It is somewhat surprising that the cumulative circuli spacing during the last third of scale growth from scale formation to the end of the winter zone was relatively poorly correlated with adult fish length (explaining 13% of the variation), whereas the middle section of scale growth during this period showed the best correlation with adult fish length (explaining 27% of the variation). This may indicate that fish growth during late summer and autumn, which determines body size at the onset of winter, is important for survival through winter. This indicates that juvenile growth at sea during the late summer and early autumn is important, but not decisive, for the size of adult fish. It appears reasonable to see this as an effect of the ability of the individual fish to respond to the feeding opportunities after the shift from coastal to oceanic waters, and that good growth during this period enables the fish to effectively utilize resources during winter and the following spring and summer, and also to experience reduced mortality due to predation.

An earlier study from the Pacific Ocean has shown that resulting size at the end of the winter zone may also be positively correlated with growth up to the onset of spawning migration and the associated sexual maturation and cessation of feeding (Heard, 1991). Differing from this, the results for Pacific pink salmon presented by Rogers (1984) and Myers (1994) indicate that scale growth during the winter period has the largest impact on adult fish size.

Previous analyses of pink salmon growth based on scale analyses have all been performed on fish from the species' native range in the Pacific. Discrepancies between our results and the results from the species' native range should be expected, as pink salmon is an invasive

introduced species in the North Atlantic and Barents Sea, and abiotic and biotic factors impacting fish growth differ among the different ocean areas. It has often been reported that populations resulting from the introduction of a species into a new environment may exhibit a number of changes in ecology and population characters compared to the donor populations. This includes pink salmon (Kennedy *et al.*, 2005; Kwain, 1987) as well as other fish species (e.g., Bøhn *et al.*, 2004). The changes may result from an adaptive (phenotypic) response to the new environment, but may also be caused by evolutionary changes (Whitney & Gabler, 2008). There have been no releases of pink salmon from the Pacific in rivers in north-west Russia since 2000 (Hindar *et al.*, 2020; Sandlund *et al.*, 2019). Thus, the pink salmon population in this region in 2017 has been exposed to selection in the new environment without interference from fish translocated from the Pacific for eight or nine generations.

In conclusion, this study showed that our hypotheses on the correlation between scale growth and fish size at spawning was only partly supported. Our results indicate that during the marine migration of invasive pink salmon, late summer and autumn may be a particularly important period for growth and survival. The data presented here provide a baseline for marine growth of pink salmon in a region with a large and apparently increasing abundance of invasive pink salmon (Berntsen *et al.*, 2020, NINA, unpublished data), from where the pink salmon are now spreading further into the North Atlantic area.

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AUTHOR CONTRIBUTIONS

T.P. initiated the project, led the field work and analysed scales. G.Ø. guided the scale analysis. O.T.S. guided writing of the manuscript, with major contributions from T.P., E.B.T. and P.F. T.P. P.F. performed the statistical tests. R.M. and S.T. helped developing the research design. All authors approved the final version of the manuscript.

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