

Article

Long-Term Trends in Freshwater and Marine Growth Patterns in Three Sub-Arctic Atlantic Salmon Populations

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Abstract: The rapid warming of the Northern hemisphere has especially challenged the evolvability of anadromous fish species, such as Atlantic salmon (*Salmo salar*), which must cope with drastically different environments depending on their life-history stage. We studied the long-term trends in, and the effects of environmental factors and life-history traits on, Atlantic salmon growth rates in both freshwater and in the ocean using c. 35,000 scale samples collected across 48 years from spawners returning to three tributaries of the subarctic River Teno in the northernmost parts of Finland and Norway (70° N). The freshwater growth has decreased in all three populations and spending more than three juvenile years in freshwater before the sea migration comes at the expense of growth. On the other hand, returning mature salmon (one-sea-winter, 1SW) showed increased growth at the sea with increasing marine temperatures, which results in larger sizes at return in 1SW spawners. We did not observe such trends in growth rates in larger, two-sea-winter salmon. Here, we report the contrasting responses in Atlantic salmon growth rates to a warming climate depending on the life-history stage.

Keywords: climate change; growth rate; marine ecosystems; river ecosystems; scales

Key Contribution: Long-term trends in Atlantic salmon growth rates in both freshwater and marine environments were studied using scale samples collected across half a century in three sub-arctic populations. The decrease in freshwater growth was associated with rising temperatures, whereas sea growth increased during the same period.



Citation: Alioravainen, N.; Orell, P.; Erkinaro, J. Long-Term Trends in Freshwater and Marine Growth Patterns in Three Sub-Arctic Atlantic Salmon Populations. *Fishes* **2023**, *8*, 441. <https://doi.org/10.3390/fishes8090441>

Academic Editor: Bror Jonsson

Received: 21 June 2023

Revised: 28 August 2023

Accepted: 29 August 2023

Published: 30 August 2023



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1. Introduction

The global climate change is affecting all natural habitats and ecosystems worldwide, and both observed and predicted effects are the most pronounced at high latitudes: the Arctic has been shown to be warming at least twice as fast as the rest of the globe on average [1]. Climate change can reduce the viability of species and the associated biodiversity loss will affect ecosystem functions and services [2,3]. Such changes may result in ecological regime shifts where functions and structures of ecosystems may change and then persist at a new equilibrium [4–6]. The adaptation capabilities of organisms under the changing climate are the key to avoid reductions in survival or reproductive rates. Adaptive responses to climate change may include physiological or behavioural changes, through phenotypic plasticity, microevolution, or their combination, that reduce the extent of mismatch between the species' phenotype and the environment [7,8].

Considering that the changing climate strongly affects various environments, anadromous fish is a special group of animal species that must cope with a variety of different habitats and highly variable environments during their life cycle, across long geographic distances and a wide salinity gradient from fresh water to full saline sea water, e.g., [9]. Such directed migrations between habitats are typically triggered by seasonal changes in the environment. The life cycle of anadromous fish typically include reproduction, egg incubation and juvenile rearing in freshwater (streams, rivers, lakes), downstream migration

through varying salinities of river outlets and brackish water estuaries, ocean migration in full sea water for effective feeding, growth, and maturation, and return migration back to freshwater for reproduction through the same environments, e.g., [10–12]. It has recently been suggested that warming climatic conditions across northern latitudes in Iceland and northern Norway have already strongly influenced the populations of anadromous salmonid fish species [13].

Atlantic salmon (*Salmo salar*, L. 1759) is an iconic, well-studied species among migratory fish that utilize and experience all the different aquatic habitats mentioned above during its life cycle. Starting from the freshwater phases of the species, changes in river temperatures are of special concern as they affect the juvenile food base and growth rate, phenology of life cycle, timing of migrations, reproductive success of spawners, and ultimately survival at various life stages. In their recent review on climate change effects on the freshwater phase of Atlantic salmon, Gillis et al. [14] concluded that climate change affects and will continue to affect instream habitats across all seasons and render challenging conditions, especially through changes in water temperature and discharge, for all Atlantic salmon life stages in freshwater. Juvenile Atlantic salmon emigrate from freshwater after having achieved a certain size and physiological stage (referred to as smolts at this life stage) in one or more years, and subsequently adapt to first estuarine and eventually full sea water and vastly increase their growth rate in the ocean. The timing of downstream migration differs among areas and rivers [15–17], but it has been shown that the initiation of the smolt seaward migration takes place earlier and earlier in association with the increasing river and ocean temperatures and has occurred 2.5 days earlier per decade since the early 1960s across the basins of the North Atlantic Ocean and the Baltic Sea [16]. Changes in phenology of habitat shifts of juvenile salmon may lead to a mismatch with the critical environmental conditions (temperature, food availability) in freshwater and at sea [15,18].

The fast growth of Atlantic salmon at sea and concurrent decisions to either return to fresh water for reproduction after one year or stay for one or more additional years in the ocean to increase more in size is dictating the key life-history patterns [10,19]. Although a strong effect of genes has been shown to largely control the age at maturity (=years spent at sea), environmental conditions play a role as well [19,20]. Recent analysis of long-term time-series data have shown temporal trends in life-history characteristics, both in years spent in fresh water and seawater, and in iteroparity, i.e., patterns in occurrence of repeated spawning [21–24]. In addition, the genetic background affecting the life-history decisions have changed over the decades in some populations in response to environmental conditions, especially the marine food web [25].

In this study, a 48-year time series data sets from three Atlantic salmon populations within a large subarctic catchment were used to investigate the long-term patterns in both freshwater and marine growth rates. Given the recent climate warming of the sub-Arctic area, we searched for possible environmental changes linked with the growth patterns of Atlantic salmon, in both freshwater and marine environments, using both abiotic and biotic environmental variables.

2. Materials and Methods

2.1. Study Area

The River Teno system (Norwegian: Tana, Sami: Deatnu) is located in northern Europe (68–70° N, 25–27° E). It forms the border between northern Finland and Norway, draining into the Tanafjord at the Barents Sea (Figure 1). More than 1100 km of different stretches of the system is accessible to anadromous Atlantic salmon, including the main stem, the large headwater branches, and numerous smaller tributaries (Figure 1). Genetic studies have revealed a highly structured population complex consisting of nearly 30 demographically independent, genetically distinct, and temporally stable population segments in tributaries and different parts of the main stem [26]. In addition, life-history variation of the Teno salmon populations is among the widest, if not the widest, within a single river system [23]. Until very recently, the River Teno has been one of the few remaining large river systems

that still supports various forms of recreational and net fisheries in the river that has yielded annual freshwater catches between 80 and 250 t, or 20,000–60,000 individual adult Atlantic salmon [23,27]. However, in recent years, the population status has strongly declined [28]. Typically, the majority (50–60%) of the salmon catch has been taken in recreational rod fishery, the next most important gear being weir and stationary gill nets, and the smallest proportion being taken with drift nets [23]. The net fisheries are practiced by locals, mostly native Sámi, and are based on special fishing rights connected to land use, ownership, or inherited rights. In addition to the extensive fishery in the main stem, salmon fishing is also operational in most of the tributaries. In most tributaries, little or no net fishing is operated or allowed, although in some larger tributaries, net fishing forms a significant share of the catch, like in the rivers studied in the present study, the Pulmankijoki, Utsjoki, and Inarijoki (Figure 1). This study is focusing on these three tributaries where long-term scale sample collections are available, which are genetically distinct [26], and represent the lower, mid, and upper parts of the catchment (Figure 1).



Figure 1. The River Teno catchment in northern Finland and Norway. The studied Atlantic salmon populations were from the tributaries Pulmankijoki, Utsjoki, and Inarijoki.

Salmon stocks of the River Teno system are managed and fisheries regulated by bilateral agreements between Finland and Norway, with the aim of conserving the wild stocks but also supporting sustainable fisheries. The border river stretches (Teno main stem, Inarijoki; Figure 1) are managed bilaterally, but tributary regulations are under national legislation in both countries. Stocking of reared fish or eggs is strictly forbidden in the entire river system.

2.2. Scale Sampling and Analyses

Scale samples were collected from 35,065 Atlantic salmon harvested over a 48-year period (1972–2020) in the Teno river system by recreational tourist anglers and local fishers using various net and rod fishing methods cf. [23]. The samples were collected by a network of trained fisherman, equipped with standard measuring boards and scales, and was established by the Finnish Game and Fisheries Research Institute (currently: Natural Resources Institute Finland (LUKE)) in the 1970s, and later complemented on the Norwegian side by the County Government of Finnmark and the Tana River Fish

Management. The network has been maintained and developed with the aim of covering all fishing methods, the entire fishing season, and different parts of the Teno river system cf. [23,27]. Based on our previous studies, the sampling from June to August virtually covers the entire run timing of these salmon populations [29,30]. The fishermen measured the length and mass of the fish in their retained catches, and recorded the sex of the fish, date of capture, and location and fishing gear used. Scales were dried and archived in paper envelopes at room temperature at the Teno River Fisheries Research station of LUKE in Utsjoki, Finland.

The river and sea age (1SW: one-sea-winter salmon; 2SW: two-sea-winter salmon, etc.) and possible previous spawning history were determined via assessment of scale patterns by trained experts following the internationally agreed guidelines for Atlantic salmon scale reading [31].

We focused on three main populations with the most coherent time series of scales and catch statistics cf. [23,26]. In general, the Teno salmon show large variability in life-history strategies, but here, we focused on the most abundant ones in these tributary populations, i.e., fish that have gone through smolting at the age of three, four, or five years, and stayed at sea on their feeding migration for one or two years before return to their natal rivers (hereafter 1SW, $n = 16,032$; and 2SW, $n = 1912$), resulting in six different life-history combinations.

For the growth analyses, a smaller subset of samples ($n = 17,944$) was analysed. The growth of the freshwater stage was defined as the total length (mm) from the nucleus to the edge of the first sea-summer growth zone (Figure 2). Respectively, the increments during sea migration were measured from the edge of the first sea-summer growth zone to the edge of the first or second sea-winter growth zone (Figure 2). For the marine phase, each alternate increments of fast- and slow-growing zones of the scales were measured (in mm). The total radius of scales correlated with the total length of the fish (Pearson's $r = 0.60$, $t = 32.958$, d.f. = 1893, $p < 0.001$). As the back-calculation of juvenile lengths from adult scales may result in life-history specific under- or over-estimations [32], and Jonsson et al. [33] showed that the potential mismatch between back-calculated juvenile length and actual length can be within ± 2 cm, we therefore abandoned such calculations.

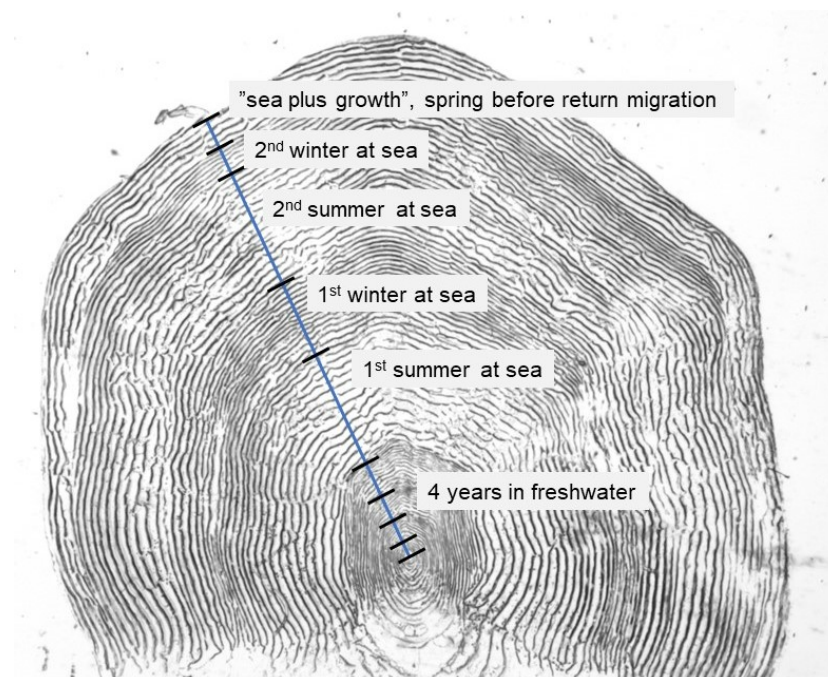


Figure 2. A sample scale from a 2SW Atlantic salmon showing growth zones in four freshwater years and two years at sea (summer and winter zones separately).

2.3. Environmental Data and Curation

The longest available temperature time series for the Utsjoki region was collected at Kevo Meteorological Station (69.75° N, 27.00° E, Finnish Meteorological Institute). The data consist of monthly mean air temperatures from the beginning of the 1960s, which we used as a proxy for a climatic impact on fish growth at the freshwater stage. The temperature data indicate how the annual 10-year rolling mean temperature has risen in the area, e.g., from −1.95 °C in 1975 to −0.26 °C in 2022.

To assess the effects of a changing climate on salmon growth at the sea stage, we used sea temperature data that are available via the ICES Data Portal [34]. We used sea temperature data collected in the Barents Sea area that is likely included in the feeding area for 1SW and 2SW Teno salmon. According to the report on ocean climate [34], the Barents Sea mean temperature has remained above the long-term average since the early 2000s, and in 2020, the mean temperatures of surface, deeper, and bottom waters were warmer than the 1981–2010 average by 1.4, 0.5, and 0.7 °C, respectively. There are two available water temperature data sets from the Barents Sea: one from the Eastern Kola Section from the surface layer (0–200 m depth; 71.5° N, 33.5° E; collected by Polar Institute of Marine Research, Russia [34]). Via the Pinro website (<http://www.pinro.vniro.ru>, accessed on 4 March 2022), the monthly mean temperature data are available from 1951 to 2017, which were used for the model where monthly mean temperatures were used as covariates (Supplementary Table S3). Another temperature data set was collected from the Western Barents Sea/ Atlantic Inflow at the Fugløya–Bear Island Section from a depth of 50–200 m (73° N, 20° E; collected by Institute of Marine Research, Norway [34]).

We also tested the association between sea growth of 1SW and 2SW salmon with the capelin (*Mallotus villosus*, Cuvier, 1829) stock variation. The high capelin biomass has been previously linked with a higher probability for late maturation in Atlantic salmon [25]. We used the acoustic trawl survey-based Barents Sea capelin stock assessment data that are available via the ICES Data Portal [35] and used both log-transformed total and immature capelin biomass and rolling average of two consecutive years when fitting the growth models for 1SW and 2SW fish.

2.4. Statistical Analysis

For data wrangling and to visualize the time series of fish growth, we used the Tidyverse-package family. To analyse the freshwater growth, we especially wanted to investigate whether a certain age at the river has a substantial effect on the total growth. We used linear mixed-effects models (LMM hereafter; lme4-package), where we first fitted birth year, smolt year, and the growth increment year as random factors. We preferred to apply the mixed effects models for growth analyses, which allows us to replace the fixed year effects with the random year effects, thus avoiding the year effects being auto-correlated with environmental effects [36]. For the fixed effects, we followed a model selection procedure, where we compared the goodness of fit of various fixed effect structures based on AIC and deviance (Supplementary Table S1). Based on the selection procedure, we ran the final model to obtain the estimates and their 95% confidence intervals and statistical probabilities. The sea growth analyses were otherwise similar, but only birth year and smolt year were used as random factors. Then, we followed a similar procedure for fixed effects (Supplementary Table S1). Sexes were merged in the analyses, as they did not indicate divergent trends in growth patterns, except in Inarijoki 2SW salmon. All the analyses were performed in the RStudio environment using R version 4.2.1.

3. Results

3.1. Freshwater Growth

Salmon parr growth in freshwater has decreased within the past c. 50 years, and the size difference among three-, four-, and five-year-old smolts seems to have disappeared (Figure 3). The best fitting LMM indicated the importance of air temperature in mid-summer and autumn impacts on juvenile salmon growth (Figure 4). Warmer air temperatures,

especially the higher mean temperatures in July or September, seemed to indicate slower growth for juvenile salmon (Figure 4). The age of fish and the annual increase in size were strongly associated showing that the first freshwater growing season has the highest impact on the total growth during the juvenile years in the river (Figure 4). The fixed effect estimates from LMM indicate that the back-calculated size of fish at the smolt stage differed significantly between populations, and the smolt size was smaller in 2SW compared to 1SW salmon (Figure 4).

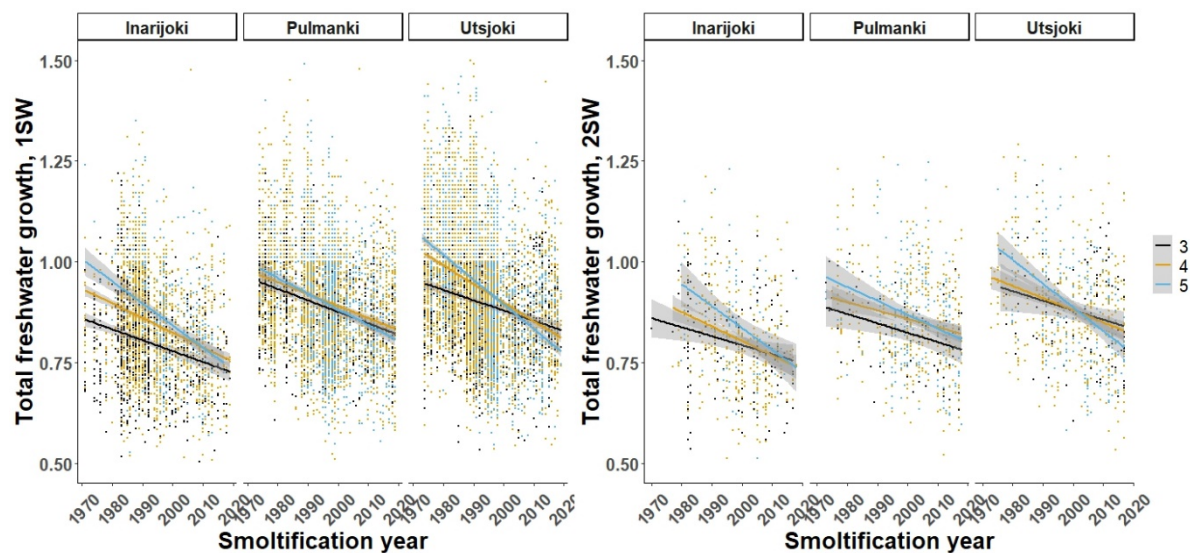


Figure 3. Total freshwater scale growth (mm) of 1SW ($n = 16,032$), and 2SW ($n = 1912$) salmon, including smolt age groups of 3, 4, or 5 from three different populations. The trend lines represent the linear regression with 95% confident intervals.



Figure 4. The fixed effect estimates of LMM of the total growth in freshwater, FWG, based on scale measures. The estimates are in relation to the 0 point of the x-axis that represents the intercept (Inarijoki pop., 1SW, 3 y-o-smolt). Mean T refers to monthly mean air temperatures. Asterisks indicate the statistical significance at the level of $\alpha < 0.05$ ("*") or $\alpha < 0.001$ ("***"). Negative estimate values are shown in red, positive in blue.

3.2. Marine Growth

When looking at the sea growth (SG) of the 1SW fish, the faster the smolt has been growing in the freshwater (i.e., smolt age 3), the larger the positive effect on sea growth the freshwater growth (FWG) had (Figure 5). The old smolting age on the other hand showed a negative impact on the sea growth (Figure 5 and Supplementary Table S2). The SG of 1SW salmon was significantly different between the three populations with the Inarijoki population showing the highest growth rate (Figure 5). The annual mean sea water temperature in the Barents Sea showed a positive association with fish growth (Figure 5). The models including the total or immature capelin biomass did not increase the goodness of fit of the model (Supplementary Table S1). When looking at the monthly mean temperatures separately, it seems that the mean temperature in September especially had a positive association with sea growth in 1SW fish (Supplementary Table S3).

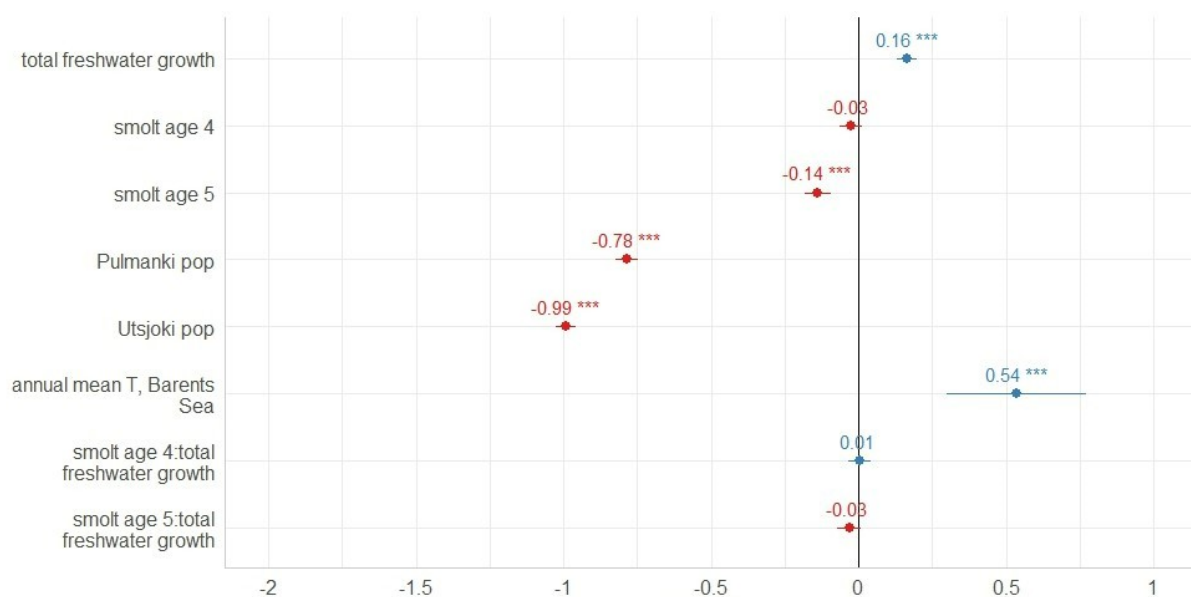


Figure 5. The fixed effect estimates of LMM of the sea growth of 1SW salmon based on scale measures. The estimates are in relation to the 0 point of the X-axis that represents the intercept (Inarijoki pop., 3 y-o-smolt). Asterisks indicate the statistical significance at the level of $\alpha < 0.001$ ("***"), Negative estimate values are shown in red, positive in blue.

Similarly, with 1SW fish, the capelin stock status nor the sea water temperature were strongly associated with SG of 2SW salmon (Supplementary Table S4). Congruently with the SG of 1SW salmon, the smolt size showed a positive association with the marine growth of 2SW salmon, and Utsjoki and Pulmanki fish were growing slower than Inarijoki salmon (Supplementary Table S4). Smolt age and FWG showed an interesting antagonistic interaction, where the older and the larger the smolts were, the slower the growth at the sea was (Supplementary Table S4).

There was an increasing trend in the total length (cm) and mass (kg) of the returning spawners since the 1970s in both 1SW and 2SW in all three populations except Inari 2SW, where size development was slightly negative (Figure 6). The total length of the returning spawners indicates concurrently that the later the fish smolt, the smaller they are at return to the tributaries, and the differences among smolt ages are potentially increasing in the Inari and Utsjoki populations (Figure 7).

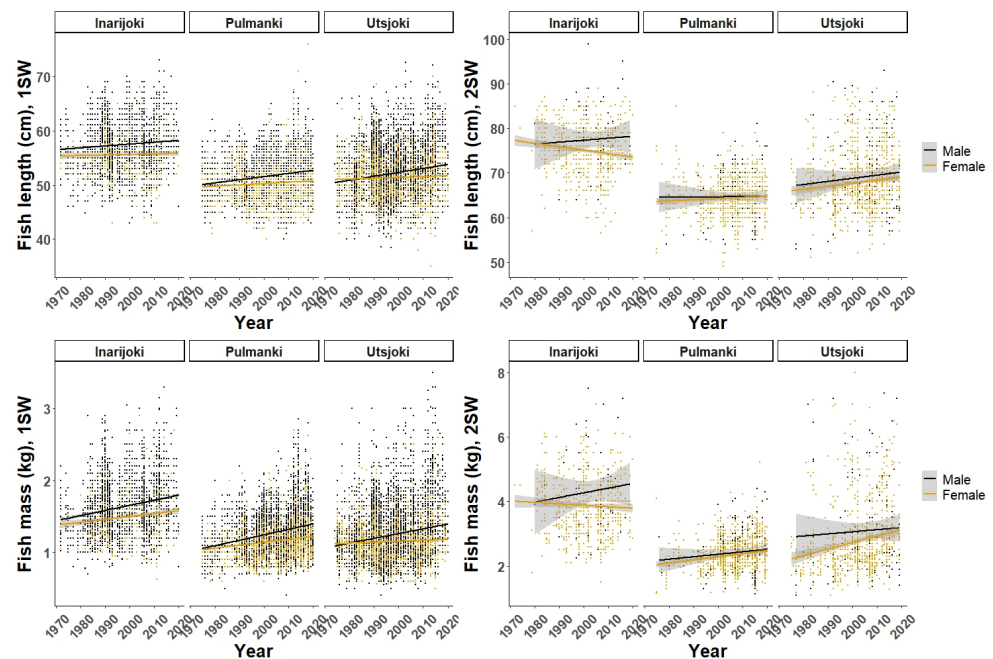


Figure 6. Total length (upper panel) and mass (lower panel) of male and female 1SW and 2SW salmon (cm) at capture from three different populations ($n = 35,065$). The trend lines represent the linear regression with 95% confident intervals.

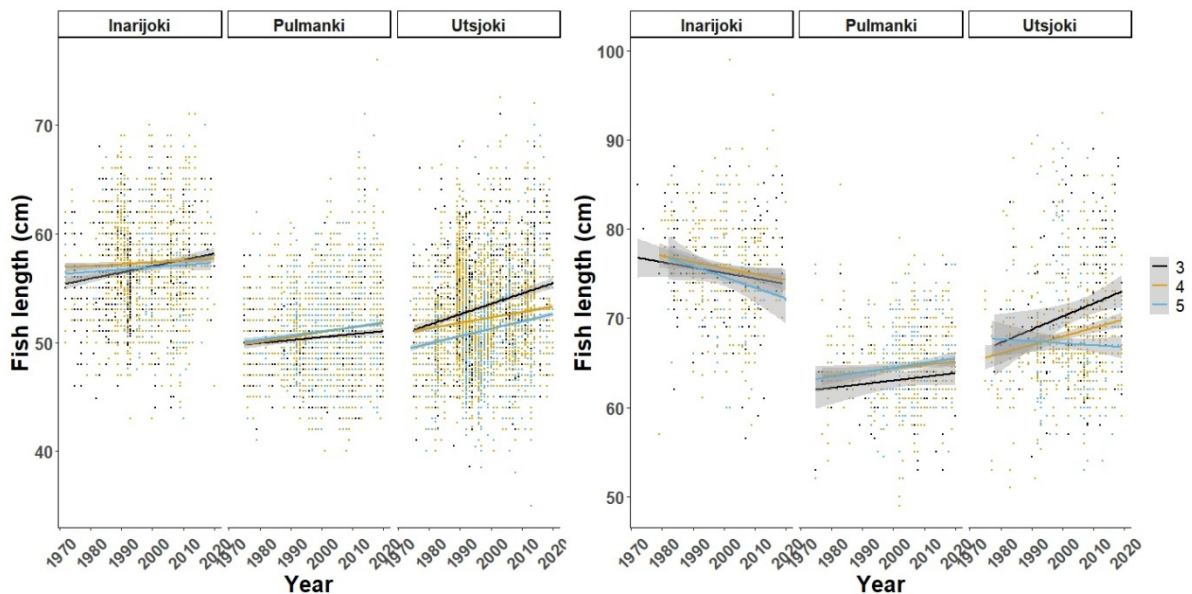


Figure 7. Total length of 1SW and 2SW salmon (cm) at capture from three different populations representing smolt ages of 3, 4, or 5 ($n = 35,065$). The trend lines represent the linear regression with 95% confident intervals.

4. Discussion

The long-term trends in Atlantic salmon growth, based on more than 35,000 catch samples and near 18,000 scales with detailed growth measurements, collected over the past 48 years, clearly indicate the life-history stage and temperature-dependent changes in growth rates. The freshwater growth has markedly decreased, whereas the sea growth of 1SW has undoubtedly increased resulting in larger sized 1SW spawners. The growth reduction was more pronounced in smolt ages four and five than in age three smolts, indicating that spending more years in the river comes with a growth cost, possibly

due to the impact of rising temperatures. The diverged growth patterns in different life-history stages likely reflect biotic and abiotic responses to increasing temperature that differ substantially between riverine and marine ecosystems.

The Increasing water temperatures during the active feeding and growing season of juvenile Atlantic salmon between mid-summer and early autumn, e.g., [37], may affect their metabolism and restrict growth at the freshwater stage. Although the temperatures in the River Teno area may not yet reach critical levels for juvenile Atlantic salmon, cf. [38], the rapid change in sub-arctic environments may cause more and more frequent surpassing of the optimal range of water temperatures for juvenile salmon growth (14–20 °C) [39], and induce varying ecological responses (see, e.g., [14,40] for reviews).

As the riverine environments may react rapidly to the temperature changes, especially in the areas of shallow and slow-running flow, the parr must either adapt to higher temperatures or escape to the refugia that buffer against the rising water temperatures even during the peak temperatures or longer waves, e.g., [14]. In such areas, food may come a limiting resource for growth via density-dependent intra-specific competition, and it has been observed that salmon parr may cease feeding altogether in cool water refugia [41], which potentially impede juvenile growth especially during summer peak temperatures, as was the case in July in our study. On the other hand, decreased feeding activity in juvenile salmon in autumn [37] may result in decreased growth (Figure 4), potentially driven by increased temperatures in September and increased basic metabolism of fish [42].

Our time series data indicate that multiple years spent in freshwater in recent years will come with a cost in the form of reduced growth compared to the situation a few decades ago. Moreover, multi-river-year smolts also grow slower in the sea and may return for spawning at a smaller size than younger, three-year-old smolts, e.g., [43]. Nevertheless, this seems to be rather population specific (c.f. Pulmanki, Figure 7). The fast growth in freshwater and early smolting seem to result in fast growth at the sea, supporting the life-history theory [44] linking fast growth with early maturation (1SW). Alternatively, if older smolts emigrate earlier, and younger smolts later in the migration window [15], there is a potential for environmental mismatch at the sea leading to growth reduction during the first year at the sea. This might cause a smaller maturation size as well. As the first year at the river shows the largest effect on total growth at the river stage, it is plausible that the unfavourable temperature conditions in the first year might have cumulative effects on the later development of juvenile fish, restricting growth in later years. This can potentially have vast cascading effects on intra-specific resource competition for habitat use and food. Competition within conspecifics may increase if formerly different-sized age-classes have utilised divergent niches, but reduced growth in old parr may drive them to compete for resources with the younger parr.

A large body of research suggests a reduction in the productivity of several marine ecosystems, including those in the Northern Hemisphere, resulting in changes in community composition and population abundances across all trophic levels [45–47]. In contrast to freshwater, the ocean environment might be less sensitive for peak air temperatures and react more slowly to the warming climate. However, the water temperature in the Barents Sea has increased in recent decades, e.g., [34,48], and such a change might have induced the observed increase in growth of 1SW fish. In contrast, the growth of 2SW fish did not covary with sea temperature, and no significant long-term trend in growth was detected within our time series. It is possible that 2SW fish have less growth potential with increased temperature since higher temperatures will increase the metabolism of larger fish more than in smaller fish, and thereby 2SW fish must allocate their energy differently compared to 1SW fish. Recent changes in the North Atlantic environment have already been shown to negatively affect growth [47] and alter genetic architecture [25] especially in larger salmon (2SW and multi-sea-winter, MSW). Tréhin et al. [49] showed that after the decline in growth during the first year at sea, growth remained stable during the later periods at sea among returning salmon, which suggests a similar lack of growth response in 2SW salmon as in our results.

Although a decline in size (total length and/or mass) of Atlantic salmon (mostly 1SW) at return to freshwater has recently been reported across several areas and rivers in the northeast Atlantic area [49–51], all three salmon populations in this study showed a long-term increase in body length for both 1SW and 2SW (with one exception) fish. Changes in marine environmental conditions, typically resulting in changes in the growth and size of salmon, appear to affect in different directions in different areas. The increase in sea water temperature in the Barents and Norwegian seas [47,48] and other possible changes in the marine environment appear to improve, at least for the time being, the marine growth of salmon in the northern populations. A slight increasing trend in growth for northern Norwegian salmon populations has been documented, whereas a decline was detected in salmon populations further south in Norway [47]. A recent study indicates, however, that the Arctic oceanic environment may change and become warmer even faster than earlier predicted, and such a scenario may further affect the growth of Atlantic salmon in an unknown direction [52].

Other interesting differences in Atlantic salmon growth patterns between different parts of the North Atlantic Ocean emerged when comparing our results to growth analyses carried out elsewhere. Both Vollset et al. and Tréhin et al. [47,49] showed recent, abrupt reductions in Atlantic salmon growth during the first year at sea in fish from a French and several southern Norwegian populations, respectively. In addition, a general decrease in marine growth rate in a Scottish salmon population has recently been documented [51]. Such rapid changes in growth indicate a large-scale shift in conditions for Atlantic salmon: a marked decrease in the extent of Arctic water in the Norwegian Sea, a subsequent warming of spring water temperature before Atlantic salmon entering the sea, and an approximately 50% reduction in zooplankton across large geographic areas of the northeast Atlantic Ocean [47]. They further concluded that these phenomena suggest an ecosystem-scale regime shift in the northeast Atlantic Ocean.

In addition, during the recent years, the proportion of early maturing 1SW salmon decreased in the Norwegian populations [47] (see also [21]). Similarly, Jonsson et al. [50] reported a decline in the proportion of 1SW salmon since the 1980s in a small Norwegian salmon population. Tréhin et al. [49] concluded that changes in age at maturity in a French salmon population support the hypothesis of a sex-specific probabilistic reaction norm: the individual probability to return after one year at sea is increasing with changes in marine growth rate. However, the proportion of both 2SW salmon and previous spawners in both the Utsjoki and Inarijoki populations have increased since the 1970s, whereas the proportion of 1SW fish has slightly decreased and showed more variable patterns in recent years compared to the past [23]. The observed patterns in growth and sea age composition in the tributary populations of the River Teno suggest more complex linkages between the variables, and alternative factors should be explored as candidate drivers of these dynamics.

If temperature acts as a growth-limiting factor, the growth of post-smolt fish may show a positive correlation with Sea Surface Temperature (SST). Previous studies have established a link between post-smolt growth and the increasing SST [53], which appears to be population specific [54]. The evidence from northeast Atlantic populations shows a negative correlation between sea growth and SST [47,54]. However, in parallel to our findings, northwest populations indicate a positive association between post-smolt growth and sea temperatures in sub-arctic and arctic marine environments [53,54]. This growth pattern can arise from either a physiological response to an optimal temperature or from the influence of certain ecosystem factors on growth. While previous evidence has established a direct link between growth and post-smolt survival [55], there are conflicting findings that suggest post-smolt growth might not always be the primary determinant of post-smolt survival [54,56]. Warming conditions during certain stages of the salmon life cycle have been associated with reduced adult recruitment. However, warming during other stages has been observed to promote salmon growth and is assumed to amplify the reproductive output of spawning fish [53]. The situation in which elevated SST leads to enhanced post-smolt growth but triggers a decline in spawner recruitment demands further

investigation, particularly regarding the potential latent effects of environmental factors, and genotype–environment interactions. Furthermore, a comprehensive understanding of the sea migration routes of sub-arctic salmon populations is essential for understanding climate effects on their dynamics.

Forage fishes defined here as small- or intermediate-sized marine pelagic species that are important or the primary food source for predators, play important roles in marine ecosystems by providing energy transfer between trophic levels [57]. In the Barents Sea and other northeast parts of the Atlantic Ocean, one of the key species is capelin, which has suffered from several population collapses over the past decades largely because of overfishing [58]. Moreover, the drastic variation in capelin population in the Barents Sea has been associated with the changes in life-history composition of the River Teno salmon and the genetic architecture behind it [25]. Changes in the food base were also associated with a reduction in marine growth of salmon in southern Norwegian populations, accompanied by a simultaneous decrease in the growth of Atlantic mackerel (*Scomber scombrus*, L. 1758) in the corresponding sea areas [47]. In our study, however, no link between capelin abundance in the Barents Sea and marine growth patterns of salmon was found. It should be remembered that the salmon sampled are the survivors who made their return to the natal rivers, and the growth patterns and other biological characteristics of these fish may not entirely reflect those that did not survive and may have suffered from changes in the environment, such as collapses of capelin stock in this case. Czorlich et al. [25] showed that the capelin collapses especially affected the large MSW salmon, and it can be speculated that the smaller 1-2SW salmon analysed in the present study may have successfully utilize other prey items, e.g., [59], and their growth rates benefited from the increasing sea water temperatures despite the periods of low capelin stock. In the sea, growing salmon shift from foraging on invertebrates to a piscivorous diet [60]. Therefore, the effect of temperature on growth may be complicated by the availability of suitable prey, which ultimately determines growth opportunities [24].

This study investigated growth patterns of Atlantic salmon from three genetically distinct populations [26], although they represent tributaries of the same large catchment. Temporal patterns in both freshwater and marine growth were largely consistent between populations, although there were differences in absolute levels. The largest 1SW and 2SW salmon were those of the Inarijoki population whereas the 1SW fish were similar in size in Utsjoki and Pulmanki, and 2SW salmon were slightly larger in the Utsjoki population. Differences in marine growth are difficult to interpret since little or nothing is known about certain aspects, e.g., the exact marine feeding areas of the salmon in these tributary populations. There are likely genetic components and local adaptations dictating marine feeding migration and growth, and a genetic component in the ontogenetic diet during the ocean feeding phase in Atlantic salmon [61]. Moreover, Jonsson et al. [20] showed that 1SW salmon tend to be larger in size in rivers with higher proportions of MSW salmon in the population, a pattern consistent with the size differences documented in the present study.

5. Conclusions

In conclusion, the rapidly progressing global change, especially in the northern areas, is affecting the anadromous fish which utilize both freshwater and ocean waters during their life cycle. Our results indicate contrasting responses in Atlantic salmon growth rates to warming climate: freshwater growth decreased whereas marine growth has largely increased. The predicted continuing and accelerating increase in water temperature and other changes in the aquatic ecosystems in the north call for carefully designed, long-term monitoring of migratory fish populations at various phases of their life cycle. There is strong evidence pointing towards the Arctic ecosystems warming more rapidly than those further south [62], which is posing particular needs for careful monitoring of changes in environmental conditions and anadromous fish populations in the northern areas, cf. [13,63].

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/fishes8090441/s1>, Table S1. Model selection procedure for FGW and SG models presenting AIC, LogLikelihood and Deviance values. The selected models are presented in bold. FWG = Freshwater growth, RG = River growth, SG = Sea growth, SST = Sea surface temperature. Rainfall and air temperatures were standardized N (0, 1). Log-transformation was used for capelin biomass (BM) and rolling averages over two years of capelin biomass (BM2y) and immature capelin biomass (Imm2y). The final models are in bold. Table S2. Summary of Linear mixed-effects models for Freshwater growth of 1SW and 2SW fish, and sea growth of 1SW fish. Table S3. Summary for LMM of 1SW fish sea growth with monthly means as covariates. SST refers sea surface temperature (°C). Table S4. Summary of Linear mixed-effects model for sea growth of 2SW fish.

Author Contributions: Conceptualization, J.E. and P.O.; Investigation, J.E. and P.O.; Data curation, P.O. and J.E.; Formal analysis, N.A.; Writing—original draft preparation, N.A. and J.E.; Writing—review and editing, N.A., J.E. and P.O. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Only the fisheries data were used in this study meaning that local fishermen have delivered the samples taken from captured and culled fish to the Natural Resources Institute Finland's collections. Living fish were not used in this study.

Informed Consent Statement: Not applicable.

Data Availability Statement: The scripts for the statistical analyses will be available online via osf.io (<https://doi.org/10.17605/OSF.IO/GJ76N>). The original data will be available on the request in accordance with the data policy of Luke.

Acknowledgments: We thank the large number of fishermen fishing the tributaries of the River Teno system who collected the large set of salmon scale samples and phenotypic data over a nearly 50-year period, and our skilful personnel who have analysed the scale material, especially, Jari Haantie, Jorma Ollila, and Matti Kylmäaho. In addition, Jorma Kuusela is thanked for organizing the complex salmon scale database.

Conflicts of Interest: The authors declare no conflict of interest.

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