



## Article

# Expected Climate Change in the High Arctic—Good or Bad for Arctic Charr?

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**Abstract:** Lakes in the High Arctic are characterized by their low water temperature, long-term ice cover, low levels of nutrients, and low biodiversity. These conditions mean that minor climatic changes may be of great importance to Arctic freshwater organisms, including fish, by influencing vital life history parameters such as individual growth rates. In this study, Arctic charr sampled from two Svalbard lakes (78–79° N) over the period 1960–2008 provided back-calculated length-at-age information extending over six decades, covering both warm and cold spells. The estimated annual growth in young-of-the-year (YOY) Arctic charr correlated positively with an increasing air temperature in summer. This increase is likely due to the higher water temperature during the ice-free period, and also to some extent, due to the winter air temperature; this is probably due to thinner ice being formed in mild winters and the subsequent earlier ice break-up. However, years with higher snow accumulation correlated with slower growth rates, which may be due to delayed ice break-up and thus a shorter summer growing season. More than 30% of the growth in YOY charr could be explained specifically by air temperature and snow accumulation in the two Arctic charr populations. This indicated that juvenile Svalbard Arctic charr may experience increased growth rates in a future warmer climate, although future increases in precipitation may contradict the positive effects of higher temperatures to some extent. In the longer term, a warmer climate may lead to the complete loss of many glaciers in western Svalbard; therefore, rivers may dry out, thus hindering migration between salt water and fresh water for migratory fish. In the worst-case scenario, the highly valuable and attractive anadromous Arctic charr populations could eventually disappear from the Svalbard lake systems.

**Keywords:** High Arctic; Svalbard lake systems; climate impact; Arctic charr; growth rate; anadromy

**Key Contribution:** Annual growth in YOY Svalbard Arctic charr correlated positively with increasing air temperature, while years with higher snow accumulation correlated with slower growth rates.



**Citation:** Svenning, M.A.; Bjørnvik, E.T.; Godiksen, J.A.; Hammar, J.; Kohler, J.; Borgstrøm, R.; Yoccoz, N.G. Expected Climate Change in the High Arctic—Good or Bad for Arctic Charr? *Fishes* **2024**, *9*, 8. <https://doi.org/10.3390/fishes9010008>

Received: 13 November 2023

Revised: 14 December 2023

Accepted: 20 December 2023

Published: 23 December 2023



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## 1. Introduction

The salmonid Arctic charr (*Salvelinus alpinus*) has a Holarctic distribution and is the only freshwater fish species in most High Arctic regions [1], including Svalbard, an archipelago in the Arctic Ocean between a latitude of 74 and 81° N. Arctic charr populations demonstrate remarkable ecological plasticity, showing various life-history adaptations to

harsh northern environments. In addition, it is the only freshwater fish species on Svalbard, forming both anadromous, resident, and landlocked stocks [2].

Lakes in the High Arctic are characterized by low water temperatures, long-term ice cover, low levels of nutrients, and low biodiversity [3]. Depending on the location, most Svalbard lakes are ice-covered for 9–12 months a year [2], with maximum water temperatures usually reaching 6–8 °C in summer–autumn [4]. The thickness of the ice, the timing of ice break-up/cover, and water temperatures during the ice-free season, however, vary among lake systems, due to local differences in air temperature and precipitation [5,6]. Studies during the early 1980s revealed that year-class strength correlates positively with mean air temperature during the two summers preceding the spawning of Arctic charr in Svalbard [7].

Temperature, which is known to influence both ingestion and metabolism, will thus influence the somatic growth rate in fishes, although the effects on growth are also influenced by interactions between temperature and food supply [8]. Although [9] suggested that as the temperature rises, somatic growth of Arctic charr would increase in high-latitude lakes, ref. [10] showed that the knowledge of fish growth in response to climate change in general remains incomplete, and that some findings are even contradictory. Svalbard Arctic charr usually experience water temperatures in June–August in the range of 1–8 °C, such that even small increases in water temperature (0.5–1 °C) may lead to significant changes in the growth of younger fish [11]. In the subalpine Lake Øvre Heimdalsvatn (>1000 m a.s.l.), an increase of 1 °C in the June air temperature resulted in a 10% growth increase in brown trout (*Salmo trutta*) [12]. In Greenland, ref. [13] recorded a positive correlation between air temperature and the growth of landlocked Arctic charr in one lake, whilst the opposite was found in another. This was probably due to differences in energy demand and food supply. In the open lake systems on Svalbard, i.e., systems containing anadromous Arctic charr with additional access to marine prey, fish density seems rather low [2,4]. As noted above, even small increases in thermal conditions may increase the growth rate in fish significantly.

Recent information on global warming shows a higher increase in air temperatures at higher northern latitudes [14,15]. In Longyearbyen, Svalbard, the annual mean temperature has increased significantly from 1912 to 2008 [6], corresponding to +0.22 °C per decade, with the highest increase shown in spring (+0.45 °C). In northeastern and southwestern Svalbard, an increase in air temperature of 8 and 3 °C, respectively, are suggested for the next 100 years [6,14]. So far, annual precipitation in the Svalbard region has been low, with a gradient from higher values in the southwest to lower values in the northeast. Precipitation, however, is also expected to increase in Svalbard during the next 100 years, especially in winter. This is predicted to lead to a larger accumulation of snow in spring, which in turn, will likely postpone the timing of ice break-up and shorten the ice-free season [16]. On the other hand, both an increasing air temperature in winter, implying thinner ice [17], and a higher temperature in spring inducing earlier ice-melt [2,18], will prolong the ice-free period. The sun's radiation will then affect the water more efficiently and this may lead to both a higher maximum water temperature as well as a higher number of degree days [5,19]. An increase in accumulated snow cover in spring has been shown by [16] in the alpine Lake Litlos (>1100 m a.s.l.) in Hardangervidda, Norway, and by [5] in Greenland lakes. This has been shown to have a strong effect on the time of ice break-up and thus a negative effect on the growth and the survival in young-of-the-year (YOY) brown trout and Arctic charr, respectively. In High Arctic and alpine lakes, a change in climate that results in higher temperatures is therefore assumed to increase growth in juvenile charr; more snowfall, on the other hand, probably induces decreased growth.

To study these opposite effects of temperature and precipitation on life history parameters in fish, access to long-term survey data covering both warm and cold periods/years is essential [20]. On Svalbard, two weather stations that have been in operation for more than 100 years [21,22] showed mainly positive air temperature trends before the 1930s, and a warm period during the 1930s and 1940s. This was followed by a negative temperature

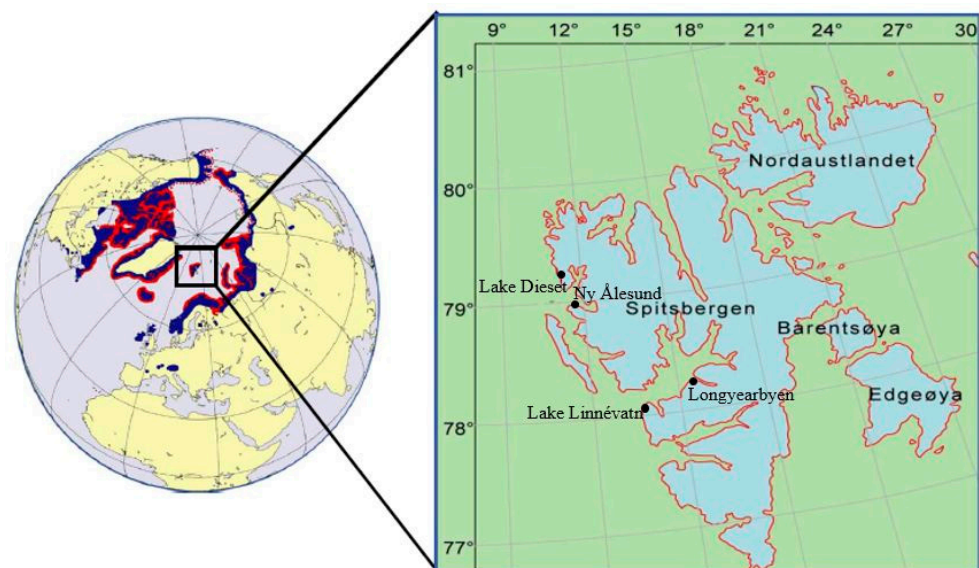
trend in the 1950s and 1960s. From the 1960s onwards there has been a general temperature increase in all seasons (see [6,14] for more details). From around 1960 to 2008, samples of Arctic charr otoliths have been collected from several populations, thus providing the possibility to use Arctic charr otoliths as flight recorders to back-calculate fish growth in juvenile Arctic charr back to the early 1950s (Gullestad, Hammar and Svenning unpublished).

Accordingly, in this study, we compare back-calculated fish growth in YOY Arctic charr from otoliths with climate indices, specifically air temperature and the accumulation of snow, in two charr populations on Svalbard, situated between 78 and 79° N. We hypothesize that both warm winters and warm summers will result in an improved growth rate in YOY Arctic charr, which may be due to thinner ice, earlier ice break-up, and a higher water temperature during the ice-free season. In years where high snowfall has occurred, however, ice break-up may be postponed, resulting in decreased growth of juvenile charr.

## 2. Materials and Methods

### 2.1. Study Sites

The Archipelago of Svalbard is situated between 74 to 81° N and 10 to 35° E, and consists of four large islands, Spitsbergen, Nordaustlandet, Barentsøya, and Edgeøya, in addition to many smaller islands (Figure 1). The climate is highly arctic, with mean July air temperatures normally being between 4 and 5 °C on western Spitsbergen, with temperatures being 2–3 °C lower on Nordaustlandet, the northernmost island [23]. The difference in temperatures between the western and northern coasts is mainly due to the influence of the Gulf Stream on the western coast of Spitsbergen, while Nordaustlandet and the eastern part of Spitsbergen are more influenced by cold, easterly air masses [24]. Annual precipitation on Svalbard is low, with 300–400 mm mostly falling as snow [23], but there are large local variations.



**Figure 1.** Map showing the circumpolar distribution area of resident (blue) and anadromous (red) Arctic charr (**left**), and the localities of Lake Dieset, Lake Linnévatr, and the meteorological stations in Longyearbyen and Ny-Ålesund (**right**).

Arctic charr is the only freshwater fish on Svalbard, with populations in approximately 200 lakes; of these, probably less than 20 lake systems contain stable anadromous populations.

Sampling has been carried out in Lake Linnévatr in the outermost part of Isfjorden, and Lake Dieset on the Mitra Peninsula, both situated on the western side of Spitsbergen (Figure 1). The lake areas are in the range of 4–4.5 km<sup>2</sup>, and both support anadromous Arctic charr in addition to resident charr [2,4]. Lake Linnévatr (78° N, 13° E) is the southernmost

of the studied lakes (Figure 1). Water temperatures are low even during summer, due to the inflow of glacier meltwater as well as being surrounded by high mountains that reduce the solar radiation of the lake [25]. Owing to glacial silting, light transmission, as characterized by the Secchi disk transparency values during summer at 0.3 m, is relatively low [4,25]. The lake is ice-covered for approximately 9–10 months of the year, but during the ice-free season, the 2.5 km outlet river to the Isfjorden Bay has a relatively stable discharge [4]. In the summers of 2008 and 2017, a fish trap was mounted in the outlet river, and approximately 2500 anadromous Arctic charr ascended the watercourse in both seasons (Svenning unpublished).

Dieset (79° N, 11° E) comprises a system of two lakes situated approximately 140 km to the north of Lake Linnévatn (Figure 1). The lakes are ice-covered for approximately 10 months of the year, but with large annual variations [2]. The discharge in the outlet river may vary considerably, and in some years Arctic charr were prevented from ascending upriver to the spawning areas due to low water flow [2]. Monitoring upstream migrations using fish traps in the 1970s [2] and in the early 1990s [26] showed that 500 to 900 individual Arctic charr ascended the water course annually. In the last 10 years, the anadromous part of the population has increased, and probably up to 2000 Arctic charr now ascend the lakes each year.

## 2.2. Meteorological Data

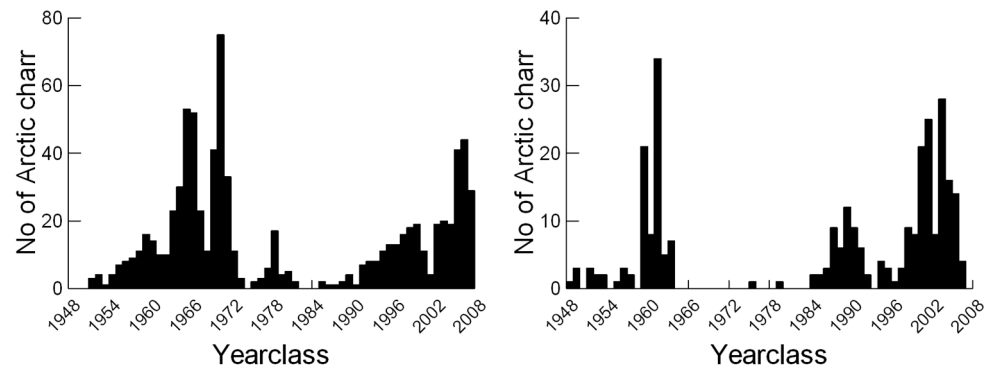
Both lakes Linnévatn and Diesetvatn are located near two meteorological stations (Figure 1). The meteorological station at Isfjord Radio was situated 4 km to the west of Lake Linnévatn, while the meteorological station at Ny-Ålesund in the Kongsfjorden Bay is situated 35 km southeast of Lake Dieset. Monthly means of air temperature and precipitation are available at Isfjord Radio from 1935 to 1976, except for the period 1941–1947, due to the evacuation of Svalbard during World War II [21]. Missing data from this latter period have been estimated using observations at Jan Mayen and the Russian station Bukta Tikhaya, on Franz Josef Land [21]. After 1976, air temperature data for Lake Linnévatn have been estimated from observations made at the Svalbard Airport and Longyearbyen stations, using regression analyses of the overlapping data with Isfjord Radio during the period 1957–1976. Monthly mean values of air temperature and precipitation were available for Ny-Ålesund from 1969 to the present, with data for the period before 1969 estimated from the Isfjord Radio records [21].

Until recently, there have been no consistent and regular measurements of snow depths made in Svalbard, in general, and only sporadic measurements of snow depth were made at the meteorological sites in Ny-Ålesund and Isfjord Radio. Long-term annual snow depth measurements are available, however, from the winter glacier mass balance records of two glaciers, Midtre Lovénbreen and Austre Brøggerbreen, in the vicinity of Ny-Ålesund [27]. Winter balance is obtained by snow-depth soundings over the glacier at the end of the winter accumulation period. The mass balance data used here cover the period 1967–2008 and comprise averages of snow thickness measurements made on the two glaciers in late April to early May, at the lowermost glacier elevations (50–250 m). While restricted spatially to these two glaciers, the data provide good proxies for spring snowfall in western Svalbard. This has been demonstrated by parallel measurements made over shorter periods from 2004 to 2008 on the Ny-Ålesund glaciers and Linnébreen near Lake Linnévatn (Jack Kohler, unpublished data).

## 2.3. Fish Data and Otolith Analyses

A total of 804 sagittal otoliths of Arctic charr from Lake Dieset and 289 from Lake Linnévatn have been used in this study. Arctic charr from Lake Dieset were sampled between 1970 and 2008 using a variety of equipment, including gillnetting in the lake ( $n = 360$ ), a trap catching ascending fish from seawater ( $n = 257$ ), electrofishing in the outlet river and in the lake ( $n = 182$ ), and rod fishing in the lake ( $n = 5$ ). In Lake Linnévatn, Arctic charr were sampled periodically from 1968 to 2006, and most fish were sampled

by gillnetting in the lake ( $n = 174$ ), while 115 were sampled by electrofishing in the lake and the outlet river. The material covers year classes of charr from 1948 to 2006 in Lake Linnévatn and from 1951 to 2008 in Lake Dieset (Figure 2). During the three periods with consistent data from YOY in both lakes (1959–1963, 1987–1991, and 1998–2006), we found no significant differences in the length of YOY between the two populations (in either period).



**Figure 2.** The number of aged Arctic charr in different year-classes in 1951–2008 from Lake Dieset (**left**;  $n = 804$ ) and 1948–2006 from Lake Linnévatn (**right**;  $n = 289$ ). Samplings of Arctic charr used for back-calculating the body length in young of the year (YOY) were conducted during the periods 1970–2008 (Lake Dieset) and 1968–2006 (Lake Linnévatn).

Arctic charr otoliths from Svalbard have a distinctive zonal differentiation between summer and winter increments, even among old individuals. They are much easier to age compared to otoliths sampled from Arctic charr populations further south, which is likely due to their slow annual growth rates, giving a clear distinction between summer and winter zones (Figure 3). Thus, age determination was carried out without any additional treatment or preparation of the otoliths, except placing them in glycerol and then viewing them under a binocular microscope.

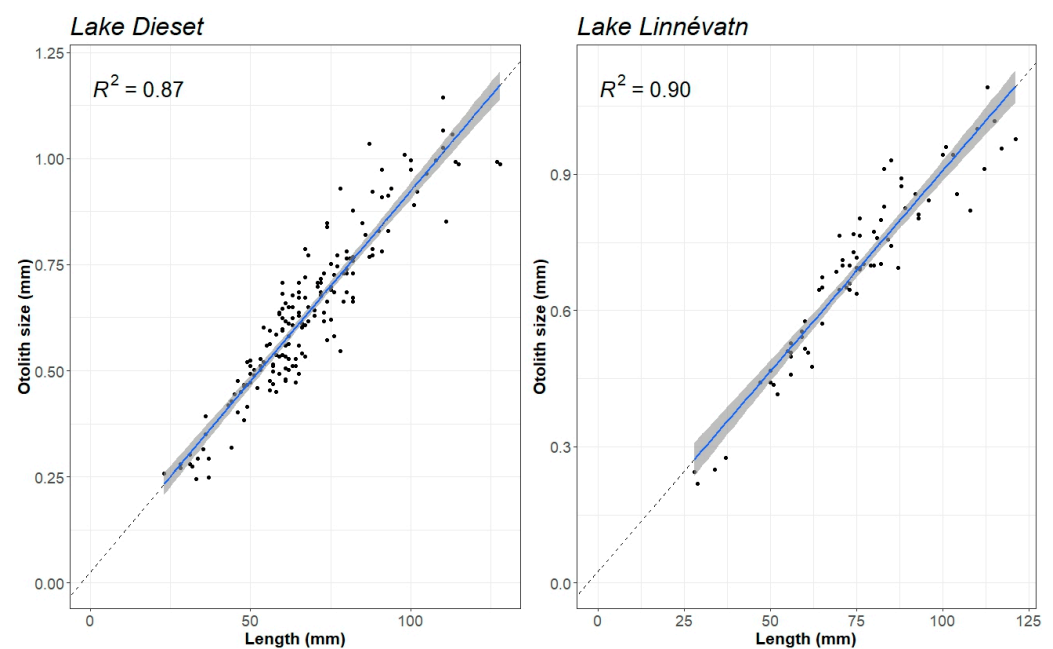


**Figure 3.** The two sagittal otoliths from a 10-year-old (winter) Arctic charr captured in Lake Linnévatn in September 1998.

Otolith increment width measurements were performed as described in [28]. The annuli were clearly visible along the rostrum, and in old fish rostrum counts have been shown to give the highest age estimates in Arctic charr [29]. Consequently, rostral radii were used for both age determination and otolith measurements; hence, relationships between fish fork length and otolith radius were evaluated.

Otoliths were photographed using a digital camera (DS-5M; Nikon Instruments Europe B.B., Kingston, Surrey, England) connected to a Leica Wild MZ8 stereo microscope and computer. Images were captured using NIS-Element software (Nikon Instruments Europe B.V., Amstelveen, The Netherlands) ([https://www.microscope.healthcare.nikon.com/en\\_EU/products/software/nis-elements](https://www.microscope.healthcare.nikon.com/en_EU/products/software/nis-elements), accessed on 1 January 2023), while the width of the otolith increments and total otolith length was measured using the image analysis program ImageJ (Version 1.41o; US National Institutes of Health, Bethesda, MD, USA). The center of each otolith was identified as precisely as possible by sight. The larval zone of the otolith is being formed when the fish larva is still in the egg and is defined as the innermost, darker part of the 0<sup>+</sup> otolith when observed with reflected light. Difficulties associated with differentiating between the end of the larval increment and the end of the first summer increment necessitated that the distance from the otolith center to the end of the first opaque (summer) increment was measured as a relative measure of the fish's first summer growth. Identified otolith growth increments of the first summer were assigned to calendar years based on the estimated age of the fish at catch.

For fish younger than 5 years of age and showing no records of anadromy, strong positive and linear correlation was observed between fish length and otolith size from both Lake Dieset ( $r^2 = 0.88$ ;  $n = 175$ ) and Lake Linnévatn ( $r^2 = 0.90$ ;  $n = 73$ ) (Figure 4). Thus, otolith increment width is a suitable predictor of somatic growth of the fish. See details in [28].



**Figure 4.** The relationship between fish length and otolith size for Arctic charr younger than 5 years of age and less than 130 mm, captured in Lake Dieset (left;  $n = 175$ ;  $Y = 0.028 + 0.0090 X$ ;  $p < 0.001$ ) and Lake Linnévatn (right;  $n = 73$ ;  $Y = 0.025 + 0.0088 X$ ;  $p < 0.001$ ).

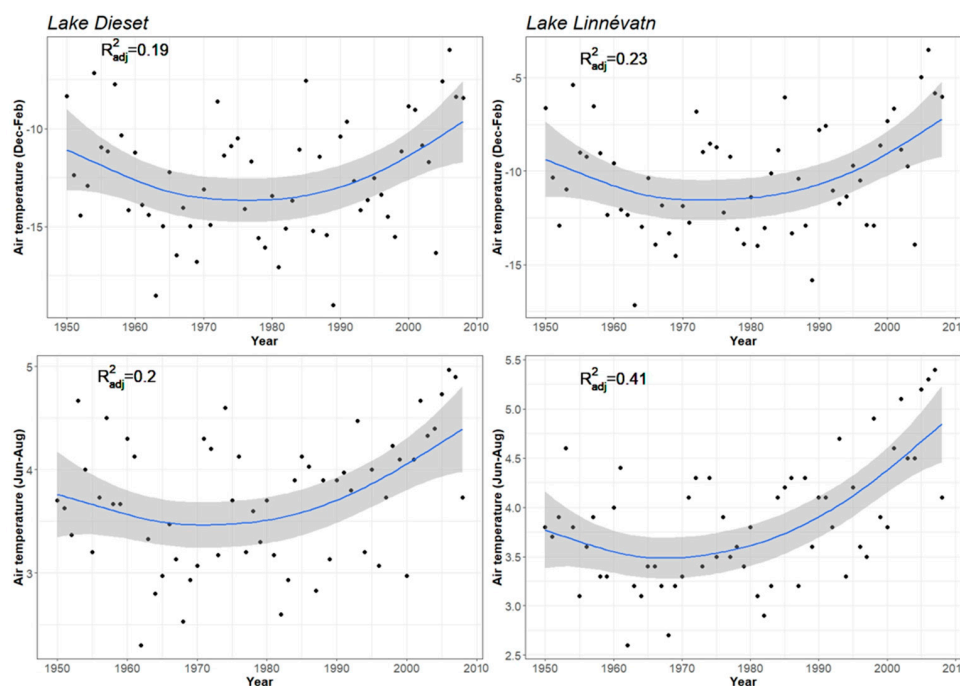
#### 2.4. Statistics

We used additive models in the R-library mgcv [30] to investigate temporal trends, effects of climatic variables, and the linearity of these effects (see [31,32] for examples). Additive models use flexible nonlinear functions to describe the relationships between response and predictor variables; here, we used the default thin-plate regression splines

of the `gam()` function to model these nonlinear relationships [30]. The effective degrees of freedom (edf) for the model, measure the degree of smoothness, with  $\text{edf} = 1$  representing a linear relationship and an edf value above 1 representing increased nonlinearity. Effective degrees of freedom are estimated using general cross-validation. However, as we were interested in the main patterns, we restricted the dimension of the spline basis to 4 so that edf would not be too large. To describe temporal trends in the first summer growth, we used the year of hatching as a predictor variable. For climatic effects, we considered mass balance (as a measure of spring snow accumulation), average winter (December to February), and summer (June to August) air temperatures as the predictor variables. All three variables were included as simple additive terms (i.e., without interaction terms such as products), and we fitted all models with one, two, and three smooth terms. We used adjusted  $r^2$  as a measure of the predictive power of each model, and together with a measure based on cross-validation (general cross-validation score), we selected the best model for predicting growth [30]. For the models with climatic variables as predictors, the figures show the partial residuals and the corresponding smoothed effect, that is, when other variables in the model are adjusted for.

### 3. Results

During the period when the individual Arctic charr were recruited to lakes Dieset and Linnévatn, the average winter (January–March) air temperatures (1950–2008) varied from  $-21.6$  to  $-5.4$  °C and from  $-18.6$  to  $-3.5$  °C at Isfjord Radio (Lake Linnévatn). In contrast, the average summer (June–August) air temperatures varied from  $1.7$  to  $5.4$  and  $2.0$  to  $5.7$  °C at Ny-Ålesund (Lake Dieset) and Isfjord Radio (Lake Linnévatn), respectively (Figure 5).

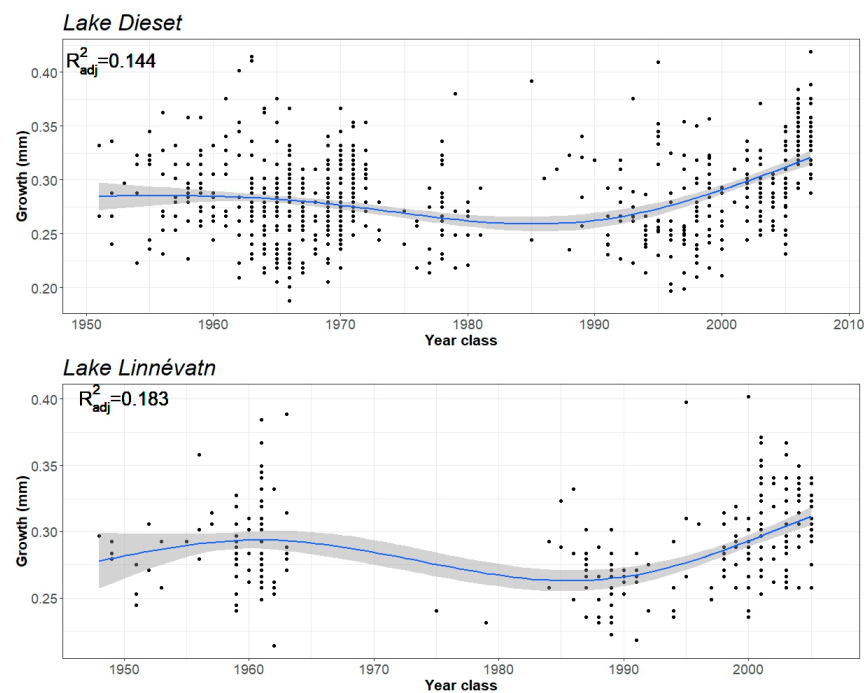


**Figure 5.** Estimated average winter (above, December–February) and summer (lower, June–August) air temperatures (°C) at Ny-Ålesund (left; Lake Dieset area) and Isfjord Radio (right; Lake Linnévatn area) in the period 1950 to 2008. The lines are smoothed by GAM.

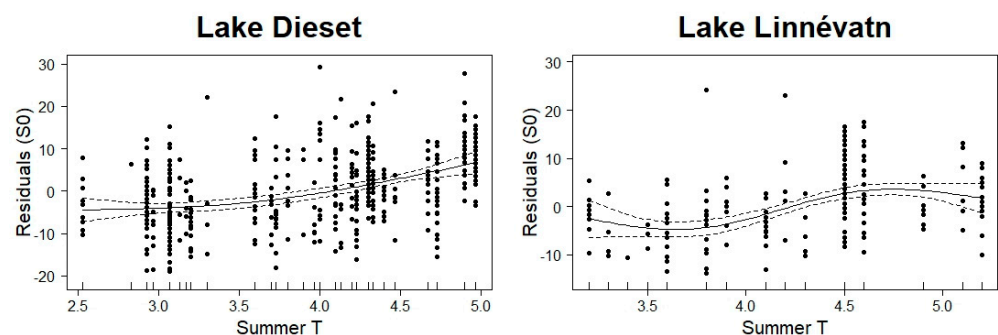
Both winter and summer air temperatures significantly co-varied between the two meteorological locations ( $r = 0.83$  and  $0.90$ , respectively;  $\text{df} = 59$ ;  $p < 0.001$ ). Both weather stations also recorded a decreasing air temperature trend (both winter and summer) from 1950 to 1978 and an increasing temperature from 1979 to 2008 (Figure 5).

The temporal trend in the back-calculated length based on measured otolith increments in YOY Arctic charr was positively associated with the shift in temperature trends related

to year class (Figure 6; Dieset:  $\text{edf} = 2.95$ ,  $p < 0.001$ ; Linnévatn:  $\text{edf} = 2.93$ ,  $p < 0.001$ ). Further, the estimated growth of YOY Arctic charr from Lake Dieset and Lake Linnévatn were both positively associated with increasing summer and winter air temperatures, and negatively correlated with the accumulated snow depth (Figure 7, Table 1). For Lake Dieset, the additive model showed an association with summer T ( $\text{edf} = 1.93$ ,  $F = 23.45$ ,  $p < 0.0001$ ), winter T ( $\text{edf} = 2.74$ ,  $F = 6.15$ ,  $p = 0.0004$ ), and snow depth ( $\text{edf} = 2.89$ ,  $F = 8.12$ ,  $p < 0.0001$ ). For Lake Linnévatn, the additive model showed an association with summer T ( $\text{edf} = 2.92$ ,  $F = 13.29$ ,  $p < 0.0001$ ), winter T ( $\text{edf} = 1.28$ ,  $F = 4.46$ ,  $p = 0.018$ ), and snow depth ( $\text{edf} = 1$ ,  $F = 5.94$ ,  $p = 0.016$ ). Based on the generalized cross-validation score, the inclusion of all three predictors (summer and winter air temperatures, and snow accumulation) explained more than 30% and 25% of the variation in YOY growth in the two lake systems of Lake Dieset and Lake Linnévatn, respectively (Table 1).

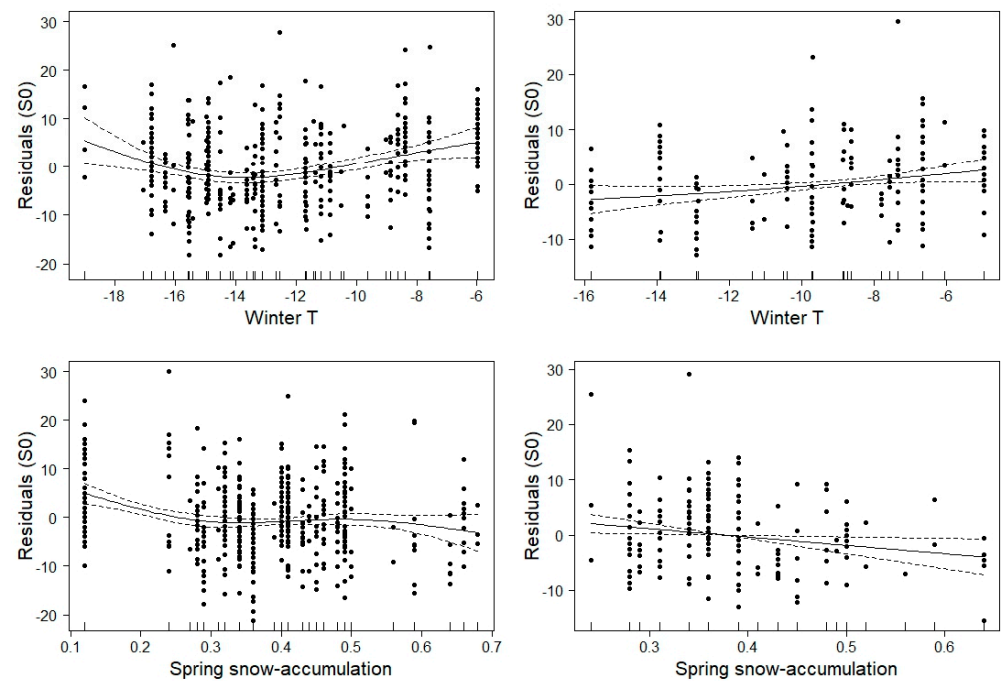


**Figure 6.** Estimated trends in fish growth in the young-of-the-year (YOY) Arctic charr from Lake Dieset (above) and Lake Linnévatn (lower), Svalbard, based on back-calculation from sagittal otoliths. The smooth lines are based on an additive model with year class as a predictor variable, and a spline basis of dimension of 4 to reduce overfitting.



**Figure 7.** Cont.





**Figure 7.** Residual plot for the first summer growth (S0) in the young-of-the-year (YOY) Arctic charr from Lake Dieset (**left**) and Lake Linnévatn (**right**), Svalbard, based on back-calculation from otoliths, and in relation to summer air temperature (above), winter air temperature (middle) and snow accumulations (lower).

**Table 1.** Influence on YOY growth explained by the different parameters (in %); summer (June–August) temperature (summer T), winter (December–February) temperature (winter T), and snow = mass balance. Percentage of variation explained (adjusted  $R^2$ ) with generalized cross-validation score (in parenthesis) for all models used to predict the first summer growth. The best models (in bold, based on GCV score) for both lakes included all three predictors. Note that the sample sizes given as [N=] differ as mass balance was not available for all years, and that  $R^2$  and GCV are not strictly comparable.

Lake	Lake Dieset	Lake Linnévatn
Year of Birth	14.4 (67.1) [N = 772]	18.3 (47.6) [N =285]
Summer T	19.6 (63.0) [N = 772]	10.9 (51.8) [N =285]
Winter T	16.0 (65.8) [N = 772]	1.9 (57.0) [N = 285]
Snow	0.00 (77.4) [N = 504]	3.9 (59.0) [N = 190]
Summer T + Winter T	20.1 (62.7) [N = 772]	10.6 (52.2) [N = 285]
Summer T + Snow	<b>30.3 (54.6) [N = 504]</b>	<b>22.5 (48.4) [N = 190]</b>
Winter T + Snow	23.9 (59.4) [N = 504]	11.6 (55.1) [N = 190]
Summer T + Winter T + Snow	<b>31.6 (53.9) [N = 504]</b>	<b>24.9 (47.1) [N = 190]</b>

#### 4. Discussion

The estimated first summer growth of young-of-the-year (YOY) Arctic charr in the two lakes Linnévatn and Dieset, Svalbard, was found to be positively correlated with the summer air temperature. To some extent, YOY growth was also positively correlated with winter air temperature. This was most probably due to thinner ice formed in mild winters, and thereby an earlier ice break-up. In contrast, we found a negative relationship between the accumulated snow depth and growth in YOY Arctic charr.

Ref. [33] found that otolith-derived water temperatures estimated from YOY Arctic charr sampled in Lake Dieset were consistent with temperatures found in the shallowest part of the littoral areas in Svalbard lakes during summer. Further, they also found that the otolith-derived temperatures differed significantly from the monitored water temperatures

recorded at the outlet river. Ref. [34] captured all age classes of juveniles in Lake Dieset as well as in the outlet river, with the exception of YOY Arctic charr that were never found in the river. This corresponds well with our sampling in both Lake Dieset and Lake Linnévatn (this study), i.e., that all YOY Arctic charr were caught close to the lake shore and at depths of less than 20 cm. These shallow areas of the littoral zone are highly influenced by solar radiation during the summer, thus explaining our findings demonstrating that summer growth of YOY Arctic charr in Lake Dieset and Lake Linnévatn was positively correlated with the summer air temperature.

Otoliths continue to form annular zones even when the growth in body length has ceased [35,36], and back-calculation of length of such fish based on annuli widths is not possible. Likewise, in periods with rapid somatic growth, for instance, in Arctic charr during the sea residence in summer [28] or when Arctic charr shift to cannibalistic behavior (Svenning, unpublished), this is not manifested in a similar marked increase in otoliths (see details in [28]). As a consequence, otoliths are highly reliable with regard to age determination. However, the uncoupling of body and otolith growth reported for many species (see, for instance [37,38]), causes the general back-calculation of body length of older fish based on annuli widths in otoliths to be problematic. The sampled otolith material from lakes Dieset and Linnévatn, covering a period of more than 50 years, has made it possible to relate the annual growth of Arctic charr to the fluctuation in climatic conditions on Svalbard during this long period. We have used the size of YOY in this study, because this age class seems to stay in the shallowest littoral area. This is contrary to the other juvenile age classes and adult fish, who use both the deeper part of the littoral, profundal, and river habitats with variable temperature regimes [33]. On the other hand, it is likely that all size classes respond similarly to variations in temperature [12,16,39], and the positive growth effect of YOY Arctic charr due to increased temperature is suggested to be representative for all age groups.

The lake water temperature during the ice-free season is mainly influenced by the timing of ice break-up and the following summer air temperature. Earlier studies have indicated that ice break-up may be explained by air temperature alone [40,41]. Meanwhile, more recent studies, such as [42], found that regional variation in ice-off dates in north-western Canada were also driven by relationships between lake size, snow thickness, and ice thickness. The annual mean air temperature in Svalbard has increased by 3–5 °C over the last four to five decades [24]. This should have led to earlier ice break-ups in Svalbard lakes. However, ref. [43] found that although the ice-free season in Lake Linnévatn has increased by 1.5 days per year in the last ten years, the time of ice break-up has been relatively constant. Further, water temperature has increased by an average of 0.06 °C per year, and stayed warm for a longer period each autumn, thus indicating a further positive effect on Arctic charr annual growth.

Mean winter and spring air temperatures have also shown an increasing trend in mainland Norway since the 1990s [44], with a significant and accelerating trend of earlier ice break-up and delayed freeze-up dates after 1991 [45]. A corresponding development has also been described for lowland and subalpine lakes elsewhere in Europe, North America, and in most of the northern hemisphere during the last decades, with a reduction in lowland areas covered by snow, earlier ice break-ups, and increasing surface water temperatures [46–48]. In the subarctic lake Takvatn, Norway, a positive effect of water temperature and a negative effect of fish abundance on somatic growth were found in individual juvenile Arctic charr [9]. This suggests that, as temperatures rise, the somatic growth of Arctic charr will increase in high-latitude lakes. Our findings suggest a similar development for YOY Arctic charr in the two Svalbard lakes studied.

Ref. [24] showed that in addition to air temperature, precipitation (both rain and snow) in Svalbard has increased in the last decades. Increasing amounts of snow on top of the ice in Svalbard lakes may compensate for increasing air temperature. Thus, this may explain the timing of ice break-up showing no change over the last 10–15 years for Lake Linnévatn [43], while dates of ice-cover have occurred later. The positive correla-

tion between air temperature, and ice break-up and water temperature found in Lake Linnévatn [43], plus a longer period with elevated temperatures in warmer years, support the findings from our study, i.e., the clear trend of a positive correlation between air temperature and YOY growth in Arctic charr, both in Lake Linnévatn and Lake Dieset. Further, the more or less constant annual timing of ice cover found for Lake Linnévatn [43] supports our second finding, i.e., a negative relationship between accumulated snow depth and growth in YOY Arctic charr.

Ice thickness in High Arctic lakes typically reaches its maximum in May [49]. Although winter air temperatures in Svalbard show an increasing trend, the December–February temperature is still well below zero. However, higher air temperatures may nevertheless affect ice thickness on the lakes, i.e., ice becomes thinner, resulting in an earlier ice break-up in summer, and a longer open-water season. In Lake Dieset, where the drainage area is 57 km<sup>2</sup>, of which more than 30% is covered by glaciers, the authors in [2], found a positive correlation between the water level in the outlet river and the air temperature. Thus, increasing air temperature obviously increases the melting of the glaciers, and depending on the summer air temperature, may have a cooling effect on the water in the lake. With future glacier loss due to melting, lakes fed by cool meltwater will more or less disappear, and lake water temperatures may become considerably higher than today. Likewise, the water flow in outlet rivers will be reduced; thereby, the access for migratory fish to feed in seawater during summer, or to swim upriver from the sea may be hindered, i.e., leading to a risk for collapse of anadromous Arctic charr populations in Svalbard and other High Arctic Lake systems.

Temperature has pervasive effects on recruitment, year-class strength, somatic growth, and other life history and behavioral traits in salmonid fishes, especially through metabolic rates and food consumption [50]. When YOY and older juveniles of anadromous Arctic charr obtain a better annual growth in length, both the survival and length of the freshwater fish remain constant until smoltification and migration to salt water may be influenced. A shorter time period in fresh water before smoltification may increase the number of smolts due to reduced predation, thereby resulting in a higher density of migratory fish. An increase in the length of YOY resident Arctic charr may also result in a higher annual survival, causing larger year classes and resulting in an increased population density. This, in turn, would lead to increased predation pressure on food resources, a lower food intake by individual fish, and stagnation in growth at a smaller size [51]. A corresponding development has been observed for brown trout on the Hardangervidda mountain plateau (>1100 m a.s.l.), i.e., low accumulation of snow in spring, early ice-free lakes and streams, and higher summer temperatures all contribute to larger and more numerous YOY [16].

As in most of the Arctic, the anadromous populations of Arctic charr in Svalbard are far more attractive for commercial fishing than resident populations, mainly due to the size and higher quality of the migratory fish. As a consequence, some of the Svalbard populations were previously heavily exploited, resulting in a strong decrease in large and spawning migratory fish. As a result of this, the Governor of Svalbard introduced a sanctuary for some of the anadromous populations in 1993. This lasted until 1997, when gillnetting was re-opened in four lakes. This was followed by a strict harvest quota for the same populations after 2008. The anadromous Arctic charr population in Lake Linnévatn has returned to a higher number than 30 years ago, but this is far less than before the 1950s.

Global warming is widespread, but it is occurring much faster in higher northern latitudes [6]. Sea surface temperatures in the Barents Sea as well as on the western coast of Svalbard have increased significantly during the last decades [52]. Thus, climate change now facilitates the northward movement of many fishes previously constrained by low temperatures from dispersal to High Arctic environments. Moreover, during the summers of 2001 and 2006, the first recorded three-spined sticklebacks, *Gasterosteus aculeatus*, were captured in Lake Linnévatn and Lake Straumsjøen, in Isfjorden, Svalbard [53]. These mature sticklebacks, observed in two Svalbard lake systems, are the only evidence of a vagrant occurrence of the species and not a verification of its establishment. Although an

established population of sticklebacks may lead to food competition with juvenile Arctic charr and/or a new vital prey for piscivorous Arctic charr, it is difficult to predict whether a potential establishment of stickleback would have negative or positive consequences for the production, life history, and harvest potential of Svalbard Arctic charr.

Even if climate warming leads to an increased somatic growth of Arctic charr in High Arctic lakes, it is still uncertain how this will influence the life history and size-structured interactions in Arctic charr populations [9]. In lakes with migratory Arctic charr in Svalbard, improved annual somatic growth could potentially lead to larger year classes and an increasing fraction of anadromous versus resident fish. This implies a potential for larger catch quotas and higher catches. However, in the longer term, warmer climates are projected to eventually lead to complete loss of many Svalbard glaciers [54,55]. With the loss of glaciers due to melting in lake catchments, rivers could potentially dry out in late summer, thus hindering migration between freshwater and saltwater environments for anadromous Arctic charr (see [28]). In the worst-case scenario, the highly valuable and attractive anadromous Arctic charr populations could eventually disappear from Svalbard lake systems.

## 5. Conclusions

The Arctic charr species complex dominates the fish communities in High Arctic rivers and lakes. Besides being an essential component of the diversity of many High Arctic fish communities, Arctic charr also comprise a significant economic resource as food for northern people. Despite being adapted to extreme environmental conditions, the distribution of Arctic charr is limited in the far north by abiotic barriers. This paper exemplifies the possible impact of changes in climate on the growth of juvenile Arctic charr in two populations in Svalbard. We further conclude that, in the longer term, a warmer climate may lead to the complete loss of most glaciers along the western coast of Svalbard, i.e., outlet rivers may dry out in summer/autumn, thus hindering migration between saltwater and freshwater environments for migratory fish. Thus, in the worst-case scenario the highly valuable and attractive anadromous Arctic charr populations could eventually disappear from Svalbard lake systems.

**Author Contributions:** Conceptualization, M.A.S.; Methodology, E.T.B., M.A.S., N.G.Y. and J.A.G.; Software, N.G.Y.; Validation, M.A.S. and R.B.; Formal Analysis, N.G.Y.; Investigation, M.A.S., J.A.G. and E.T.B.; Resources; Data Curation, M.A.S., E.T.B. and J.A.G.; Writing—Original Draft Preparation, M.A.S., E.T.B. and J.A.G.; Writing—Review and Editing, M.A.S., R.B., J.H., J.K. and N.G.Y.; Visualization, M.A.S., N.G.Y. and R.B.; Supervision, M.A.S.; Project Administration, M.A.S. and J.A.G.; Funding Acquisition, M.A.S. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research received no external funding.

**Institutional Review Board Statement:** In accordance with Norwegian and European legislation related to animal research, formal approval of the experimental protocol by the Norwegian Animal Research Authority (NARA) was not required, because the regulation only applies to procedures on live animals. All samples (otoliths) from this study were taken from animals that were already dead.

**Data Availability Statement:** The data that support the findings of this study are available from the corresponding author upon reasonable request.

**Acknowledgments:** This study is based on the sampling of Arctic charr in two Svalbard lake systems over the period of 1960–2008. We would like to dedicate this work to Nils Gullestad, who started collecting Svalbard Arctic charr otoliths with great enthusiasm in the early 1960s, continuing for almost two decades, but who sadly passed away last autumn before the project was completed. We would also like to thank Sigmund Spjelkavik, Thomas Olsen, and the staff at Isfjord Radio for collecting Arctic charr from Lake Linnévatn, and to Hanne Hegseth who sampled Arctic charr in both Lake Linnévatn and Lake Dieset. We also thank Eirik Førland, Knut Langeland, Bård Jørgen Bårdsen, Brian Dempson, and Mike Power for their valuable input during the project period.

**Conflicts of Interest:** Author Eigil T. Bjørvik was employed by the company CFEED. The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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