Rising temperatures in a subarctic lake lead to increased somatic growth rates for Arctic charr (*Salvelinus alpinus,* (L.))

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Abstract

Cold water species living at high latitudes are expected to respond rapidly to climate change due to their sensitivity to increasing temperature. Water temperature strongly affects the ecology of fish, influencing food intake and conversion, and ultimately somatic growth rate. In a lake, somatic growth rates will also be contingent on food availability, which is negatively affected by fish abundance. Abundance plays a key role in competitive interactions and the scope for food acquisition and is hence an important constraint on temperature-dependent growth. The current field study addresses gradients of both water temperature and relative abundance affecting somatic growth in juvenile fish at high latitudes over nearly 40 years. A sclerochronological analysis was conducted using sagittal otoliths extracted from Arctic charr annually from the early 1980s up to 2016. Otolith growth measurements from individual fish were used to obtain length-at-age data, via statistical models, to investigate whether water temperature variability and abundance translates into changes in somatic growth. Results revealed a clear positive effect of water temperature on somatic growth in juvenile individuals and a clear negative effect of abundance. Temperature-dependence in growth was significant for average and fast-growing individuals across all investigated age classes with the only exception of 2-year-old fish. Abundance had a consistently negative effect on growth rates for all age classes considered. These findings suggest that as global temperatures rise, somatic growth of Arctic charr will correspondingly increase in high latitude lakes, up to an optimum, past which they will likely decline. This will have direct consequences for cold-water fish populations at high-latitudes, affecting fish length at age, maturation schedules and ultimately fish demographics.

Acknowledgements

I will forever be indebted for the love and support I received from family and friends during my time away from them in Tromsø - without which none of this would have been possible.

To my mother, Helen, I would like to express my deepest gratitude and sincerest thanks for everything you do for your family, this would not have been possible without your unconditional love and support.

To my father, Paul, from an early age you instilled in me a relentless passion for nature, and I am forever grateful. I hope that one day I may pass this passion on as you did for me.

My two brothers, Dimitri and Zachary, thank you for the memories and adventures, and providing me with the inspiration to pursue my passion. To many more adventures.

Megan, I promise, no more extended trips away from home… I am forever grateful to have you in my life. I look forward to the future and making many more memories.

I would like to extend my sincerest thanks and appreciation to my supervisors and mentors, Aslak and Raul. You have both been tremendously patient, insightful, encouraging and helpful. Without the both of you, this paper would not have fallen into place as it has. I wish you all the best in the future and hope our paths cross again soon.

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Contents

1. Introduction

Body temperature is conceivably the most important ecophysiological factor affecting the performance of ectotherms. Biological processes, rates and functions such as metabolic rate, locomotion, immune function, sensory input, foraging ability, courtship, and rates of feeding and growth are all influenced by temperature (Huey et al. 1979; Angilletta et al. 2002; Kuperinen et al. 2011). The significant role ambient temperature plays for ectotherms is particularly evident in aquatic environments. Aquatic ectotherms principally exchange heat with the water through conduction, and thus their body temperature closely resembles that of the surrounding environment (Narum et al. 2013; Siikavuopio et al. 2014). Fish are obligate poikilotherms, meaning they lack the necessary mechanisms for internal temperature regulation. However, fish may thermoregulate through behavioural and physiological interactions with the environment, for example, by actively seeking preferred temperatures when thermal gradients exist (Brett 1971; Larsson 2005; Fitzgerald et al. 2011). As thermal conformers, fish are acutely sensitive to water temperatures and can perceive temperature fluctuations as low as <0.5 °C and generally maintain body temperatures within 1-2 °C of ambient water temperatures (Block et al. 1993; Kristensen et al. 2006; Elliot & Elliot 2010). For fish, water temperature is thus an essential property of its habitat and a defining component of its niche (Magnuson et al. 1979; Elliot & Elliot 2010).

Water temperature strongly affects the ecology of fish, influencing food intake and conversion, and ultimately somatic growth rate (Jobling 1983; Rubin 1993; Larsson & Berglund 2005; Siikavuopio et al. 2014). Fluctuations in vital rates mediated by temperature-dependent growth have implications for entire fish populations, affecting: population size, age structure and total biomass (Pankhurst et al. 2011). When ration is not a limiting factor, increasing temperatures are generally associated with increasing growth rates along a thermal performance curve, up to an optimum temperature, beyond which growth rates decline due to metabolic costs exceeding energy intake (Jobling 1983; Larsson & Berglund 2005; Payne et al. 2016). Within a normal temperature range, growth for fish progresses faster at warmer temperatures, approximately at exponential rates (Gillooly et al. 2001; Kingslover et al. 2008; Zuo et al. 2011). The relationship between water temperature and growth rate has been described empirically for many fish species, which show great variability in both temperature range and optimum for growth (Mortensen et al. 2007; Siikavuopio et al. 2014). Thermal tolerances for fish vary widely according to species and environment (Wysocki et al. 2009)

and thermal guild may be partially categorized by either being stenothermal or eurythermal. Stenothermal fish exhibit a narrow temperature range and are unable to tolerate extreme fluctuations in temperature changes, while eurythermal fish may generally tolerate wider temperature ranges (Becker et al. 1979; Pörtner 2001; Heino et al. 2009). Consequently, stenothermic fish are more vulnerable to temperature changes; particularly younger age classes such as fry and juveniles, which are considerably more sensitive to temperature and lack the capacity to thermoregulate (Elliot & Elliot 2010; Réalis-Doyelle et al. 2016). Accordingly, fluctuations and trends in water temperature due to climate variability and warming will have effects on fish growth that are species specific (Elliot & Klemetsen 2002; Larsson et al. 2005; Siikavuopio et al. 2010). Furthermore, an important mechanism which often limits ration availability and consequently growth, is high fish abundance. High intraspecific densities may restrict food availability resulting in competitive interactions for limited resources, and as individuals within the same species have highly similar resource requirements, the intensity of intraspecific competition may be severe and strongly related to population density (Amundsen et al. 2007).

Cold water species living at high latitudes are expected to respond rapidly to climate change due to their sensitivity to increasing temperature and to the high rate of warming experienced (Hein et al. 2012; Karjalainen et al. 2015). The Arctic is warming at twice the global average and lakes respond with a prolonged, warmer ice-free season (Ficke et al. 2007; Heino et al. 2009; Myers et al. 2017). Consequently, growth and survival of cold-water species such as the Salmonids, are expected to be impacted (Reist et al, 2006a). Salmonids are the most species rich and the most studied group of freshwater fish in the Arctic, including ecological key species such as Arctic charr *Salvelinus alpinus,* Atlantic salmon *Salmo salar* and Brown trout *Salmo trutta* (Klemetsen et al. 2003; Reist et al. 2006a). Within this family, no species is found as far north as Arctic charr. Distributed throughout the Holarctic as far as ~84°N (Larsson & Berglund 1998), Arctic charr can live in lakes where ice-cover remains throughout the summer, for some or most years (Klemetsen et al. 2003; Reist et al. 2006b).

Arctic charr is the most cold-water adapted salmonid (Siikavuopio et al. 2009), capable of surviving and feeding at temperatures as low as ~0°C (Elliot & Klemetsen 2002; Klemenstan et al. 2003). Conversely, Arctic charr are the least tolerant of high water temperatures, with critical thermal limits for survival at 26–27 °C compared to 30-33 °C and 26-30 °C, for Atlantic salmon and Brown trout respectively (Elliot & Elliot 2010). For most populations of

Arctic charr, growth may begin at 1-3 °C (Larsson et al. 2005), and the temperature range within which they may feed while exhibiting no signs of abnormal behavior is 3-16 °C (Jensen et al. 1989). The effect of temperature on the growth of Arctic charr has been studied extensively. Laboratory experiments have demonstrated that increasing temperatures are associated with increased growth, up to an optimum range of 11-14°C (Jobling 1983; Jensen et al. 1989; Larsson & Berglund 1998; 2005; Larsson et al. 2005; Siikavuopio et al. 2010) past which growth steeply declines. Interestingly, Arctic charr have exhibited preferential water temperatures lower than the ranges for optimal growth and tend to choose temperatures more conducive for food conversion (Larsson & Berglund 1998; Larsson et al 2005; Elliot & Elliot 2010). Additionally, optimal and preferential water temperatures are similar throughout Arctic charr's extensive distributional range, with no evidence of adaptation to warmer waters at lower latitudes (Baroudy & Elliot 1994; Elliot & Elliot 2010; Elliot & Klemetsen 2002; Klemetsen et al. 2003). Despite the temperature affinity and sensitivity of Arctic charr, it is difficult to obtain reliable and consistent field evidence of climatic effects on charr growth (e.g. Kristensen et al. 2006; Michaud et al. 2010; Murdoch et al. 2013).

The current field study addresses temperature variability and abundance on juvenile Arctic charr growth at high latitudes over nearly 40 years. Emphasis is placed on the early life stages, since the effect of temperature on growth is particularly evident during this critical life phase (McCauley & Huggins 1979; Otterlei et al. 1999; Imslad et al. 2005; Kingslover et al. 2008; Siikavuopio et al. 2014). The study site, Lake Takvatn, is a subarctic, oligotrophic lake in Northern Norway (69 °N) where broadscale monitoring has been ongoing for over four decades. Arctic charr was introduced in Takvatn in the 1930's from neighbouring Lake Fjellfrøsvatn, and research on the charr population has been ongoing since 1979 (Klemetsen et al. 1989). A sclerochronological analysis using sagittal otoliths extracted from Arctic charr annually through 1983 to 2016 is carried out. Otolith growth measurements from individual fish are used to obtain length-at-age data, via statistical models, to investigate whether water temperature variability and rates of abundance translate into changes in somatic growth. Considering present knowledge and understanding of somatic growth and thermal performance of Arctic charr, I pose three hypotheses:

1. I expect to find higher somatic growth of Arctic charr for years which exhibit warmer water temperatures.

2. The increase in somatic growth will be the most pronounced for the 0+ young-of-the-year and 1+ juveniles and will dissipate as the charr reaches ages 2+ and 3+.

3. Somatic growth will decline with increasing Arctic charr abundance.

2. Materials and Methods

2.1 Study Location

The Arctic charr were sampled from Takvatn, a subarctic lake located in Northern Norway (69°07′N, 19°05′E), connected to the Målselv River system (Fig. 1.). The lake is oligotrophic, dimictic, and situated 214 m above sea level. Takvatn has a surface area of 14.2 km^2 and two main basins, both of which have an approximate depth of 80 m (Klemetsen et al. 1989). The climate is subarctic, with an average air temperature in July of 13.2 °C. Midnight sun occurs from May 26th to July 24th. The lake is ice free from end of May or early June to November (Klemetsen 1989; Amundsen et al. 1997; 2013). Mid-summer surface temperatures are approximately 12 °C, with a maximum temperature of 14 °C (Amundsen et al. 2013), followed by autumn circulation which brings winter temperatures to 2 °C or lower (Klemetsen 1989). Takvatn supports a fish community composed of Arctic charr (*Salvelinus alpinus*, hereafter charr), Brown trout (*Salmo trutta*, hereafter trout), and three-spined stickleback (*Gasterosteus aculeatus*) (Klemetsen 1989). Trout is the only native fish species found in the lake, as charr were introduced from a neighboring lake, Fjellfrøstvatn, in the 1930's due to the declining trout fishery - a result of an increase in fishing pressure. This was followed by the introduction of the three-spined stickleback in the 1950's from Sagelvvatn, a lake located in a separate watercourse than Takvatn (Klemetsen 1989). Although Takvatn is part of the Målselv River system, anadromous species are prevented from entering the lake due to the Målselv waterfall, consequently all species of fish in Takvatn are permanent lake residents.
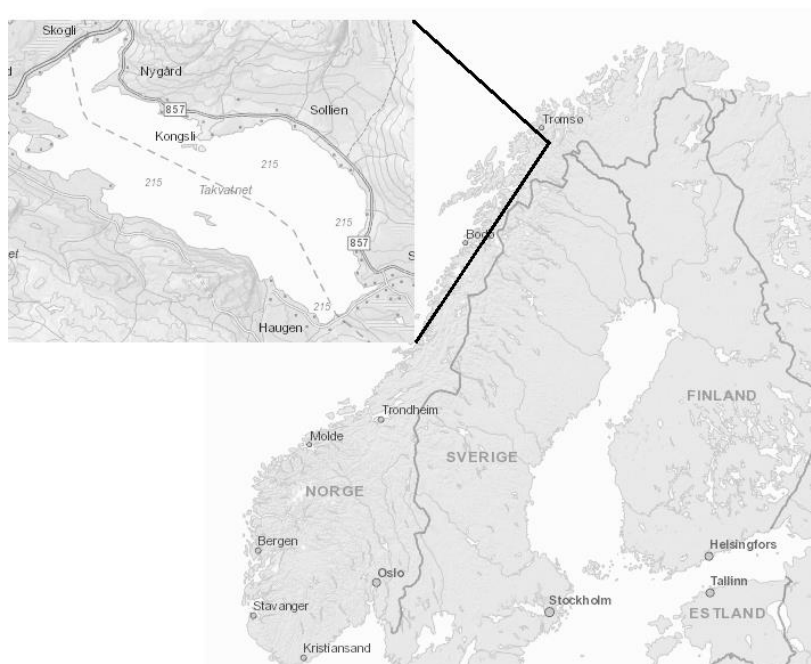

Fig. 1. Map of study location in north Norway, inset map of lake Takvatn (atlas.nve.no, Version 2.8.2.0001.)

2.2 Field Sampling

This study uses sagittal otolith samples collected between 1983 and 2016. Field sampling procedures have been standardized and protocols for Takvatn have been conducted similarly for all years. Briefly, monofilament gill nets were set in the East end of the lake, in three habitats, the littoral, profundal and pelagic, all placed for approximately the same duration of fishing hours (12h), over all sampling years. Multi-mesh gillnets were used in all three habitats, Norwegian 'Benthic Gillnet Overview' (BGO) gillnets (L=40 m, W=1.5 m) were used for the littoral zone (0-15m) and profundal zones (>20m), and Norwegian 'Floating Gillnet Overview' (FGO) gillnets (L=40m, W=6m) were placed in the pelagic zone (0-6m). Both BGO and FGO gillnets have 10, 12.5, 15, 18, 22, 26, 35 and 45mm mesh sizes – measured from knot to knot and alternate at 5m intervals horizontally. All captured fish were sampled and recorded at the Takvatn field station. Each fish was given a number, followed by fork-length (mm) and weight (g) measurements. Otoliths were extracted and aged using surface reading techniques, then the pair of sagittal otoliths were placed in a vial containing 96% ethanol. The body cavities were opened to inspect for parasites in the swim bladder and intestines, the stomach was extracted for diet content analysis. Fish were additionally visually sexed, and the maturity stage was assessed based on gonad development.

2.3 Laboratory analysis

Otoliths

Sagittal otoliths (i.e. ear bones or stones) extracted from charr at the Takvatn field station were analyzed in the laboratory to determine age and growth of individual fish. Otoliths are paired calcified structures used for balance and/or hearing in all teleost fish, the composition of which is dominated primarily by calcium carbonate (Campana 1999). Otoliths exhibit a pattern of alternating opaque and hyaline (transparent) growth increments (Holden & Raitt 1974; Campana 1985). The differentiation between the opaque and hyaline zones is the result of seasonal differences in growth rate, with rapid growth during summer months resulting in the hyaline zone, and slow or no growth in winter leading to the opaque zones (Holden & Raitt 1974; Barber et al. 1987; Mendoza 2006). Accordingly, 'a full year of growth' is characterised by one translucent zone followed by an opaque zone. Otolith reading was performed at the freshwater ecology laboratory of the Norwegian College of Fisheries Sciences in Tromsø, Norway. The total number of otoliths sampled was 693. The otoliths analyzed were distributed over 28 years encompassing extensive climatic variability, with

marked inter-annual differences in mean air temperatures. Only otoliths that were extracted between June and October were analyzed. To reduce error due to difficulty in estimation, fish older than 6 years were excluded from the study, as growth zone structures become finer on older otoliths, a consequence of decreasing growth rates as fish age (Holden & Raitt 1974). Otolith measurements and aging were validated by randomly selecting 40 otoliths, which were independently measured and aged a second time by two researchers, to evaluate precision consistency of measurements and aging.

Preparation of Otoliths

Preparation of otoliths for aging and growth measurements were done by pipetting glycerol into a cavity of a black viewing slide. Glycerol was used as a medium to increase clarity of annual growth zones (Holden & Raitt 1974) and facilitate easier handling, while the black dish increased contrast (Floro-Larsen et al. 2016). Next, one sagittal otolith was removed from a sample tube containing a pair of otoliths preserved in 96 % ethanol. Using forceps, the otoliths were individually immersed in the glycerol filled cavity, while being illuminated from above (VisiLED MC 1000). Each otolith was positioned with the posterior nucleus side facing upwards and the sulcus-side downwards (Appendix Fig. A1.). A stereo-microscope and integrated camera (Carl Zeiss SteREO Discovery. V8; Zeiss Axiocam ERc5s) were used to photograph otoliths, with components set as follows: objective = 1, optovar = 3.2x, total magnification = 1.6x. One picture was taken of each otolith, and two copies were made, one was a raw image, which did not include any measurements and was kept as a control for validating age and growth measurements (Appendix Fig. A1.), and a second image, which was used to measure annual growth zones in a separate file (Appendix Fig. A2.). All images were analyzed with Carl Zeiss - Zen (blue edition) 2011, software (version 1.0.0.0).

Age and Annual Growth Measurements

First, to asses the age of each otolith, hyaline and opaque zones were counted until the last full year of growth. Once the fish was aged, growth was evaluated by measuring the width of annual growth increments. The first measurement taken was total otolith length, a transect was initially positioned from the center of the primordium to the last full year of growth, on the ventral side, toward the anterior end of the otolith; the resultant total otolith length is representative of total fish length. Next, another transect line was positioned from the centre of the primordium, at the same location as the first transect above, and stretched out to the end of the nucleus, the resultant transect produced a length measurement for the first year of

growth (+0). Following these two transects, additional measurements were made by positioning transects at the beginning of each subsequent hyaline zone to the end of the proceeding opaque zone, resulting in annual length measurements, this was done for each full year of growth (both hyaline and opaque zones) (Appendix Fig. A2.). A summary of the number of otoliths per age group, along with mean total otolith lengths and fish lengths is shown (Table 1). Age appears to be a good predictor of mean total otolith length and mean fish length, which increase steadily as fish grow older (Fig. 2).

Table 1. Summary of sampled fish and otoliths, listing age of the fish at capture, number of sampled otoliths by fish age, and the mean total otolith lengths and fish lengths at capture.

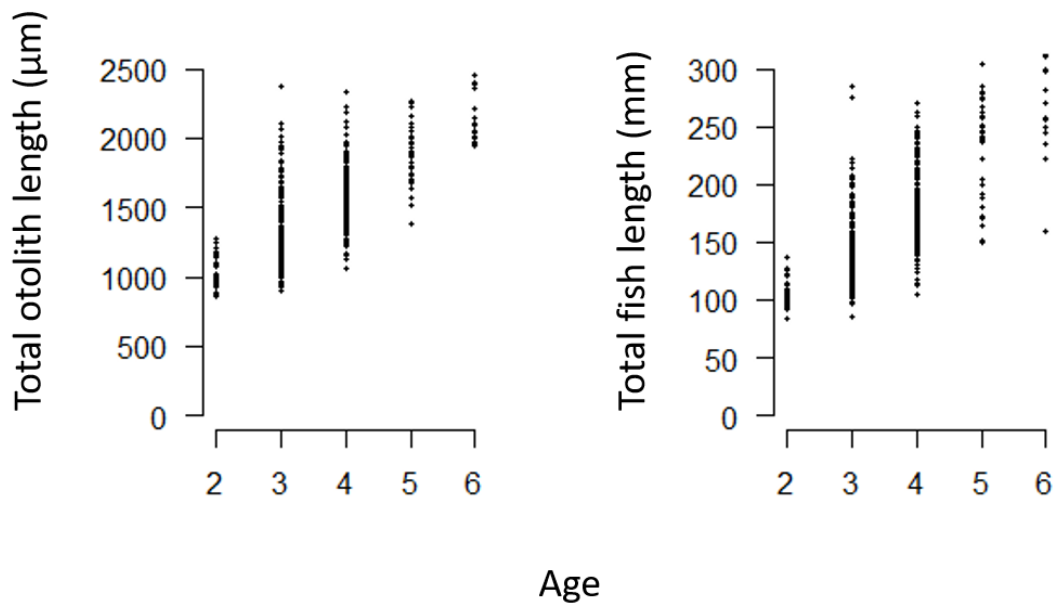| Age	N	Mean total otolith length (µm)	Mean fish length (mm)
2	35	1040.27 ± 145.61	105.62 ± 11.18
3	363	1278.21 ± 217.22	141.39 ± 25.41
4	236	1540.06 ± 190.97	181.33 ± 34.31
5	39	1888.93 ± 176.18	235.71 ± 38.57
6	17	2140.91 ± 176.23	269.29 ± 42.75

Fig. 2. Total otolith length at age (left panel) and body length at age (right panel) in Arctic charr.

2.4 Temperature Data

Temperature data, as well as other climactic parameters (precipitation, wind, etc.) have been collected daily since 1957 at the Bardufoss meteorological stations located in the Målselv region and were used as inputs for modelling water temperature. Additionally, water temperature data for Lake Takvatn were collected for the month of August since 1980 for most years, and for the entire open water season on a few years, which were used for calibrating the General Lake Model. For Lake Takvatn water temperature was modelled with a 1D, air-to-water limnological model (General Lake Model, R package GLMr). The limnological model for lake Takvatn was forced using several climatic variables obtained from the nearby Bardufoss meteorological station and provided estimated daily water temperatures along the water column. Inputs for the water temperatures were summarized as annual means and open-water seasonal mean temperatures for the top 1-10m of water in Takvatn. Open-water seasonal mean temperatures were chosen to encompass middle of May to beginning of November, to include ice break up and freeze up times (Fig. 3).
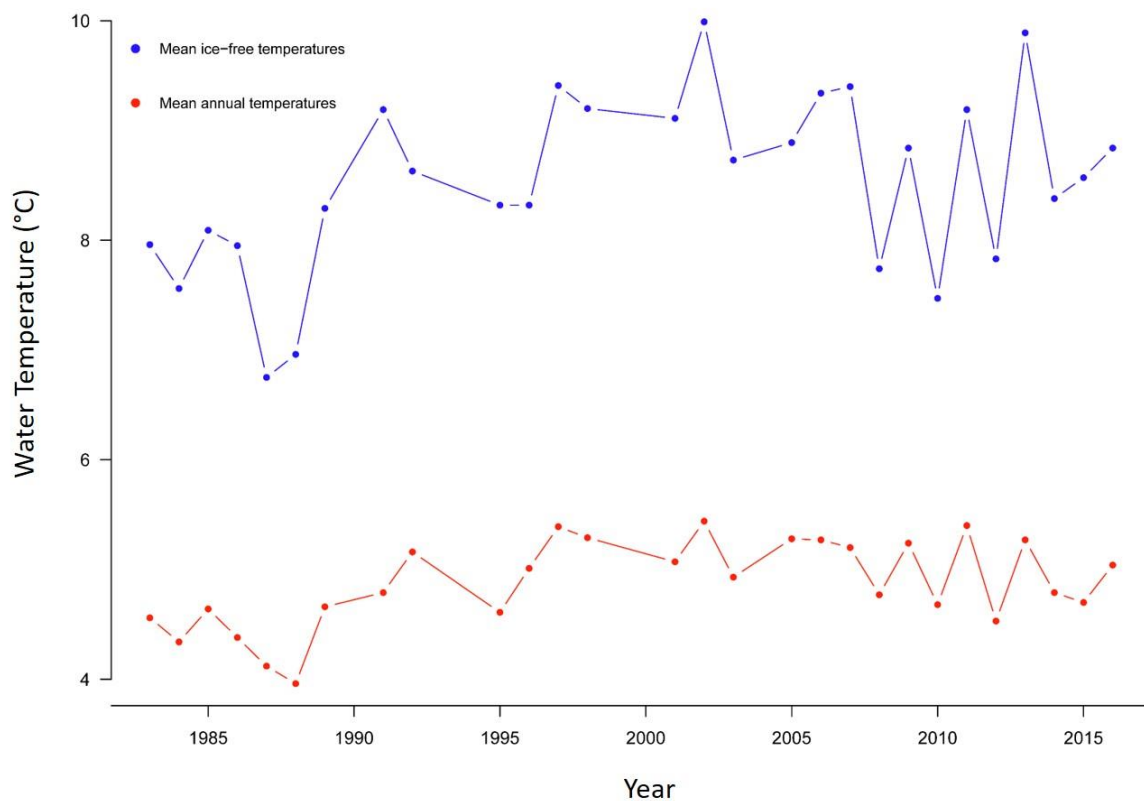

Fig. 3. Mean modelled temperatures of ice-free periods (May to November) (Blue line) and mean modelled annual temperatures (Red line).

2.5 Catch Per Unit Effort Data

Catch per unit effort (CPUE) data were collected by gillnetting fish in the littoral zone (<15m) of Lake Takvatn. CPUE data are given as number of fishes $100m^{-2}$ net $night^{-1}$, for the month of August each year. Refer to (Klemetsen et al. 2002) for a detailed overview of Takvatn CPUE and the culling which removed 666 000 individual charr from the lake between 1984 and 1989. The CPUE of charr declined considerably during the late 1980s and the trout CPUE was low (Fig. 4.). Prior to the culling the littoral zone had a high density of small and slow-growing charr and very few trout (Klemetsen et al. 2002). After the culling, charr numbers displayed damped oscillations and brown trout abundance increased; eventually the CPUE of both species stabilized to similar levels (Fig. 4.).

Fig. 4. Temporal developments of catch per unit effort (CPUE) during the study period for Arctic charr (black) and Brown trout (grey) in lake Takvatn.

2.6 Statistical analysis

Backcalculation

Backcalculation of growth is done to obtain length-at-age data. Charr is a slow growing species (Barber et al. 1987; Morita & Matsuishi 2001), an uncoupling between somatic and otolith growth can occur known as an age-effect, such that, as the fish gets older and somatic growth stagnates otolith accretions may still develop (Stormer et al. 2016; Ashworth et al.

2017; Thaulow et al. 2017). Given the age effect present in charr otoliths (Barber et al. 1987; Morita & Matsuishi 2001), the statistical model for backcalculation proposed by Finstad (2003) was applied. The Finstad model adds an interaction term to a backcalculation method developed by Morita & Matsuishi (2001), where an age effect was initially included to account for the otolith size increasing continuously during periods with little, or no somatic growth.

Finstad (2003) model:

$$L_t = [O_t O_T^{-1} (\beta_0 + \beta_1 L_T + \beta_2 T + \beta_3 L_T T) - \beta_0 - \beta_2 t] (\beta_1 + \beta_3 t)^{-1}$$

Where L_t is the back calculated length at age t, T is age at capture, O_t is the measured otolith radius at age t, O_T is the observed otolith size at the time of capture and L_T is the observed fish length at the time of capture. The $\beta_0,$ β_1, β_2 and β_3 are coefficients estimated by least squares multiple regression (Finstad 2003).

KT model – Temperature-dependent growth

To investigate the potential eco-physiological effect of inter-annual water temperature variability for charr growth in lake Takvatn, this study uses a temperature-growth relationship specifically parametrized for charr (Smalås et al. 2019 – In review). The temperature-dependent growth rate coefficient Kt follows a dome shaped curve (Fig. 5.), reaching a maximum at the temperature optimum for growth.

$$K_t = \frac{K_{max}(T_t - T_{min})(T_t - T_{max})}{(T_t - T_{min})(T_t - T_{max}) - (T_t - T_{opt})^2}$$

Where K_{max} is the maximum growth coefficient parameterized for Takvatn charr, T_t is the experienced average daily water temperature (°C), and $T_{max},$ T_{min} and T_{opt} are the maximum, minimum and optimum temperatures for growth which for charr correspond to 20 °C, < 1 °C and 14.1 °C respectively (Larsson & Berglund 1998; 2005; Larsson et al. 2005; Siikavuopio et al. 2010)
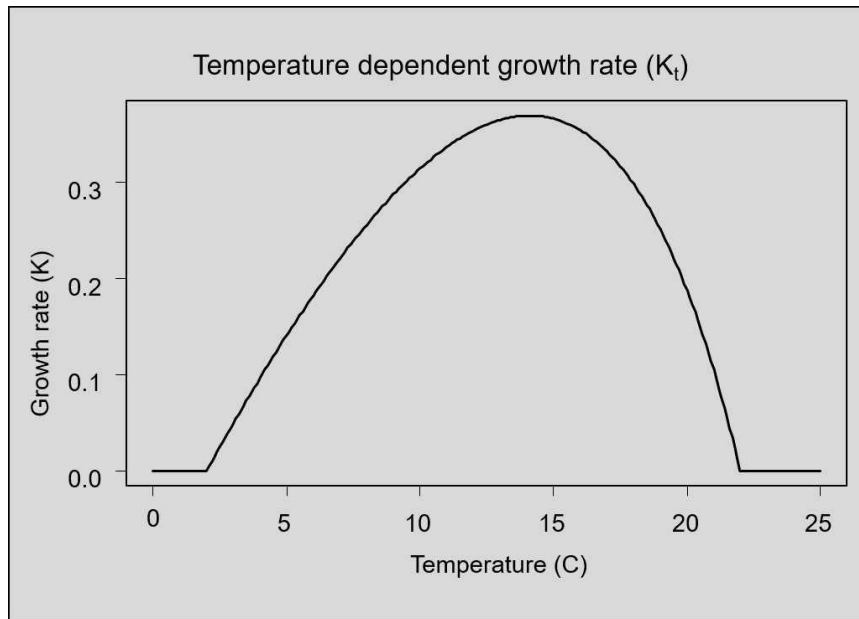
Fig. 5. Temperature-dependent growth rate curve for Arctic charr. Growth rate increases with water temperature up to an optimum of 14°C for Arctic charr, after which growth rate declines rapidly.

Regression models

Both parametric and non-parametric regression models were used to investigate the effects of inter-annual relative abundance (CPUE) and water temperature variability on somatic growth across age classes of charr. To study abundance and temperature effect on mean growth, linear regression models were applied that included CPUE and annual mean water temperature as explanatory variables and age specific backcalculated growth as response variable. To analyse abundance and temperature effects on charr displaying higher within-year growth performances and to cope with variance heterogeneity, quantile regression models for median, 75th and 90th percentile growth were applied using the same explanatory variables as in the linear regression models.

Computations, statistical analyses and graphics were made in R (R version 3.5.0) using the package 'quantreg' for quantile regression model estimation and statistical inference.

3. Results

3.1 Backcalculated Lengths

A verification of backcalculated lengths showed a good performance of the Finstad (2003) model (Fig. 6.) with a satisfactory agreement between backcalculated lengths (i.e. sum of all backcalculated yearly length increments for each fish) and observed lengths at capture ($R^2 = 0.93$; p<0.001)
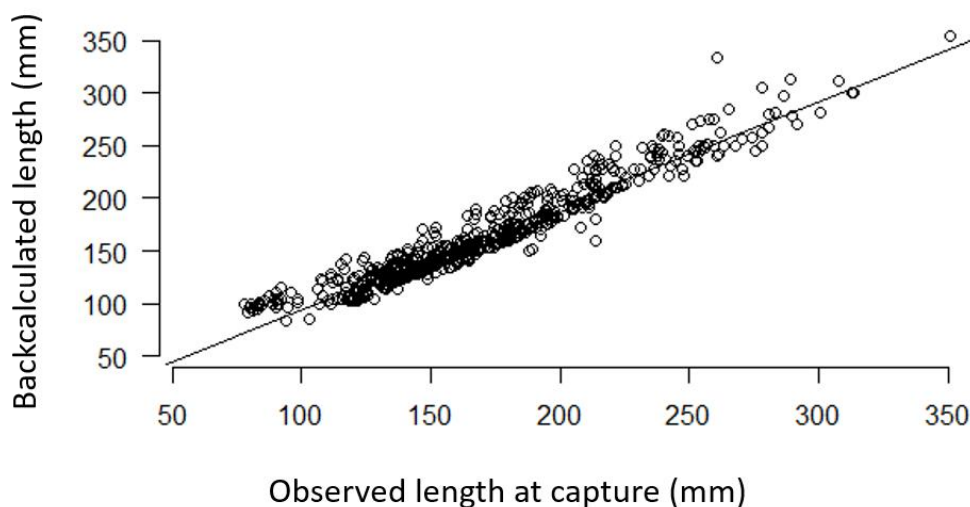

Fig. 6. Relationship between backcalculated lengths and observed lengths at capture for all fish included in the analyses (N=693). The trend line was obtained by linear regression.

3.2 Effects of abundance and temperature on somatic growth

Linear regression results show the dependence of charr growth on water temperature and CPUE for 0+ charr to be highly significant ($F_{2,690} = 21.94$, $p < 0.001$, $R^2 = 0.057$). For the 1+ aged charr water temperature and CPUE explained the most variation between years ($F_{2,690} = 43.73$, $p < 0.001$, $R^2 = 0.1099$). Additionally, the magnitude of the effect of water temperature on growth was the highest for the 1+ age class, which showed that, on average, with a 1°C increase in temperature, somatic growth would increase by 4.97mm (Appendix Table A2). The models showed significant effects, although accounting for less variation in growth, also for the 2+ ($F_{2,655} = 15.16$, $p < 0.001$, $R^2 = 0.041$) and 3+ ($F_{2,655} = 17.54$, $p < 0.001$, $R^2 = 0.048$) age classes.

Somatic growth increased with water temperature in all age classes except for 2+ individuals, and water temperature showed the strongest effect for the 3+ age group (Fig. 7.). Quantile regression revealed that for median and fast-growing individuals, increased water temperature led to increased growth rates for all age classes except for 2+ fish. For example, quantile regression results for 0+ charr showed a significant, positive effect of water temperature on growth (2.02, 95% CI = 1.2, 4.06) at 50th percentile and for the 90th percentile (4.14, 95% CI = 0.34,6.43) (Appendix Table A5.), this translates to a doubling from the 50th to 90th percentile. Results for 1+ charr showed positive significant relationships between water temperature and growth for all regressions; 50th percentile (4.76, 95% CI = 3.02, 6.51), 75th percentile (5.72, 95% CI = 2.56,7.65) and 90th percentile (7.65, 95% CI = 3.53,11.93) (Appendix Table A6.). 3+ charr in Takvatn showed a positive significant relationship with water temperature at the 50th percentile (4.89, 95% CI = 0.53, 8.24) and 75th percentile (6.82, 95% CI = 1.28, 11.31) (Appendix Table A8.). In addition, the 90th percentile clearly demonstrated that the fast-growing individuals take advantage of the increased water temperature more than average growing individuals (10.83, 95% CI = 2.1, 14.85), the temperature effect for this percentile translates to a 10.83mm increase per °C (Appendix Table A8.).

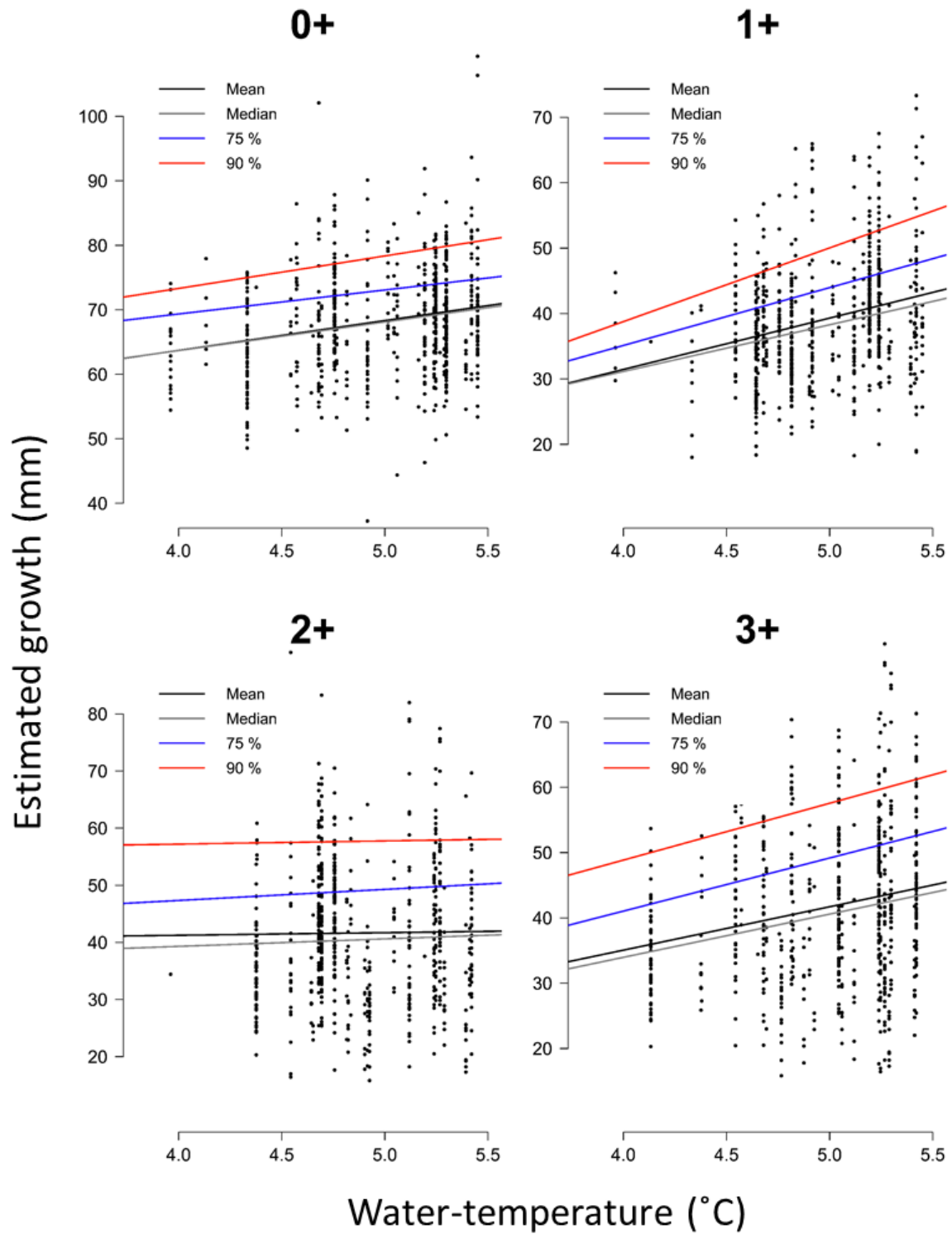Fig. 7. Estimated annual somatic growth (mm · year^{-1}) plotted against water temperature (°C) by age group. The plots for the four age classes include linear and percentile regression lines, with mean, median, 75th and 90th percentiles.

Strong negative effects of CPUE on somatic growth were visible for all age classes of charr in Lake Takvatn (Fig. 8.), although notably having the strongest effects on 2+ and 3+ individuals. Quantile regression of CPUE on growth for the 0+ charr showed a significant negative effect (-0.32, 95% CI = -0.51, -0.23) for the 50th percentile, (-0.18, 95% CI = -0.48, -0.008), 75th percentile, and 90th percentile (-0.20, 95% CI = -0.45, -0.02) (Appendix Table A5.). Quantile regression results for 1+ charr showed significant negative CPUE regressions at the 50th percentile (-0.46, 95% CI = -0.6, -0.34), 75th percentile (-0.42, 95% CI = -0.62-0.29) and for 90th percentile (-0.53, 95% CI = -0.74, -0.18) (Appendix Table A6.). Quantile regression results for 2+ CPUE effect showed a significant negative relationship only at the 50th percentile CPUE (-0.91, 95% CI = -1.11, -0.79) and 75th percentile (-1.34, 95% CI = -1.52, -0.97) (Appendix Table A7.). CPUE was negative and not significant for two percentiles for the 3+ age class: 50th (-0.63, 95% CI = -1.03, 0.21), 75th (-0.41, 95% CI = -1.35, 0.88) and 90th percentile was positive although not significant (0.43, 95% CI = -1.55, 1.27) (Appendix Table A8.).

A Kt coefficient plot is shown to demonstrate that temperature (°C) translates to the empirically derived growth rate for charr (Appendix Fig. A4.). There is a corresponding a mean annual temperature-dependent growth coefficient plotted against year show in (Appendix Fig. A3.).
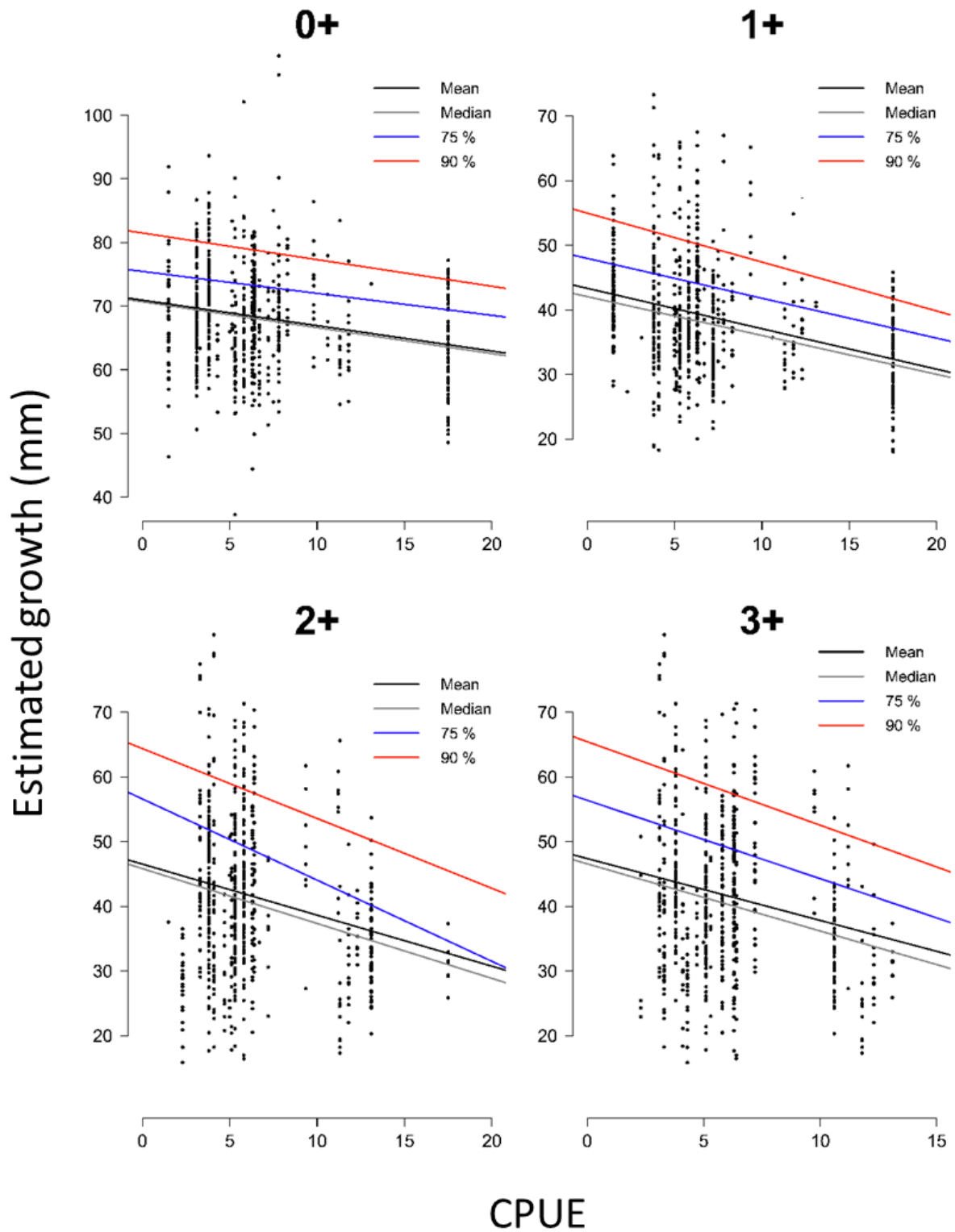
Fig. 8. Estimated fish growth (mm · year^{-1}) plotted against catch-per-unit-effort (CPUE), given as number of fishes 100m^{-2} net-night^{-1}, by age group. The plots for the four age classes include linear and percentile regression lines, with mean, median, 75th and 90th percentiles.

4. Discussion

This study demonstrated the significant role temperature and abundance have on the somatic growth of a wild population of subarctic fish. Water temperature showed a clear positive relationship with somatic growth for juvenile charr in lake Takvatn, while high abundance was associated with decreased individual somatic growth rate. The propensity for fish to increase somatic growth rates was the most pronounced for average and fast-growing individuals. Younger individuals displayed a strong temperature-dependence in growth, which was substantially more distinct than in 2+ fish, in line with expectations. This is consistent with previous studies suggesting that younger fish are better able to optimize temperature-dependent growth (Elliot & Elliot 2010; Réalis-Doyelle et al. 2016). Contrary to my expectations, the 3+ individuals showed a considerably strong temperature-dependent effect on growth. Abundance had a distinctly negative effect on growth, with higher CPUE leading to decreased somatic growth rates. There was a considerable amount of variation in growth between years that could not be explained by temperature and was only partially accounted for by variation in abundance. In addition to variation between years, there was also substantial variation among individuals within a year across age classes. My findings suggest that as temperatures rise, somatic growth of charr will correspondingly increase in high latitude lakes, given that abundance does not limit ration availability.

4.1 Temperature-dependent growth

Data derived from nearly 40 years has provided considerable *in-situ* evidence of temperature-dependent growth for a subarctic fish specie. The documented positive relationship between mean-annual water temperatures and somatic growth rates of individual fish confirms the ecological importance of climate variability at these high latitudes and provides one of the few field corroborations of the hypothesis for charr. In previous studies the relationship between temperature and growth of charr has only consistently been seen in controlled laboratory settings (e.g Baroudy & Elliot 1994; Larsson & Berglund 2005; Elliot & Elliot 2010), whereas field studies have shown variable findings (e.g Power et al. 2000; Kristensen et al. 2006; Godiksen et al. 2010; Michaud et al. 2010; Murdoch et al. 2013). Two potential reasons why field studies have not been conclusive in the past is the ample within year variation in growth among individuals and the limited climatic/temperature variability between years in short term studies. Despite the observed overall proclivity for charr to

increase somatic growth rates with increased temperature, the variability between individuals within the same years suggests that not all individual fish have the same scope for temperature related increases in somatic growth. For example, the 1+ individuals would on average experience an increase of 4.76mm per 1°C of warming, contrasted to the top 90th percent of the same year class, which demonstrated 7.65mm of growth per 1°C of warming, almost a 50% increase in the scope for temperature-dependent growth. In addition, for the 3+ individuals, mean growth was 4.89mm per 1°C of warming and a two-fold increase at the 90th percentile which exhibited 10.83mm of growth per 1°C.

The latter findings can perhaps be accounted for by the fact that temperature is not static, nor uniform in subarctic lakes, particularly in large oligotrophic lakes such as Takvatn which commonly encompass three major habitats i.e. the profundal, pelagic and littoral, and accordingly different thermal regimes (Klemetsen et al. 1989; 2003). A primary factor likely responsible for the variability between individuals within the same year was habitat use, which can differ substantially between individual fish. The habitat fish seek are often naturally prescribed by inter- and intraspecific competition, food profitability and predation risk (Adams et al. 1988; L'Abée-Lund et al. 1993; Byström et al. 2004; Sinnataby et al. 2012; Klemetsen et al. 1989; 2013; Kratochvil et al. 2014). Different habitats will determine the thermal range an individual fish may experience, the temperature differences between habitats are particularly evident in oligotrophic lakes where large thermal gradients exist between warm epilimnetic and cold hypolimnetic waters (Klemetsen et al. 1989; Murdoch et al. 2013). For example, individuals in the littoral zone would not only have experienced increased temperatures, but perhaps also increased foraging opportunities compared to individuals in the profundal zone (Klemetsen et al. 2002; Byström et al. 2004), therefore compensating for increased metabolic demands and resulting in higher growth rates (Kristensen et al. 2006; Zuo et al. 2012; Payne et al. 2016). Conversely, individuals which displayed below average growth may have been relegated (through intraspecific competition or predation) to cooler waters typical of the profundal zone. These are suitable habitats for predator avoidance, although deficient in optimal thermal conditions and food profitability, leading to slower somatic growth (L'Abèe-lund et al. 1993; Godiksen et al. 2011).

4.2 Age and temperature-dependent growth

Temperature-dependent influences on growth vary according to age and consequently ontogenetic life stages and size (McCauley & Huggins 1979; Jobling 1983; Otterlei et al. 1999; Imslad et al. 2005; Siikavuopio et al. 2014). The current study demonstrated age-dependent temperature effects on wild individual fish growth, specifically that younger age groups responded to temperature positively, as the 0+ and 1+ showed a strong correlation between increased temperature and consequent increases in growth rates. Young-of-the-year size-at-age has previously been linked positively with warm water and air temperatures in high latitude regions (Godiksen et al. 2010). Younger fish have generally shown a preference for warmer waters compared to larger conspecifics (Otterlei et al. 1999; Handeland et al. 2008; Siikavuopio et al. 2014). The affinity for younger fish to preferentially choose warmer temperatures could be to optimize growth preceding intralacutstrine habitat-shifts to deeper and colder profundal zones and/or to increase chances of first over-wintering success (McCauley & Huggins 1979; Klemetsen et al. 1989; 2003; Bystrom et al. 2004; Godiksen et al. 2010; Siikavuopio et al 2014). Similarly, 0+ subarctic gadids, display a higher temperature for optimal growth, a supposed adaptation to maximize first summer-growth before transitioning to deeper, colder water (Laurel et al. 2017). It is probable that in Takvatn, when warmer water is available, most of the young-of-the-year and 1+ juvenile charr preferentially select the warmer thermal regime of the littoral zone, particularly if food availability is high and the risk of predation is low. The abrupt loss of the temperature signal in growth rates for the 2+ age class suggests that during this ontogenetic phase most of the fish are likely not in an ideal thermal habitat. Residency in the profundal waters, characterized by nutrient deficient foraging and cold thermal regimes (L'abèe-lund et al. 1993; Godiksen et al. 2011) could have played a principal role in mitigating the temperature-dependent growth relationship for the 2+ age group. Surprisingly, the steepest relationship between growth and temperature was for the 3+ age class. This was despite hypothesising that temperature-dependent growth would dissipate past juvenile ages, as temperature has less of an effect on larger fish (Kingsolver et al. 2008; Emmrich et al. 2014). It is probable that the older juveniles are better able to realize the potential for growth from increases in temperature through thermoregulation. Additionally, larger, older fish are generally capable of withstanding negative temperature effects and sudden fluctuations in temperature, given their size which acts as a buffer (Elliot & Elliot 2010; Murdoch et al. 2013). At 3+ the charr which inhabited the profundal zone likely emigrate back to shallower waters (Klemetsen et al. 1989), as risks associated with predation have decreased with body size (Wankowski 1979) and seek better foraging. These

individuals may also have a wider dietary niche and access to more nutritious food, providing a greater opportunity to meet metabolic demands.

4.3 Food availability and Intraspecific competition

High abundances of charr and their ecological effects in Takvatn have been documented extensively, notably having a considerable impact on the fish populations dynamics, food availability, individual fitness and somatic growth (Amundsen et al. 1988; 1993; 2007; Klemetsen et al. 1989; 2002). The clear negative relationship documented between CPUE and growth stresses the importance of high abundance for somatic-growth. This contribution offers a clear example of abundance effects on growth in Takvatn based on individual growth, previous studies were all aggregated population estimates. Intraspecific competition exerts powerful selective forces on fish and has direct effects on the competitive success of individual fish (Ward et al. 2006). In Takvatn, during periods of high densities prior to the culling (1984 to 1989), fish exhibited a unimodal size structure and small over-all body sizes (Klemetsen et al. 2002). Competition and the ensuing resource scarcity lead to a truncated charr population, food consumption was low, and it was established that the low somatic growth rates of individual fish were the direct result of high densities of charr (Amundsen et al 2007). The local availability, quantity, and quality of food present for fish plays a vital role in enabling the growth benefits of increased temperatures (Kaushik 1986). For fish, food availability and ration size play a fundamental role in growth and can constrain the positive effects temperature may have on accelerating growth rates (Jobling 1983). Fundamentally, increases in temperature lead to increases in metabolic demands of ectotherms (Kristensen et al. 2006; Zuo et al. 2012). Metabolic rates can increase exponentially within normal temperature ranges (Zuo et al. 2012), if the increases in ambient temperature are not subsequently met with increases in food supply fish will likely experience retarded growth and lower overall fitness (Kristensen et al. 2006; Zuo et al. 2012). Food availability was likely a key contributing factor to both the inter- and intra-annual variation. For example, the optimum temperature of 14.1 °C derived from laboratory studies is for charr being fed on maximum rations. This optimum fluctuates strongly with ration sizes (Larsson & Berglund 2005; Elliot & Elliot 2010), and food availability is closely linked to intra-specific competition (Klemetsen 1989; Amundsen 1997; 2013). Previous *in-situ* studies on the temperature effects on growth have shown that food availability and productivity play a major role in a fish's capacity to realize the growth benefits from increased temperatures (Kristensen

et al. 2006; Michaud et al. 2010; Murdoch et al. 2013). Following the intensive fishing at Takvatn, feeding rates increased and showed a strong inverse relationship between population density and food consumption rates; in addition, there was substantial variation in growth rates which also showed considerable negative correlations with population density (Amundsen et al. 2007). Moreover, intraspecific competition exerted a tremendous force on habitat selection. Prior to the culling there was a predominance of very young, small, and immature charr found in profundal samples where water temperature would be the coolest (Klemetsen et al. 1989). These juveniles were potentially relegated to this zone by intra-specific competition from larger and older conspecifics. It would be intuitive to at least, in part, associate the poor growth during this time to the relatively cooler and less productive profundal region of Takvatn.

4.4 Predation and inter-specific competition

Predation is an important biological interaction which commonly affects the growth of fish. Predation and competition between trout and charr characterise the dynamics between these two salmonid species when they coexist, particularly due to the trout's piscivorous tendencies (Amundsen et al. 2007; Finstad et al. 2011; Persson et al. 2013; Hernandez et al. 2014). The trout is generally considered a superior predator and outcompetes charr in the littoral zone for better forage such as zoobenthos (Forseth et al. 2003; Klemetsen et al. 2003) and is a markedly better piscivorous feeder than charr when they coexist (Persson et al. 2013; Hernandez et al. 2014). In contrast, the charr have a diversified dietary niche, which is wider than that of the rival trout (Forseth et al. 2003; Klemetsen et al. 2003; Eloranta et al. 2013). Surprisingly, in Takvatn, evidence shows the trout pose little significant negative pressure on individual charr performance (Persson et al. 2013). Previous studies on the lake have demonstrated that the performance of charr was better explained by intraspecific density dependence (Amundsen et al. 1993), rather than the density of predacious trout - which neither explained individual charr growth rate or habitat use (Persson et al. 2013). Once the charr reaches the 1+ age they likely lose the ability to hide amongst the structurally complex littoral zone (Bystrom et al. 2004); their larger size and lack of physical refuge may make them more appealing prey items for trout and consequently affected the populations growth. Interspecific competition between the charr and sticklebacks is likely a larger factor which played a part in the between year variability of charr growth. In Takvatn, there was a strong relationship between years with extremely low densities of cladocerans (*Daphnia and*

Eurycercus) and years with high-density scores of sticklebacks and conversely low growth rates for young charr (Klemetsen et al 2000). Years with low stickleback densities correlated well with excellent growth in small charr (Klemetsen et al 2000). Therefore, competition for resources in a resource limited lake likely played a larger role than predatory forces from trout.

4.5 Future implications

The temperature-dependent growth established here has several future implications for fish in comparable systems across the Holarctic. If temperatures increase as anticipated, then cold-water fish species will correspondingly increase in size, granted that thermal tolerances are not exceeded, and food availability meets the higher demand. Individual fish will therefore attain greater size at age, which might have multiple reverberating effects, influencing entire fish populations. For example, body size determines the strength of predator-prey interactions, body-size-abundance relationships and energy fluxes in food webs (Emmrich et al. 2014). Recent temperature-dependent modelling on somatic growth rates of charr (specifically calibrated for Takvatn) have predicted higher water temperatures will lead to higher growth rates of charr and consequently lead to larger sizes at age (Smalås et al, 2019 – In review). The current findings corroborate these predictions, as it is evident temperature has already had an impact on the growth-rates of fish in Takvatn. Furthermore, the observed variability within and between years is likely to increase, as increasing temperatures will also have effects on other environmental and biological mechanisms that act on fish growth (Finstad et al. 2011). These inferences are based on fish which still have leeway with regards to temperature flexibility, such as many subarctic fishes which have yet to experience significant increases in water temperature. For example, other fish species associated with warm water, already at thermal limits have shown decreased growth due to climate change (Reist et al. 2006a), therefore, thermal guild will play a large role in determining the extent to which species are affected by climate induced shifts in temperature. This is likely the case with other predicted climate change scenarios such as species shifts/extinctions, phenological and genetic changes (Reist et al. 2006a; Ficke et al. 2007; Hein et al. 2012). The current outcomes in conjunction with previous studies highlight the high degree in which local variability will play on temperature-dependent growth and should be taken into consideration by managers (Murdoch et al. 2013). Managing fish such as the ones found in Takvatn in the future will likely raise novel issues such as changing fish demographics. Managers will have

to look further then just abundances and biomass, but also at size and age distributions to monitor population demographics (Smalås et al. 2019 – In review).

Importantly, temperatures seldom exceeded thermal optimums in the current study. In other words, temperatures were seldom high enough to elicit tolerance-related responses, nor were they high enough to produce negative effects as seen in previous studies (Kristensen et al. 2006; Murdoch et al. 2013). Therefore, it is likely that there will be a net overall benefit of increasing temperatures for growth performance in the coming years in lakes such as Takvatn where water temperature can stay relatively cold, as predicted temperatures for the next 80 years are unlikely to exceed the thermal optimum for charr for prolonged periods (Smalås et al. 2019 – In review). However, how fish respond to changing temperature regimes will be specific to locality and other biological and environmental mechanisms at play (Heino et al. 2009). Moreover, it is probable that certain characteristics of Takvatn and study design made the temperature effect more pronounced. For example, Takvatn has a homogenous charr population, that is, only one resident morph and no anadromous forms (Klemetsen et al. 1989). Different morphs may experience variable life-histories and display pronounced phenotypic variation such as different egg sizes leading to different alevin sizes after hatching; subsequently resulting in variable sizes at older ages - even under identical thermal regimes (Vøllestad & Lillehammer 2000; Godiksen et al. 2010).

4.6 Limitations and Study perspectives

This contribution exclusively focused on the somatic growth of charr, future studies may wish to incorporate trout otolith data, to have comparable data which would be particularly interesting to see in Takvatn as their early life histories differ considerably. In addition to studying other species, incorporating more variables such as parasite load and stomach contents may help account for the within year variability and provide an even clearer picture of how temperature shapes growth trajectories.

5. Conclusions

The present study documented how somatic growth rates of charr in wild settings increase with increasing water temperatures. These findings corroborate empirical research which has previously shown somatic growth rates in charr to increase with increases in temperature. Moreover, this contribution provides one of the first *in-situ* studies on temperature-dependent growth with conclusive results, demonstrating the significant role temperature plays in mediating charr growth in wild populations. In addition to temperature, abundance was shown to be a fundamental factor in modulating individual growth rates, notably having a negative effect on somatic growth. These findings suggest that as temperatures continue to rise in high latitude lakes, cold-water adapted species such as Arctic charr will have a greater scope for overall somatic growth. This will have reverberating effects on entire fish populations and fundamentally affect the characteristics of fish communities. In response, managers will have to anticipate changing fish demographics and consequently focus on strategies to mitigate any potential stressors which may exacerbate this impact.

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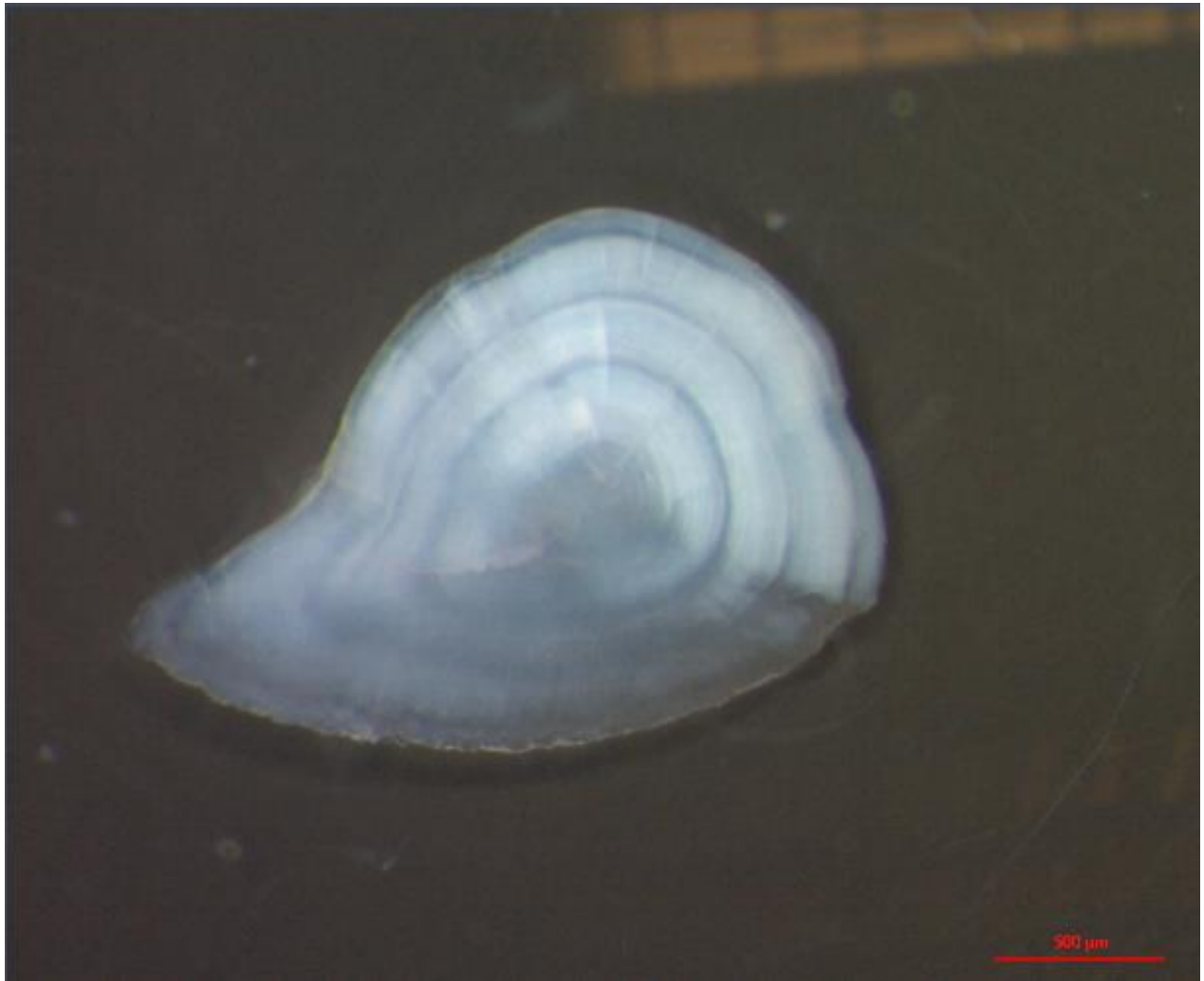
Appendix

Fig. A1. Raw photo of otolith with the posterior nucleus side facing upwards. Does not include measurement. Scale 500µm.
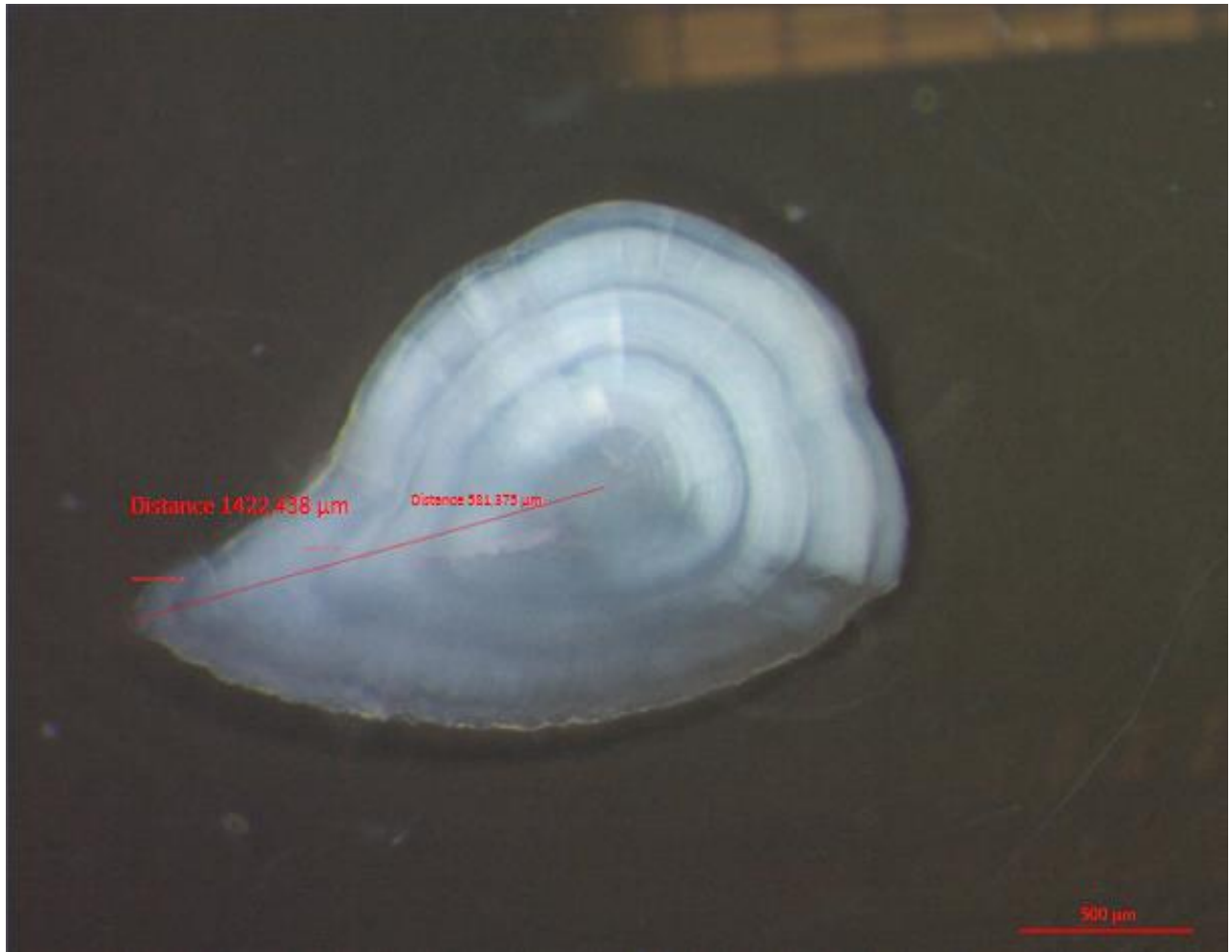
Fig. A2. Photo of otolith with the posterior nucleus side facing upwards. Transects of total otolith length, and annual growth transects. Scale is 500µm.
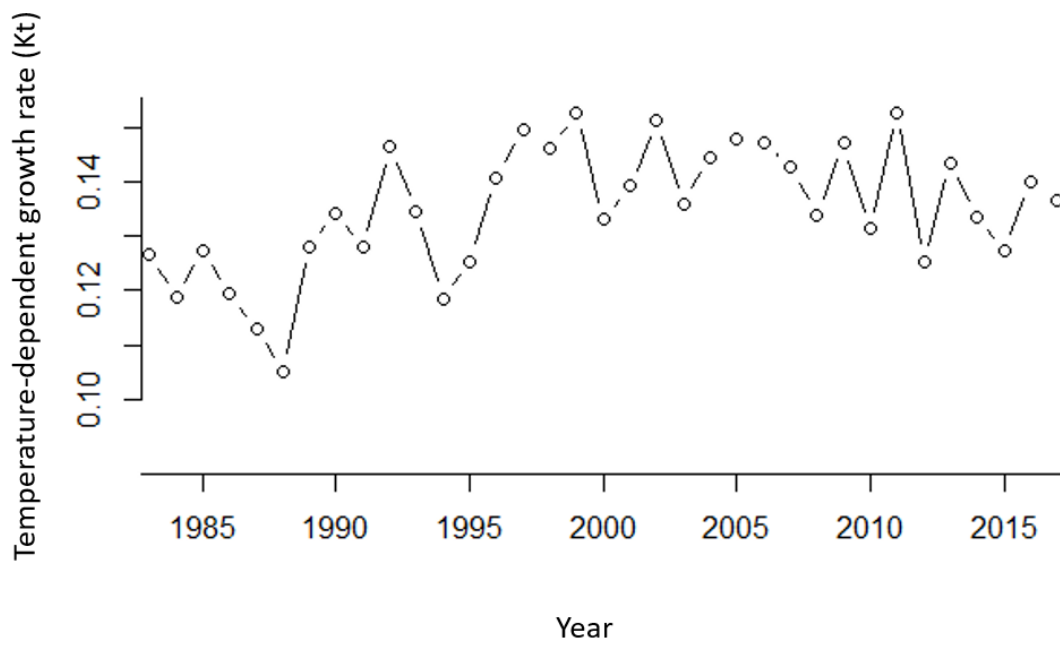
Fig. A3. Mean annual temperature-dependent growth coefficient plotted against year

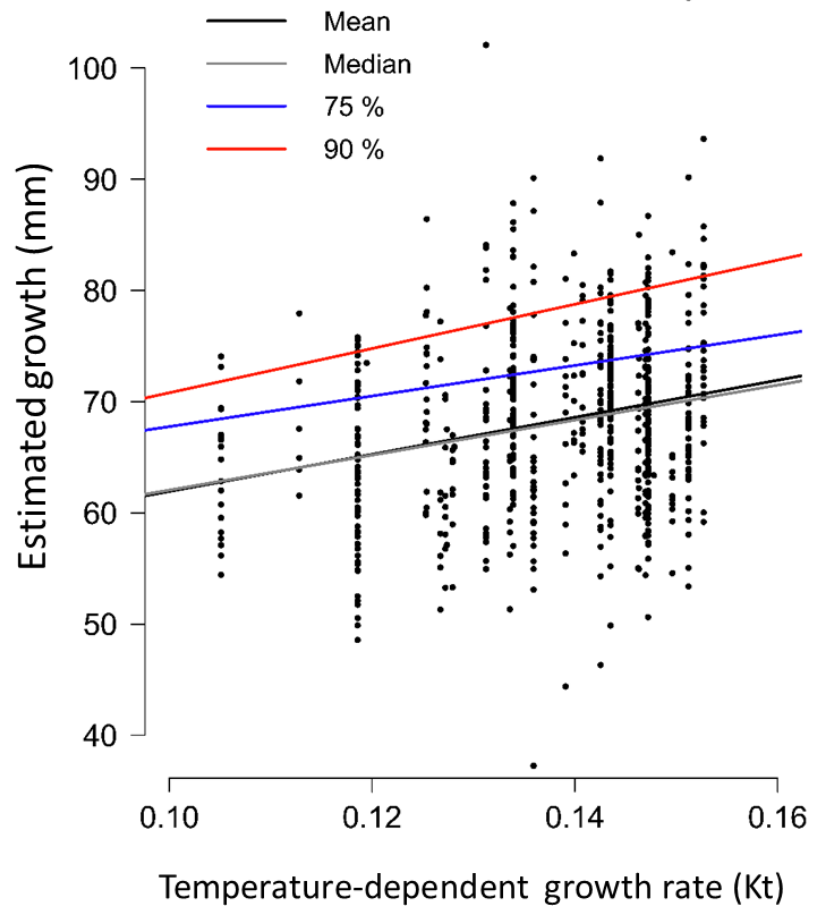Fig. A4. Estimated growth (mm · year^{-1}) plotted against temperature-dependent growth rate (Kt) for 1+ fish. The plot includes linear and percentile regression lines, with mean, median, 75th and 90th percentiles.

Linear regression:

Table A1. Regression results for estimated growth (mm) dependent on water temperature and CPUE for 0+ Arctic charr in Takvatn ($F_{2,690} = 21.94$, $p < 0.001$, $R^2 = 0.057$).

	Regression coefficient	Confidence interval	t-value	P-value
Intercept	54.31	± 9.64	11.03	<0.001
Water temperature	3.15	± 1.81	3.4	<0.001
CPUE	-0.25	± 0.16	-3.08	<0.001

Table A2. Regression results for estimated growth (mm) dependent on water temperature and CPUE for 1+ Arctic charr in Takvatn ($F_{2,690} = 43.73$, $p < 0.001$, $R^2 = 0.1099$).

	Regression coefficient	Confidence interval	t-value	P-value
Intercept	17.79	± 12.28	2.840	=0.005
Water temperature	4.97	± 2.38	4.094	<0.001
CPUE	-0.50	± 0.16	-6.209	<0.001

Table A3. Regression results for estimated growth (mm) dependent on water temperature and CPUE for 2+ Arctic charr in Takvatn ($F_{2,655} = 15.16$, $p < 0.001$, $R^2 = 0.041$).

	Regression coefficient	Confidence interval	t-value	P-value
Intercept	56.97	± 15.83	7.05	<0.001
Water temperature	-2.07	± 3.1	-1.3	=0.193
CPUE	-0.85	± 0.3	-5.5	<0.001

Table A4. Regression results for estimated growth (mm) dependent on water temperature and CPUE for 3+ Arctic charr in Takvatn ($F_{2,655} = 17.54$, $p < 0.001$, $R^2 = 0.048$).

	Regression coefficient	Confidence interval	t-value	P-value
Intercept	22.94	± 15.83	2.74	=0.006
Water temperature	4.45	± 3.1	2.96	=0.003
CPUE	-0.59	± 0.3	-2.61	=0.009

Quantile regression:

Table A5. Quantile regression results for back-calculated growth (mm) dependent on water temperature and CPUE for 0+ Arctic charr in Takvatn (50th, 75th and 90th percentile).

	Percentile	Regression coefficient	Lower 95% CL	Upper 95% CL
Intercept	0.5	60.07	49.3	64.71
Water temperature		2.02	1.2	4.06
CPUE		-0.32	-0.51	-0.23
Intercept	0.75	57.53	50.48	75.3
Water temperature		3.34	-0.005	4.85
CPUE		-0.18	-0.48	-0.008
Intercept	0.90	59.01	46.8	81.14
Water temperature		4.14	0.34	6.43
CPUE		-0.20	-0.45	-0.02

Table A6. Quantile regression results for back-calculated growth (mm) dependent on water temperature and CPUE for 1+ Arctic charr in Takvatn (50th, 75th and 90th percentile).

	Percentile	Regression coefficient	Lower 95% CL	Upper 95% CL
Intercept	0.5	17.28	8.66	26.28
Water temperature		4.76	3.02	6.51
CPUE		-0.46	-0.6	-0.34
Intercept	0.75	17.96	7.83	34.61
Water temperature		5.72	2.56	7.65
CPUE		-0.42	-0.62	-0.29
Intercept	0.90	15.76	-6.84	34.59
Water temperature		7.65	3.53	11.93
CPUE		-0.53	-0.74	-0.18

Table A7. Quantile regression results for back-calculated growth (mm) dependent on water temperature and CPUE for 2+ Arctic charr in Takvatn (50th, 75th and 90th percentile).

	Percentile	Regression coefficient	Lower 95% CL	Upper 95% CL
Intercept	0.5	59.72	46.66	74.19
Water temperature		-2.80	-5.42	0.24
CPUE		-0.91	-1.11	-0.79
Intercept	0.75	64.6	46.59	84.31
Water temperature		-1.15	-5.73	1.89
CPUE		-1.34	-1.52	-0.97
Intercept	0.90	84.3	28.94	110.73
Water temperature		-3.97	-8.87	6.34
CPUE		-1.27	-1.86	0.02

Table A8. Quantile regression results for back-calculated growth (mm) dependent on water temperature and CPUE for 3+ Arctic charr in Takvatn (50th, 75th and 90th percentile).

	Percentile	Regression coefficient	Lower 95% CL	Upper 95% CL
Intercept	0.5	23.02	-0.68	42.99
Water temperature		4.89	0.53	8.24
CPUE		-0.63	-1.03	0.21
Intercept	0.75	17.74	-14.61	48.9
Water temperature		6.82	1.28	11.31
CPUE		-0.41	-1.35	0.88
Intercept	0.90	0.89	-21.38	59.02
Water temperature		10.83	2.1	14.85
CPUE		0.43	-1.55	1.27