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**Long-Term Effects on Somatic Growth, Life History Traits and Population  
Biology of Arctic Charr (*Salvelinus alpinus*) Following the Fish Culling  
Experiment in Takvatn**

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Freshwater ecology

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## ABSTRACT

Stunting in fish populations is a special case of density-dependent growth characterized by old slow-growing individuals with low recreational and resource use value. The phenomenon is commonly observed in lacustrine populations of Arctic charr (*Salvelinus alpinus*) in temperate regions. In Takvatn, a subarctic lake in northern Norway, stunted growth of Arctic charr was attributed to food shortage in the overcrowded fish population. A large-scale culling experiment removing 31 tons (666 000) of Arctic charr was carried out between 1984 and 1989. The culling resulted in a substantial reduction in the population density, with a decrease of almost 80% in the littoral zone by the end of the culling. The present study investigates the long-term changes in somatic growth and life history traits – age and size at maturity – of Arctic charr over four decades during and following the culling experiment and addresses how these responses are reflected at the population level. Somatic growth of Arctic charr was shown to increase substantially the initial years following the culling before stabilizing at an enhanced level over time, as a response to the increased food availability for the remaining charr. Furthermore, an investigation of the impact of increasing water temperature due to climate warming on somatic growth revealed no clear temperature effect, suggesting that the changes in population density plays the most significant role in explaining the growth enhancement observed in Takvatn. The study further demonstrated a shift in maturation schedule towards maturation at earlier age but larger sizes, likely as a compensatory response to the reduced population density. In addition, males and females appeared to respond differently to the density reduction the initial years after the culling started. Finally, the responses of the culling at the population level were manifested in a shift in the age- and size structure from a dominance of small-sized old fish pre-culling to a higher proportion of younger individuals as well as larger individuals. The new demographic structure has persisted for more than three decades, emphasizing its strong resilience. The present study highlights the importance of a detailed examination of individual-level responses to culling to increase our understanding of density-related implications on the demographic structure at the population level. Such insights, when applied to management practices, enable the assessment of population status and the establishment of fishery regulations grounded in scientific research.

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# 1 INTRODUCTION

Fish make up almost half the total number of the recognized existing vertebrate species and demonstrate an enormous diversity and plasticity in growth regimes and life history strategies (Talbot, 1993; Winemiller, 2005; Dunlop et al., 2009). In contrast to higher vertebrates such as birds and mammals, where body size has a large genetic component and growth naturally ceases once full adult size is achieved, fish can typically continue to grow throughout their natural lifespan if the conditions allow for it (Asdell, 1946; Sebens, 1987). For fish and other organisms exhibiting indeterminate growth, the environmental conditions are often more important than the genetic component in determining fish growth and final adult body size. Both biotic and abiotic factors (e.g., competition, predation, food availability, water temperature) are known to affect fish growth (McDowall, 1994; Brander, 1995; Wootton, 2012). Growth and adult body size are also tightly connected to life history events such as size and age at maturity as there exists an important trade-off between present reproduction and future growth (Cook et al., 1999; Wootton, 1985, 2012; Smalås et al., 2013). When a fish matures, a shift in energy allocation occurs, from solely investing in somatic growth to investing in both somatic growth as well as the development of gonads, secondary sexual characters and reproductive activity (Calow, 1979; Wootton, 1985; Smalås et al., 2013). The growth rate and maximum adult size achieved by fish may therefore strongly influence age and size at sexual maturity of fish and vice versa (Stearns, 1992; Wootton, 1985, 2012). Due to differences in reproductive investment between males and females, where the females invest more energy in egg production compared to the sperm production by males, different strategies regarding timing of maturation may evolve between the sexes to maximize fecundity (Stearns, 1992). Differences in environmental selection pressures can therefore lead to large variations in somatic growth and maturity patterns among individuals within the same population and between different populations (Sebens, 1987)

Sufficient food availability in terms of prey abundance and quality (including both type and size) is crucial for fish to meet their energy requirements to maintain vital life functions and invest in future growth and reproduction (Jonsson & Jonsson, 2001). It has been recognized for many years that there exists an inverse relationship between population density and individual somatic growth in fish which is usually assumed to be related to density-dependence of food availability (Post et al., 1999; Amundsen et al., 1993; 2007; Lorenzen, 2002; De Roos et al., 2007). As the population density increases, fish tend to decrease their growth rate as a response

to higher intraspecific competition for food resources (Amundsen et al., 2007; Svedäng, 2014). In events of severe resource limitations and starvation, fish and other organisms displaying high plasticity in somatic growth and life-history traits, have shown an exceptional ability to cope with prolonged periods of feeding rates below the necessary maintenance level (Fishelson, 1997; McCue, 2010; Bar & Volkoff, 2012). This ability to adapt to their local condition enables fish to alleviate the acute mortality effects associated with food deprivation and is a useful tool for fish exposed to harsh and unpredictable environmental condition (Amundsen et al., 2007; Hammar, 2014). However, the high flexibility of fish in adjusting their growth rates to local conditions may also increase the risk of overcrowding and stunting (Amundsen et al., 2007).

Overcrowding and stunting are very common for many freshwater fish populations in temperate regions and represents a major problem regarding the management of these lakes (Amundsen et al., 1993, 2002; Linløkken et al., 1996; Ylikarjula et al., 1999; Svenning et al., 2015). Overcrowded populations are characterized by an accumulation of old, slow-growing individuals that reach sexual maturity early, resulting in a high proportion of the population being mature (Klemetsen et al., 2002; Chizinski et al., 2010; Jonsson & Jonsson, 2011). Overpopulation and stunting are especially common in Arctic charr *Salvelinus alpinus* (hereafter referred to as charr) populations as the species have a high recruitment capacity and thus often rely on mechanisms regulating the population density, such as predatory species or cannibalism (Amundsen & Klemetsen, 1988; Langeland, 1986; Langeland & Jonsson, 1990; Byström et al., 2004; Finstad et al., 2006). A food consumption study on stunted charr, performed in lake Takvatn, a subarctic lake in northern Norway, supported that food restriction was the explanation for the stunting observed in the overcrowded population (Amundsen, 1984; Amundsen & Klemetsen, 1988). In an attempt to alleviate the stunting, a large-scale density reduction through intensive fishing was proposed and carried out from 1984 to 1989 (see section 2.2 for more information). Several studies covering different aspects of fish biology and ecology regarding e.g., changes in habitat utilization, food consumption, growth and parasite loads have been carried out following the culling experiment (e.g., Amundsen, 1989; Klemetsen et al., 1989; Amundsen et al., 1993, 2007, 2019; Henriksen et al., 2016, 2019). An important effect of the culling was a strong reduction in the density of charr, which further led to a substantial improvement in somatic growth (Amundsen et al., 2007) as well as the establishment of an alternative stable state regarding the population structure (Persson et al., 2007). However, there has been given little or no attention to the changes in life history strategy of charr, which should be implemented to increase our understanding of how the individuals

respond to the culling, which have further implications for the population structure. Moreover, despite the numerous studies carried out in Takvatn, including Klemetsen et al. (2002) 's work covering 20 years, further research is needed to examine the long-term trends and dynamics of the charr population following the culling experiment, as such ecological and evolutionary responses may take decades to unfold (Strayer et al., 2006). The aim of the present study is to examine the long-term changes in growth and life history traits of charr over the four decades during and following the culling. The study further aims to elucidate how these individual-level responses manifest in the size and age structure at the population level, which can provide insight to the resilience of the demographic structure.

In general, there exist few studies addressing long-term ecosystem-based data series, as the maintenance and funding of such studies often are challenging (Jackson & Fureder, 2006; Amundsen et al., 2019). However, studies spanning over decades may be crucial in order to gain a comprehensive understanding of the mechanisms and processes forming the population and community dynamics, which in the context of conservation and management is of great importance (Hampton et al., 2019). Extensive data from long-term studies may also provide a unique opportunity to investigate the potential impacts of climate change, which have received increasing attention in recent decades as temperature are increasing at a higher rate today than in periods in the past (ACIA, 2005; Ficke et al., 2007; Elliott & Elliott, 2010). High-latitude environments are particularly vulnerable because of the high rate of warming in the arctic (ACIA, 2005; Parmesan, 2006; Reist et al., 2006; Coumou et al., 2018). Water temperature is considered the most important environmental factor impacting fish growth rate under conditions where food availability is not limiting (Jobling, 1983; Viadero, 2005; Elliott & Elliott, 2010; Árnason et al., 2022). Metabolic rate is frequently reported to increase with increasing temperature, which in turn might lead to enhance fish growth rate until the optimum temperature is reached (Gillooly et al., 2001; Gårdsmark & Huss, 2020). Studies have also shown that increasing temperature can modify a range of phenotypic traits such as timing and thus size at maturity (Árnason et al., 2022). The Arctic charr is the northernmost freshwater species and highly cold-water adapted (Klemetsen et al., 2003) and growth is observed to begin at temperatures as low as -1.7 °C (Larsson et al., 2005). The optimum temperature range for growth is found to occur between 11-17 °C (Swift, 1964; Jobling, 1983; Larsson & Berglund, 1988, 2005; Larsson et al., 2005; Gunnarsson, 2011), suggesting that charr in Takvatn experiences temperatures at the lower end of their temperature range. Thus, the potential impact

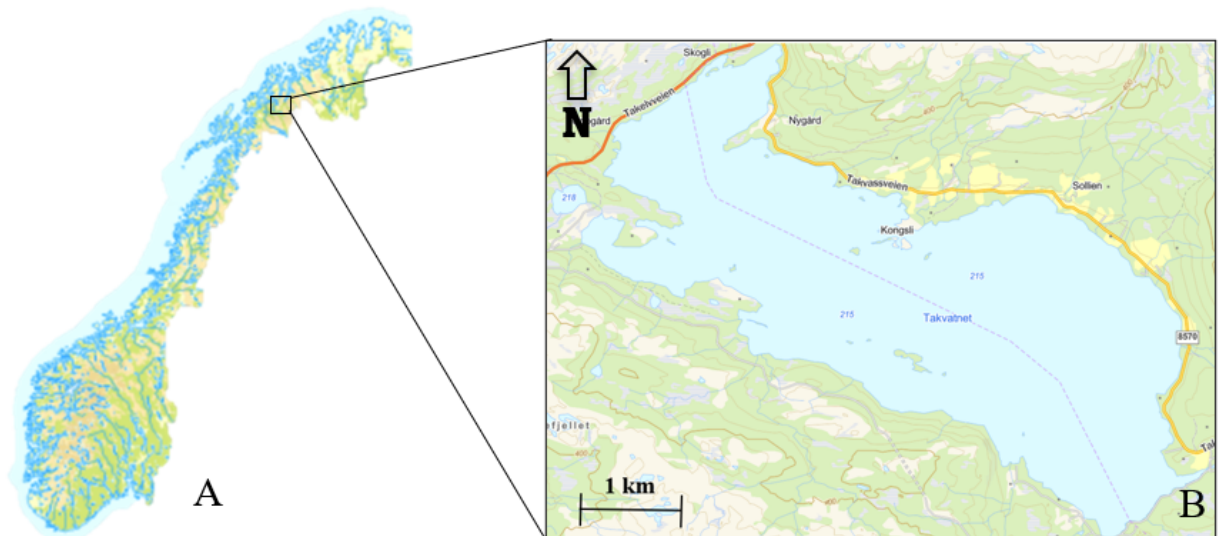
and importance of increasing water temperature on somatic growth of charr will also be explored.

The present study reviews the long-term developments of the charr population in Takvatn over a four-decade period from 1980-2020, exploring the hypotheses that (1) the reduced charr density from the culling experiment led to a marked improvement in growth performance in the initial years following the culling before stabilizing at an enhanced level over time, (2) annual somatic growth rate and length increment of charr will increase with increasing water temperature, (3) the culling resulted in a change in the onset of sexual maturity of charr and (4) there has been a change in the population structure of charr from a dominance of small-sized, older individuals pre-culling to a higher proportion of younger individuals as well as larger fish.

## 2 MATERIAL AND METHODS

### 2.1 Study Area

Takvatn (69°07'N 19°05'E) is a subarctic, oligotrophic dimictic lake connected to the Målselv River system, in Troms and Finnmark county, northern Norway (**Fig.1**). The lake is situated at 214 meters above sea level and has a total area of 15.2 km<sup>2</sup> and a catchment area of 66 km<sup>2</sup>. It is divided into two main basins, both having a maximum depth around 80 m (Klemetsen et al., 1989). The vegetation around is primarily dominated by birch (*Betula pubescens*) forests. Throughout the year, the lake experiences large seasonal variation regarding both temperature and light conditions, with the ice-free period normally lasting from May/June to November/December and midnight sun from end of May to end of July (Prati et al., 2020).



**Fig. 2** Location of the study area. **A** Map of Norway, the square marks the location of lake, Takvatn. Map retrieved from Norgeskart.no. **B** Map of lake Takvatn (69°07'N 19°05'E). Map modified from Norges vassdrags- og energidirektorat; retrieved from <https://temakart.nve.no/prosjekt/f7cc70a3-4bd4-468b-97a4-30b0a44df79a/1643105312> on 20 February 2023.

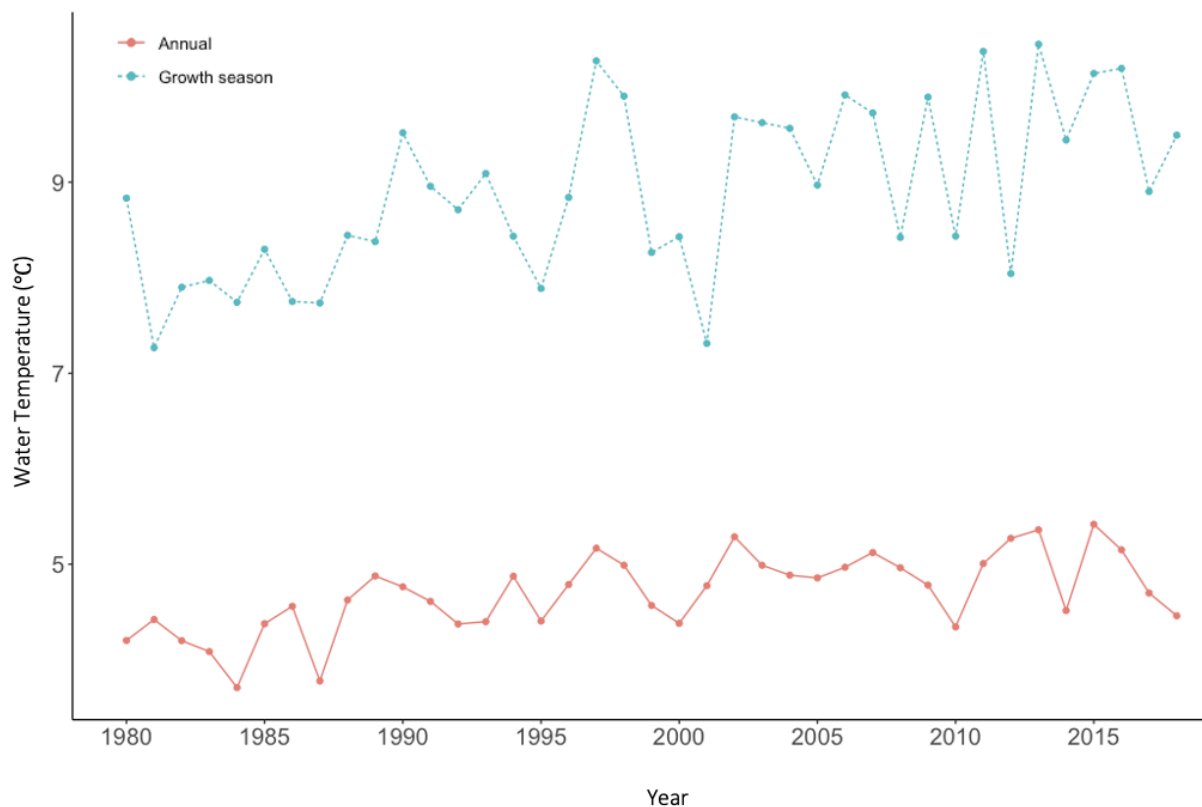
## 2.2 Takvatn and the Whole-Lake fish culling experiment

Takvatn consisted originally of brown trout as the only fish species back in the beginning of the 20<sup>th</sup> century. However, due to size-selective fishing for larger individuals, the trout population was almost eliminated from the lake by the end of the 1920s (Amundsen et al., 2015). charr from Fjellfroskvatn, a lake situated in a tributary to the downstream river from Takvatn, was introduced in 1930 (Klemetsen et al., 1989). However, due to continued selective fishing for larger individuals in the already overfished trout population, charr soon became the dominant fish species in the system as the population rapidly increased. The high population density of charr further led to poor individual growth, which seemed to be related to food shortage (Amundsen, 1989; Svenning & Grotnes, 1991). As an attempt to provide the charr with additional prey, three-spined stickleback (*Gasterosteus aculeatus*) was introduced from the nearby lake Sagelvvatn in the 1950s. However, the introduction of three-spined stickleback only led to higher interspecific competition for food, and a shift in the diet of charr to copepods leading to higher infection rate by the two parasitic tapeworms, *Dibothriocephalus dendriticus* and *Dibothriocephalus ditremus* (Amundsen et al., 2015). By the late 1970's, the lake was dominated by a highly overcrowded and parasitized charr population with stunted growth. Earlier studies on fish from stunted populations had shown that density reduction or transplantation to less crowded environments led to improved growth (Green, 1955; Burrough & Kennedy, 1979; Donald & Alger, 1989). It was therefor decided that large-scale culling through an intensive fishing program was the best cultivation strategy in Takvatn (Amundsen et al., 1993). During the whole-lake culling experiment in Takvatn, funnel traps mostly baited with salted fish roe from Atlantic cod (*Gadus morhua*) was used to remove a total of 666 000 charr or 31.3 metric tons. The heaviest fishing effort lasted from 1984 to 1989, with an annual removal of roughly 100 000 charr (**Appendix, Table S1**). Some additional fishing was performed in 1990 and 1991 with an annual yield of 25 000 charr (Klemetsen et al., 2002).

## 2.3 Temporal Variation in Water Temperature

Daily temperature data, along with other climatic parameters (precipitation, solar radiation, wind, cloud cover and humidity) has been taken at Bardufoss meteorological station (-19 km from Takvatn) since 1957. These data have been used to force a one-dimensional air-to-water temperature model (General Lake Model, Rpackage GLMr). For calibrating the model, water temperature from Takvatn, measured in August most years since 1980, as well as for the entire

ice-free season over some years, were used. The model provided daily estimated water temperature in lake Takvatn from 1957-2020 (Kotowych et al., 2023). As the annual fish sampling for the present study chiefly was carried out in August, the mean water temperature from August 1st of the previous year to July 31st of the year under consideration was chosen to represent the annual mean water temperature. The mean water temperatures for the months of August, September, and October were chosen to represent the mean water temperature during the main growth season (**Fig. 2**).



**Fig. 2** Mean modelled annual mean water temperature (red line) and mean temperature during main growth season (Sept, Oct, Nov) (blue line) in lake Takvatn.

## 2.4 Fish Sampling

The study is based on data from the long-term ecological studies carried out in Takvatn from 1980 to 2020. The study material includes a total of 5235 charr caught by standardized gillnet sampling of fish carried out in August and September in 1980 and 1981 and then annually from 1985 to 2020. Samples were taken from the littoral (<15 m depth) and profundal (>25 m depth) zones using benthic gillnets and in the epipelagic (upper 0-6 m at >30 m depth) zone using floating gillnets. For the majority of the time, multi-meshed gillnets have been used for all habitats, whereas prior to 1989, single mesh-sized gill nets were used including 1.5 x 30 m

bottom nets with bar mesh sizes (knot to knot) from 10-52 mm in the littoral and profundal, and 6 x 30 m floating nets with mesh sizes from 10-25 mm in the pelagic (Klemetsen et al., 1989; Amundsen et al., 1993). From 1989 and onward, 1.5 x 40 m multi-meshed 'Benthic Gillnet Overview' (BGO) nets were used in the littoral and profundal, and 6 x 40 m multi-meshed "Floating Gillnet Overview" (FGO) in the pelagic (Klemetsen & Dahl-Hansen, 1995), both made up of eight 5 m panels of different bar mesh-sizes ranging from 10-45 mm (10, 12.5, 15, 18, 22, 26, 35 and 45 mm). In recent years, 1.5 x 45 m 'Bottom Gillnet Nordic' (BGN) has gradually been replacing the BGO in the littoral and profundal, including nine panels of different mesh-sizes ranging from 10-55 mm (10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm). Given the large similarity in the mesh sizes of the gillnet series that have been used over the study period, their selectivity is considered to be similar.

Weight and fork length (hereafter referred to as length) were measured, and sex and stage of maturity were determined for each fish in the field. Otoliths were collected and preserved in 96% ethanol for later age determination. Fish age was estimated in the lab by reading the surface of the otoliths immersed in glycerol under a binocular microscope.

## 2.5 Catch Per Unit Effort (CPUE)

The relative density of fish each year has been quantified by catch per unit effort (CPUE) estimates of charr and brown trout based on the littoral, profundal and pelagic gillnet catches in August. CPUE is defined as the mean number of fish caught per 100 m<sup>2</sup> gillnets per night (Klemetsen et al., 1989). CPUE estimates from 1980 have been used as a representative reference point before the culling experiment started in 1984, as the relative population density prior to the culling was not expected to vary significantly (Klemetsen et al., 2002).

## 2.6 Data- and Statistical Analysis

All statistical analysis were conducted in RStudio (ver. 2023.03.1 + 446) statistical computing program. In order to strengthen the dataset, especially for the older age-classes, the 40-year study period from 1980 to 2020 has been divided into eight 5-yr periods (**Table 1**) for all analyses except the exploration of any temperature effects on somatic growth (see section 2.3).



**Table 1** Overview of the eight 5-yr periods lasting from 1980 to 2020, with corresponding n-values for the various periods.

Period	1	2	3	4	5	6	7	8
Year	1980-1985	1986-1990	1991-1995	1996-2000	2001-2005	2006-2010	2011-2015	2016-2020
n	433	1035	652	683	655	594	572	499

### 2.6.1 von Bertalanffy Growth Model

Two different mathematical models for describing fish growth have been applied for comparison of growth patterns of charr between the eight periods, based on size-at-age data; **(1)** the reparameterization of the traditional von Bertalanffy growth model (VBGM) by Gallucci and Quinn (1979), and **(2)** the Quince-Boukal-Dieckmann (QBD) Biphasic model based on the biphasic growth model by Quince et al. (2008a, 2008b). In the present study, fish older than 12 years were grouped together with 12-yr-old fish when fitting the growth curves for both growth models. This was done in order to strengthen the dataset for the older age-groups with fewer individuals, and was justified by no significant differences being found in length at age between 12-, 13-, 14- and 15-year-old charr (one-way ANOVA,  $F=2.021$ ,  $p > 0.05$ ; **Appendix, Fig. S1**)

The traditional von Bertalanffy growth model (1938, 1957) is a widely used model for describing growth patterns of fish and has been used across a diverse range of organisms exhibiting asymptotic indeterminate growth (Lester et al., 2004). It is often used *a priori* before even exploring alternative models that might be more appropriate for the specific data (Lugert et al., 2016). The model assumes that the growth in length per unit time decreases as the individual grows, and is described by the following equation (1a):

$$l_t = L_\infty(1 - e^{-K(t-t_0)}), \quad (1a)$$

where  $l_t$  is the expected length of the fish at time or age  $t$ ,  $L_\infty$  is the asymptotic length where growth is 0,  $K$  is the growth coefficient which describes how fast  $L_\infty$  is achieved, and  $t_0$  is the theoretical age when size is 0. Because  $K$  describes the growth rate relative to the difference between the asymptotic size ( $L_\infty$ ) and the current size ( $l_t$ ) of the organism,  $K$  as a growth rate is impossible to interpret without knowledge of  $L_\infty$ . If  $L_\infty$  in a given population is high, the time at which  $L_\infty$  is reached is longer leading to a low  $K$ -value and opposite if  $L_\infty$  is low. In other

words, these two parameters are highly interdependent, which the model has been criticized for. Mooji et al. (1999) recommends an alternative parameterization of the VBGM provided by Gallucci and Quinn (1979), which attempts to avoid this problem by incorporating  $G_{init} = K x L_{\infty}$ . In the present study the reparameterization by Gallucci and Quinn has therefore been used and is described by the following equation (1b):

$$l_t = L_{\infty} - (L_{\infty} - L_0) e^{- (G_{init}/L_{\infty})t}, \quad (1b)$$

where  $L_0$  is the length of the fish when time or age is 0 ( $t=0$ ).  $L_0$  were set to 1.8 cm, the length of charr at hatching. The two growth parameters estimated from the VBGM are  $G_{init}$  which describes the absolute initial growth rate or the maximum growth rate (cm/year) and  $L_{\infty}$ , the asymptotic size (**Table 2**).  $G_{init}$  and  $L_{\infty}$  were estimated for all eight periods from the model (**Appendix, Table S2**). Growth curves based on the estimated parameters were compared for all eight periods with non-linear least square (nls) regression (**Appendix, Fig. S2**).

### 2.6.2 The Biphasic Growth Model

Despite of the fact that the VBGM seems to provide good descriptions of somatic growth and its wide range of applications, the model has been criticized for lacking a mechanistic basis in terms of change in energy allocation when a juvenile fish becomes mature and thus having very little biological significance (Lester et al., 2004; Boukal et al., 2014; Kestemont et al., 2015). In contrast to juvenile fish that allocate all surplus energy to somatic growth, mature fish starts to allocate a proportion of the surplus energy to reproduction as well. Thus, the VBGM tends to fail in describing somatic growth before the fish reach maturity, as the model uses exclusively one growth equation when fitting all the data regardless of stage of maturity (Lester et al., 2004). Biologically and mechanistically meaningful growth models based on allocation decisions have therefore become increasingly important to better model and understand different life history strategies (Boukal et al., 2014).

Quince et al. (2008a, b) introduced an improved growth model, the biphasic growth model, which explicitly takes the cost of reproduction into account when modeling fish growth. In contrast to the VBGM, the biphasic model assumes distinct phases of growth by integrating two separated growth function for immature (prematuration phase) and mature individual (postmaturation phase). The model assumes that immature fish invest all surplus energy towards growth, while mature individuals invest a proportion of the surplus energy in

reproduction, and consequently a decreased proportion of energy in growth (Lester et al., 2004). Thus, by incorporating maturation as a distinct life-history transition, trade-off between present reproduction and future somatic growth is accounted for. In addition, the model allows for various allometries of net energy acquisition depending on body weight in contrast to most growth models assuming a given allometric exponent for net energy intake,  $\beta$  usually of  $2/3$  or  $3/4$  (Boukal et al., 2014). The energy acquisition exponent  $\beta$  describes how much energy an organism has available for growth and reproduction based on its body size and is a result from the difference between energy intake and energy expenditure on metabolism. Larger individuals with higher metabolic rate need more nutrients to gain the same amount of nutrients per body mass as smaller individuals. Despite the flexibility of the model proposed by Quince et al., which allows  $\beta$  from deviating from its standard, the application of the model is somehow restricted as body size is measured in units that depends on  $\beta$ , instead of the more familiar units of length or weight. In the present study, an alternative formulation of the Quince et al. model (2008a, 2008b), the QBD- Biphasic model (Boukal et al., 2014), where unit of size is expressed as length or weight, has been used. The interannual growth in terms of length is described by the following equation (2a):

$$l_{t+1} = \frac{(1-\beta)^\alpha \sqrt{l_t^{(1-\beta)\alpha} + (1-\beta)cb^{-(1-\beta)}}}{\sqrt{1+q^{-1}(1-\beta)r_{t+1}}}, \quad (2a)$$

where  $l_t$  is the expected length of the fish at time or age  $t$ ,  $\beta$  is the allometric exponent which was set to 0.67 in the present study,  $q$  is the ratio of energy requirement of producing somatic tissue per unit of weight and gonadic tissue, which were assumed to be equal ( $q=1$ ) in the present study,  $\alpha$  is the scaling exponent describing the relationship between weight and length while  $b$  scales this weight and  $r_{t+1}$  is the relative reproductive investment measured as the ratio of gonadic weight to somatic weight  $G_t/W_t$  at age  $t+1$ . The juvenile growth trajectory follows by inserting  $r_t = 0$  as immature individuals allocate all energy to somatic growth and can be described by the following equation (2b):

$$l_t = \frac{(1-\beta)^\alpha \sqrt{l_0^{(1-\beta)\alpha} + c(1-\beta)b^{-(1-\beta)}t}}{\sqrt{1+q^{-1}(1-\beta)r_t}}, \quad (2b)$$

For adults, in contrast, there exist an important trade-off between reproductive investment and somatic growth, which means that the adult growth depends on  $r_t$ . For adult growth, the

reproductive investment is assumed to be constant ( $r_t = r$ ) and can be described by the following equation (2c):

$$l_t = \sqrt{{}^{(1-\beta)\alpha} R^{t-t_{mat}} (l_0 {}^{(1-\beta)\alpha} H t_{mat}) + \frac{RH}{1-R} (1 - R^{t-t_{mat}})}, \quad (2c)$$

where  $H=c(1-\beta)b^{-(1-\beta)}$  and  $R=[1+q^{-1}(1-\beta)r]^{-1}$  (Boukal et al., 2014). Age at maturity ( $t_{mat}$ ) for each period were defined as age at which 50% of the population is mature (A50), estimated using logistic regression (see 2.6.4). The two growth parameters estimated from the QBD- Biphasic model are the energy acquisition parameter  $c$  which represents the energy available for growth and describes the immature growth capacity, and  $r$  the relative reproductive investment, which describes the proportion of energy consumed that is allocated to reproduction by mature individuals (**Table 2**). The energy acquisition parameter and relative reproductive investment were estimated for all eight periods (**Appendix, Table S2**).

Non-linear regression (nls) was used when fitting the QBD- biphasic model. The *nls.QBD* function in R allows for different statistical weightings (swe) for the different age classes: **(1)** Each age class receives the same total weight in fitting regardless of the number of individuals sampled within each age class (swe=1). In practice, this means that older age groups with fewer sampled individuals are up-weighted relative to abundant young age classes. This weighting often provides a better fit for the older age groups, but a less accurate fitting for the younger age groups **(2)** No weighting (swe=0), meaning each individual receives the same total weight in fitting, which in contrast to the latter often provide a better fit for the abundant younger age classes but a less accurate fit for the less abundant older age classes, and **(3)** Intermediate weighting (swe=0.5) which may provide a good compromise between the two. The observed and estimated data were compared and visualized for all eight periods to find the weighting that gave the best fit (**Appendix, Fig. S3**). In the present study, swe=1 (i.e., equal weighing for each age class) have mostly been used as that provided the best fit for all periods except period 8, where intermediate weighting rather was adopted. Growth curves based on the QBD- Biphasic model (hereafter referred to as biphasic growth model) and the VBGM, have been compared for all eight periods (**Appendix, Fig. S4**).

**Table 2** Estimated growth parameters from the VBGM and the biphasic growth model.

Estimated parameter	Model	Symbol	Unit
Asymptotic length	VBGM	$L_{\infty}$	cm
Initial growth rate	VBGM	$G_{init}$	cm/year
Energy acquisition parameter	Biphasic growth model	$c$	$g^{1-\beta}yr^{-1}$
Reproductive investment	Biphasic growth model	$r$	Dimensionless

### 2.6.3 Water Temperature and Somatic Growth

Simple linear regression was used to model the linear relationship between temperature and specific growth rate (SGR) as well as annual length increment from 1980 to 2020. Mean annual SGR and length increment were estimated for the most common age-classes of charr (2–6-year-old fish) during the study period from 1980 to 2020. Only those years with a sample size exceeding 10 individuals for each specific age-class were included, to ensure a representative dataset. The following equations were used (3, 4):

$$SGR = \ln W_t - \ln W_{t-1} \quad (3)$$

and

$$\text{Annual length increment} = L_t - L_{t-1} \quad (4)$$

where  $W_t$  and  $L_t$  are the mean body weight and length, respectively, of a year-class in the year under consideration and  $W_{t-1}$  and  $L_{t-1}$  are the mean body weight and length of the same year-class in the previous year. The relationship between length increment and age-classes was tested, showing no correlation (Pearson correlation test;  $P > 0.05$ ,  $R = -0.01$ ; **Appendix, Fig. S5**), thus indicating a linear growth between the age-classes. In an effort to circumvent the years during which density was observed to strongly affect somatic growth, an additional analysis excluding the years prior to 2000 was conducted (**Appendix, Fig. S6**).

### 2.6.4 Length and Age at Maturity

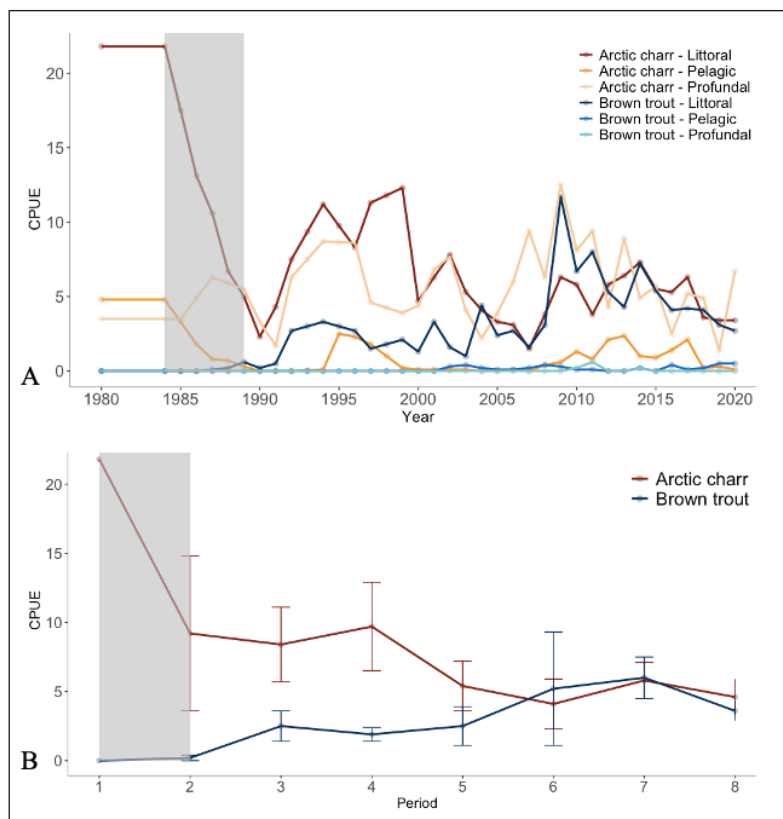
Length and age at maturity expressed as the length and age at which 50% of the individuals in a population are mature ( $L_{50}$  and  $A_{50}$ ) were estimated using the logistic regression model ( $R\text{-glm}()$ , stats package base R), with maturity expressed as a binary value of either 1 (mature) or 0 (immature) (Cook et al., 1999; Doll & Lauer, 2013). A sigmoid curve fitted to the observed data was produced from the logistic regression and visualized using ggplot from the *ggplot2*-

package.  $L_{50}$  and  $A_{50}$  were extracted from the *dose.p* function within the *MASS*-package in R. Estimation of  $L_{50}$  and  $A_{50}$  was carried out for both sexes for all eight periods (**Appendix, Table S3; Fig. S7-S10**). Statistically significant differences in age and length at maturity between the sexes were tested for all periods using likelihood ratio test (**Appendix, Table S4**).

## 3 RESULTS

### 3.1 Relative Abundance Based on CPUE

The relative population density of charr and brown trout in lake Takvatn based on CPUE estimates changed considerable during the 40-year study period during and following the fish culling experiment (**Fig. 3A, B**). Charr generally inhabited both the littoral, profundal and pelagic zones. In contrast, trout predominantly inhabited the littoral, with limited to no appearances in the pelagic and profundal zones (**Fig. 3A**). The charr population declined by almost 80% in the littoral from 1984 prior to the culling to 1989 at the end of the culling (**Fig. 3A**). In contrary, the littoral density of trout, which was almost absent in period 1, started to increase in the catches from period 2 and onwards. In the years following the culling experiment and over most of the study period, trout has shown a persistent, gradual increase in population density in the littoral, whereas the littoral density of charr has remained at relatively low levels, with some moderate year-to-year fluctuations. From around 2005 and onwards (i.e., period 6-8), the trout and charr densities have been of similar magnitudes in the littoral (**Fig. 3A, B**).



**Fig. 3** Average catch per unit effort (CPUE), calculated as the mean number of fish per 100m<sup>2</sup> gillnets per night, of Arctic charr and brown trout in **A**) the littoral, profundal, and pelagic zones of Takvatn each year from 1980-2020 and **B**) in the littoral zone of Takvatn for each 5-yr period. Error bars represents  $\pm$  standard deviation (SD). The grey shaded area represents the time period when the prime intensive fishing occurred.

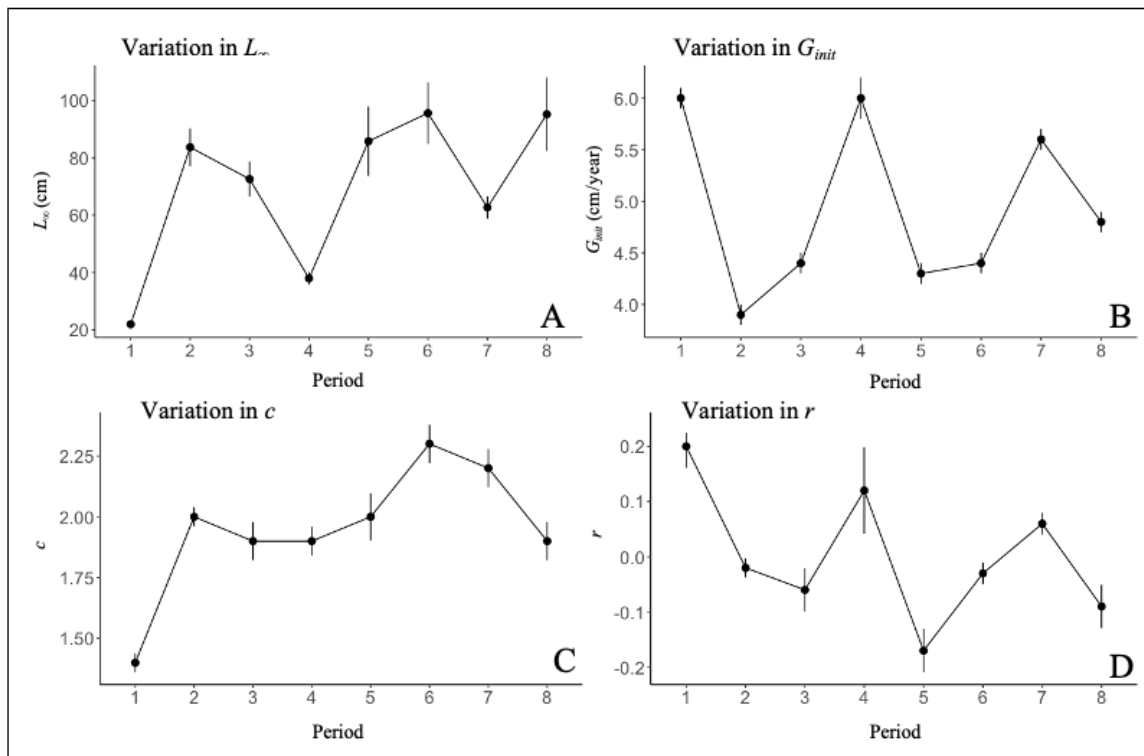
## 3.2 Temporal Variation in Growth

### 3.2.1 Growth Parameters

The estimated growth parameters  $L_{\infty}$ ,  $G_{init}$ ,  $c$  and  $r$  showed great variation, but no consistent trends over the duration of the study. No statistical significance difference in growth performance was found between the two sexes (ANCOVA test; **Appendix, Table S5, S6**), thus the estimated growth parameters are representative for both. Asymptotic length,  $L_{\infty}$ , increased rapidly from period 1 (**Fig. 4A**;  $L_{\infty}$ =22.0 cm) to period 2 (**Fig. 4A**;  $L_{\infty}$ =83.7 cm), after which it chiefly fluctuated with a slight increase throughout the study period and two notable dips in period 4 (**Fig. 4A**,  $L_{\infty}$ =38.0 cm) and period 7 (**Fig. 4A**,  $L_{\infty}$ =62.7 cm). For the initial growth rate,  $G_{init}$ , an opposite pattern was shown, with the highest growth rate in period 1, 4, and 7 (**Fig. 4B**), coinciding with the periods when  $L_{\infty}$  was at the lowest (**Fig. 4A**). Accordingly, a strong negative correlation was revealed between  $L_{\infty}$  and  $G_{init}$  (Pearson correlation test;  $P < 0.05$ ,  $R = -0.85$ ; **Appendix, Fig. S11**). Thus, the biological interpretation of  $G_{init}$  will not be further emphasized, as it seems to be highly dependent on  $L_{\infty}$ .

From the biphasic growth model, the estimated allometric coefficient  $c$  of net energy acquisition, describing the immature growth capacity, shows a rapid increase from period 1 (**Fig. 4C**;  $c = 1.4$ ) to period 2 (**Fig. 4C**;  $c = 2.0$ ). Afterward, immature growth capacity has generally remained stable throughout the study period, with a small increase during period 6. The temporal variations in the relative reproductive investment  $r$  showed a more or less similar trend as  $G_{init}$ , which again showed the opposite pattern as  $L_{\infty}$ . Reproductive investment was highest in period 1 (**Fig. 4D**;  $r = 0.2$ ), followed by a decrease in period 2 (**Fig. 4D**;  $r = -0.02$ ) and has shown a slight decreasing trend over the course of the study period, with some fluctuations. A notable increase was shown for period 4 (**Fig. 4D**;  $r = 0.12$ ) and 7 (**Fig. 4D**;  $r = 0.06$ ), similar to the increase in  $G_{init}$ .



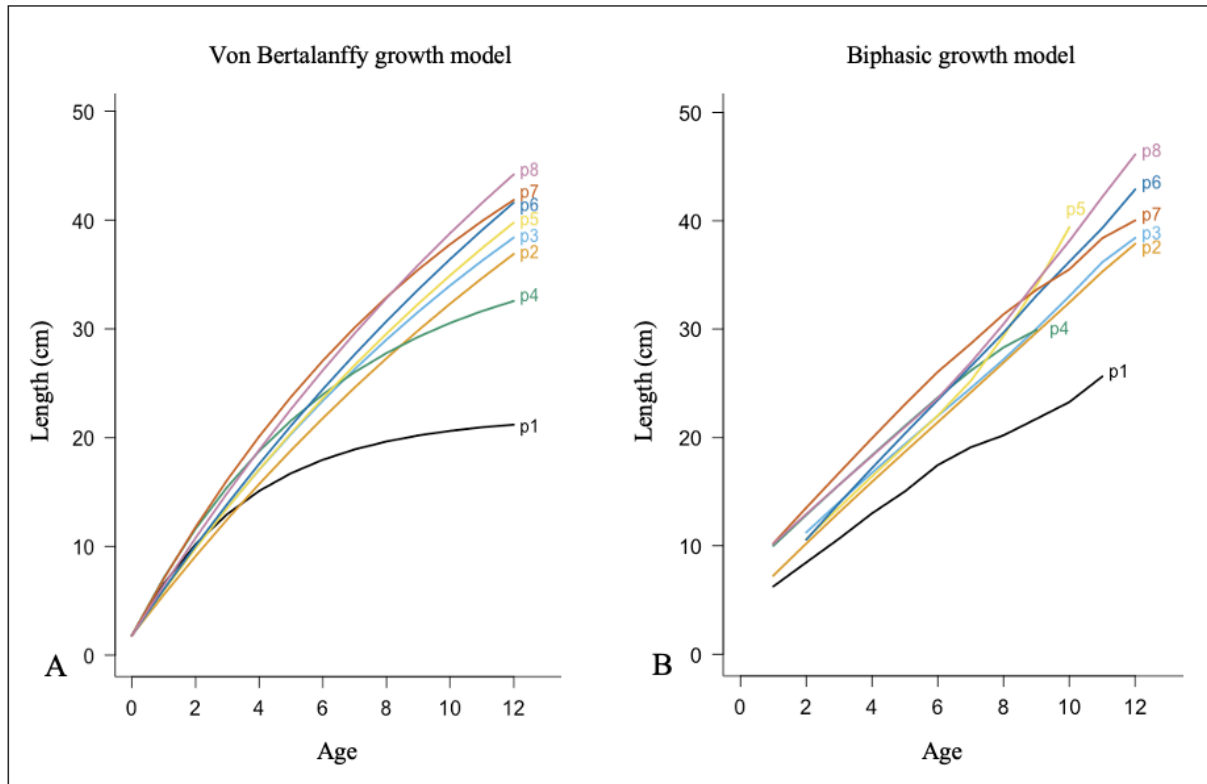


**Fig. 4** Temporal variation in growth rate based on growth parameters **A)**  $L_{\infty}$  (cm) and **B)**  $G_{init}$  (cm/ year) estimated from the von Bertalanffy growth model, and **C)** energy acquisition parameter,  $c$  and **D)** relative reproductive investment,  $r$ , estimated from the biphasic growth model. Error bars indicate 95% confidence interval.

### 3.2.2 Growth Curve Comparisons

A visual inspection of the growth curves produced from VBGM (**Fig. 5A**) and the biphasic growth model (**Fig. 5B**), reveals that the two models provide fairly similar depictions of how growth has changed over the study period. Both models suggest an improved growth over the study period, with particularly two periods standing out. For period 1 and 4, growth appears to be relatively poor compared to the other periods, which can be seen in both growth models (**Fig. 5**). However, despite the similarities between the two models, there are especially one important difference, which lies in the extent to which they capture variation in adult growth. This becomes particularly evident in period 5 where adult growth seems to rapidly increase according to the biphasic growth model (**Fig. 5B**), whereas the VBGM seems not capture this change in growth (**Fig. 5A**). Due to the fact that VBGM assumes a decrease in growth with increasing size, it appears that the model underestimates the growth in period 5, when adult growth experiences an increase. Thus, the biphasic growth model, including two separate growth functions for immature and mature fish, appears to capture variation in growth more

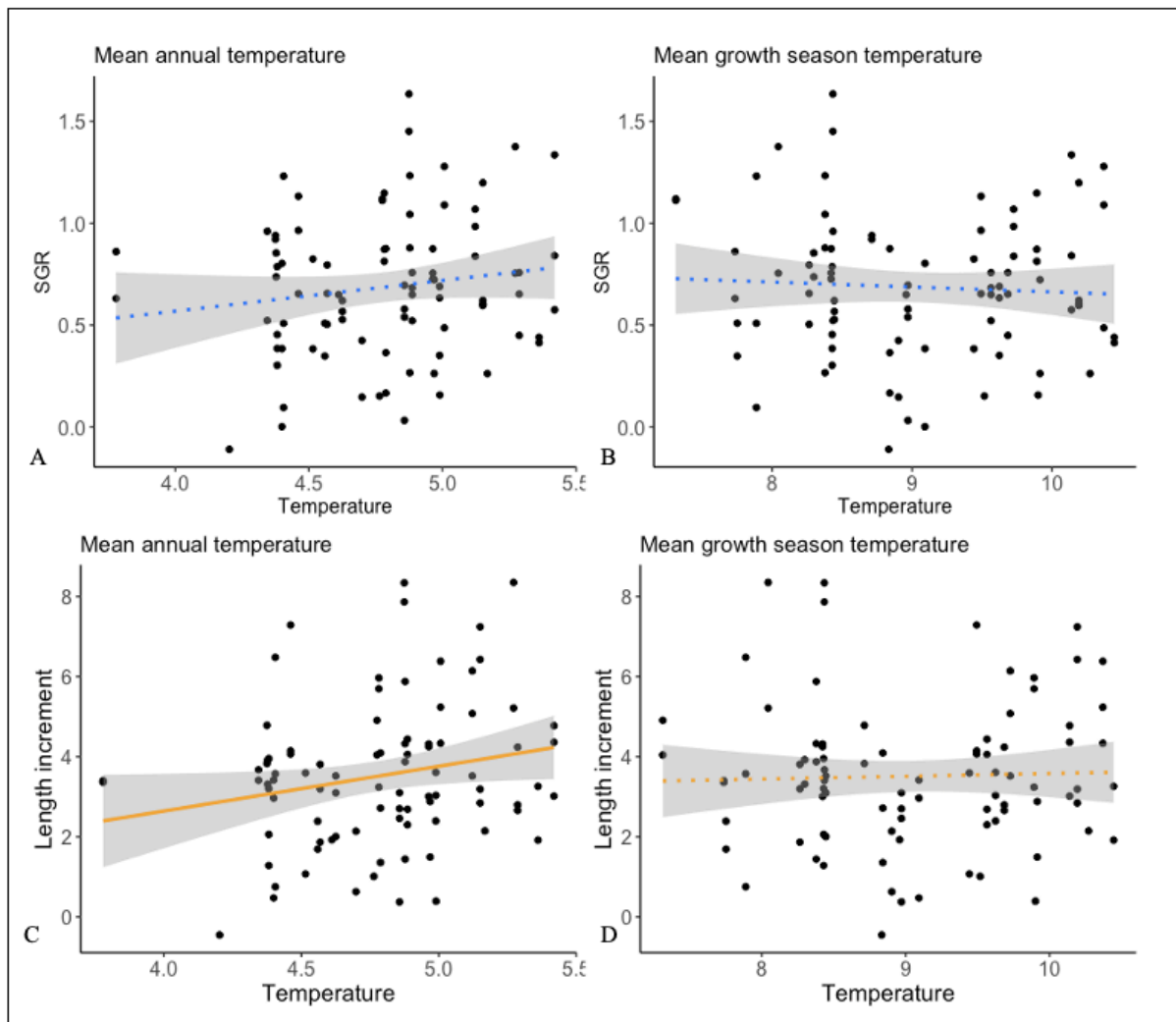
effectively, and therefore seemingly describes the growth pattern more accurately (**Appendix, Fig. S4**).



**Fig. 5** Fitted growth curves based on **A**) von Bertalanffy growth model for all periods combined and **B**) the biphasic growth model for all periods combined in lake Takvatn.

### 3.3 Water Temperature and Somatic Growth

The mean annual specific growth rate (SGR) of charr showed no significant correlation with water temperature (**Appendix, Table S7; Fig. 6A, B**), both with respect to mean annual water temperature and mean summer water temperature. No significant correlation was further found between mean annual length increment and mean summer temperature, whereas a statistically significant positive correlation was found between mean annual length increment and mean annual temperature ( $p\text{-value}=0.04$ ,  $r^2 = 0.0046$ ; **Appendix, Table S7; Fig. 6C, D**). However, less than 1% of the variance in length increments was explained by water temperature. An additional analysis excluding the years before 2000, a period characterized by substantial density fluctuations of charr and increasing abundance of brown trout, both expected to influence the charr growth, yielded almost similar results, but with none of the analysis being statistically significant (**Appendix, Table S7**). Hence, there is insufficient evidence to conclude that a meaningful relationship exists between annual length increment and water temperature.

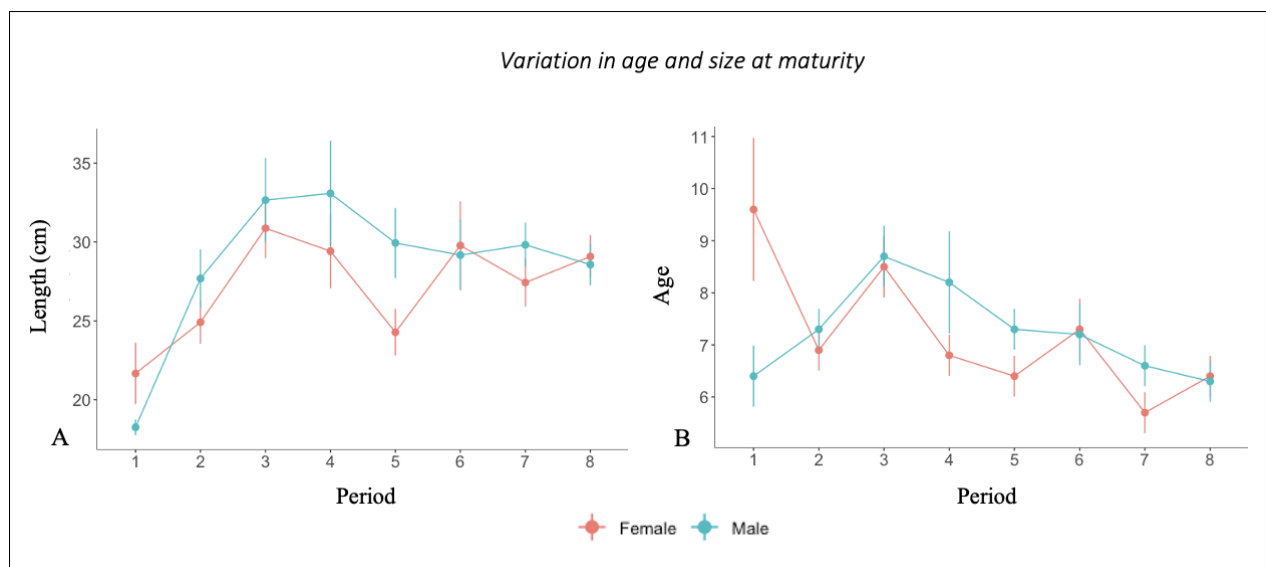


**Fig. 6** Linear regression analysis: Illustrating the relationship between **A)** specific growth rate (SGR) and mean annual temperature (1. August to 31. July the subsequent year) **B)** SGR and mean growth season temperature (1. August- 31. October) **C)** length increment and mean annual temperature **D)** length increment and mean growth season temperature. The grey shaded area shows the 95% confidence interval along the line.

### 3.4 Size- and Age at Maturity

There was an overall increase in length at 50% maturity (L50) for both males and females over the course of the study (**Fig.7A**), with the most notable increase over the three first periods from 1980-1995. Prior to the fish culling, male and female matured at relatively small sizes at 18.3 cm and 21.7 cm, respectively. Following the intensive fishing, L50 increased with nearly 15 cm for males and 10 cm for females from period 1 to period 3, to reach 32.7 cm and 30.9 cm, respectively. However, from period 3, there was a slight decline in L50, before stabilizing around 29 cm for both sexes from period 6 and onwards. In contrast to L50, which showed a

clear and similar increase for both males and females during the first three periods, age at 50% maturity ( $A_{50}$ ) showed a more variable pattern especially in relation to differences between the sexes over the two first periods. From period 1 to 2,  $A_{50}$  increased from 6.5 years to 7.3 years for males, while declined from 9.6 to 6.9 years for females (**Fig. 7B**). However, from period 3 and onwards,  $A_{50}$  has followed a similar declining trend for both males and females despite the fact that  $L_{50}$  remained stable from period 6 to 8. These findings suggest that charr matured earlier in life over the last three study periods, but at a similar size as in the periods before. Even though the observed changes in  $A_{50}$  and  $L_{50}$  over the 40-year study period primarily showed similar trends for males and females (**Fig. 7A, b**), there were significant differences between the sexes in half of the periods (Likelihood ratio tests; **Appendix, Table S4**).

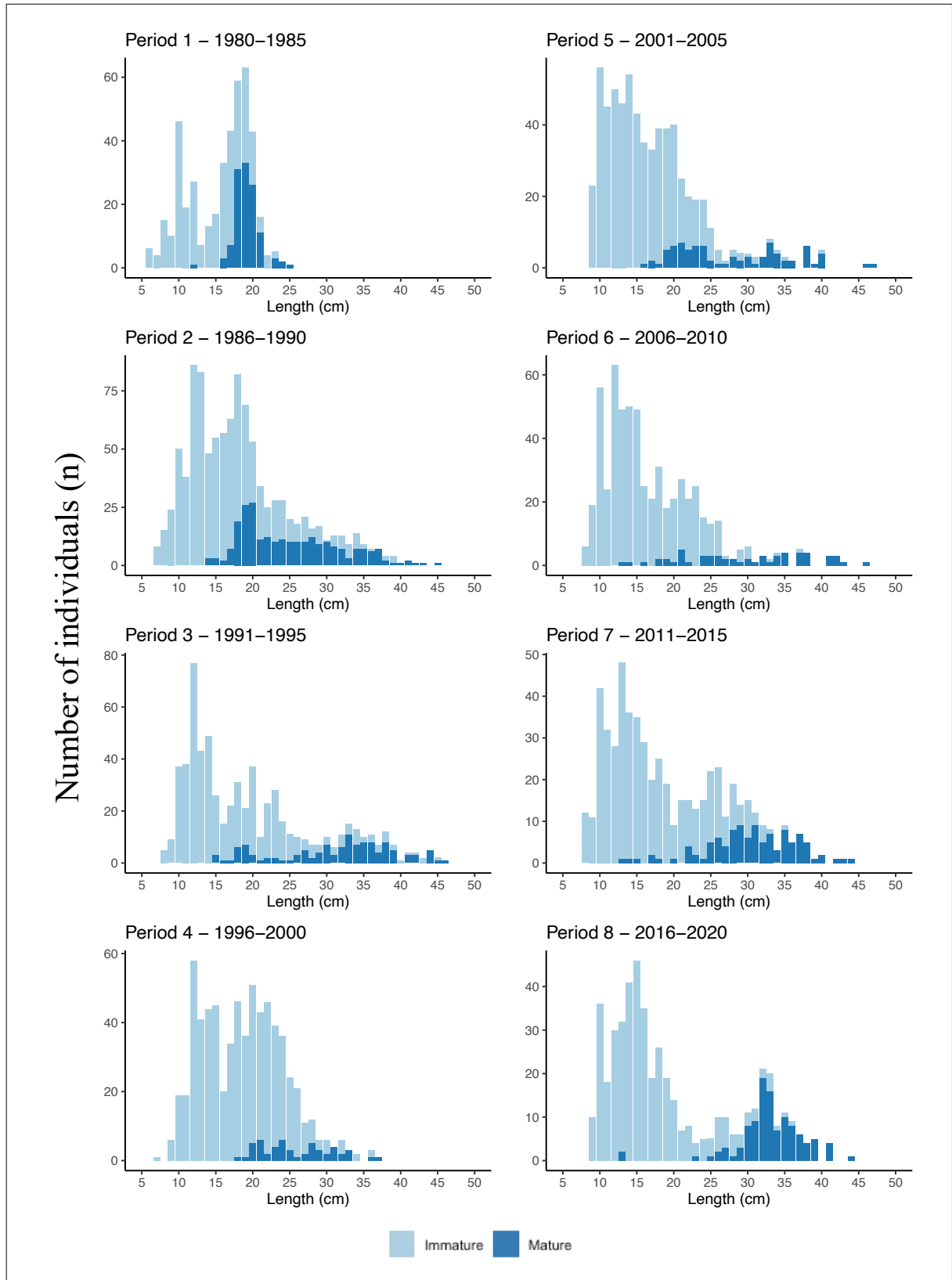


**Fig. 7** Temporal variation in **A)** length (cm) at which 50% of the population is mature ( $L_{50}$ ) and **B)** age at which 50% of the population is mature ( $A_{50}$ ) over the eight periods. Blue and red line represents males and females, respectively. Error bars indicate 95% confidence interval.

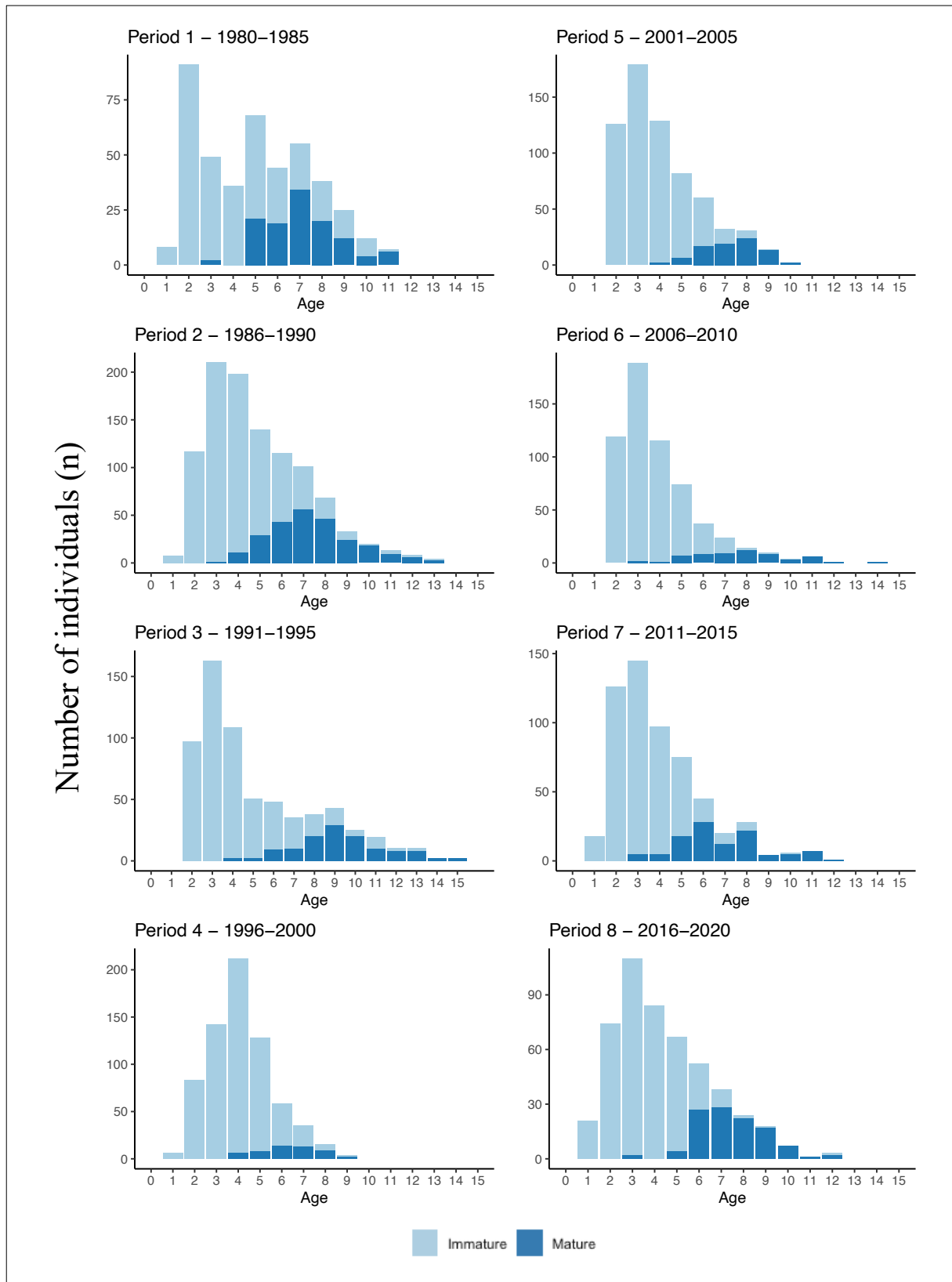
### 3.5 Size- and Age Distribution of Arctic Charr

The fish culling experiment led to drastic changes in the size- and age structure of the charr population. Before the fish removal, the population was dominated small-sized fish, where the largest fish reached a maximum length of ~25 cm (**Fig.8; Period 1**), and a large proportion of the population were old mature individuals (**Fig. 9; Period 1**). Already by period 2, the largest individuals in the catches reached sizes > 40 cm (**Fig. 9**). In addition, the proportion of older mature individuals had declined, while the numbers of younger fish in the catches had increased, showing a regularly high contribution since (**Fig. 9**). In period 4 (1996-2000), the

contribution of older individuals as well as larger size-classes had notably diminished with few fish older than 8 years or larger than 35 cm in the catches (**Fig. 8, 9; period 4**). From period 5 and onwards, larger and older individuals reappeared, reaching a maximum size >45 cm (**Fig. 8, 9**). The population has since comprised two distinct modes of the length frequency distribution, the first mode consisting of smaller individuals (<25 cm) and the second consisting of larger individuals (> 25 cm).



**Fig. 8** Length distribution of Arctic charr caught in the littoral, profundal and pelagic zones of Takvatn for all periods. Proportion of mature fish is illustrated by coloration: Light blue bars indicate immature fish, and dark blue bars indicate mature fish. Note the different scales on the y-axes.



**Fig. 9** Age distribution of Arctic charr caught in the littoral, profundal and pelagic zones of Takvatn for all eight periods. Proportion of mature fish is illustrated by coloration: Light blue bars indicate immature fish, and dark blue bars indicate mature fish. Note the different scales on the y-axes.

## 4 DISCUSSION

The long-term ecosystem-based data series available from lake Takvatn makes it possible to explore the long-term development in a subarctic fish population following a whole-lake culling experiment. Additionally, it offers a unique opportunity to investigate the effect of increasing water temperature on somatic growth rate of charr in a subarctic lake. In line with previous studies (Amundsen, 1989; Amundsen et al., 1993, 2007; Klemetsen et al., 2002) and with the hypothesis presented, somatic growth of charr demonstrated a marked improvement over the initial years following the culling before stabilizing at an enhanced level over time. This was supported by the outcome of both the growth models applied in the present study, which overall depicted the same trend in growth patterns for all study periods. However, contrary to my predictions, no clear water temperature effects on somatic growth rate of charr were found, suggesting other factors being more important in determining growth than increasing water temperature in lake Takvatn. Furthermore, age and size at sexual maturity, which were hypothesized to be influenced by density reduction and improved growth performance, exhibited an overall trend toward earlier maturation at larger sizes following the culling experiment. However, some interesting differences were found between the sexes regarding the onset of maturity over the initial years following the culling, suggesting that females and males responded differently to the impact of the fish culling. Lastly, and in accordance with the hypothesis presented, the responses of the culling at the population level, reflected the responses at the individual level. The population structure shifted from a dominance of small-sized, older individuals pre-culling to a broader size distribution with a clear lower and upper size-mode and a higher proportion of younger individuals post-culling.

The culling experiment led to drastic changes in the population density of both charr and brown trout. During the period when the heaviest fishing efforts took place (1984-1989), the littoral density of charr was reduced to about 20% of the density of the overcrowded population prior to the culling (**Fig. 3A**). The strong reduction suggests that the charr population was unable to compensate for the high mortality effect from fishing through increased recruitment during that period. In the initial decade following the culling, i.e., during period 3 to 4 (1991-2000), the charr population oscillated in abundance, which could raise doubts about the success of the culling in establishing an alternative stable state. However, the population density gradually stabilized during period 5 (2001-2005), suggesting that the fluctuations over the initial years



chiefly reflected a transient phase in the process of establishing a new stable state (Persson et al., 2007). The reduction in charr density further led to a gradual long-term recovery of the brown trout population, which has been suggested to be a result of density compensation following competitive release in the littoral zone (Amundsen et al., 2007). The charr population showed no return to the stunted population structure on the cessation of the intensive fishing, and Amundsen et al. (1993) suggested that more than one stable state could develop in charr lakes if the perturbations were strong enough, as seemingly was the case in Takvatn. Charr and brown trout have for the past 15 years comprised about 50% each of the littoral catches, providing additional support for the establishment of a new stable state. However, addressing the long-term temporal changes in growth and life history traits of charr after the culling and how these individual-level responses translate to the population level is essential for evaluating the resilience of the new stable state which may have further implications for the management of such lakes.

The immediate effect of the culling in Takvatn was a significant improvement in somatic growth of charr, which was most pronounced in the early years following the culling, before the growth stabilized at an enhanced level in accordance with the first hypothesis. The estimated asymptotic length and immature growth capacity rapidly increased following the culling, which was also reflected by the growth curves produced by both growth models, i.e., the VBGM and the biphasic growth model (**Fig. 4A, 4C, Fig. 5**). A food consumption study of charr in Takvatn, suggested that the stunted growth observed in the overcrowded population prior to the culling was related to restricted food resources as the daily food intake rates were found to be very low (Amundsen & Klemetsen, 1988). A direct effect of the density reduction was an improved growth performance among the remaining charr, supporting an inverse relationship between population density and somatic growth. Amundsen et al. (2007) demonstrated that this negative relationship between population density and somatic growth was a direct result of density-dependent impacts on the food consumption rate of charr in Takvatn. Furthermore, the growth improvement could also be related to the qualitative composition of prey, which changed towards larger and more valuable prey types after the density reduction of charr (Amundsen, 1989; Knudsen et al., 1996). The effect consumers may have on the prey community size distribution due to size-selective predation has been documented in several studies (Galbraith, 1967; Mittelbach, 1983; Amundsen et al., 2019).

In the later post-culling periods, the growth performance showed some smaller variations between periods. However, a notably poor growth was observed in period 4 (1996-2000), where

estimated asymptotic length was very low compared to the other periods after the culling (**Fig. 5**). This result may simply reflect a lower food consumption rate by charr due to increased competition for resources. However, the abundances of potential competitors were not higher in period 4 compared to other periods, and the relatively high energy acquisition parameter during that period (**Fig. 4C**) further indicate that food restriction may not be the explanation for the poor growth (see also Dahl-Hansen, 1995; Klemetsen et al., 2002). An examination of the demographic structure further reveals the absence of older and larger individuals in period 4 (**Fig. 8, Fig. 9**), which may be attributed to the mortality of the strong year-classes that appeared following the culling. Increased exploitation of fish populations is often accompanied by increased recruitment (Healey, 1980), which in Takvatn resulted in particularly strong 1982, 1983 and 1984 year-classes (Amundsen et al., 1993; Klemetsen et al., 2002). During period 4, these strong year-classes probably died out as the maximum longevity of charr in Takvatn is about 15 year (Klemetsen et al., 2002). This can be further supported as older and larger individuals reappeared in period 5 (2001-2005) (**Fig. 8, Fig. 9**), suggesting new groups of strong year-classes were able to grow into the population. Thus, the seemingly poor individual growth observed in period 4 appeared to be a result of the absence of older and larger individuals rather than a change in the growth conditions of the fish.

As previously mentioned, the replacement of  $K$  with  $G_{init}$  in the VBGM reparametrized by Gallucci and Quinn (1979) did not yield the intended effect, which was to avoid the dependency of  $K$  on  $L_{\infty}$ . In contrast to Mooji et al. (1999)'s recommendation of Gallucci and Quinn's model to avoid this problem, the result from the current study suggests that these two parameters (i.e.,  $G_{init}$  and  $L_{\infty}$ ) are still highly negatively correlated (**Fig. 4A, 4B**). This becomes particularly evident in period 1 and 4 when the estimated asymptotic length was very low while the initial growth rate was very high. According to the model output, the younger charr in these periods appear to grow exceptionally well before reaching the asymptotic length. This, however, is likely not the case as there are no biological explanations for the exceptional high growth rate observed in the younger charr during these periods, especially given the high population density in period 1 (1980-1985). Thus, the biological interpretation of  $G_{init}$  appeared to be just as dubious as for  $K$  in the original von Bertalanffy model, and prudent consideration is warranted when interpreting  $G_{init}$  from a biological standpoint.

A visual inspection of the growth curves produced from the VBGM and the biphasic growth model reveals that growth increases in an almost linear fashion with age, which do not align with the models' underlying assumptions. Both the VBGM based on bioenergetic principles,

and the biphasic growth model founded on the evolutionary principle of a trade-off between reproduction and growth in the allocation of energy, assume a decelerating growth with increasing age before gradually approaching the characteristic asymptotic shape primarily arising from the allocation of energy to reproduction by mature individuals (Heino & Kaitala, 1999; Lester et al., 2004; Wilson et al., 2018). Consequently, the biphasic growth model fails in estimating reproductive investment, which becomes particularly evident in periods when the estimated relative reproductive investment was zero or even negative (**Fig. 4D**; 2, 3, 5, 6 and 8), indicating that the proportion of energy allocated to reproduction by mature individuals is zero or less than zero, which have no biological support. In reality, these results simply reflect the ability of charr to retain growth even after maturation through ontogenetic niche shifts, which may compensate for the energy costs associated with reproduction. The dietary need of fish increases during ontogeny due to higher costs related to maintenance, swimming and feeding (Elliott, 1976; Jobling, 1982; Laegdsgaard & Johnson, 2001). For growth to continue at larger sizes, many species including charr may exhibit ontogenetic niche shifts (e.g., changes in feeding behavior, habitat preferences, and morphology) which typically has been related to distinct growth phases in the species life history (Werner & Gilliam, 1984; Kimirei et al., 2013; Young et al., 2021). The timing of ontogenetic niche shift and maturity appear to be tightly connected, suggesting that as the charr reaches sexual maturity it is also able to change its feeding behavior towards larger prey (Forseth & Jonsson, 1994). In the overcrowded situation when there were small opportunities for charr to undergo ontogenetic niche shifts, the growth curve for period 1 follows the more typical pattern where growth decelerates at older ages towards an asymptotic size. However, in the post-culling periods, the increasing food availability for the charr population gave the charr an opportunity to expand their feeding niche to include larger and more valuable prey types as they grew larger. Several studies suggests that juvenile charr primarily feed on zooplankton, and as they grow, they start feeding on larger zooplankton species and benthic invertebrates, and the largest ones may even turn over to a piscivore diet (Forseth et al., 2003; Klemetsen et al., 2003; Jonsson et al., 2008; Prati et al., 2021). This has also been demonstrated to be true for charr in Takvatn (Moe, 2011; Sanchez-Hernandez et al., 2022), and Amundsen (1994) even found that 5% of the charr larger than 20 cm were cannibalistic. Another important factor for maintaining growth may be related to the ability of charr as a generalist to shift between benthic and pelagic trophic niches, depending on the degree of resource competition (Nilsson, 1967; Quevedo et al., 2009; Eloranta et al., 2013). High individual niche specialization in charr is often induced by strong intraspecific competition, leading to some individuals being more efficient zooplankton feeders, while others

primarily feed on various zoobenthos in the littoral (Bolnick et al., 2010; Amundsen, 1995; Eloranta et al., 2013). Such trophic dietary plasticity has been documented in Takvatn as well (Prati et al., 2021) and appeared to increase over the ontogeny (Sanchez-Hernandez et al., 2022), suggesting that territorial behavior and the monopolization of resources could contribute to retaining growth. Thus, the estimated negative proportion of energy allocated to reproduction is an artifact of the underlying model assumptions which are not met as none of the models specifically accounts for the shifts or specialization in diet that may occur. These findings emphasize the importance of acknowledging that all growth models are simplifications of reality and should therefore be interpreted carefully if the assumptions are not met. More complex growth models that capture fluctuations in food availability are necessary for a more precise description of how growth patterns respond to ecological changes, like e.g., ontogenetic niche shifts.

In the periods following the culling, the individual growth of the charr appeared to stabilize at an enhanced level. However, a modest yet consistent growth enhancement could be observed throughout the entire 40-year study period (period 4; 1996-2000 excluded), especially from the VBGGM, while the biphasic growth model showed some more temporal variations. These results may be related to changes in water temperature which is the most important environmental factor influencing fish growth rate (Jobling, 1982; Viadero, 2005; Árnason et al., 2022). In Takvatn, a gradually increasing trend in water temperature has been documented over the study period (1980-2020) (**Fig. 2**). Increasing water temperature was hypothesized to have a positive effect on somatic growth of charr, as the charr in Takvatn experiences temperatures below their optimum in which growth may improve with climate warming. However, based on the temperature-growth analysis from the current study, just one out of the four analyses showed a statistically significant positive effect of temperature on growth (**Fig. 6C**). Most studies that have demonstrated a positive effect of increasing temperature on somatic growth of charr come from controlled experimental laboratory studies (Jobling, 1983; Baroudy & Elliott, 1994; Larsson & Berglund, 2005; Elliott & Elliott, 2010; Árnason et al., 2022), while field studies have shown more inconsistent results (Power et al., 2000; Kristensen et al., 2006; Murdoch et al., 2013). A recent paper has, however, demonstrated a positive effect of warming on juvenile growth rate of charr in Takvatn (Kotowych et al., 2023). Kotowych et al. used back-calculation of growth to obtain length-at-age data, which may capture inter-individual variation in growth more effectively and thus allows for a more detailed examination of growth patterns than the current mean-length-at-age approach. In their regression model, both temperature and CPUE

estimates were included as predictor variables to account for the effect of population density on growth (Kotowych et al., 2023). The model used in the present study could not account for density-dependence, which may have implications for understanding the drivers of growth variability of the Takvatn charr. For example, in 1980, unusually high water-temperatures were reported in Takvatn (Amundsen, 1989), potentially enhancing the growth rate. However, the abundance of charr was very high that year, likely suppressing the temperature signal and resulting in a low individual growth rate despite the high temperatures, hereby affecting and potentially biasing the outcome of the temperature analysis. Thus, understanding the effect of multiple stressors and how they interact in field studies is often challenging, as also experienced in other studies (Woodward et al., 2010; Smalås et al., 2020). Still, the outcome of the temperature analysis in the current study suggests that the population density of charr is likely more important than temperature in explaining the inter-annual variation in the somatic growth of charr observed in Takvatn. Additionally, the fluctuating and increasing abundance of brown trout may have concealed any temperature effects on somatic charr growth.

The growth rate and maximum adult size achieved by fish may have implication for maturation schedules as growth and reproduction are tightly linked through trade-off (Stearns, 1992; Wootton, 1985; Cook et al., 1999). Different selection pressure (e.g., population density, predation, temperature) may affect the trade-off regime leading to variation in age and size at maturity as adaptive responses to specific ecological or environmental conditions to maximize overall fitness throughout life (Winemiller, 2005; Smalås et al., 2013). Thus, the growth enhancement mediated by reduced intraspecific competition following the culling was hypothesized to alter the size and age at sexual maturity of charr in Takvatn (Jonsson & Jonsson, 2011; Ward et al., 2016). Over the 40-year study period, an overall trend towards earlier maturation at larger sizes was observed. Early maturation has previously been associated with a reduction in population size as a compensatory response to large density reduction, providing more food and higher growth rate (Colby & Nepszy, 1981; Trippel, 1995; Ali et al., 2003). Several studies have shown that a reduction in population density shifts maturation schedules towards earlier maturation as an adaptive response to maximize lifetime reproductive output as the fish may mature earlier but at the same or even larger size (Healey, 1980; Diana, 1983; Helser & Almeida, 1997; Jonsson & Jonsson, 2011, Moncrief et al., 2018). In the present study, charr attained maturation at younger ages but at larger sizes over the first three periods (1980-1995) and thereafter maintained a similar maturation size over the last periods (1996-2020),

suggesting that the trend towards earlier maturation was a compensatory response to the strong density reduction that took place during the culling.

Females and males demonstrated differences in size and age at maturation and their developments during and in the first decade following the culling (from period 1 to 2; 1980-1990), suggesting that they responded differently to the culling and growth enhancements. Females exhibited a trend towards earlier maturation at a larger size, while males seemed to delay maturation with an associated increase in size at maturity over the first years after the culling started. Female fecundity is known to increase with body size (Stearns, 1992; Roff, 1993), and several studies have shown that female maturing later at larger sizes produces larger as well as a higher number of eggs than their smaller conspecifics (van den Berghe, 1989; Sandlund et al., 1992; Hsieh et al., 2010; Loewen, 2010). Charr typically mature at a size range between 20-40 cm (Klemetsen et al., 2003), which was also supported by the findings in the present study. Prior to the culling, both males and females matured at small sizes ( $L_{50} \approx 20$  cm), which was likely a consequence of the restricted food availability, which limited the opportunities for growth (**Fig. 7A**). The low mortality rates through cannibalism or predation from brown trout, which were almost absent in the pre-culling period, possibly allowed a delayed reproduction of females until an appropriate size regarding maximizing fecundity was attained. Moreover, the results suggest that the reproductive success of females is more dependent on body size compared to males. This may be explained by the fact that body size directly affects fecundity and egg size, access to breeding territories, and probability of nest destruction (van den Berghe & Gross 1989; Fleming, 1996, 1998). Thus, there might be a selection towards larger body size at maturity in females (Forseth et al., 1994). In contrast, age at maturation in males are usually more variable which appear to be associated with different spawning behavior (Jonsson & Jonsson, 2001; Sandlund et al., 1992). Males may deploy alternative mating tactics, including a sneaking spawning behavior, which has frequently been documented both in charr and in several other salmonid species (Sigurjónsdóttir & Gunnarsson, 1989; Brattli et al., 2018). Thus, selection may favor both larger males using guarding tactics and aggression in the competition for mates as well as smaller males deploying sneaking spawning behavior.

Following the culling, the shift in maturation schedule in females towards earlier maturation at larger sizes, can be explained by life history theory which states that it is beneficial to mature early due to increased likelihood for surviving until maturity, as a result of spending less time in the vulnerable juvenile stage (Johnson & Belk, 2001; Walsh & Reznick, 2008). If predation

pressure is high, prey investing more in reproduction early in life at the expense of the quality of offspring should be favored (Stearns, 1992; Smalås, 2013). In addition, individuals maturing earlier increase their lifetime fecundity because of shorter generation time relative to slowly maturing conspecifics (Stearns, 1992). In contrast, males matured later and at larger sizes compared to the pre-culling situation, which was likely driven by sexual selection in their contests for females and successful fertilization (Roff, 1993). Larger males often experience a reproductive advantage over smaller males, as they are more aggressive. Moreover, smaller males may even be ignored or bullied by the females. A field study with charr demonstrated that females exhibited an aggressive behavior towards small-sized sneakers, which can be a defense mechanism against egg predation or might indicate a female preference for larger males (Sigurjónsdóttir & Gunnarsson, 1989).

The individual-level responses to the culling, which were improved somatic growth and an overall trend towards earlier maturation, were further hypothesized to be reflected at the population level. The population structure was hypothesized to shift from a dominance of small-sized, older individuals to a higher proportion of younger individuals as well as larger fish. In the pre-culling situation, the size distribution was dominated by small-sized fish and the age distribution revealed a high proportion of old individuals in the population (**Fig. 8, 9**). The high population density which caused intense intraspecific competition for resources (Amundsen et al., 2007) prevented individuals to grow large. Furthermore, the observed late age at maturation resulted in lower reproduction rate, and thus a lower production of small-sized young individuals relative to biomass. Prior to the culling, the largest charr dominated in the most productive littoral zone of the lake, while the small-sized charr were confined to the profundal zone through an ontogenetic habitat shift (Klemetsen et al., 1989). Thus, the size distribution in the littoral zone were found to be highly unimodal (Klemetsen et al., 2002) which had implications for the ecological interactions within the lake system, making the demographic structure where few charr grew larger than 25 cm very resilient. This resilience was attributed to the absence of larger cannibalistic individuals and the low abundance of sympatric predatory brown trout, which could regulate charr density through increased juvenile mortality, thereby limiting recruitment (Amundsen et al., 1993; Klemetsen et al., 2002; Persson et al., 2007). The habitat segregation between small and larger individual, limited the possibilities of charr tuning into cannibals because of the small size differences between the potential cannibal and prey in the littoral (Amundsen, 1994; Klemetsen et al., 2002). In addition, the encounter rate between brown trout and charr within the preferable prey-size were found to be very low, which

prohibited an increase in brown trout abundance (Persson et al., 2007). Thus, it appeared that the equilibrium situation of a dense charr population prior to the culling reflected a stable state in which neither cannibalism nor predation from brown trout had the potential to shift the population structure (Amundsen et al., 1993; Persson et al., 2007). In the post-culling situation, the size distribution shifted to an upper size mode include larger individuals than previously ( $> 25$  cm) and the age distribution changed towards a higher proportion of younger and smaller individuals (**Fig. 8, 9**). The density reduction of old charr and reduced intraspecific competition for resources in the littoral allowed the numerous smaller juveniles to move into the more productive habitat, despite increased predation risk from larger conspecific and brown trout (Amundsen et al., 1993). The appearance of small-sized vulnerable charr, creating a lower size mode in the littoral, increased the encounter rate with both cannibalistic charr and predatory brown trout (Amundsen, 1994; Klemetsen et al., 2002). This became an important factor for the recovery of the brown trout population (Persson et al., 2007, 2013). Thus, in the post-culling situation, both larger charr and brown regulated the population density of charr through increased mortality of juveniles and thus reducing recruitment. The shift in the size-distribution of charr in the littoral from a unimodal structure to a bimodal structure induced by food-dependent growth appeared to be essential for the establishment of an alternative stable state (Persson et al., 2007).

The culling appeared to succeed in establishing an alternative stable state with both brown trout and charr present. In the low-density equilibrium state, the individual growth of charr rapidly improved with a corresponding increase in length-at-age leading to a higher recruitment of larger individuals into the population. In light of the ongoing climate change, rapidly increasing water temperature at high latitudes may accelerate somatic growth of charr (Smalås et al., 2020; Kotowych et al., 2023), thus potentially boosting this effect. The presence of two distinct size modes of individuals smaller and larger than 25 cm, has persisted for over three decades and have become even more pronounced over the last decade (**Fig. 8**), despite some oscillating in population abundance over the study period. Thus, the new equilibrium of charr and brown trout seems to have increased in resilience over time, suggesting that the population can withstand moderate perturbation through e.g., fishing without retuning to its original size structure. However, if the lake is not being appropriate managed, intense exploitation can quickly return the population to the overcrowded state as fishing practices are often size-selective and targets larger and thus also older individuals. This can lead to a shift in the population structure of the exploited species by truncating the age and size distribution



(Berkeley, 2004; Ottersen, 2008; Hsieh, 2010), which as shown in Takvatn may have implications for size-structured interactions and consequently growth and maturation schedules of the overexploited species. Understanding how changes in various life-history traits (e.g., growth, size, and age at maturity) have consequences for the population dynamics has received increased attention and recent research emphasizes the importance of incorporating the intricate interplay of different life-history traits in fisheries management (Rose, 2002, 2005; De Roos et al., 2003; Lorenzen, 2008; Lester et al., 2014). Addressing these complexities are crucial for establishing sustainable exploitation rate to endure the long-term health and balance of aquatic ecosystems.

## 5 CONCLUSIONS

The present study provides valuable insights into the short- and long-term effects of fish culling on growth, maturity, and population dynamics of charr based on a four-decade-long survey in the subarctic lake Takvatn. The immediate effect of the culling was a substantial improvement in the somatic growth of charr, and this effect has persisted over the whole study period. The density reduction and growth enhancement had further implications for the age and size at maturity, leading to a general trend of earlier maturation. The fish still reached maturity at larger sizes than those in the overcrowded population, which further emphasize the improved living condition after the culling. These responses at the individual level were also reflected at the population level, manifested in a shift from a dominance of old slow-growing individuals pre-culling to a broader size-distribution including both small and large fish and a higher proportion of juveniles charr post-culling. This shift in the demographic structure of charr appears to be essential for the establishment of an alternative stable state, where both charr and brown trout are present. Finally, the study suggests that the new stable state may have increased its resilience over time, which may indicate that increasing water temperatures over the same time period may have contributed to this stability. However, such an effect could not be demonstrated in the present investigation.

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## APPENDIX

**Table S1** Yearly Arctic charr removal during the stock depletion experiment in lake Takvatn from 1984-1989.

<b>Year</b>	<b>Number of fish</b>	<b>Weight (tons)</b>
1984	126 000	7.7
1985	104 000	7.0
1986	112 000	3.9
1987	129 000	4.5
1988	95 000	3.9
1989	100 000	4.3
<b>Total</b>	<b>666 000</b>	<b>31.3</b>

**Table S2** Estimated growth parameters ( $\pm 95\%$  confidence interval) from von Bertalanffy growth model and the biphasic growth model for all periods.

Period	$L_{\infty} \pm SE$	$g \pm SE$	$c \pm SE$	$r \pm SE$	$c \pm SE$	$r \pm SE$
			swe=0.5	swe=0.5	swe=1	swe=1
Period 1: 1980-1985	22.0 $\pm$ 0.6	6.0 $\pm$ 0.2	1.5 $\pm$ 0.06	0.07 $\pm$ 0.04	1.4 $\pm$ 0.04	0.2 $\pm$ 0.04
Period 2: 1986-1990	83.7 $\pm$ 12.9	3.9 $\pm$ 0.2	2.0 $\pm$ 0.03	-0.03 $\pm$ 0.04	2.0 $\pm$ 0.04	-0.02 $\pm$ 0.02
Period 3: 1991-1995	72.6 $\pm$ 12.0	4.4 $\pm$ 0.2	1.8 $\pm$ 0.1	-0.12 $\pm$ 0.08	1.9 $\pm$ 0.08	-0.06 $\pm$ 0.04
Period 4: 1996-2000	38.0 $\pm$ 4.3	6.0 $\pm$ 0.4	1.9 $\pm$ 0.06	0.06 $\pm$ 0.08	1.9 $\pm$ 0.06	0.12 $\pm$ 0.08
Period 5: 2001-2005	85.8 $\pm$ 23.7	4.3 $\pm$ 0.2	2.1 $\pm$ 0.08	-0.13 $\pm$ 0.06	2.0 $\pm$ 0.1	-0.17 $\pm$ 0.04
Period 6: 2006-2010	95.6 $\pm$ 21.0	4.4 $\pm$ 0.2	2.3 $\pm$ 0.08	-0.07 $\pm$ 0.06	2.3 $\pm$ 0.08	-0.03 $\pm$ 0.02
Period 7: 2011-2015	62.7 $\pm$ 7.6	5.6 $\pm$ 0.2	2.1 $\pm$ 0.08	0.07 $\pm$ 0.04	2.2 $\pm$ 0.08	0.06 $\pm$ 0.02
Period 8: 2016-2020	95.2 $\pm$ 25.1	4.8 $\pm$ 0.2	1.9 $\pm$ 0.08	-0.16 $\pm$ 0.06	1.9 $\pm$ 0.08	-0.09 $\pm$ 0.04

**Table S3** Length and age at 50% sexual maturity ( $L_{50}$  and  $A_{50}$ )  $\pm 95\%$  confidence interval for all periods and between sexes.

Period	n (Total)	$A_{50} \pm 95\%$ CI (Total)	$A_{50} \pm 95\%$ CI (Females)	$A_{50} \pm 95\%$ CI (Males)	$L_{50} \pm 95\%$ CI (Total)	$L_{50} \pm 95\%$ CI (Females)	$L_{50} \pm 95\%$ CI (Males)
1	433	7.6 $\pm$ 0.6	9.6 $\pm$ 1.4	6.4 $\pm$ 0.6	19.2 $\pm$ 0.6	21.7 $\pm$ 1.9	18.3 $\pm$ 0.5
2	1035	7.1 $\pm$ 0.2	6.9 $\pm$ 0.4	7.3 $\pm$ 0.4	26.4 $\pm$ 1.2	24.9 $\pm$ 1.4	27.7 $\pm$ 1.8
3	652	8.5 $\pm$ 0.4	8.5 $\pm$ 0.6	8.7 $\pm$ 0.6	31.8 $\pm$ 1.6	30.9 $\pm$ 1.9	32.7 $\pm$ 2.7
4	683	7.5 $\pm$ 0.6	6.8 $\pm$ 0.4	8.2 $\pm$ 1.0	31.4 $\pm$ 2.2	29.4 $\pm$ 2.4	33.1 $\pm$ 3.3
5	655	6.8 $\pm$ 0.2	6.4 $\pm$ 0.4	7.3 $\pm$ 0.4	27.2 $\pm$ 1.4	24.3 $\pm$ 1.5	29.9 $\pm$ 2.2
6	594	7.3 $\pm$ 0.4	7.3 $\pm$ 0.6	7.2 $\pm$ 0.6	29.4 $\pm$ 1.8	29.8 $\pm$ 2.8	29.2 $\pm$ 2.2
7	572	6.2 $\pm$ 0.4	5.7 $\pm$ 0.4	6.6 $\pm$ 0.4	28.7 $\pm$ 1.0	27.4 $\pm$ 1.5	29.8 $\pm$ 1.4
8	499	6.3 $\pm$ 0.2	6.4 $\pm$ 0.4	6.3 $\pm$ 0.4	28.8 $\pm$ 1.0	29.1 $\pm$ 1.4	28.6 $\pm$ 1.3

**Table S4** Summary of results from the likelihood ratio test (LRT) on differences in age and length at maturation between sex. Statistical significance was approximated using p-values: \*\*\*p < 0.001; \*\*p < 0.01; \*p < 0.05; •p < 0.1. Grey boxes represent non-statistical significance p-values > 0.1.

Period	1	2	3	4	5	6	7	8	Hole period
Age p-value	***	>0.05	>0.05	*	***	>0.05	*	>0.05	>0.05
Length p-value	***	>0.05	>0.05	*	***	>0.05	**	>0.05	>0.05

**Table S5** Summary of results from ANCOVA test on differences in length at age between the two sexes for all 8 periods. Statistical significance was approximated using p-values: \*\*\*p < 0.001; \*\*p < 0.01; \*p < 0.05. Grey boxes represent non-statistical significance p-values > 0.5.

Period	1	2	3	4	5	6	7	8	Hole period
p-value	>0.05	*	>0.05	>0.05	>0.05	>0.05	>0.05	**	>0.05

**Table S6** Summary of results from Mann-Whitney U Test (Wilcoxon Rank-Sum Test) on differences in length at age between the two sexes for all 8 periods. Statistical significance was approximated using p-values: \*\*\*p < 0.001; \*\*p < 0.01; \*p < 0.05. Grey boxes represent non-statistical significance p-values > 0.5.

Period ⇒	1	2	3	4	5	6	7	8
Age ↓								
2		*		**	*			
3								*
4				**	*			
5								
6								
7								
8								
9								
10								

**Table S7** Summary of results from linear regression analysis of relationship between **A)** specific growth rate (SGR) and temperature and **B)** length increment and temperature. All years included (left), and only years after 2000 (right). Statistical significance was approximated using p-values: \*\*\*p < 0.001; \*\*p < 0.01; \*p < 0.05.

Comparison		(1980-2020)		(2000-2020)	
		r2	p-value	r2	p-value
A	SGR vs. mean annual temperature	0.023	0.16	0.002	0.75
	SGR vs. mean growth season temperature	0.003	0.59	0.011	0.46
B	Length increment vs. mean annual temperature	0.046	0.04*	0.016	0.38
	Length increment vs. mean growth season temperature	0.001	0.77	0.0001	0.94

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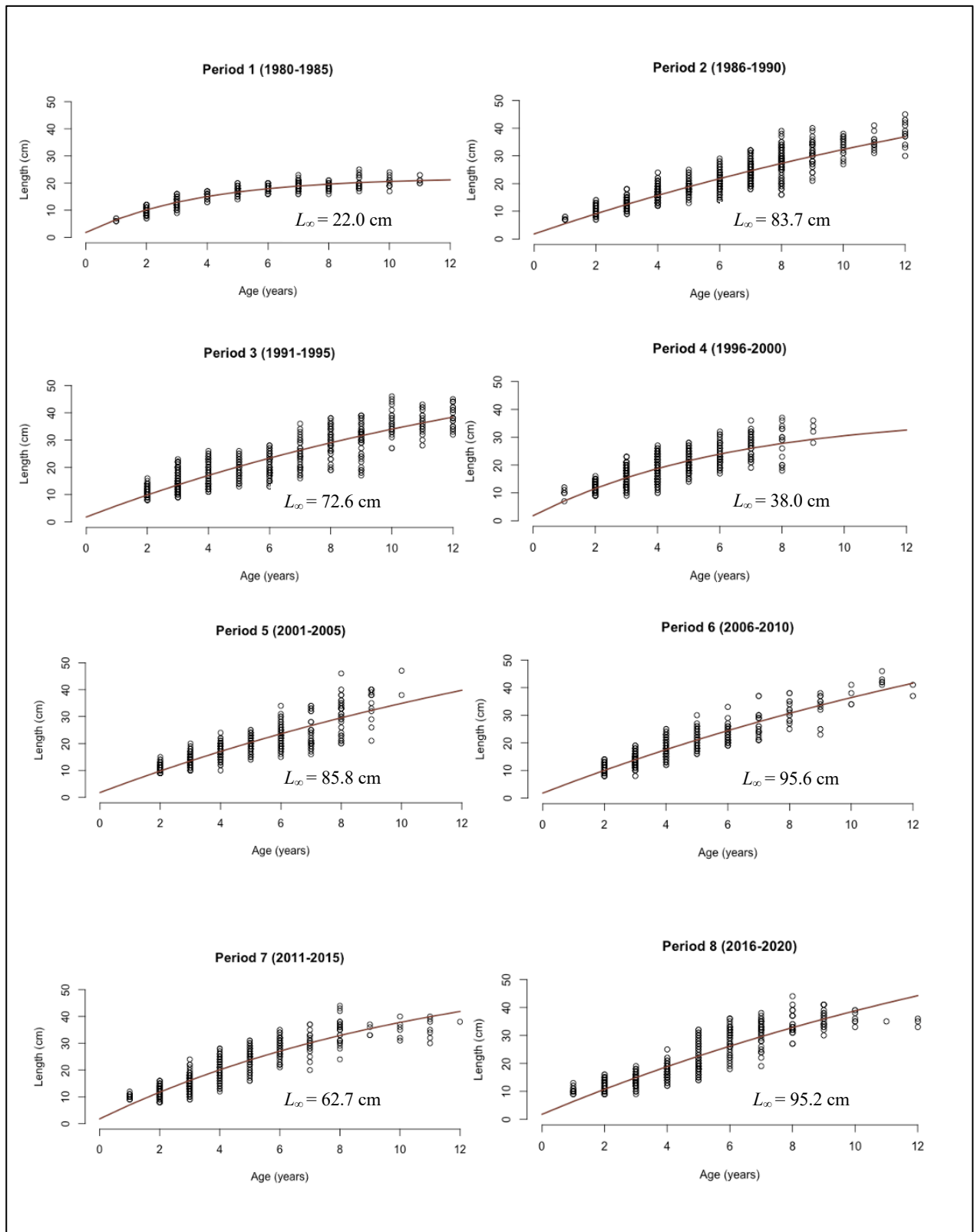
> summary(anova_result)
      Df Sum Sq Mean Sq F value Pr(>F)
Age      5  79210   15842   4.159 0.00139 **
Residuals 165 628502    3809
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

$Age
      diff      lwr      upr      p adj
11-10 13.85948 -17.988503  45.70747 0.8088617
12-10 59.58467  17.232198 101.93714 0.0010659
13-10 32.37970 -19.378875  84.13827 0.4661039
14-10 47.57018 -57.185602 152.32595 0.7795121
15-10 83.73684 -43.747653 211.22134 0.4095173
12-11 45.72518   1.288996  90.16137 0.0397188
13-11 18.52022 -34.956818  71.99725 0.9178259
14-11 33.71069 -71.904724 139.32611 0.9408166
15-11 69.87736 -58.314450 198.06917 0.6182494
13-12 -27.20497 -87.531005  33.12107 0.7845092
14-12 -12.01449 -121.257586  97.22860 0.9995662
15-12 24.15217 -107.044538 155.34889 0.9948537
14-13 15.19048 -98.031747 128.41270 0.9988603
15-13 51.35714 -83.170904 185.88519 0.8804617
15-14 36.16667 -126.291384 198.62472 0.9876219

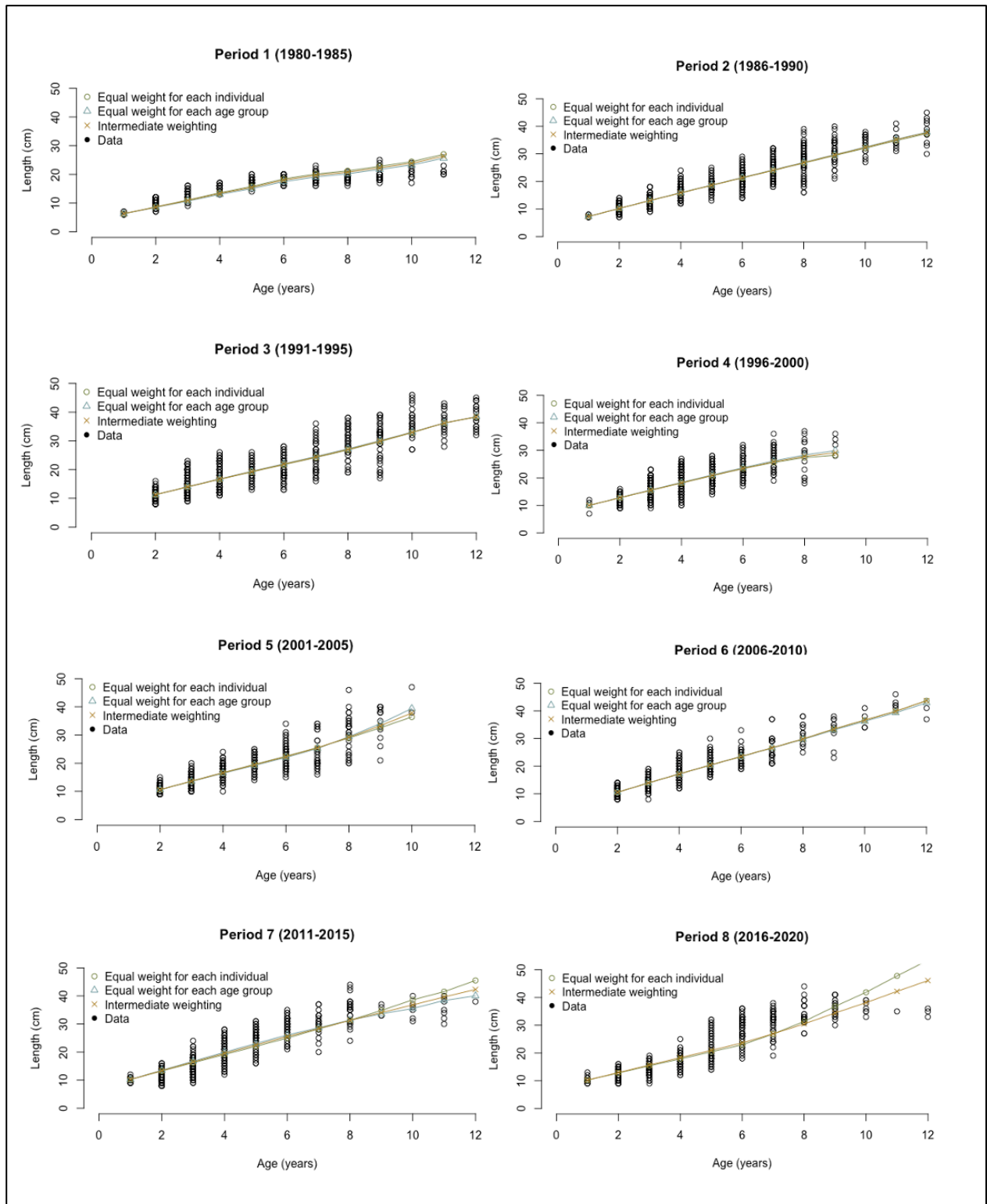
      Df Sum Sq Mean Sq F value Pr(>F)
Age      3   8726    2909   2.021 0.127
Residuals 38  54686    1439

```

**Fig. S1** Summary of ANOVA-test, testing differences in length between **A)** 10, 11-, 12-, 14- and 15-year-old Arctic charr. Tukey's HSD test ("honestly significant difference") was used to identify the means that were significantly different from each other **B)** 12, 13-, 14- and 15 year-old Arctic charr

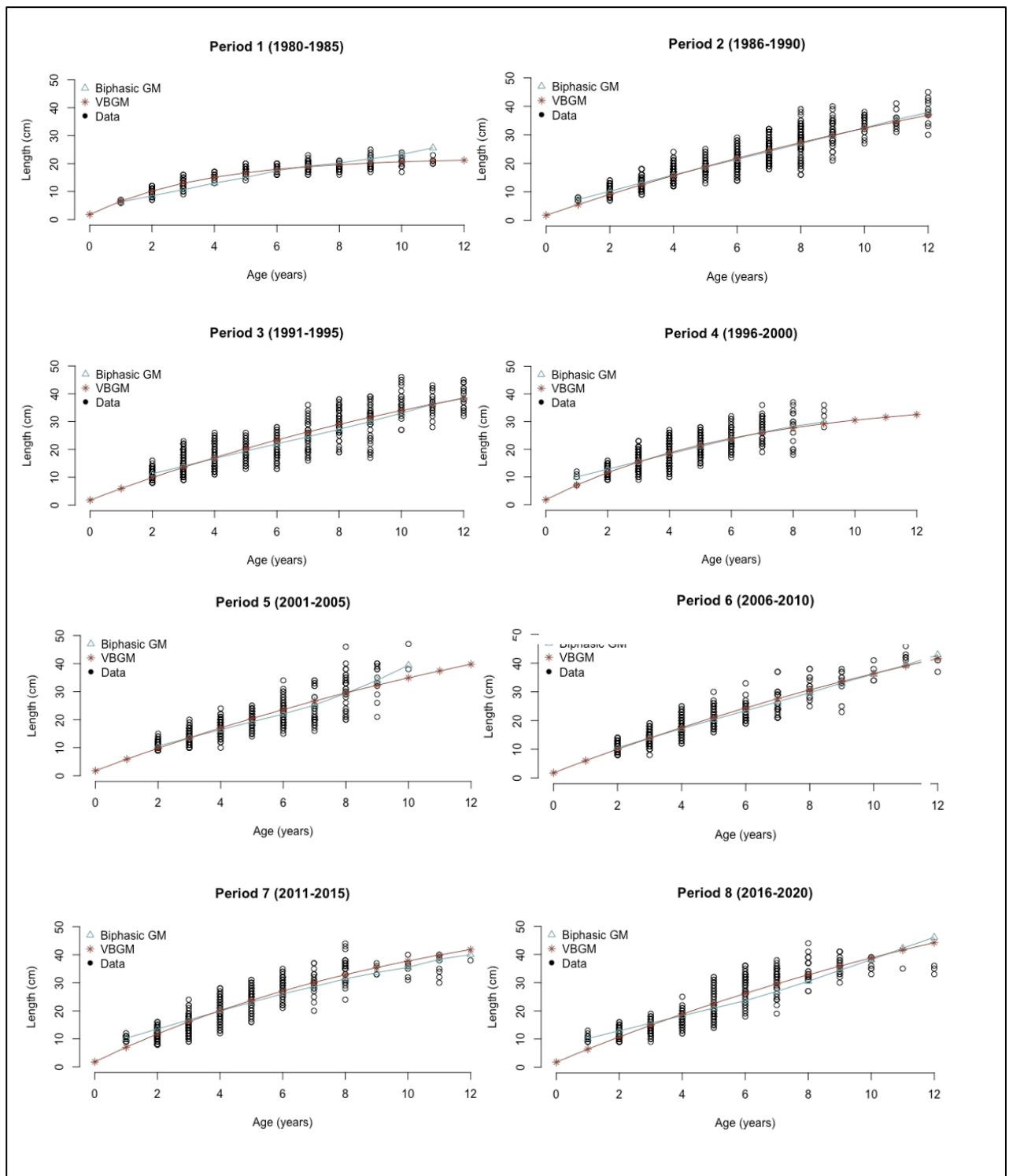


**Fig. S2** Growth curves (green lines) based on estimated regression parameters from the von Bertalanffy growth model for all periods in lake Takvatn. The open dots are the observed individual size (length at age).

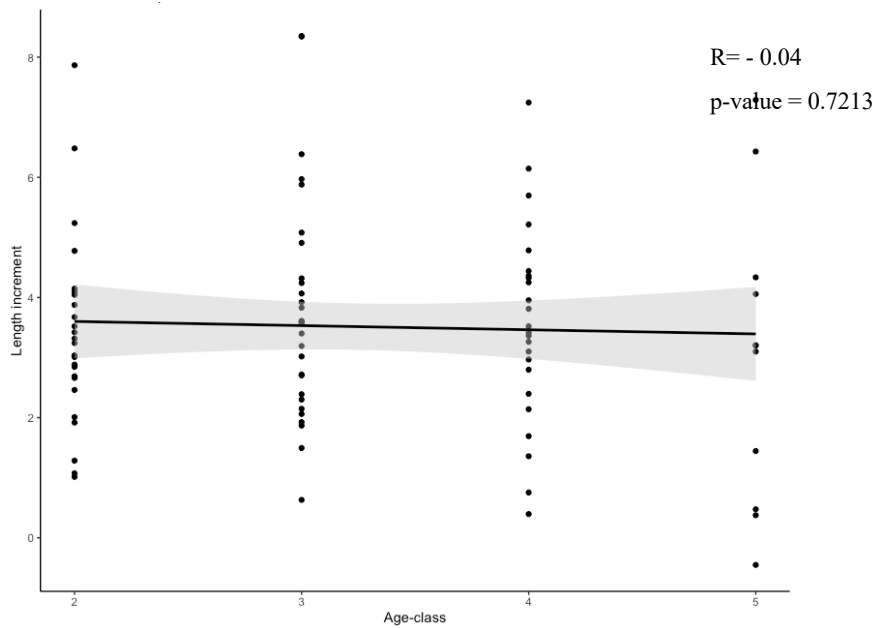


**Fig. S3** Growth curves based on the estimated regression parameters from the biphasic growth model with three different weighting factors (swe) for all periods; Equal weight for each individual (green line, open circle), equal weight for each age group (blue line, open triangle) and intermediate weighting (yellow line, cross). The black open circles are the observed data.

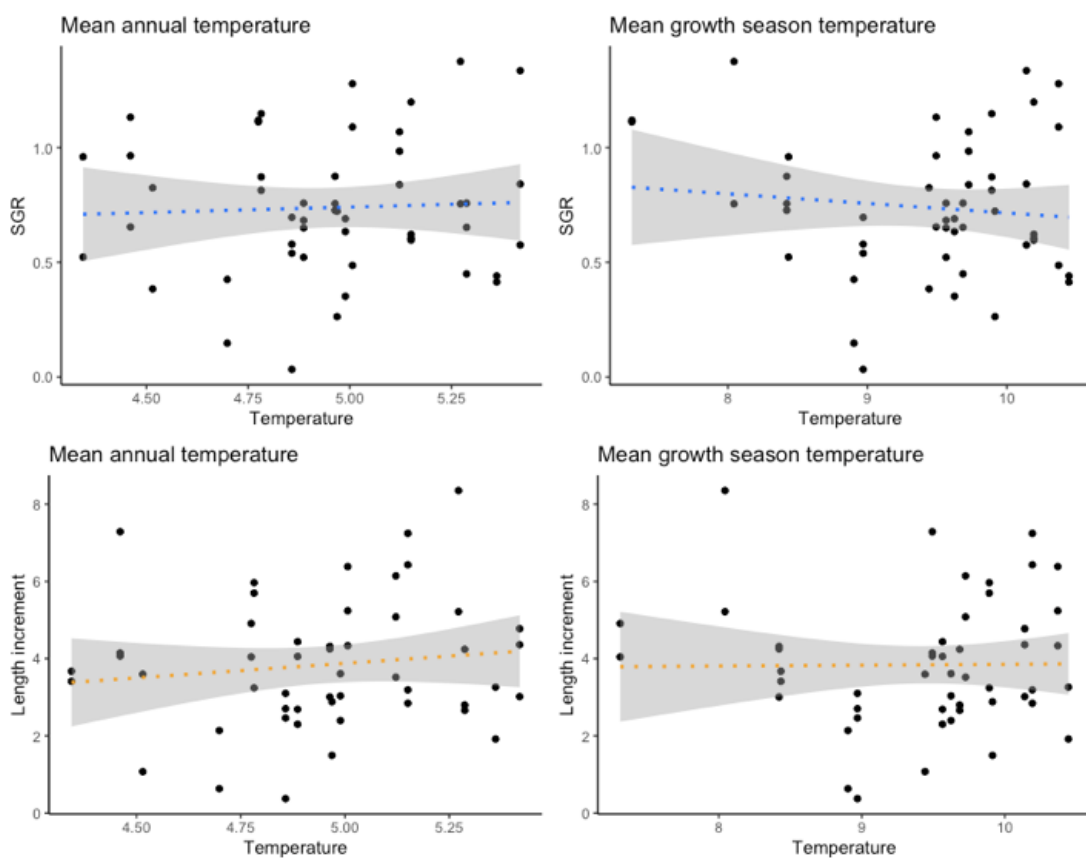




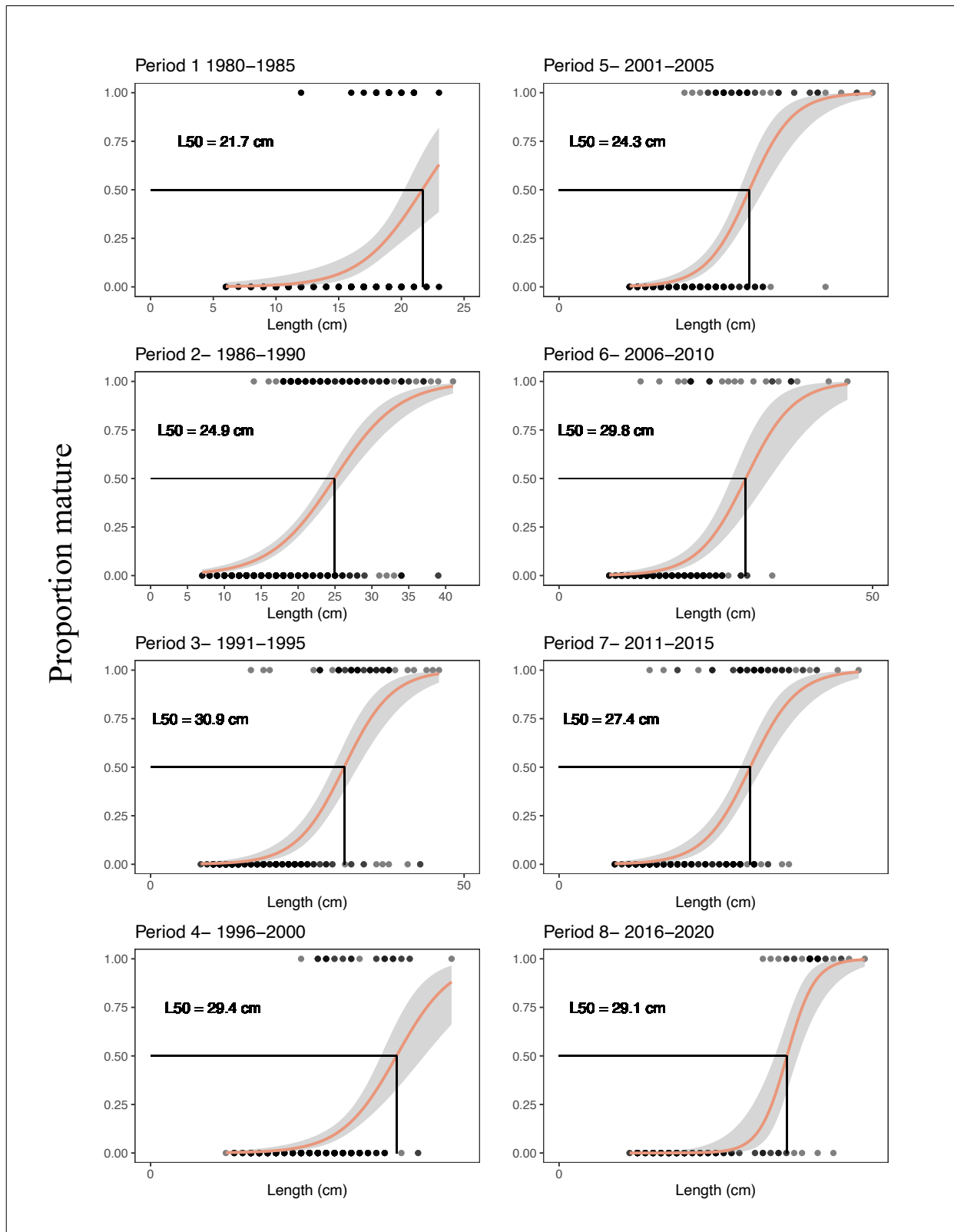
**Fig. S4** Comparison of the growth curves based on the two different growth models; the von Bertalanffy growth model (VBGM) (red line) and the biphasic growth model (blue line) for all period. The black open circles are the observed data.



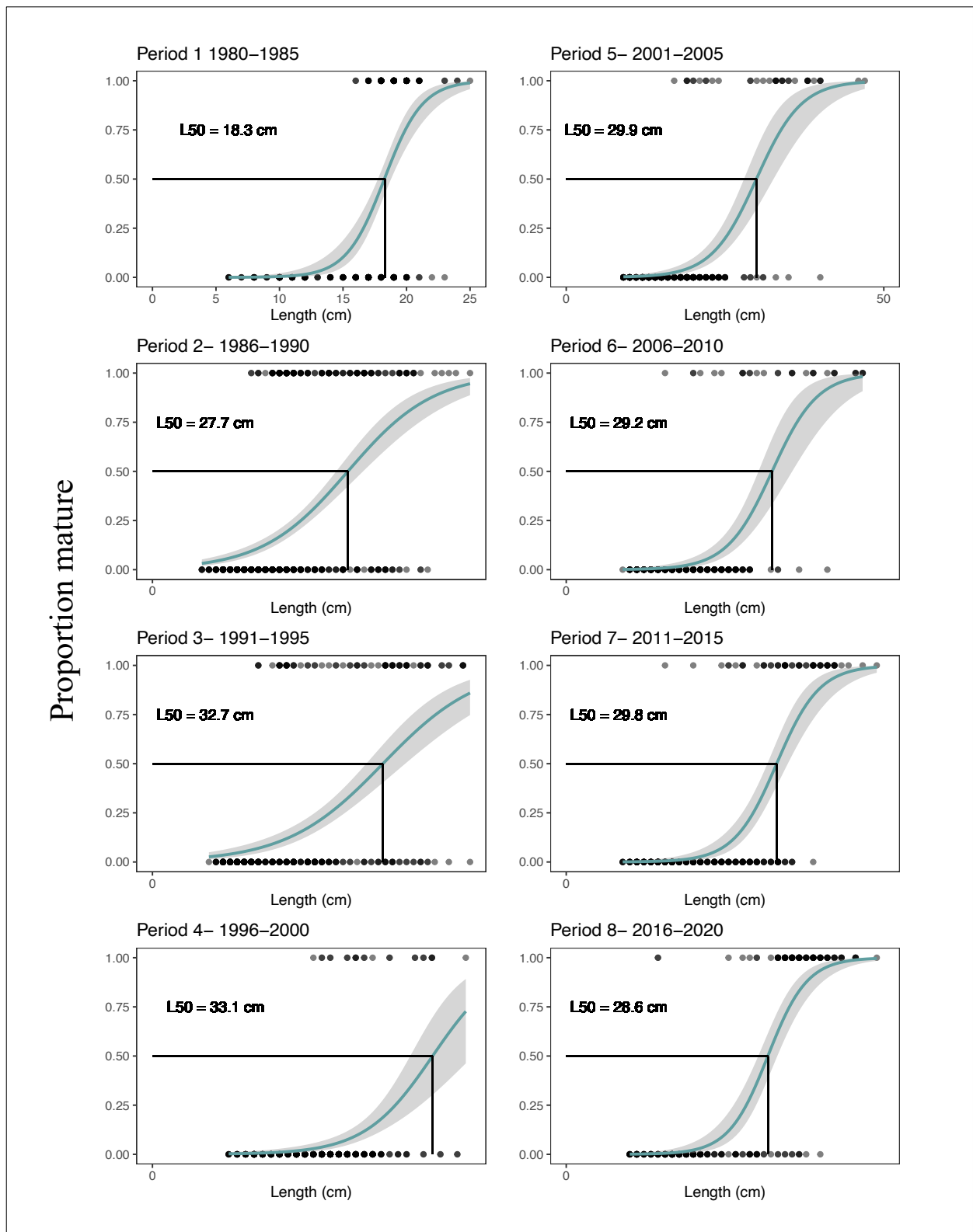
**Fig. S5** Pearson correlation test; testing the correlation between age-class and annual length increment



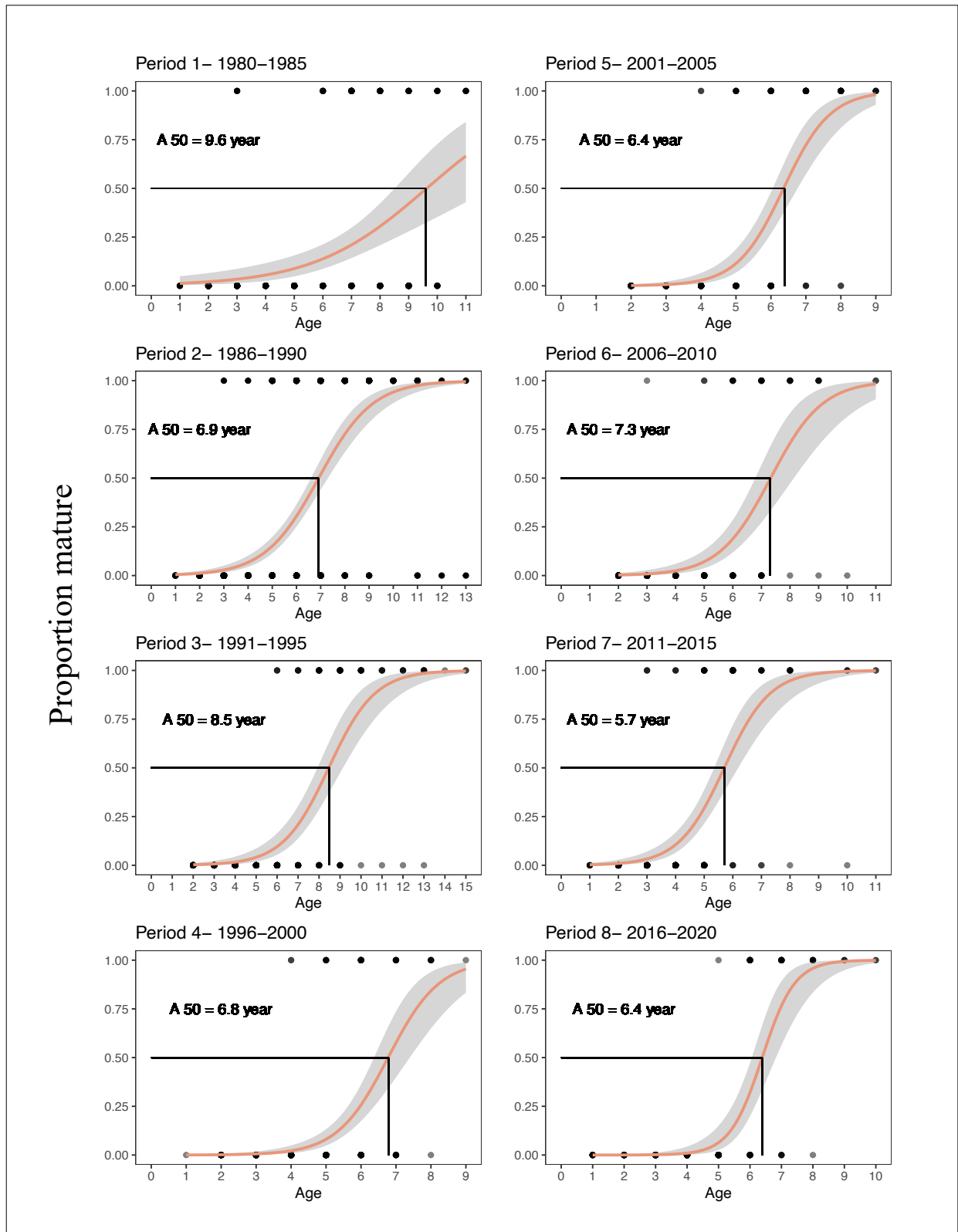
**Fig. S6** Linear regression analysis (1980-2020): Illustrating the relationship between **A)** specific growth rate (SGR) and mean annual temperature (1. August to 31. July the subsequent year) **B)** SGR and mean growth season temperature (1. August- 31. October same year) **C)** length increment and mean annual temperature **D)** length increment and mean summer temperature. The grey shaded area shows the 95% confidence interval along the line.



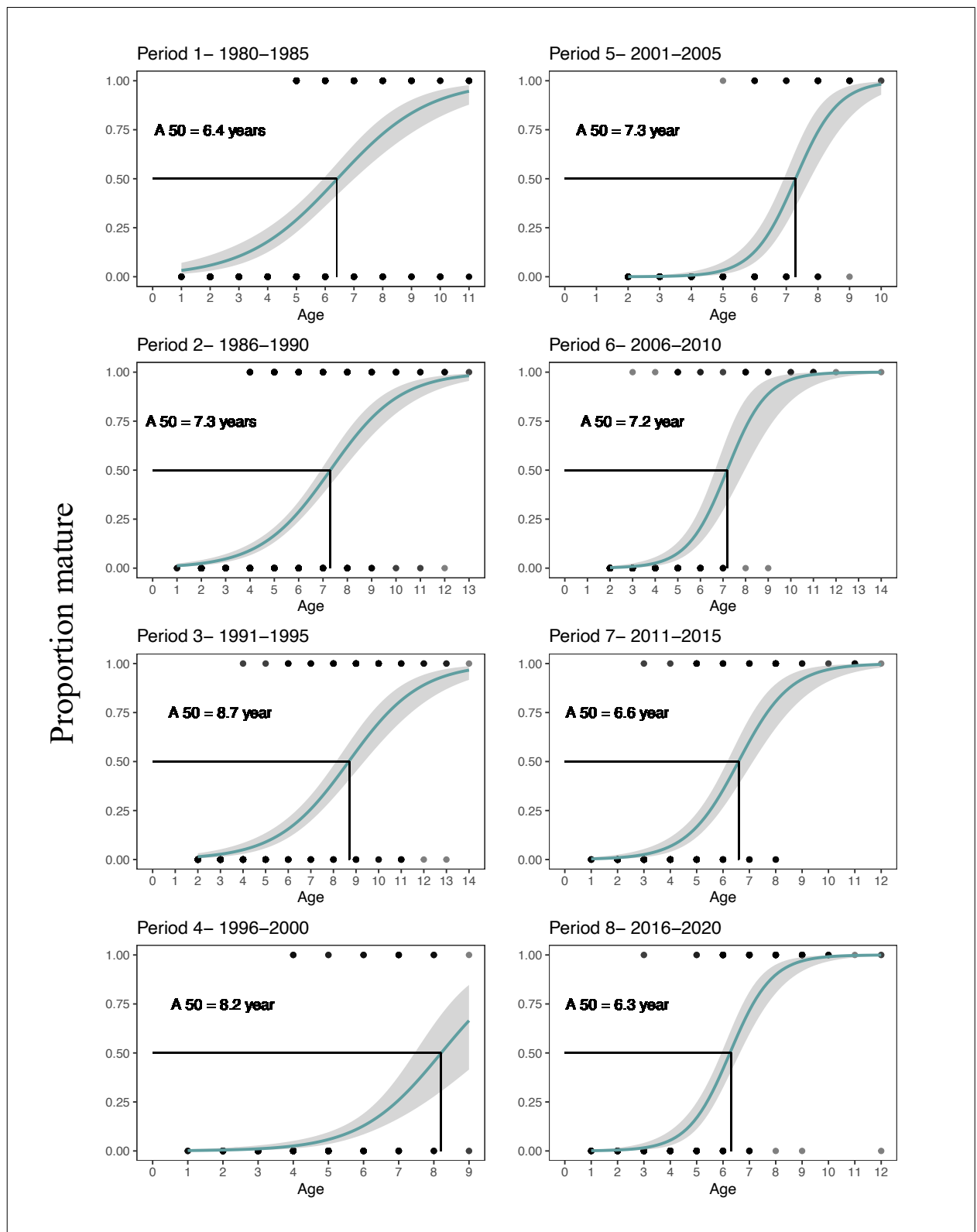
**Fig. S7** Maturity ogives for female Arctic charr in Takvatn for each period. Black dots are the observed data. The curve shows the fitted generalized linear regression to the data  $\pm$  95% confidence interval (grey area). The black lines marks the L<sub>50</sub> value for each period.



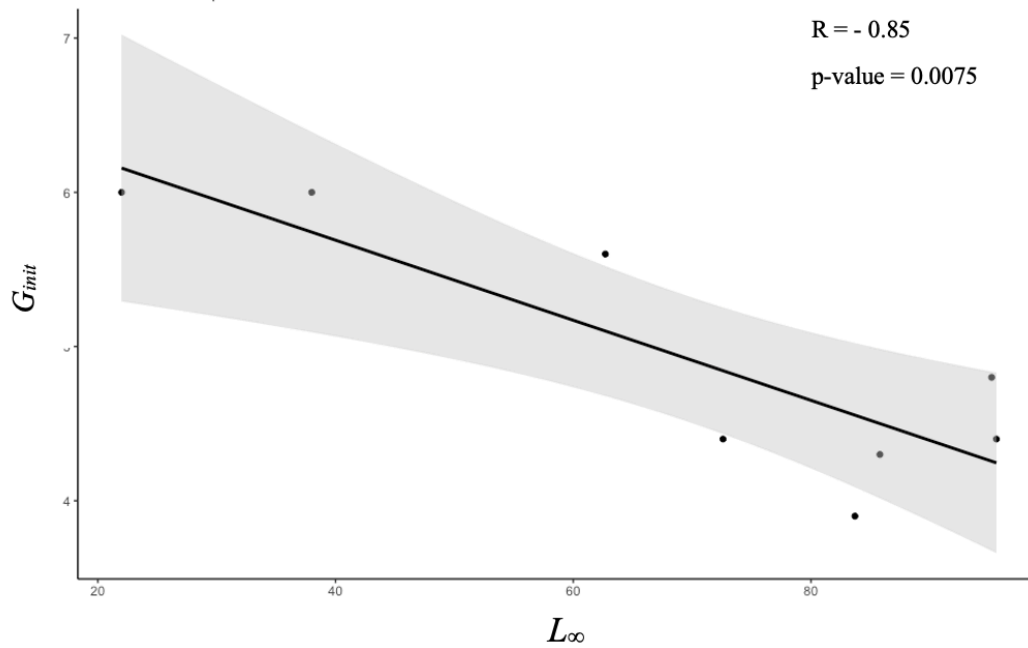
**Fig. S8** Maturity ogives for male Arctic charr in Takvatn for each period. Black dots are the observed data. The curve shows the fitted generalized linear regression to the data  $\pm$  95% confidence interval (grey area). The black lines marks the L<sub>50</sub> value for each period.



**Fig. S9** Maturity ogives for female Arctic charr in Takvatn for each period. Black dots are the observed data. The curve shows the fitted generalized linear regression to the data  $\pm$  95% confidence interval (grey area). The black lines marks the A<sub>50</sub> value for each period.



**Fig. S10** Maturity ogives for male Arctic charr in Takvatn for each period. Black dots are the observed data. The curve shows the fitted generalized linear regression to the data  $\pm$  95% confidence interval (grey area). The black lines marks the  $A_{50}$  value for each period.



**Fig. S11** Pearson correlation test; testing the correlation between  $L_\infty$  and  $G_{init}$ . The Pearson correlation coefficient  $R$  measures the strength and direction of the linear relationship between two variables, which goes from -1 to 0, where 1 indicates a perfect negative linear correlation, +1 indicates a perfect positive linear correlation, and 0 indicates no linear correlation.

