



UiT The Arctic University of Norway

Faculty of Biosciences, Fisheries and Economics

Department of Arctic and Marine Biology

Growth and Maturation of a Subarctic Fish Community Under a Changing Climate

Atle Johannes Hætta Stangeland

BIO-3950 Master's thesis in Biology June 2021



Picture: N rve Stubbraaten Johansen

Acknowledgments

I want to give a special thanks to my all-knowing supervisor Rune Knudsen, who has given me valuable wisdom of fish, feedback on my work, and helped with the progress of planning and structuring the master's thesis. Thanks to my co-supervisors Karl-Øystein Gjelland at NINA for fieldwork experience and statistical help, and Aslak Smalås at UiT for help with statistical analyses, data interpretation and a lot of valuable feedback.

Big thanks to Runar Kjær at UiT for moral support, feedback and for spending his valuable time answering a massive amount of emails. A lot of thanks to Per-Arne Amundsen who voluntarily joined the team and has given me valuable feedback and knowledge. I could never have done this without you all!

In this project I got to be part of a fieldwork with great and skillful people from Norsk Institutt for Naturforskning (NINA), Narve and my co-supervisor Karl-Øystein. Lille Rostavatn offered a beautiful scenery the two days we were there. I learned a lot, and got a lot of field-experience.

Cesilie at The University of Tromsø (UiT) taught me how to read otoliths, and together with my fellow student Adrian, we drank a lot of coffee while we age-determined all the fish from the fieldwork-sampling of 2020. Also, a big thanks to NINA – Tromsø for providing me with an office and laboratory.

I also want to thank the Freshwater Ecology group at UiT for two fantastic years of interesting courses, both in the classroom and field. Thanks to my fellow students Sonja, Vegar and Eivind for two remarkable years at UiT.

Thanks to Biret Merete for proofreading “čeahkkáigeassu”. Thanks to my family, and especially my sister, Aili Biriita, for her feedback and criticism of my thesis, and Andrea for her knowledge of English and support during long nights of writing.

At last I want to thank all the fish that no longer live in Lille Rostavatn, as they voluntarily swam into the gillnets to support this thesis.

Čoahkkáigeassu

Jávriid liegganeapmi, dálkkádaga riev dama dihte, sáhtta váikkuhit sáivačáhceguliid eallinvuohke-strategiijaide, erenoamážit davvi jávriin. Guollešlájaid eallinvuohke-strategiijat govvidit birrasa gos guolit ellet, ja dálkkádaga liegganeapmi sáhtta váikkuhit dasa makkár eallinvuohke-strategiijat leat ovdamunnin šaddamii ja reproduseremii.

Dás mun guorahalan movt guliid eallinvuohke-strategiijat sáhttet rievdat go dálkkádat lieggana, Davvi-Norgga jávris. Guhkkodat, ahki ja guliid rávisvuohta, golmma áigodaga bivddus guoktelogigolmma jagi áigodagas, adnojuvvojit modelleret ja buohtastahttit rievdadusaid guovtti eallinvuohke-strategiijas: ahtanuššan ja ahki-ja-sturrodat go guolit rávásmuvvet.

Guolit mat leat hávjánan galbmačáhcai, nugo rávdu (*Salvelinus alpinus*) ja njáhká (*Lota lota*), leat vátnon iskkadeami áigodagas, seammás leat guolit mat leat hávjánan lieggasit čáhcai, nugo dápmot (*Salmo trutta*) ja hárru (*Thymallus thymallus*), lassánan jávris. Seamma áigodagas lea jávri jahkásaš gaskamearalaš temperatuvra lassánan ovttain grádain.

Ahtanuššan paramehterat, L_∞ ja G_i , leaba modellerejuvvon muddejuvvon von Bertalanffy modeallain. G_i -paramehter lassánii buot guollešlájain, earret rávdus, ja L_∞ lassánii buot guollešlájain earret njágas, iskkadeami áigodagas. Dát gávdnosat sáhttet čujuhit ahte dálkkádaga liegganeapmi lea guliide muhtin muddui ovdamunnin. Sihke guolit mat leat hávjánan galbmačáhcai ja guolit mat leat hávjánan lieggasit čáhcai leat nuorabut ja oaneheappot go rávásmuvvet, mii orru leamen negatiiva váikkuhus badjánan temperatuvrra dihte.

Dálkkádaga liegganeami váikkuhusaid guliid eallinvuohke-strategiijaide lea váttis guorahallat danin go leat olu fáktorat mat váikkuhit guliide. Leat máŋga guollešlájaid mat čuhcet guhtet guoibmáseaset dán jávris gos leat vel máŋggadáfot eallinbirrasat. Čázi temperatuvrra badjáneapmi orru váikkuheame guliid eallinvuohke-strategiijaide máŋga dáfus.

Abstract

Increasing water temperatures from novel climate change may alter freshwater fish life history strategies, especially those of fish populations in northern latitudes. Fish species life history strategies are reflected by their environments and increasing water temperature may alter the most favorable strategies considering growth and reproductive patterns.

In this study, life history traits of a fish community will be investigated to reveal any supposable climate change effects on life history strategies of a subarctic lake in northern Norway. Length, age, and maturity data from three periods of sampling over a 23-year period is used to model and compare changes over time of two life history traits: growth and age-and-size at maturation.

The current lake has experienced a community-shift, with decreased relative contribution of the cold-water adapted species Arctic charr (*Salvelinus alpinus*) and burbot (*Lota lota*) and a corresponding increase of the cool-water adapted species brown trout (*Salmo trutta*) and grayling (*Thymallus thymallus*). At the same time, there has been a mean annual water temperature increase of 1 degree.

The growth parameters, L_{∞} and G_i , are modelled with a modified von Bertalanffy equation. There was an increase in G_i for all species, except for Arctic charr, and an increase in L_{∞} for all species, except for the burbot during the period of study. These findings suggest that the fish species benefit somewhat of climate change, to this day. The calculated maturation patterns reveal decreased A_{50} and L_{50} for both cold-water adapted species, which could indicate a negative temperature effect.

The effects of climate change on life history strategies are difficult to distinguish. As there are many factors affecting life history traits in a complex fish community in a heteromorphic lake. Climate change seems to affect life history traits both directly and indirectly through various mechanisms.

Table of contents:

List of figures:.....	v
List of tables:	v
1 Introduction.....	1
2 Materials and Methods	5
2.1 Study Area and Temperature Data	5
2.2 Field Sampling.....	6
2.3 Laboratory Analysis - Age Determination	7
2.4 Statistical Analysis	8
2.4.1 Growth.....	9
2.4.2 Age and Size at Maturity.....	10
3 Results.....	11
3.1 Age and length structure.....	11
3.2 Growth.....	13
3.3 Age-and-size at maturity	15
4 Discussion.....	16
4.1 Climate Change Effect on Growth	17
4.2 Comparison of Growth of Cold- and Cool-Water Adapted fish	21
4.3 Maturation Strategies in a Changing Climate.....	22
5 Concluding remarks.....	25
References.....	27
Appendix.....	33

List of figures:

Figure 2.1: Study Location.....	5
Figure 3.1: Sample Overview - Length Structure	11
Figure 3.2: Sample Overview - Age Structure	12
Figure 3.3. Von Bertalanffy - Model Parameters	13
Figure 3.4: Age-and-Sie at 50% Maturation	15

List of tables:

Table 2.1: Sample Sizes	7
Table 3.1: Mean and Median Length of Arctic Charr	14

1 Introduction

Life history strategies of freshwater fish highly reflect the conditions of the environment they occupy (Hutchings, 2002). With the ongoing global warming, and especially the warming of northern and subarctic lake systems (O'Reilly *et al.*, 2015; EEA, 2016), there will be, and are already shown prominent impacts on freshwater environments (Woodward *et al.*, 2010; Goldman *et al.*, 2012; Rolls *et al.*, 2017). For example, climate change is shown to negatively affect the mean body size of ectotherms globally (Gardner *et al.*, 2011). The growth of fish, and especially age-and-size at maturity, are key life history traits for describing individuals' fitness in various environments, as different life history strategies are beneficial only under given conditions (Hutchings, 2002). As most fish are ectothermic, their metabolism and performance is closely related to the temperature of their environment (Jeppesen *et al.*, 2012), and climate change is shown to have great effects on northern fish populations and their life history traits, such as growth and reproduction strategies (Myers *et al.*, 2017; Rolls *et al.*, 2017). I will here study the growth and age-and-size at maturity of a subarctic freshwater fish community to reveal potential effects of climate change on the fish community.

Life history theory explains organisms' general life cycle, considering the allocation of resources for growth and reproduction. In life history theory there are several traits that evolutionary forces act upon, for example: brood size, age at maturity, growth pattern, birth size and lifespan (Stearns, 1992). Organisms' fitness is a feature of these life history traits, where different combinations of life history traits will have diverse effects on organisms' fitness and thereby have an effect on reproductive success (Stearns, 1976). Natural selection favors the species that are most adapted to their environment (Watt, 2001). These adaptations are reflected in organisms' life history strategies, where some strategies are more favorable than others in given environments. Different strategies are determined by genetics with a plasticity to environmental gradients which allows species to tolerate a range of environmental factors (Hutchings, 2002).

There is a tradeoff between somatic growth and reproduction (Stearns, 1992), and therefore interesting to investigate the relationship between growth and maturation in a changing environment, with some organisms maturing early at a small size, while others delay maturation until they are larger (Hutchings, 2002). Delayed maturation is generally beneficial as fecundity increases with body size (Stearns, 1992). However, if the mortality is high, early maturation is favorable as individuals that mature early have higher chances of reproducing and thereby acquire higher fitness (Fišer, 2019).

In a changing environment, the genotypes and the accompanying life history traits that are most beneficial for reproductive success, will be evolutionary favored and thus increase in frequency within a population (Hutchings, 2002). There are variations in life histories between fish species, populations and even among fish within the same population (Hutchings, 2002), which reflect the great plasticity to environmental gradients. However, novel climate changes are rapidly altering freshwater environments and species might have problems evolving fast enough to keep up (Berteaux *et al.*, 2004).

Reist *et al.* (2006) lists three possible outcomes of organisms facing rapid temperature increases due to climate change: local population extinction induced by thermal stress, northwards range shift, and rapid natural selection to tolerate the altered habitat. Freshwater communities are expected to have a pronounced response to climate changes as they possess a poorer ability to disperse compared to e.g. terrestrial organisms, as their habitats are more spatially isolated (Heino *et al.*, 2009). At the same time, the abundance of cold-water fish is decreasing, while cool- and warm-water fish seem to benefit from novel climate change (Myers *et al.*, 2017). Global warming is more critical for the survival of cold-water species, as they lack areas to expand to northwards, while cool- and warm-water species can expand their range northwards as the temperature increases (Chu *et al.*, 2005). In large, deep lakes, cold-water adapted fish populations with no possibility of range shift, may display habitat shifts to persist. For example, high surface lake temperatures during summer stratification can induce a habitat-shift of cold-water fish species to use the colder deep waters as a thermal refugia (Elliott & Elliott, 2010; Myers *et al.*, 2017).

A synthesis by Rolls *et al.* (2017) has collected information of subarctic freshwater fish response to climate change and the effect on the fishes life history strategies. The synthesis describes a general decrease in growth and age-and-size at maturity for fish populations due to

thermal stress factors and a size dependent temperature-induced metabolism cost. However, if the water temperature is within fishes' optimal temperature of growth and there is sufficient food availability, smaller individuals seem to benefit from warmer water, regarding growth rate (Elliott & Elliott, 2010) and larger individuals fish are shown to have a lower optimal temperature of growth than smaller individuals (Morita *et al.*, 2010). Warmer water may also increase the competition pressure on cold-water adapted species from cool-water adapted species. Warmer-water adapted species benefit from increasing temperatures which can amplify their reproduction output and invasion success and thereby increase their competitive impact (Rolls *et al.*, 2017). Thermal stress and increasing competition and predation from cool-water adapted species, may lead to increased mortality of the cold-water adapted fish species. Since high mortality is shown to reduce both age-and-size at maturity for cold-water adapted fish species (Perrin & Rubin, 1990; Fišer, 2019) it is likely to expect earlier maturation and at smaller sizes for cold-water adapted species.

In this semi-long-term study, the life history traits of a subarctic lacustrine fish community in northern Norway, has been investigated to see if climate change has affected the populations growth and maturation traits. There are six fish species in the studied lake; Arctic charr (*Salvelinus alpinus*), burbot (*Lota lota*), brown trout (*Salmo trutta*), grayling (*Thymallus thymallus*), minnow (*Phoxinus phoxinus*) and salmon parr (*Salmo salar*), of which the first four species are included in this study, with a special emphasis on the cold-water adapted Arctic charr and burbot. During the 21-year period from 1997 to 2018 the mean growth season (June-November) water temperature has increased about 1 °C (Dalbak, 2020). At the same time, there has been a general decline in the abundance of cold-water adapted arctic charr and burbot, while the abundance of cool-water adapted grayling and brown trout has increased (Dalbak, 2020), although the total fish density has not changed. The diet of the species has been stable with an intermediate diet overlap between the species, indicating a stable habitat and resource segregation throughout the time-period (Dalbak, 2020).

Based on the available information of climate change impacts on cold-water adapted fish species, I here address the effect of climate change on life history traits of a lacustrine, subarctic fish community based on the following hypotheses:

1. Increasing water temperatures lead to increased initial maximum growth rate (G_i) of the studied fish species, while the maximum asymptotic length (L_∞) will decrease for cold-water adapted species and increase for cool-water adapted species.
2. Cool-water adapted fish species grow faster than cold-water adapted fish species with increasing temperatures.
3. Increasing temperatures result in reduced age-and-size at 50% maturity for the cold-water adapted species.

2 Materials and Methods

2.1 Study Area and Temperature Data

The study lake, Lille Rostavatn, is located within the subarctic climate zone in northern Norway (Figure 2.1). Subarctic climate regions are mostly found between 50° and 70°N. These regions have short summers and long winters, and are known for large seasonal temperature variations (Stepanova, 1958). The growth season is relatively short and is modelled to be between 91 and 120 days (Hanssen-Bauer *et al.*, 2009). However, at the latitude of lake Lille Rostavatn, the midnight sun occurs for two months between May 20th and July 22nd, which partly may compensate for the short growth season (Wetzel, 2001). The lake is ice-covered 6-7 months between November-/December and May/June (Knudsen *et al.*, 2010; Eloranta *et al.*, 2013).

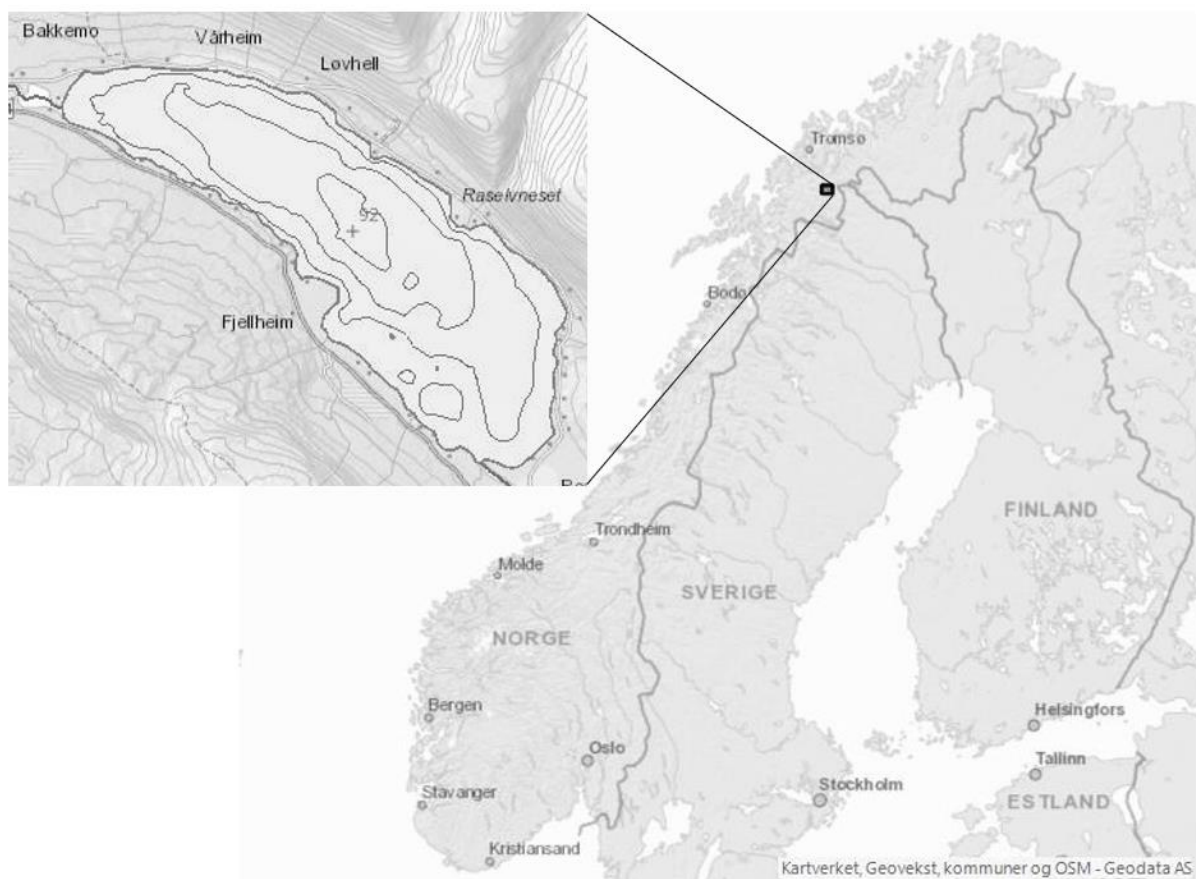


Figure 2.1: Map of Lille Rostavatn with 10 m, 40 m, and 80 m depth curves, and the lake's location in Norway (69°0'N, 19°6'E, 102 m a.s.l.) (NVE, 2021).

Lake Lille Rostavan is located in the Målselv watercourse in Troms og Finnmark county, Northern Norway. The lake is oligotrophic and dimictic with a surface area of 13.3 km² and a maximum depth of 92 meters (NVE, 2021). The lake has well developed littoral, pelagic and profundal habitats, where the littoral zone (<10 meter) compose about 30% of the total surface area (NVE, 2021). The fish community in the lake consist of six species: Arctic charr, burbot, brown trout, grayling, minnow, and salmon parr. The lake has an estimated retention time (the mean time water spends in the lake) of 0.7 years (NVE, 2021). The basin bed in Lille Rostavatn is covered in sand and stone with widely scattered emergent macrophytes. Pine dominates the forest on the west side of the lake, while birch dominates the east-side forest along with some farming areas.

There is no available temperature data from Lille Rostavatn itself. The assumption of increased water temperature in Lille Rostavatn is based upon temperature data collected from two locations in the outlet river of Lille Rostavatn, about 40 km downstream the lake, from 1991 to 2018 by Norges vassdrags- og energidirektorat (NVE). From the available data, mean water temperature is calculated for three annual seasons: growth season (June-November), summer (June-September) and fall (September-November), by Dalbak (2020). There was found a significant increase of the mean water temperature of all seasons from 1991 to 2018 (Dalbak, 2020). There was also found a significant increase of the mean water temperature during the growth season from 1997 to 2018, from 6 to 7.2 °C, respectively (Dalbak, 2020).

2.2 Field Sampling

The fish samples were collected by fishing with multi-mesh gillnets in 1997, 2010, 2016, 2018 and 2020 (Table 2.1). The gillnets were placed in the water in the evening and retrieved in the morning, giving each net approximately 12 hours of fishing per night. The aim of the fishing was to assemble a representative overview of the habitat distribution and size composition of the present fish populations in the lake. Therefore, multi-mesh gillnets were distributed through the whole lake area and across the three main habitats: the littoral, pelagic, and profundal zone. There were used several types of gillnets, both standard size (SS) and multi-mesh gillnets; NORDIC, FGO and BGO nets. The NORDIC net is a benthic multi-mesh gill net measuring 30 m long and 1.5 m deep. The NORDIC net is made up of 12 randomly distributed sectors (2.5 m long x 1.5 m deep) of different mesh sizes, ranging from 5 to 55 mm knot-to-knot (Appelberg

et al., 1995). The second net type is called FGO net, which is a multi-mesh floating gillnet used in the pelagic zone. It measures 40 m long and 6-meter-deep with 8 randomly distributed sectors (5 m long x 6 m deep) of different mesh-sizes, which measure from 10 to 45 mm knot-to-knot. The BGO nets are 40 m long and 1,5 m deep benthic multi-mesh gillnets, with mesh sizes ranging from 10 to 45 mm knot-to-knot.

All fish were measured in mm (total length for burbot and fork length for the other species) and weighted in grams. The sex and maturity status were determined. The maturity status was determined as either immature or mature. Fish that do not spawn current year, but have spawned previously, were determined as mature.

Table 2.1: Sampling overview from Lille Rostavatn from August 1997, 2010, 2016, 2018 and 2020, in addition to October samples from 1997 and 2018. Presented with number of Arctic charr, brown trout, grayling, and burbot per sampling, and percentage of the total number of fish per sampling in parentheses.

Period	Month	No. of fish	No. of Arctic charr (%)	No. of brown trout (%)	No. of grayling (%)	No. of burbot (%)
1997	August	315	227 (72)	20 (6)	2 (1)	66 (21)
1997	October	334	260 (78)	8 (2)	4 (1)	62 (19)
2010	August	211	122 (59)	35 (17)	45 (21)	9 (4)
2016	August	165	87 (53)	35 (21)	36 (22)	7 (4)
2018	August	282	136 (48)	41 (15)	87 (31)	18 (6)
2018	October	262	114 (44)	46 (18)	34 (13)	68 (26)
2020	August	226	112 (50)	25 (11)	67 (30)	22 (10)

2.3 Laboratory Analysis - Age Determination

The fish age determination was done by analyzing the sagittal otoliths located in the inner ear of the fish. The otoliths are made out of several concentric zones, which appear either as hyaline or opaque depending on the amount of organic carbon in the zones (Agger *et al.*, 1974; Mendoza, 2006). The otolith zones reflect the different growth rate of fish during summer and winter, where temperature affects the metabolism and available food (Agger *et al.*, 1974). Therefore, the opaque zones are formed during summer when the individual growth is good, while the hyaline zones are formed during winter when the growth is poor (Mendoza, 2006).

The sagittal otoliths were collected by removing the top of the skull of the fish, with a scalpel, to expose the brain. The otoliths are located on each side beneath the brain and were collected with tweezers. The otoliths were marked and stored in small plastic sample tubes with a 96% ethanol liquid until they were read. The fish age was determined by surface readings of the otoliths with a stereo microscope. The otoliths were soaked in glycerol and placed on a dark surface with direct light from above, when being read, to better distinguish the otolith ring structures. The hyaline zones were counted to determine the fish's age. Since the Arctic charr and brown trout hatch during spring season and their actual age is therefore the count of hyaline zones plus the months between hatching and sampling time as the opaque zone for the current year has already formed.

2.4 Statistical Analysis

The sampled data is separated as three sample periods: The August and October samplings from 1997 are combined as the first period, the 2010 sampling is the second period and the 2016, 2018 and 2020 samples are combined as the third period. There were generally small sample sizes of all fish species in 2010 due to lower sampling effort compared to the other sampling periods. A previous study of the lake shows low densities of brown trout and grayling in 1997 (Dalbak, 2020), which reflect the low sample sizes of these species in 1997. The species with few sampled individuals in 1997 and 2010 are combined as a 1997-2010 sample period for the growth and maturation analyses.

All individuals included in the statistical analyses are length measured, while not all individuals are age or maturity determined. Therefore, the number of individuals differ for each analysis. For age-and-length structure, only individuals sampled with multi-mesh gillnets are presented as standard-size gillnets has a size-selective catchability and will not give a representative overview of the age-and-length structure. Samples of both standard-size and multi-mesh gillnets are included for growth and maturity analyses.

As the smallest gillnet mesh-size which is mutual for all years of sampling is 10 mm, all fish individuals below 9 cm are excluded from the statistical analysis (See: Finstad *et al.*, 2000; Borgstrøm *et al.*, 2019).

2.4.1 Growth

A modified version of the von Bertalanffy growth equation was used to model the somatic growth of the fish. The von Bertalanffy model (VBGM) is well-known and widely used (Lester *et al.*, 2004; Katsanevakis & Maravelias, 2008). The von Bertalanffy growth equation describes the growth of fish with an asymptotic curve. The asymptotic growth curve assumes a reduction in somatic growth of adult individuals as there is a tradeoff between energy allocated to growth and reproduction (Lester *et al.*, 2004). Therefore, the asymptotic curve is good at describing somatic growth of mature individuals where it is assumed that energy is allocated to maintenance and reproduction, at the cost of growth. The somatic growth curve is less suitable at describing premature individual growth, as their somatic growth, in many cases, is close to linear (Lester *et al.*, 2004).

In the von Bertalanffy growth equation:

$$L(t) = L_{\infty}(1 - e^{-k(t-t_0)}) \quad (1)$$

the $L(t)$ is the length at age t . The modelled parameter L_{∞} is the mean asymptotic length as age approaches infinity, k (Brody's growth coefficient) is the growth coefficient which describes the rate the length is approaching L_{∞} , and t_0 is the age at which the length is zero. Since t_0 is the age where fish length is zero, it will often be a negative (Lester *et al.*, 2004) number and do not provide much biological importance.

The modified von Bertalanffy growth equation (Mooij *et al.*, 1999) was used to model fish growth:

$$L(t) = L_{\infty} - (L_{\infty} - L_0) \cdot e^{-(G_i L_{\infty}^{-1})t} \quad (2)$$

In this model the G_i is the initial maximum growth rate, which occurs early in life. The G_i is easier to interpret, compared to k , as it has a mathematical unit of $length \cdot age^{-1}$. In the von Bertalanffy model (1), the growth rate, k , is highly dependent on L_{∞} as the k describes the rate that fish growth is approaching L_{∞} . In model (2), G_i is less dependent on L_{∞} which provides a good comparison of the initial maximum growth rate changes over time. The L_0 is the length where the fish age is zero (yr), which is a more biologically understandable parameter than the t_0 in model (1). G_i and L_{∞} were estimated with non-linear least-square regression based on mean length-at-age data. The L_0 was fixed to a suitable length for each fish species at age zero, based on former studies of length at age zero: 20 mm for Arctic charr and brown trout

(Wallace & Aasjord, 1984; Klemetsen *et al.*, 2003), 14 mm for grayling (Thomassen *et al.*, 2011), and 3 mm for burbot (Ghan, 1990; Ryder & Pesendorfer, 1992; Harzevili *et al.*, 2004). With a fixed L_0 there will be less parameters for the model to estimate, which gives more robust estimations of the remaining parameters.

To further investigate differences in somatic growth over time, the mean and median length per age group were calculated for Arctic charr. The non-parametric Wilkison rank-sum-test was used to test differences over time, of the median length for each age-class.

2.4.2 Age and Size at Maturity

The age, A_{50} , and size, L_{50} , where 50% of the population is mature were calculated to investigate any changes over time. The length at which 50% of the population is mature is one of the most common methods of investigating sexual maturity (Tsikliras *et al.*, 2014). Logistic regression with individuals as immature or mature as binomial predictor variables were used to determine A_{50} and L_{50} . The probability (p) of maturation is described by the logistic function:

$$p(x) = \frac{e^{(\beta_0 + \beta_1 x)}}{1 + e^{(\beta_0 + \beta_1 x)}} \quad (3)$$

Where the coefficients β_0 is the intercept and β_1 is the slope of the sigmoid curve that describes the probability of maturation at a given age or length (x).

To compare the age and length at which the fish populations mature during the study, the age (A_{50}) or length (L_{50}) where 50% of the population have reached sexual maturity were calculated by using the coefficients β_0 and β_1 :

$$A_{50} \text{ or } L_{50} = -\frac{\beta_0}{\beta_1} \quad (4)$$

3 Results

3.1 Age and length structure

The length structure of most fish populations varied between sampling periods (Figure 3.1). There was a notable increase in the frequency of larger individuals for all species, except for burbot, in 2016–2020 compared to 1997 and 2010. For Arctic charr, there were high frequencies of the smallest length groups in all years, especially in 2016–2020. In 1997, the highest frequencies of individuals were in the medium-sized length groups. In 2010, the Arctic charr had a bimodal length distribution with peaks for the smallest and medium-sized length groups. There were few individuals of Arctic charr above 29 cm in both 1997 and 2010. The 2016–2020 samples of arctic charr had a wide length distribution, with relatively low frequencies of medium-sized individuals. The highest proportion of mature individuals of Arctic charr were amongst the medium-size groups in 1997. In 2016–2020, most of the largest charr were mature, while few individuals of Arctic charr were mature in 2010.

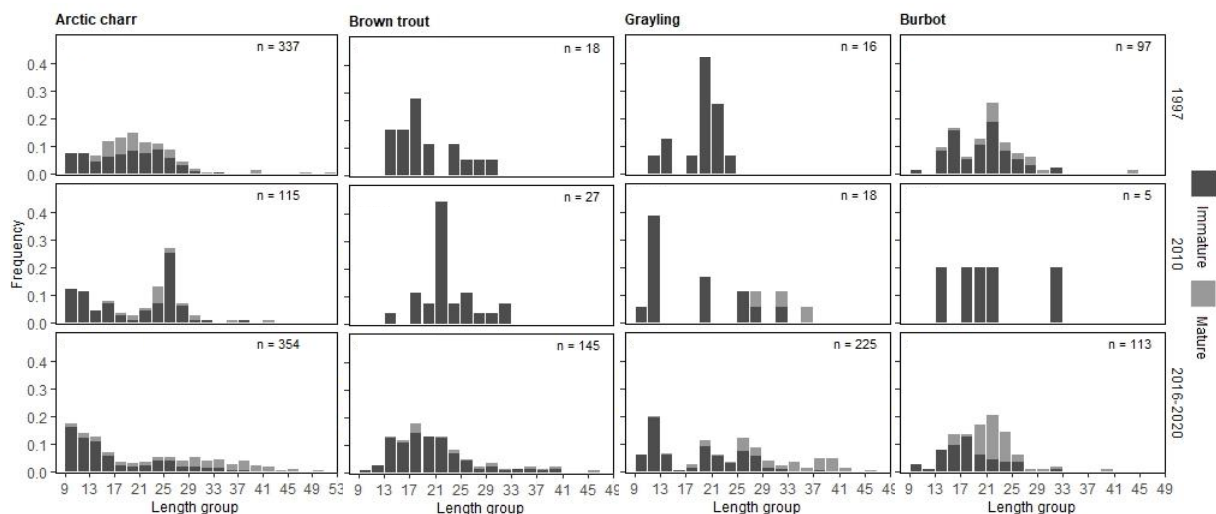


Figure 3.1: Frequency of length structure of 2 cm length groups of Arctic charr, brown trout, grayling, and burbot per sampled year (1997, 2010 and 2016–2020) split up in sexual mature (light shaded bars) and immature (dark shaded bars) individuals, with number of individuals (n) per sampled year and species.

There was no large change in the length distribution of burbot between sampling periods, but the sampling size was low in 2010 and cannot be compared with the remaining years. There was a higher proportion of mature burbot in 2016–2020 compared to 1997.

Brown trout and grayling had wider length distributions in 2016–2020, with both smaller and larger individuals caught, than in the previous years. Small sampling sizes in 1997 and 2010 may influence the length distribution of brown trout and grayling. In 2016–2020, brown trout had high frequencies of medium-sized individuals, while grayling had a multimodal length distribution with peaks for small, medium, and large individuals. Most individuals of brown trout were immature for all length groups, and most graylings above 29 cm were mature in 2016–2020.

There was a slight increase in the frequency of older individuals of Arctic charr in 2016–2020 compared to 1997 and 2010 (Figure 3.2). Brown trout had a wider age distribution in 2016–2020, compared to earlier years, at which small sample sizes may influence the age distribution. Grayling had no comparable change in the age structure between years. Burbot had higher frequencies of young individuals in 2016–2020 compared to 1997, and small sample size in 2010 gives no room for comparison.

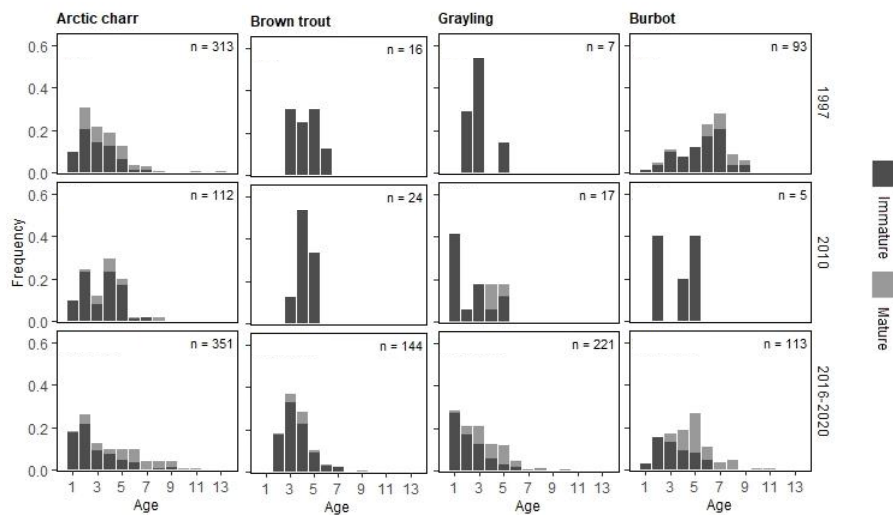


Figure 3.2: Age structure (frequency) of Arctic charr, brown trout, grayling and burbot per sampled year (1997, 2010 and 2016–2020) split up in sexual mature (light shaded bars) and immature (dark shaded bars) individuals, with number of individuals (n) per sampled year and species.

3.2 Growth

The growth parameters, L_∞ and G_i , modelled with the modified von Bertalanffy growth model (MVBGM) (2), varied throughout the study period (Figure 3.3). L_∞ increased for all species, except for burbot, which had a slight and insignificant decrease in L_∞ . Arctic charr had a significant increase in L_∞ , with non-overlapping 95% confidence intervals, from 1997 to 2016-2020. In 2010, the L_∞ of Arctic charr was intermediate compared to the first and last period, but with overlapping 95% confidence intervals (*CI*) with both of those periods. Grayling had a non-significant increase in L_∞ , from 1997-2010 to 2016-2020.

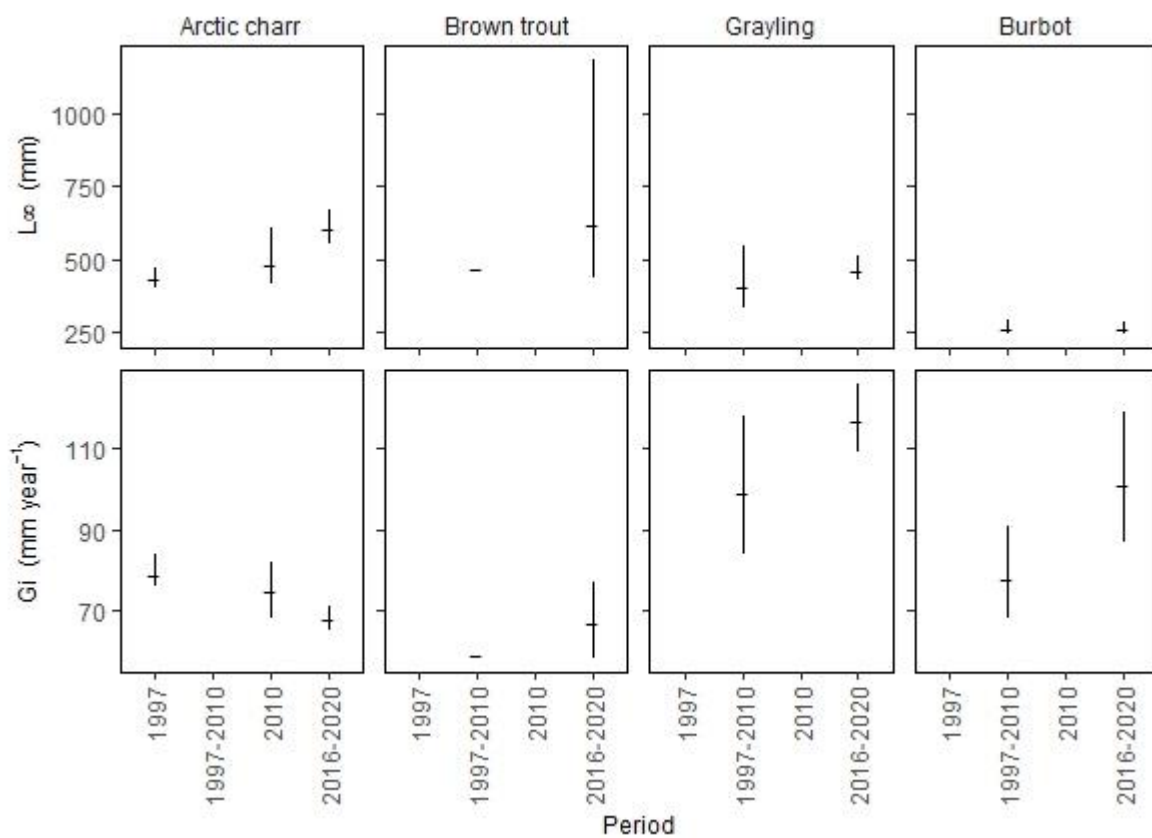


Figure 3.3. Modelled parameters, L_∞ (top panel) and G_i (bottom panel), of the modified version of von Bertalanffy growth model (2), for Arctic charr, brown trout, grayling, and burbot, based on length and age data per period. Error bars indicate parameters' 95% confidence interval. Error bars for brown trout for the 1997–2010 period is not included.

All species, except Arctic charr, had an increased initial maximum growth rate G_i , during the study period (Figure 3.3). Arctic charr had a significant decrease in G_i from 1997 to 2016-2020, with non-overlapping *CI*. The 2010 G_i of charr was intermediate compared to the first and last period, with overlapping *CI* with both of those periods. Burbot and Grayling had significantly

increased G_i from 1997-2010 to 2020-2016, with slightly overlapping CI . The confidence intervals of brown trout for the 1997-2010 period were not obtainable due to low sample sizes and large individual variations of length within age-groups and are therefore not presented. See Appendix D for visual presentation of growth curves. More detailed information of the growth model parameter values is available in Appendix E.

The growth of Arctic charr, regarding mean and median length at age, has changed significantly for two- to five-year-old individuals during the study period (Table 3.1). For one-year old Arctic charr there was no significant change in the median length ($p=0.678$). Two and three-year-old Arctic charr had a significantly lower median length in 2016–2020 compared to 1997 ($p<0.001$). Four and five-year-old individuals of Arctic charr had a significant higher median length in 2016–2020 compared to 1997 ($p=0.015$ and $p<0.001$).

Table 3.1: Mean and median fork length in mm, for Arctic charr in 1997 and 2016–2020, divided in age-classes (1–5 years). n is the number of individuals per age-class and sampling period. P-values for the Wilcoxon-rank-sum-test of difference in median fork length per age-class.

Species	Age (yr)	Period	No. of fish	Length (mm)		P-value
				Mean \pm SD	Median	
Arctic charr	1 ⁺	1997	49	102.4 \pm 13.0	98.0	0.6784
		2016–2020	64	103.4 \pm 13.0	99.0	
	2 ⁺	1997	138	159.3 \pm 26.5	156.5	<<0.0001
		2016–2020	92	130.9 \pm 16.8	129.5	
	3 ⁺	1997	114	196.7 \pm 19.1	197.0	<<0.0001
		2016–2020	43	168.3 \pm 28.4	168.0	
	4 ⁺	1997	87	226.9 \pm 23.5	234.5	0.01516
		2016–2020	35	239.4 \pm 32.5	240.0	
	5 ⁺	1997	56	246.1 \pm 22.2	253.0	<0.001
		2016–2020	34	277.7 \pm 42.8	265.0	

3.3 Age-and-size at maturity

There was an overall decrease in the estimated age and length (A_{50} and L_{50}) at which 50% of the fish populations were sexually mature for, Arctic charr, grayling, and burbot during the study period (Figure 3.4). A_{50} and L_{50} was unattainable for brown trout for the 1997–2010 period as only one mature individual was observed. For Arctic charr there was a large increase of both A_{50} and L_{50} from 1997 to 2010, before it dropped in 2016-2020, to a slightly lower value than in 1997. Burbot and grayling had a decrease in both A_{50} and L_{50} from 1997-2010 to 2016-2020. See Appendix F; G; for visual presentation of A_{50} and L_{50} fitted generalized linear regression curves. More detailed information of the growth model parameter values is available in Appendix H.

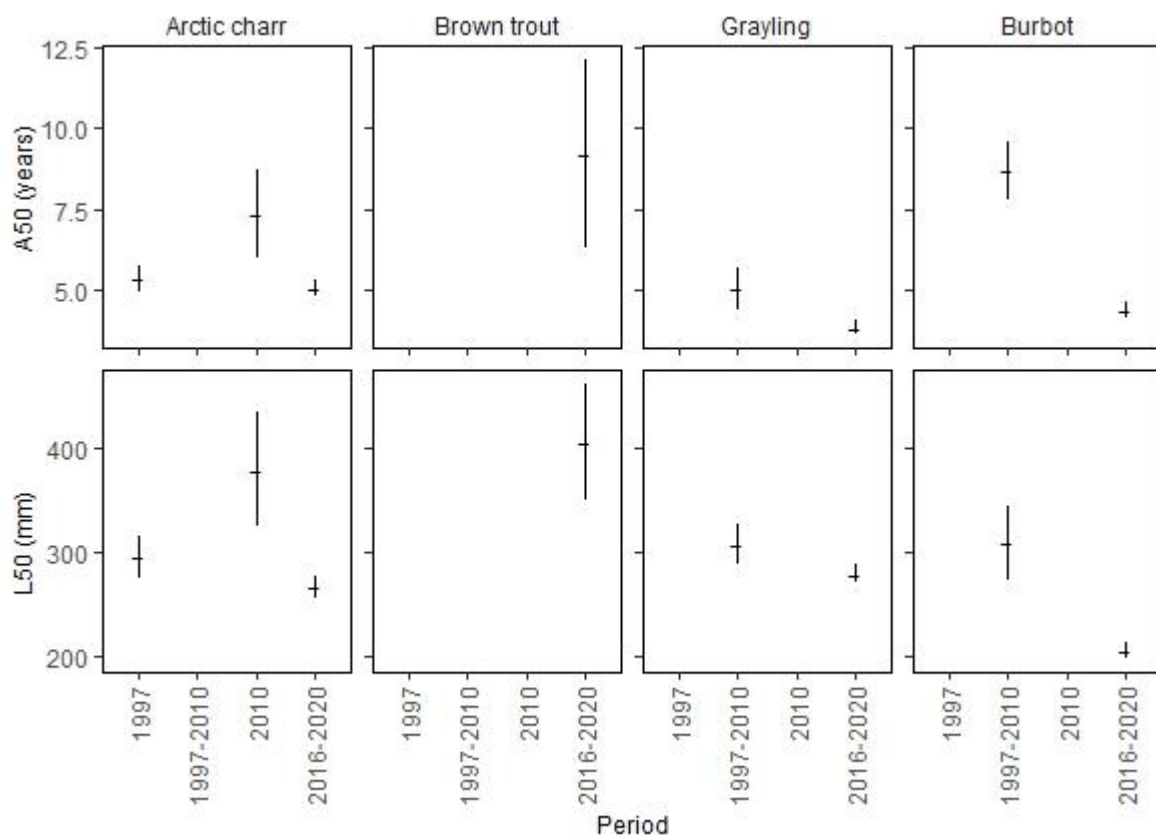


Figure 3.4: Age in years (top panel) and length in mm (bottom panel) where 50% of individuals are mature, for Arctic charr, brown trout, grayling, and burbot, per sampling period. Error bars indicate standard error.

4 Discussion

Three periods of sampling over a period of 23 years, from 1997 to 2020, have demonstrated changes in growth and maturation parameters of a lacustrine subarctic fish community. During the same period, there was a temperature increase of 1.2 °C, based on measurements in the lake's outlet-river from 1997 to 2018. It was also observed an increase in the relative proportion of cool-water adapted fish species in the lake, with a corresponding decrease in the proportion of cold-water adapted fish species (Dalbak, 2020).

The increased water temperature was expected to adversely affect the cold-water adapted fish species and benefit the cool-water adapted fish species of the lake, regarding growth and maturation patterns. The initial maximum growth rate (G_i) was expected to increase for all studied species, while the maximum asymptotic length (L_∞) was expected to decrease for cold- and increase for cool-water adapted species. The G_i increased for burbot, brown trout and grayling, in accordance with the hypothesis, in contrast to the decrease in G_i for Arctic charr. The L_∞ increased for both cool-water adapted species, in accordance with the hypothesis, while the L_∞ increased, unexpectedly, for Arctic charr, while burbot had a slight decrease in L_∞ , as hypothesized.

It was expected that the cool-water adapted species would grow faster than the cold-water adapted species as the mean growth-season temperature increased in Lille Rostavatn. However, brown trout had the lowest G_i of all species, throughout the whole period, while grayling had the highest G_i . The G_i of Arctic charr and burbot was intermediate compared to the cool-water adapted species in all years sampled, separately.

It was observed a decrease in age-and-size at maturity for both coldwater adapted species, and for one of the cool-water adapted species, grayling. Due to the lack of mature individuals of brown trout in the samples from 1997–2010, brown trout is only presented with A_{50} and L_{50} 2016–2020. The decrease in age-and-size at 50% maturity for both cold-water adapted species, Arctic charr and burbot, over time, is in accordance with the hypothesis that increased water temperatures would reduce A_{50} and L_{50} of both cold-water adapted species. However, the decreased A_{50} and L_{50} of grayling was not expected from the hypothesis.

4.1 Climate Change Effect on Growth

Contradictory effects on the growth parameters were observed for the cold-water adapted species. Only burbot had a significant and considerable increase in G_i , and a slight, non-significant decrease in L_∞ , of which both effects were hypothesized. Arctic charr had a decreased G_i and increased L_∞ , of which both results were significant, but opposite of the expectations from theory. Further, there was found a significantly lower mean length of 2–3⁺ charr and increased mean length of 4–5⁺ charr in 1997 compared to 2016–2020, which may indicate a poorer growth for 2–3⁺ year old charr, and better growth for 4–5⁺ year old charr. There was no significant difference in the mean length of 1⁺ Arctic charr during the study period.

The cool-water adapted species, brown trout and grayling, had increased G_i and L_∞ during the study period, in accordance with the hypothesis. The increase in G_i was significant for both species, opposed to the increase in L_∞ , which was non-significant.

Other studies of juvenile somatic growth have found contractionary effects of increasing water temperatures in populations of Arctic charr. Godiksen *et al.* (2012) observed positive effects on growth, during periods of high spring and summer temperatures, on 1⁺ year old Arctic charr, and no effect on 0⁺ and 2⁺ and 3⁺ charr. Kotowych (2019) found a strong, temperature correlated, positive growth effect on juvenile Arctic charr aged 0⁺, 1⁺ and 3⁺, and no growth correlation for 2⁺ charr. Both studies included subarctic charr populations in northern Norway. The study of lake Lille Rostavatn does not include fish of age 0⁺. However, the growth parameter, G_i , explains the growth during the fishes first year and is comparable to growth of 0⁺ fish of other studies.

To my knowledge there are few similar studies, such as the current study of Lille Rostavatn, that compares the L_∞ of a long-term dataset of a lacustrine fish population experiencing increasing temperature. However, a study by Michaud *et al.* (2010) of an anadromous Arctic charr population in Northern Labrador, Canada, observed a significant positive effect on growth in periods with higher water temperatures of individuals aged 6–12 years. In addition, the study found an increase in the calculated L_∞ of anadromous charr that experienced warmer seasonal water temperature during growth at sea.

Studies of juvenile growth of brown trout have differing observations of thermal effect on growth. A study by Forseth *et al.* (2009) found no correlation between temperature and growth of juvenile brown trout in lakes at different latitudes (57–66 ° N), with varying degree-days, while a study by Bærum *et al.* (2013) of brown trout in a south-eastern-Norwegian river found a positive seasonal temperature effect on growth of juvenile brown trout, similarly to the findings in the present study of Lille Rostavatn. Further, a study by Mallet *et al.* (1999) found an increased growth of grayling during periods of warmer water, compared to earlier years with colder water, which may reflect the increased G_i . The growth was however negatively affected when water temperature exceeded 21 °C for long periods.

The contradicting effects on growth from other studies, referred to above, demonstrates that there are diverse factors from climate change that affect fish populations, in addition to the effect of temperature alone. The impact of climate change on life history is complicated, and hard to explain as climate change affect populations both directly through physiological processes, and indirectly by altering ecosystems and population dynamics (Stenseth *et al.*, 2002).

Increasing water temperatures will in theory provide faster growth of fish, as the metabolism and performance is temperature-dependent (Huey & Kingsolver, 1989; Jeppesen *et al.*, 2012). The positive temperature effect on growth applies until the temperature exceeds fishes' optimal temperature for growth (Elliott & Elliott, 2010). Thermal effect on growth of Arctic charr follows a dome shape curve with an optimum of growth within 14–16 °C (Larsson & Berglund, 1998, 2005; Elliott & Elliott, 2010). The temperature data from the outlet river of Lille Rostavatn (See: Dalbak, 2020) has no mean summer-season temperatures above 11 °C, and temperature increase should therefore have a positive effect on G_i of Arctic charr, as the mean summer temperatures do not exceed the optimal temperature of growth. A study by Smalås *et al.* (2020) in Lake Takvatnet, a lake nearby and similar to Lille Rostavatn, could support the assumption that juvenile charr growth should increase with increasing temperatures. The study by Smalås *et al.* (2020) predicted improved growth of Arctic charr with modelled scenarios of future rising temperatures. Even in a modelled climate scenario with a future 1.5 °C water temperature increase, only a few days during summer were predicted to exceed the optimal temperature of growth of Arctic charr, and thus not restrain growth of char (Smalås *et al.*, 2020).

Increasing temperatures is globally shown to negatively affect the mean adult body size (Gardner *et al.*, 2011), but there are examples of the opposite effect in species in seasonal environments (Chown & Klok, 2003). The increase in L_{∞} of Arctic charr, brown trout, and grayling from 1997 to 2016-2020, may therefore indicate a positive response from the presumably elevated water temperatures in Lille Rostavatn. Other studies, for example Michaud *et al.* (2010) have linked increased L_{∞} of Arctic charr to raised water temperatures. However, there are various factors that impact L_{∞} , such as maturation patterns (Stearns, 1976; Lester *et al.*, 2004), resource competition (Ohlberger & Fox, 2013; Amundsen *et al.*, 2015) and harvesting (Ahti *et al.*, 2020; Smalås *et al.*, 2020). The observed increase in L_{∞} in Lille Rostavatn of Arctic charr, brown trout, and grayling can therefore not be related directly to a positive temperature effect on growth from.

The response on fish populations from climate change is dependent on lake morphometry (Kristensen *et al.*, 2006; Murdoch & Power, 2013). For example, populations in shallow lakes are more susceptible to climate change than populations in large lakes, as large-lake populations have the possibility to move between habitats in accordance to their optimal temperature of growth throughout their life stages (Baroudy & Elliott, 1994; Morita *et al.*, 2010; Murdoch & Power, 2013). Individuals in large lakes may use the deep profundal zone for thermal refugia. However, the profundal habitat is less attractive for feeding, and utilizing the profundal habitat may reduce growth (Klemetsen *et al.*, 1989; Murdoch & Power, 2013). Sampled data from Lille Rostavatn show an increased number of charr individuals aged 1⁺-3⁺ in the profundal zone, while there are less of the same age-classes in the littoral zone in 2016-2020 compared to 1997 (See: Appendix B). Therefore, the reduced G_i of Arctic charr may be a cause of habitat shift, and a subsequent limitation in growth from restricted food availability and decreased metabolism in the cold water. Similar evidence of reduced growth of 0⁺ charr that occupy the profundal zone is found by Godiksen *et al.* (2012) and Kjellman and Eloranta (2002).

Lille Rostavatn had a major shift in community structure, with declined abundance of cold-water adapted species and a corresponding increase of cool-water adapted species. The shift in community structure might explain the depressed growth of juvenile Arctic charr by the habitat shift. Increased interspecific interactions, followed by the community shift, such as predation and competition coerce juvenile charr to utilize the profundal habitat (Klemetsen *et al.*, 1989; Godiksen *et al.*, 2011). Therefore, the habitat shift and following decreased G_{∞} of charr in Lille Rostavatn, can be an indirect effect of climate change as climate warming enhance the

abundance of cool-water adapted species (Comte *et al.*, 2013; Myers *et al.*, 2017; Rolls *et al.*, 2017; Svenning *et al.*, 2021).

The Arctic charr aged 4–5⁺ show no change in the habitat-use in Lille Rostavatn over time, and most 4–5⁺ charr are caught in the littoral zone in all periods of sampling (Appendix B). The significantly increased mean length of the 4–5⁺ charr does not indicate any restriction on growth from increased water-temperature. Although, as growth rate of each age class of Arctic charr is not calculated, the increased mean size of 4–5⁺ only indicates a better growth rate in 2016–2020, as the younger charr in 2016–2020 are smaller than in 1997 on average, while the mean length of 4–5⁺ is larger in 2016–2020 than in 1997.

Opposed to the decreased G_i of Arctic charr, it was observed an increase in G_i of the other cold-water adapted species, burbot, and both of the cool-water adapted species. The increased growth parameters G_i of brown trout and grayling over time corresponds with the increased water temperatures as both species have slightly higher optimal temperatures of growth, compared to the cold-water adapted species, at respectively 14–17 °C (Elliott & Hurley, 2000) and about 17 °C (Mallet *et al.*, 1999). Burbot has a similar thermal optimum of growth as the charr, at about 14–16 °C for both juvenile and adult burbot (Pääkkönen & Marjomäki, 2000; Hofmann & Fischer, 2003), and a preferred temperature of juvenile burbot at around 11 °C, and 14 °C for adult burbot (Hofmann & Fischer, 2002). The water temperatures of Lille Rostavatn supposedly do not exceed the optimum for growth, and the increased temperature during growth season seems to amplify growth of juvenile burbot, reflected by the observed increased G_i . Burbot is shown to grow quickly during their first year (McPhail & Paragamian, 2000) and a prolonged growth season from climate change increases the length of growth season, and enhance the juvenile growth of fish (Jonsson & Jonsson, 2009), and may explain the increased G_i of burbot, grayling and brown trout.

Burbot had an observed constant L_∞ in Lille Rostavatn, with a slight decrease, during the study period. It may indicate that the L_∞ of burbot is not directly negatively affected by temperature, as the temperature does not exceed the preferred temperature of feeding and growth.

Most of the juvenile burbot is caught in the littoral zone (Appendix B). This trend is constant during the study period, and burbot show no change in habitat-use, as observed for Arctic charr. Even though there is an increased dominance of cool-water adapted species in the littoral habitat, burbot does not seem to escape to the profundal zone for predatory, nor competition avoidance. Burbot is, however, known to have a thermal habitat selection based on feeding, and

reproduction periods (Harrison et al., 2016). Burbot is dependent on cold water ($< 2\text{ }^{\circ}\text{C}$) to reproduce as egg-survival is sensitive to temperatures, while it prefers higher temperatures for feeding (Harrison *et al.*, 2016).

4.2 Comparison of Growth of Cold- and Cool-Water Adapted fish

Arctic charr was the only species that displayed a significant decrease in G_i , while the remaining species had increased G_i , significantly only for burbot. Since the reduced G_i of Arctic charr is explained by using the profundal zone, to supposedly avoid increased competition in the littoral zone. It seems that the reduced G_i of Arctic charr is an indirect effect of climate change, by altered interspecific interactions through changes in community structure.

The highest increase in G_i , and supposedly the species benefitting the most from temperature-increased related growth of 0^+ was the burbot, followed by grayling, and brown trout, at 99–118 $\text{mm}\cdot\text{yr}^{-1}$, 79–102 $\text{mm}\cdot\text{yr}^{-1}$, 59–67 $\text{mm}\cdot\text{yr}^{-1}$, respectively. In comparison, the G_i of Arctic charr declined from 80–75–68 $\text{mm}\cdot\text{yr}^{-1}$. As, the decline in G_i of Arctic charr is related to the indirect effect of a possible temperature induced elevated abundance of grayling and brown trout as competitors and predator (brown trout), Arctic charr presumably have had the least advantage of increased mean growth-season temperature. The large increase in G_i of grayling might reflect climate change effects on the lake populations by prolonged growth seasons. This effect can possibly have a large positive impact on the spring-spawning grayling as timing of the juveniles emerging is crucial, since too early emergence leads to starvation, while too late emerging reduces the length of time period of growth (Wedekind & KÜNg, 2010).

According to the modelled growth with MVBGM, the high juvenile growth of burbot quickly declines and becomes asymptotic (Appendix E). Before the age of 2 years the burbot has the slowest growth when comparing growth curves. In 2016-2020 grayling showed the fastest growth of all species, until the age of about 10 years. Arctic charr and brown trout had similar growth curves until the age of 9 years, of which after, brown trout had better growth. There were not caught brown trout over 9 years old, but the large estimated L_{∞} of brown trout, implies that individuals >10 years grow better than the other species, although this is not significant compared to Arctic charr and grayling. The fast growth of grayling, and older age-classes for brown trout and arctic charr, may also reflect the probable relation between climate change and longer growth season, which provides a longer growth season, and thus better growth.

The large uncertainty in the L_{∞} of brown trout may be a result of few sampled individuals aged > 5 years, and no individuals < 3 years of age. Kritzer *et al.* (2001) recommend at least 7-10 individuals per age class for precise parameter estimations with the von Bertalanffy growth model. There were large ranges in length per age classes for the brown trout in Lille Rostavatn, which will also affect the model precision (Kritzer *et al.*, 2001). The large range in length within age groups 4–6 years could indicate different life history strategies considering maturity patterns, as maturation leads to decreased growth (Stearns, 1976; Jobling & Baardvik, 1991). Very few individuals of sampled brown trout were mature, and this does not account for the few individuals with higher than average size at age. However, a switch to a piscivorous diet of brown trout is known to enhance growth, compared to invertebrate feeding individuals of the same species (Klemetsen *et al.*, 2003; Hughes *et al.*, 2019), and thus explain the large L_{∞} .

4.3 Maturation Strategies in a Changing Climate

In accordance with the expectations, it was observed a decreased age-and-size at maturity for both coldwater adapted species. The decrease in age-and size at maturity of the cool-water adapted species, grayling, was not expected. The only estimation of age-and-size at maturity for brown trout was available from in 2016-2020 data, and was highest of all species, though not significantly. The results of A_{50} and L_{50} , of grayling and brown trout have low accuracy, displayed by the large standard errors, due to low sample sizes of mature individuals of grayling and brown trout in 1997-2010 (See: Appendix E; F; G). For some sampling periods, age-and-size at maturity are estimates, not modelled results, as the modelled regression curve does not even cross the probability of 50% maturity. The low statistical power can be a reason for the observed decrease in A_{50} and L_{50} of grayling over time.

Arctic charr had a large A_{50} and L_{50} in 2010 compared to early and late years. A possible explanation for this can be the large samples of fish from the pelagic habitat. Very few charr were caught in the littoral habitat, and about half of the individuals were sampled in the pelagic zone. Arctic charr that utilize the pelagic habitat are on average younger than the average age in the littoral zone, and fewer individuals are mature (Klemetsen *et al.*, 1989; Appendix C). The proportionally large samples of charr caught in the pelagic habitat in 2010 is therefore likely to have caused the large estimates of A_{50} and L_{50} . However, it remains unclear why there were large sample sizes of charr in the pelagic zone in 2010, and a corresponding increase in the catch-per-unit effort that year (Dalbak, 2020).

Experiments of reared populations of Arctic charr in water temperatures of 9, 12 and 15 °C show an increased gonadosomatic index, and thereby earlier maturation of juvenile charr exposed to high temperatures (Gunnarsson *et al.*, 2011). Norrgård *et al.* (2014) demonstrates that reared juvenile fish, exposed to high qualities and quantities of food has the same effect as temperature on early maturation, with earlier maturation. However, the early maturation of reared fish displays a poorer growth after maturation than for the immature fish (Jobling & Baardvik, 1991).

The age-and-size at maturation is shown to be affected by temperature. An experimental study by Kuparinen *et al.* (2011) showed that age-and-maturation of nine-spined-stickleback was lower within a warm-water treatment, compared to a cold-water treatment. For males in the study, both A_{50} and L_{50} were reduced. For females, only A_{50} was reduced while the L_{50} remained unchanged. This study might reflect that temperature is an important factor for age-and-size at maturation, as fish populations at high latitudes are shown to mature later and at larger length than populations at lower latitudes (Blanck & Lamouroux, 2007).

The optimal timing and size at maturity are variable life history strategies that depend on environmental conditions, such as temperature, food availability, predation pressure and competition (Stearns, 1992; Hutchings, 2002). The effect of predation on maturation is two-fold (Heibo & Magnhagen, 2005); high predation risk may induce faster growth and thereby later maturation as prey need to grow fast to exit the size-dependent predatory risk; on the other hand, high mortality from predation induces a resource-competitional release and prey may grow larger before maturation. Decreases in age at maturity correlates with longevity as individuals with short lifespan seek to start reproducing early, to compensate for the shorter lifespan of producing offspring (Fišer, 2019), while individuals with long life span can delay maturation and start reproducing at a larger size, which is beneficial as fecundity increases with body-size (Stearns, 1992). However, the mortality of Arctic charr and burbot in Lille Rostavatn is not known and cannot be investigated as a possible factor for changes in age-and-maturity patterns. There are caught older fish individuals of all species in the latest time period which could indicate an increased longevity with later onset of maturation, but there is no evidence of that.

Maturation may reduce growth, as there is a tradeoff between the energy located to growth and reproduction during the growth season (Stearns, 1976; Jobling & Baardvik, 1991). Populations within the same species, at high latitudes, grow slower and mature later than low-latitude populations (Blanck & Lamouroux, 2007; Lappalainen *et al.*, 2008) and increasing temperature may decrease the age-and-length at maturity of subarctic fish populations (Rolls *et al.*, 2017). Therefore, the earlier maturation and increased growth rates of Arctic charr (by comparing the modelled growth curves separately) in Lille Rostavatn are contradictory outcomes, as there is a negative effect from early maturation on the allocation of energy on growth, which leads to lower asymptotic length of fish (Lester *et al.*, 2004). The reduced size at maturity of Arctic charr does not reflect the increased growth considering the tradeoff between growth and reproduction. To continue to grow after maturation, the Arctic charr must have fulfilling food availability. With high quantities of food, there might be an advantage to mature early and at a smaller size to increase the time-span of reproduction. Females invest more energy in reproduction than males and male reproduction success is less size-dependent (Stearns, 1992) and there might be differing thermal effects on age-and-size at maturity of males and females with increasing water temperatures.

The observed decrease of age-at-maturity of burbot and grayling, in Lille Rostavatn, is a possible effect of the increased initial growth rate, G_i . Optimal temperatures for growth and sufficient food availability during early life stages leads to earlier maturation (Forseth *et al.*, 1994; Heibo & Magnhagen, 2005) and reduced adult growth (Jobling & Baardvik, 1991). These studies suggest that increased G_i leads to earlier maturation and may explain the observed decreased G_i of grayling and burbot. The decreased age-at maturity of grayling has, however, not resulted in poorer growth of older individuals as the modelled growth curve is steeper in the latest sampling period (Appendix B).

The early maturation of burbot and grayling, because of increased G_i , does not, however, explain the decreased size at maturation. If the size at maturation for burbot and grayling would have been stable, over time, faster juvenile growth would be a good explanation of decreased age-at-maturity. Therefore, earlier maturation and at a smaller size can be reflected by other factors than just the initial growth rate. High mortality is a factor that reduces both age-and-size at 50% maturation, as individuals need to start reproduction early to have higher chances of reproduction (Perrin & Rubin, 1990).

Despite all the possible factors influencing A_{50} and L_{50} above, burbot is shown to have a stability in life history traits across environmental gradients (Cott *et al.*, 2013), and it is therefore not likely to believe that temperature increase has nearly reduced the A_{50} of burbot to half, during the study period with a 1 degree water temperature increase. In 1997 there were observed immature individuals of burbot aged 7 to 9 years old. In 2016-2020 no burbot aged 7 to 9 years were immature. Burbot is shown to skip spawning seasons if they have low energy reserves (McPhail & Paragamian, 2000). In some populations over 60% mature female individuals were in non-spawning condition during spawning season (Cott *et al.*, 2013). If there are large proportions of spawn-skipping individuals in Lille Rostavatn, it can explain the large A_{50} and L_{50} in early years. It can be difficult to determine the correct maturity status of spawn-skipping mature individuals, due to their lack of gonads development. And mature, spawn-skipping individuals may be falsely determined as immature. The data samplings and examination of individuals are done by various people over the study period, and the determination of maturity state can be affected by different interpretations.

5 Concluding remarks

This study has demonstrated various effects of a 1-degree temperature increase on the growth and age-and-size at maturity of a subarctic lake fish community during a 23-year period. From available literature of climate change effects on fish growth and maturation we expected the following results from this study: (1) Increasing temperature will result in increased growth of juvenile fish, which was found in all studied species except for Arctic charr. The mean maximum asymptotic length of cold-water adapted species will decrease in contrast to an increase for cool-water adapted species, which was true for both cool-water adapted species, and for burbot, while Arctic charr faced an increased mean asymptotic length. (2) The cool-water adapted species were expected to grow faster than the cold-water adapted species, which was not confirmed for juvenile fish as the initial growth rate was highest for burbot, followed by grayling, Arctic charr, and at last, the brown trout. The growth curves, however displayed a poor growth of older burbot. Grayling grew fastest till the age of 10, from where brown trout had the best growth. The growth curve of Arctic charr and Brown trout were similar, but the growth of Arctic charr stagnated at a lower size. (3) At last, it was expected That the age-and-

size at maturity would decrease for cold-water adapted species, which was observed in both Arctic charr and grayling.

The increased growth rate of juvenile burbot, grayling and brown trout seems to be a direct effect of climate change and increased temperature induced growth rate. The decline in growth rate of juvenile Arctic charr, on the other hand, is explained by a thermally induced community shift, with the following increase of competition and predation pressure, which forced the juvenile charr to utilize the profundal habitat. The changes in mean asymptotic length is highly connected to maturation patterns, but the observed earlier maturation of fish contradicts with the increased asymptotic length. The increased juvenile growth can explain the earlier maturation pattern observed in Lille Rostavatn, but to a smaller degree the smaller size at maturation. Shift to a piscivorous diet may enhance growth in some individuals, even after maturation. Burbot is known to have a high juvenile growth as they can feed on large invertebrates early, compared to other fish (McPhail & Paragamian, 2000) and may explain the high juvenile growth, compared to the other fish species. The decreased age-and-size at maturation of Arctic charr, grayling and burbot could be in some degree affected by temperature via increased juvenile growth rate, as it is shown to reduce both age-and-size at maturity. Low statistical power in some of the estimated maturation patterns might have had a large influence on the differing results.

This study has demonstrated that climate change does affect life history traits of freshwater fish species, both through direct physiological changes (e.g. metabolism and growth) and indirect through changed interactions with other species (e.g. change in competition and predation). The effects of climate change on life history strategies are difficult to distinguish and there are many factors affecting life history traits in a complex fish community in a heteromorphic lake, like Lille Rostavatn. This study does not address all possible explanations on altered life history strategies, but it confirms that climate change influences northern fish populations, but predicting the effects is difficult as many factors impacts the outcome. Further research on heteromorphic lakes with high species diversity should be investigated to understand and predict the large variety of possible effects from climate change.

References

- Agger, P., Bagge, O., Hansen, O., Hoffman, E., Holden, M. J., Kesteven, G. L., . . . Williams, T. (1974). Manual of Fisheries Science Part 2 - Methods of Resource Investigation and their Application. In M. J. Holden & D. F. S. Raitt (Eds.), *FAO Fisheries Technical Paper - 115 Rev.1*. Rome: FAO.
- Ahti, P. A., Kuparinen, A., & Uusi-Heikkilä, S. (2020). Size does matter — the eco-evolutionary effects of changing body size in fish. *Environmental reviews*, 28(3), 311-324. doi:10.1139/er-2019-0076
- Amundsen, P.-A., Smalås, A., Knudsen, R., Kristoffersen, R., Siwertsson, A., & Klemetsen, A. (2015). Takvatnprosjektet - Forskning og kultivering av en overbefolka røyeberstand. (5). doi:10.7557/7.3420
- Appelberg, M., Berger, H. M., Hesthagen, T., Kleiven, E., Kurkilahti, M., Raitaniemi, J., & Rask, M. (1995). Development and intercalibration of methods in nordic freshwater fish monitoring. *Water, air and soil pollution*, 85(2), 401-406. doi:10.1007/BF00476862
- Baroudy, E., & Elliott, J. M. (1994). The critical thermal limits for juvenile Arctic charr *Salvelinus alpinus*. In (pp. 1041-1053). London :.
- Berteaux, D., Réale, D., McAdam, A. G., & Boutin, S. (2004). Keeping Pace with Fast Climate Change: Can Arctic Life Count on Evolution?1. *Integrative and Comparative Biology*, 44(2), 140-151. doi:10.1093/icb/44.2.140
- Blanck, A., & Lamouroux, N. (2007). Large-scale intraspecific variation in life-history traits of European freshwater fish. *Journal of Biogeography*, 34(5), 862-875. doi:10.1111/j.1365-2699.2006.01654.x
- Borgstrøm, R., Bergum, K., Børresen, T. E., & Svenning, M. A. (2019). Gillnet catchability of brown trout *Salmo trutta* is highly dependent on fish size and capture site. *Fauna norvegica*, 39, 30-38. doi:10.5324/fn.v39i0.2536
- Bærum, K. M., Haugen, T. O., Kiffney, P., Moland Olsen, E., & Vøllestad, L. A. (2013). Interacting effects of temperature and density on individual growth performance in a wild population of brown trout. *Freshw Biol*, 58(7), 1329-1339. doi:10.1111/fwb.12130
- Chown, S. L., & Klok, C. J. (2003). Altitudinal body size clines: latitudinal effects associated with changing seasonality. *Ecography*, 26(4), 445-455. doi:10.1034/j.1600-0587.2003.03479.x
- Chu, C., Mandrak, N. E., & Minns, C. K. (2005). Potential Impacts of Climate Change on the Distributions of Several Common and Rare Freshwater Fishes in Canada. *Diversity and Distributions*, 11(4), 299-310. doi:10.1111/j.1366-9516.2005.00153.x
- Comte, L., Buisson, L., Daufresne, M., & Grenouillet, G. (2013). Climate-induced changes in the distribution of freshwater fish: observed and predicted trends. *Freshwater Biology*, 58(4), 625-639. doi:10.1111/fwb.12081
- Cott, P. A., Johnston, T. A., & Gunn, J. M. (2013). Stability in Life History Characteristics among Burbot Populations across Environmental Gradients. *Transactions of the American Fisheries Society (1900)*, 142(6), 1746-1756. doi:10.1080/00028487.2013.811101
- Dalbak, K. (2020). The effect of climate change on the fish community in Lille Rostavatn, northern Norway. In: UiT Norges arktiske universitet.
- EEA. (2016). *Climate change, impacts and vulnerability in Europe 2016* (EEA Report No 1/2017). Retrieved from <https://www.eea.europa.eu/publications/climate-change-impacts-and-vulnerability-2016>

- Elliott, J. M., & Elliott, J. A. (2010). Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change. *Journal of Fish Biology*, 77(8), 1793-1817. doi:10.1111/j.1095-8649.2010.02762.x
- Elliott, J. M., & Hurley, M. A. (2000). Daily energy intake and growth of piscivorous brown trout, *Salmo trutta*. *Freshwater Biology*, 44(2), 237-245. doi:10.1046/j.1365-2427.2000.00560.x
- Eloranta, A. P., Knudsen, R., & Amundsen, P. A. (2013). Niche segregation of coexisting Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) constrains food web coupling in subarctic lakes. *Freshwater Biology*, 58(1), 207-221. doi:10.1111/fwb.12052
- Finstad, A. G., Jansen, P. A., & Langeland, A. (2000). Gillnet selectivity and size and age structure of an alpine Arctic char (*Salvelinus alpinus*) population. *Canadian journal of fisheries and aquatic sciences*, 57(8), 1718-1727. doi:10.1139/f00-071
- Fišer, G. (2019). Life histories. In W. B. W. D. C. C. T. Pipan (Ed.), *Encyclopedia of caves* (3 ed., pp. 652-657).
- Forseth, T., Larsson, S., Jensen, A. J., Jonsson, B., Näslund, I., & Berglund, I. (2009). Thermal growth performance of juvenile brown trout *Salmo trutta*: no support for thermal adaptation hypotheses. *J Fish Biol*, 74(1), 133-149. doi:10.1111/j.1095-8649.2008.02119.x
- Forseth, T., Ugedal, O., & Jonsson, B. (1994). The Energy Budget, Niche Shift, Reproduction and Growth in a Population of Arctic Charr, *Salvelinus alpinus*. *The Journal of animal ecology*, 63(1), 116-126. doi:10.2307/5588
- Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. (2011). Declining body size: a third universal response to warming? *Trends Ecol Evol*, 26(6), 285-291. doi:10.1016/j.tree.2011.03.005
- Ghan, D. (1990). Ecology of larval and juvenile burbot (*Lota lota*): Abundance and distribution patterns, growth, and an analysis of diet and prey selection. In: ProQuest Dissertations Publishing.
- Godiksen, J. A., Borgstrøm, R., Dempson, J. B., Kohler, J., Nordeng, H., Power, M., . . . Svenning, M. A. (2012). Spring climate and summer otolith growth in juvenile Arctic charr, *Salvelinus alpinus*. *Environmental biology of fishes*, 95(3), 309-321. doi:10.1007/s10641-012-9998-0
- Godiksen, J. A., Svenning, M. A., Sinnatamby, R. N., Dempson, J. B., Borgstrøm, R., & Power, M. (2011). Stable isotope-based determinations of the average temperatures experienced by young-of-the-year Svalbard Arctic charr (*Salvelinus alpinus* (L.)). *Polar Biology*, 34(4), 591-596. doi:10.1007/s00300-010-0907-8
- Goldman, C. R., Kumagai, M., & Robarts, R. D. (2012). *Climatic Change and Global Warming of Inland Waters: Impacts and Mitigation for Ecosystems and Societies* (2. Aufl. ed.). New York: New York: Wiley-Blackwell.
- Gunnarsson, S., Imsland, A. K., Árnason, J., Gústavsson, A., Arnarson, I., Jónsson, J. K., . . . Thorarensen, H. (2011). Effect of rearing temperatures on the growth and maturation of Arctic charr (*Salvelinus alpinus*) during juvenile and on-growing periods. *Aquaculture research*, 42(2), 221-229. doi:10.1111/j.1365-2109.2010.02615.x
- Hanssen-Bauer, I., Drange, H., Førland, E. J., Roald, L. A., Børsheim, K. Y., Hisdal, H., . . . Ådlandsvik, B. (2009). Klima i Norge 2100. Bakgrunnsmateriale til NOU Klimatilpassing. In: Norsk klimasenter.
- Harrison, P. M., Gutowsky, L. F. G., Martins, E. G., Patterson, D. A., Cooke, S. J., & Power, M. (2016). Temporal plasticity in thermal-habitat selection of burbot *Lota lota* a diel-migrating winter-specialist. *J Fish Biol*, 88(6), 2111-2129. doi:10.1111/jfb.12990

- Harzevili, A. S., Dooremont, I., Vught, I., Auwerx, J., Aqutaert, P., & Charleroy, D. D. (2004). First feeding of burbot, *Lota lota* (Gadidae, Teleostei) larvae under different temperature and light conditions. *Aquaculture research*, *35*(4), 419-422. doi:10.1111/j.1365-2109.2004.01047.x
- Heibo, E., & Magnhagen, C. (2005). Variation in age and size at maturity in perch (*Perca fluviatilis* L.), compared across lakes with different predation risk. *Ecology of freshwater fish*, *14*(4), 344-351. doi:10.1111/j.1600-0633.2005.00108.x
- Heino, J., Virkkala, R., & Toivonen, H. (2009). Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biol Rev Camb Philos Soc*, *84*(1), 39-54. doi:10.1111/j.1469-185X.2008.00060.x
- Hofmann, N., & Fischer, P. (2002). Temperature Preferences and Critical Thermal Limits of Burbot: Implications for Habitat Selection and Ontogenetic Habitat Shift. *Transactions of the American Fisheries Society (1900)*, *131*(6), 1164-1172. doi:10.1577/1548-8659(2002)131<1164:TPACTL>2.0.CO2
- Hofmann, N., & Fischer, P. (2003). Impact of temperature on food intake and growth in juvenile burbot. *Journal of Fish Biology*, *63*(5), 1295-1305. doi:10.1046/j.1095-8649.2003.00252.x
- Huey, R. B., & Kingsolver, J. G. (1989). Evolution of thermal sensitivity of ectotherm performance. *Trends Ecol Evol*, *4*(5), 131-135. doi:10.1016/0169-5347(89)90211-5
- Hughes, M. R., Hooker, O. E., Leeuwen, T. E., Kettle-White, A., Thorne, A., Prodöhl, P., & Adams, C. E. (2019). Alternative routes to piscivory: Contrasting growth trajectories in brown trout (*Salmo trutta*) ecotypes exhibiting contrasting life history strategies. *Ecology of freshwater fish*, *28*(1), 4-10. doi:10.1111/eff.12421
- Hutchings, J. A. (2002). Life Histories of Fish. In P. J. B. Hart & J. D. Reynolds (Eds.), *Handbook of Fish Biology and Fisheries: Fish Biology* (Vol. 1, pp. 149-174). Oxford, UK: Oxford, UK: Blackwell Publishing Ltd.
- Jeppesen, E., Mehner, T., Winfield, I., Kangur, K., Sarvala, J., Gerdeaux, D., . . . Meerhoff, M. (2012). Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes. *The International Journal of Aquatic Sciences*, *694*(1), 1-39. doi:10.1007/s10750-012-1182-1
- Jobling, M., & Baardvik, B. M. (1991). Patterns of growth of maturing and immature Arctic charr, *Salvelinus alpinus*, in a hatchery population. *Aquaculture*, *94*(4), 343-354. doi:10.1016/0044-8486(91)90178-A
- Jonsson, B., & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *J Fish Biol*, *75*(10), 2381-2447. doi:10.1111/j.1095-8649.2009.02380.x
- Katsanevakis, S., & Maravelias, C. D. (2008). Modelling fish growth: multi-model inference as a better alternative to a priori using von Bertalanffy equation. *Fish and fisheries (Oxford, England)*, *9*(2), 178-187. doi:10.1111/j.1467-2979.2008.00279.x
- Kjellman, J., & Eloranta, A. (2002). Field estimations of temperature-dependent processes: case growth of young burbot. *Hydrobiologia*, *481*(1), 187-192. doi:10.1023/A:1021249620773
- Klemetsen, A., Amundsen, P.-A., Muladal, H., Rubach, S., & Solbakken, J. I. (1989). Habitat shifts in a dense, resident arctic charr *Salvelinus alpinus* population. *Physiol. Ecol. Japan, Vol. 1*, 187-200.
- Klemetsen, A., Amundsen, P. A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F., & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories.

- Ecology of freshwater fish*, 12(1), 1-59. doi:<https://doi.org/10.1034/j.1600-0633.2003.00010.x>
- Knudsen, R., Amundsen, P.-A., & Klemetsen, A. (2010). Arctic charr in sympatry with burbot: Ecological and evolutionary consequences. *Hydrobiologia*, 650(1), 43-54. doi:10.1007/s10750-009-0077-2
- Kotowych, N. V. (2019). Rising temperatures in a subarctic lake lead to increased somatic growth rates for Arctic charr (*Salvelinus alpinus*, (L.)). In: UiT The Arctic University of Norway.
- Kristensen, D. M., Jørgensen, T. R., Larsen, R. K., Forchhammer, M. C., & Christoffersen, K. S. (2006). Inter-annual growth of Arctic charr (*Salvelinus alpinus*, L.) in relation to climate variation. *BMC Ecol*, 6(1), 10-10. doi:10.1186/1472-6785-6-10
- Kritzer, J. P., Davies, C. R., & Mapstone, B. D. (2001). Characterizing fish populations: effects of sample size and population structure on the precision of demographic parameter estimates. *Canadian journal of fisheries and aquatic sciences*, 58(8), 1557-1568. doi:10.1139/cjfas-58-8-1557
- Kuparinen, A., Cano, J., Loehr, J., Herczeg, G., Gonda, A., & Merilä, J. (2011). Fish age at maturation is influenced by temperature independently of growth. *Oecologia*, 167(2), 435-443. doi:10.1007/s00442-011-1989-x
- Lappalainen, J., Tarkan, A. S., & Harrod, C. (2008). A meta-analysis of latitudinal variations in life-history traits of roach, *Rutilus rutilus*, over its geographical range: linear or non-linear relationships? *Freshwater Biology*, 53(8), 1491-1501. doi:10.1111/j.1365-2427.2008.01977.x
- Larsson, S., & Berglund, I. (1998). Growth and food consumption of 0+ arctic charr fed pelleted or natural food at six different temperatures. *Journal of Fish Biology*, 52(2), 230-242. doi:10.1006/jfbi.1997.0575
- Larsson, S., & Berglund, I. (2005). The effect of temperature on the energetic growth efficiency of Arctic charr (*Salvelinus alpinus* L.) from four Swedish populations. *Journal of thermal biology*, 30(1), 29-36. doi:10.1016/j.jtherbio.2004.06.001
- Lester, N. P., Shuter, B. J., & Abrams, P. A. (2004). Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *Proc Biol Sci*, 271(1548), 1625-1631. doi:10.1098/rspb.2004.2778
- Mallet, J. P., Charles, S., Persat, H., & Auger, P. (1999). Growth modelling in accordance with daily water temperature in European grayling (*Thymallus thymallus* L.). *Canadian journal of fisheries and aquatic sciences*, 56(6), 994-1000. doi:10.1139/cjfas-56-6-994
- McPhail, J. D., & Paragamian, V. L. (2000). *Burbot: biology, ecology, and management* (D. W. W. I. B. b. Edited by: V. L. Paragamian, ecology, and management Ed.). Spokane, Washington: American Fisheries Society.
- Mendoza, P. R. (2006). OTOLITHS AND THEIR APPLICATIONS IN FISHERY SCIENCE. *Ribarstvo*, 64(3), 82-102.
- Michaud, W. K., Dempson, J. B., & Power, M. (2010). Changes in growth patterns of wild Arctic charr (*Salvelinus alpinus* (L.)) in response to fluctuating environmental conditions. *Hydrobiologia (The Hague)*, 650(1), 179-191. doi:10.1007/s10750-010-0091-4
- Mooij, W. M., Van Rooij, J. M., & Wijnhoven, S. (1999). Analysis and comparison of fish growth from small samples of length-at-age data: Detection of sexual dimorphism in Eurasian perch as an example. *Transactions of the American Fisheries Society (1900)*, 128(3), 483-490. doi:10.1577/1548-8659(1999)128<0483:AACOFG>2.0.CO2

- Morita, K., Fukuwaka, M.-a., Tanimata, N., & Yamamura, O. (2010). Size-dependent thermal preferences in a pelagic fish. *Oikos*, *119*(8), 1265-1272. doi:10.1111/j.1600-0706.2009.18125.x
- Murdoch, A., & Power, M. (2013). The effect of lake morphometry on thermal habitat use and growth in Arctic charr populations: implications for understanding climate-change impacts. *Ecol Freshw Fish*, *22*(3), 453-466. doi:10.1111/eff.12039
- Myers, B., Lynch, A., Bunnell, D., Chu, C., Falke, J., Kovach, R., . . . Paukert, C. (2017). Global synthesis of the documented and projected effects of climate change on inland fishes. *Reviews in Fish Biology and Fisheries*, *27*(2), 339-361. doi:10.1007/s11160-017-9476-z
- Norrgård, J. R., Bergman, E., Greenberg, L. A., & Schmitz, M. (2014). Effects of feed quality and quantity on growth, early maturation and smolt development in hatchery-reared landlocked Atlantic salmon *Salmo salar*. *J Fish Biol*, *85*(4), 1192-1210. doi:10.1111/jfb.12523
- NVE. (2021, 3. June). Vassdrag - Innsjødatabase, Elvenett. Retrieved from <https://temakart.nve.no/tema/innsjodatabase>
- O'Reilly, C. M., Sharma, S., Gray, D. K., Hampton, S. E., Read, J. S., Rowley, R. J., . . . Zhang, G. (2015). Rapid and highly variable warming of lake surface waters around the globe. *Geophys. Res. Lett*, *42*(24), 10,773-710,781. doi:10.1002/2015GL066235
- Ohlberger, J., & Fox, C. (2013). Climate warming and ectotherm body size — from individual physiology to community ecology. *Functional ecology*, *27*(4), 991-1001. doi:10.1111/1365-2435.12098
- Perrin, N., & Rubin, J. F. (1990). On Dome-Shaped Norms of Reaction for Size-to-Age at Maturity in Fishes. *Functional ecology*, *4*(1), 53-57. doi:10.2307/2389652
- Pääkkönen, J.-P. J., & Marjomäki, T. J. (2000). Feeding of Burbot, *Lota lota*, at Different Temperatures. *Environmental biology of fishes*, *58*(1), 109-112. doi:10.1023/A:1007611606545
- Reist, J. D., Wrona, F. J., Prowse, T. D., Power, M., Dempson, J. B., King, J. R., & Beamish, R. J. (2006). An Overview of Effects of Climate Change on Selected Arctic Freshwater and Anadromous Fishes. *Ambio*, *35*(7), 381-387. doi:10.1579/0044-7447(2006)35[381:AOOEOC]2.0.CO2
- Rolls, R., Hayden, B., & Kahilainen, K. (2017). Conceptualising the interactive effects of climate change and biological invasions on subarctic freshwater fish. *Ecology and Evolution*, *7*(12), 4109-4128. doi:10.1002/ece3.2982
- Ryder, R. A., & Pesendorfer, J. (1992). Food, growth, habitat, and community interactions of young-of-the-year burbot, *Lota lota* L., in a Precambrian Shield lake. *Hydrobiologia*, *243-244*(1), 211-227. doi:10.1007/BF00007037
- Smalås, A., Strøm, J. F., Amundsen, P. A., Dieckmann, U., Primicerio, R., & Heino, J. (2020). Climate warming is predicted to enhance the negative effects of harvesting on high-latitude lake fish. *The Journal of applied ecology*, *57*(2), 270-282. doi:10.1111/1365-2664.13535
- Stearns, S. C. (1976). Life-history tactics: a review of the ideas. *The Quarterly review of biology*, *51*(1), 3-47. doi:10.1086/409052
- Stearns, S. C. (1992). *The evolution of life histories*. Oxford: Oxford University Press.
- Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K.-S., & Lima, M. (2002). Ecological Effects of Climate Fluctuations. *Science*, *297*(5585), 1292-1296. doi:10.1126/science.1071281
- Stepanova, N. A. (1958). On the lowest temperatures on earth. *Monthly weather review*, *86*(1), 6-10. doi:10.1175/1520-0493(1958)086<0006:OTLTOE>2.0.CO2

- Svenning, M. A., Falkegård, M., Dempson, J. B., Power, M., Bårdsen, B. J., Guðbergsson, G., & Fauchald, P. (2021). Temporal changes in the relative abundance of anadromous Arctic charr, brown trout, and Atlantic salmon in northern Europe: Do they reflect changing climates? *Freshwater Biology*. doi:10.1111/fwb.13693
- Thomassen, G., Barson, N. J., Haugen, T. O., & Vøllestad, L. A. (2011). Contemporary divergence in early life history in grayling (*Thymallus thymallus*). *BMC Evol Biol*, *11*(1), 360-360. doi:10.1186/1471-2148-11-360
- Tsikliras, A. C., Tsikliras, A. C., Stergiou, K. I., & Stergiou, K. I. (2014). Size at maturity of Mediterranean marine fishes. *Reviews in Fish Biology and Fisheries*, *24*(1), 219-268. doi:10.1007/s11160-013-9330-x
- Wallace, J. C., & Aasjord, D. (1984). The initial feeding of Arctic charr (*Salvelinus alpinus*) alevins at different temperatures and under different feeding regimes. *Aquaculture*, *38*(1), 19-33. doi:10.1016/0044-8486(84)90134-0
- Watt, W. B. (2001). Adaptation, Fitness, and Evolution. In N. J. Smelser & P. B. Baltes (Eds.), *International encyclopedia of the social and behavioral sciences* (Second edition / editor-in-chief, James D. Wright, University of Central Florida, Orlando, FL, USA ed.).
- Wedekind, C., & KÜNg, C. (2010). Shift of Spawning Season and Effects of Climate Warming on Developmental Stages of a Grayling (*Salmonidae*): Climate Change and Spawning Season. *Conservation Biology*, *24*(5), 1418-1423. doi:10.1111/j.1523-1739.2010.01534.x
- Wetzel, R. G. (2001). *Limnology : lake and river ecosystems* (3rd ed. ed.). San Diego: Academic Press.
- Woodward, G., Perkins, D. M., & Brown, L. E. (2010). Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Phil. Trans. R. Soc. B*, *365*(1549), 2093-2106. doi:10.1098/rstb.2010.0055

Appendix

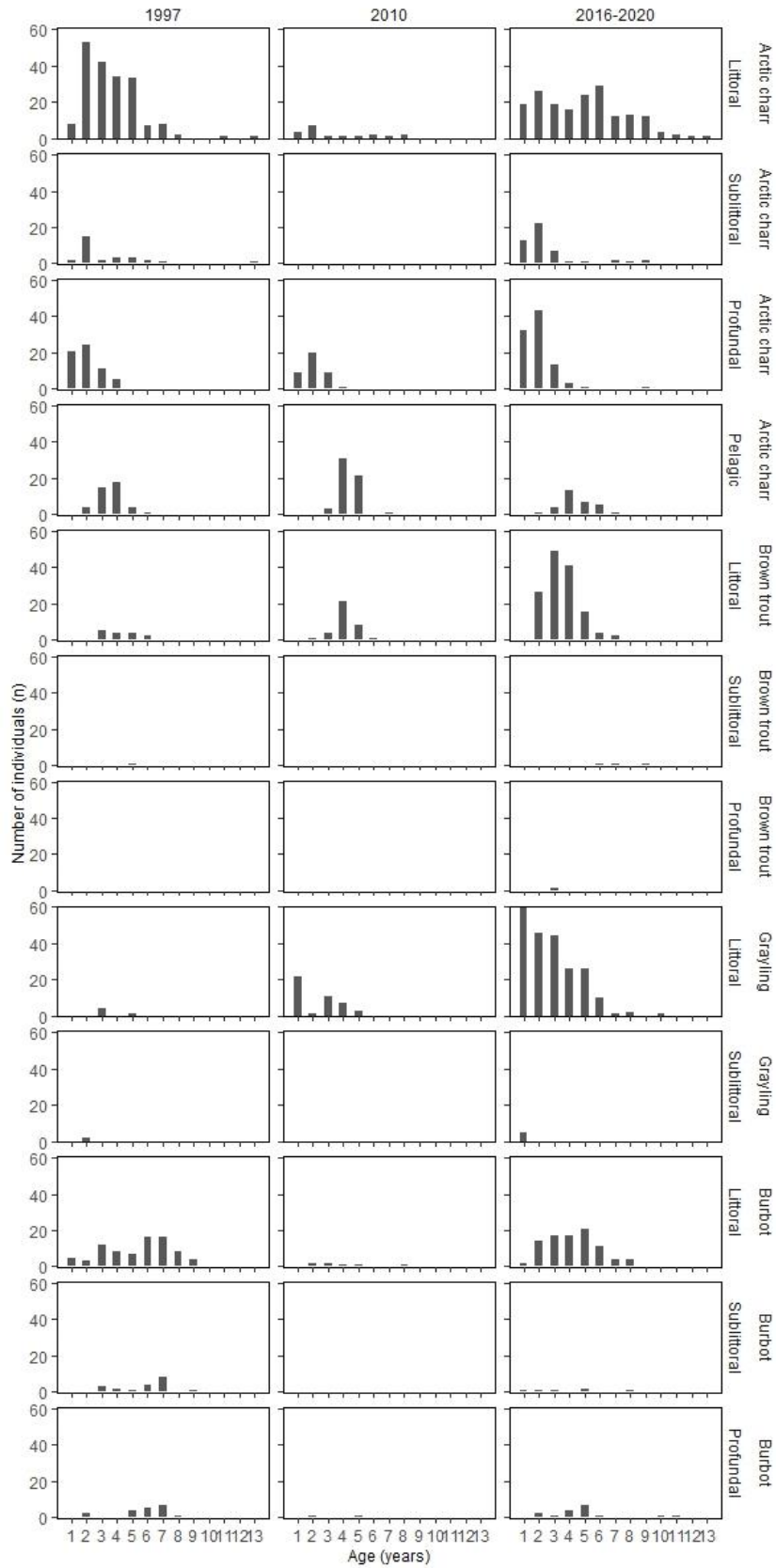
Appendix A

Sample size per gillnet type and period of sampling for, Arctic charr, brown trout, grayling, and burbot.

Species	Period	Gillnet type	No. of fish
Arctic charr	1997	Multi-mesh	351
		FGO	46
		SS	196
	2010	Multi-mesh	59
		FGO	57
		SS	3
	2016–2020	Multi-mesh	337
		FGO	22
	Brown trout	1997	Multi-mesh
SS			15
2010		Multi-mesh	38
2016–2020		Multi-mesh	146
		SS	1
Grayling	1997	Multi-mesh	16
		SS	1
	2010	Multi-mesh	75
		SS	1
	2016–2020	Multi-mesh	231
Burbot	1997	Multi-mesh	223
		SS	51
	2010	Multi-mesh	9
	2016–2020	Multi-mesh	116

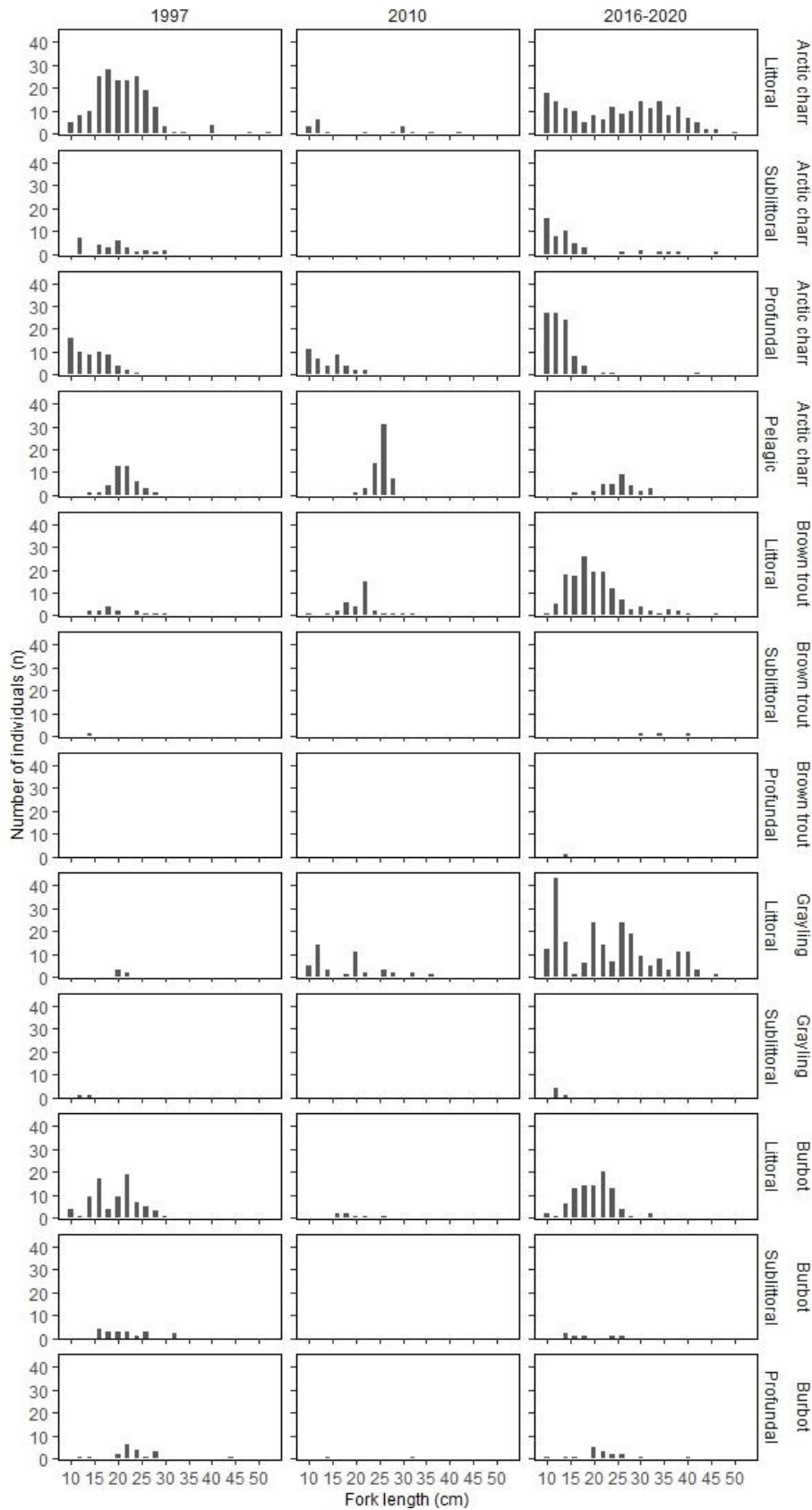
Appendix B

Number of individuals per age class (*yr*) of Arctic charr, brown trout, grayling, and burbot in gillnet samples within littoral, sublittoral, profundal, and pelagic lake habitats, per period of sampling.



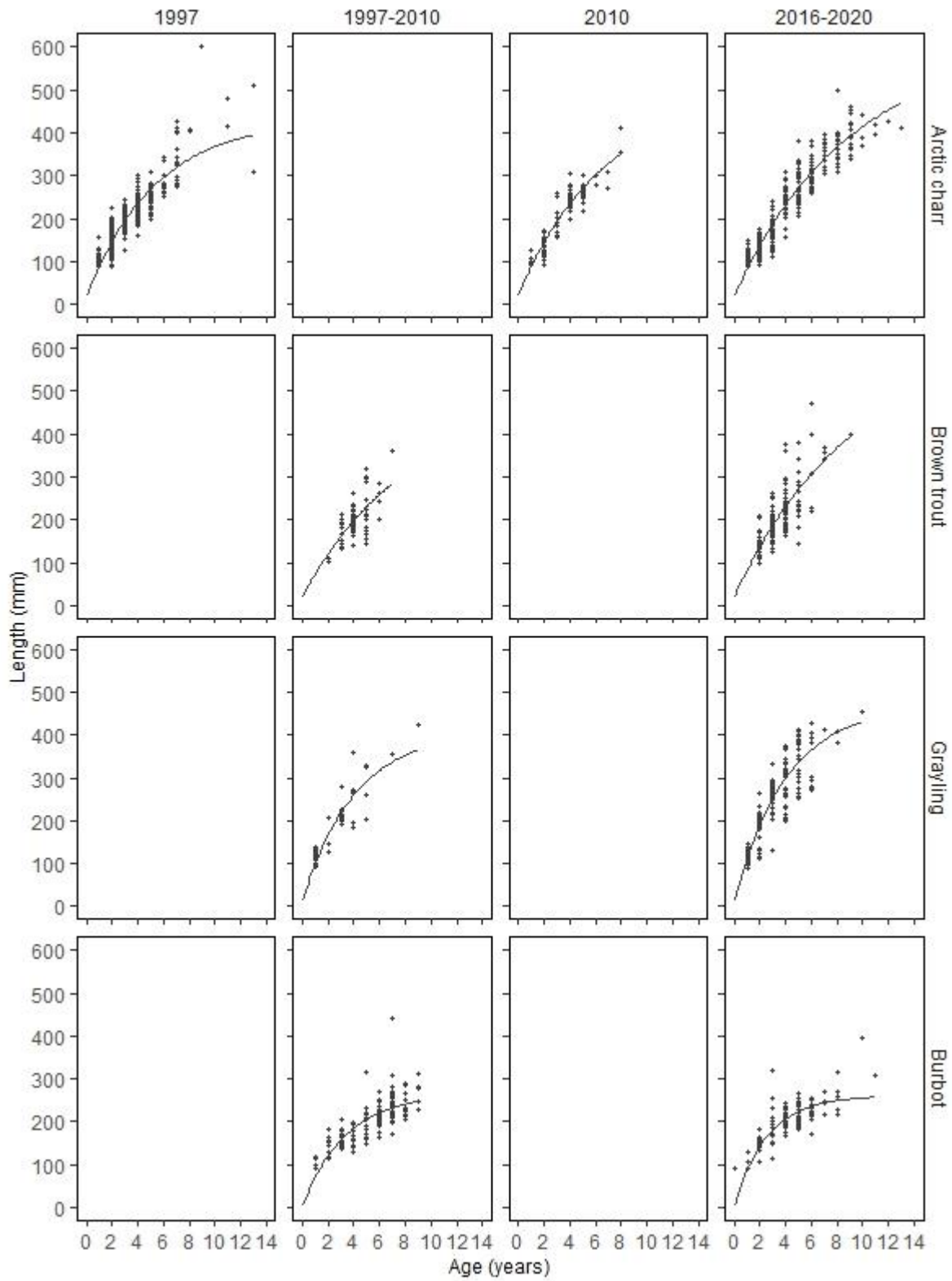
Appendix C

Number of individuals per length group of 2 cm, of Arctic charr, brown trout, grayling, and burbot in samples within littoral, sublittoral, profundal, and pelagic habitats per period of sampling.



Appendix D

Plots of length (*mm*) per age (*yr*) class with the modified von Bertalanffy growth curve of Arctic charr, brown trout, grayling and burbot per period of sampling.



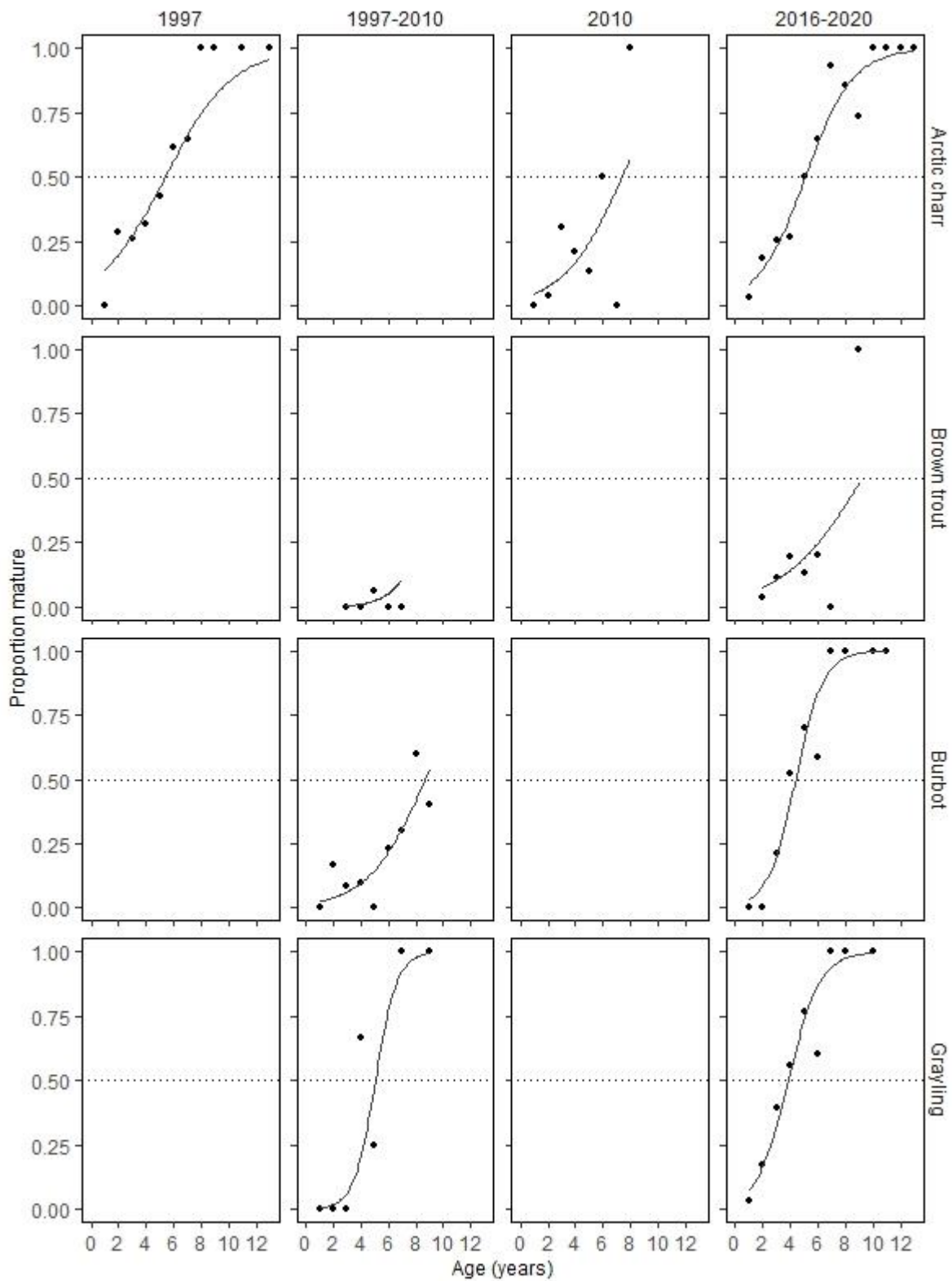
Appendix E

Growth parameters \pm standard error (95% confidence interval) of the modified von Bertalanffy growth model (2), for Arctic charr, brown trout, grayling, and burbot pr sampling period, with number of individuals. L_{∞} is the asymptotic length as age approaches infinity and G_i is the initial maximum growth factor in mm per year.

Species	Period	No. of fish	$L_{\infty} \pm SE$ (CI)	$G_i \pm SE$ (CI)
Arctic charr	1997	481	433 \pm 16 (400–471)	80 \pm 1.8 (76.2–84.0)
	2010	113	487 \pm 46 (413–607)	75 \pm 3.6 (68.7–82.9)
	2016–2020	352	605 \pm 29 (556–668)	68 \pm 1.6 (65.1–71.3)
Brown trout	1997–2010	65	474 (–)	59 \pm 8.8 (–)
	2016–2020	145	622 \pm 137 (439–1179)	67 \pm 4.6 (58.5–77.5)
Grayling	1997–2010	53	410 \pm 43 (334–542)	99 \pm 7.4 (84.2–118.2)
	2016–2020	224	466 \pm 22 (428–514)	118 \pm 4.2 (109.7–126.1)
Burbot	1997–2010	153	266 \pm 11 (246–294)	79 \pm 5.4 (68.2–91.7)
	2016–2020	114	261 \pm 10 (241–288)	102 \pm 7.0 (87.7–119.0)

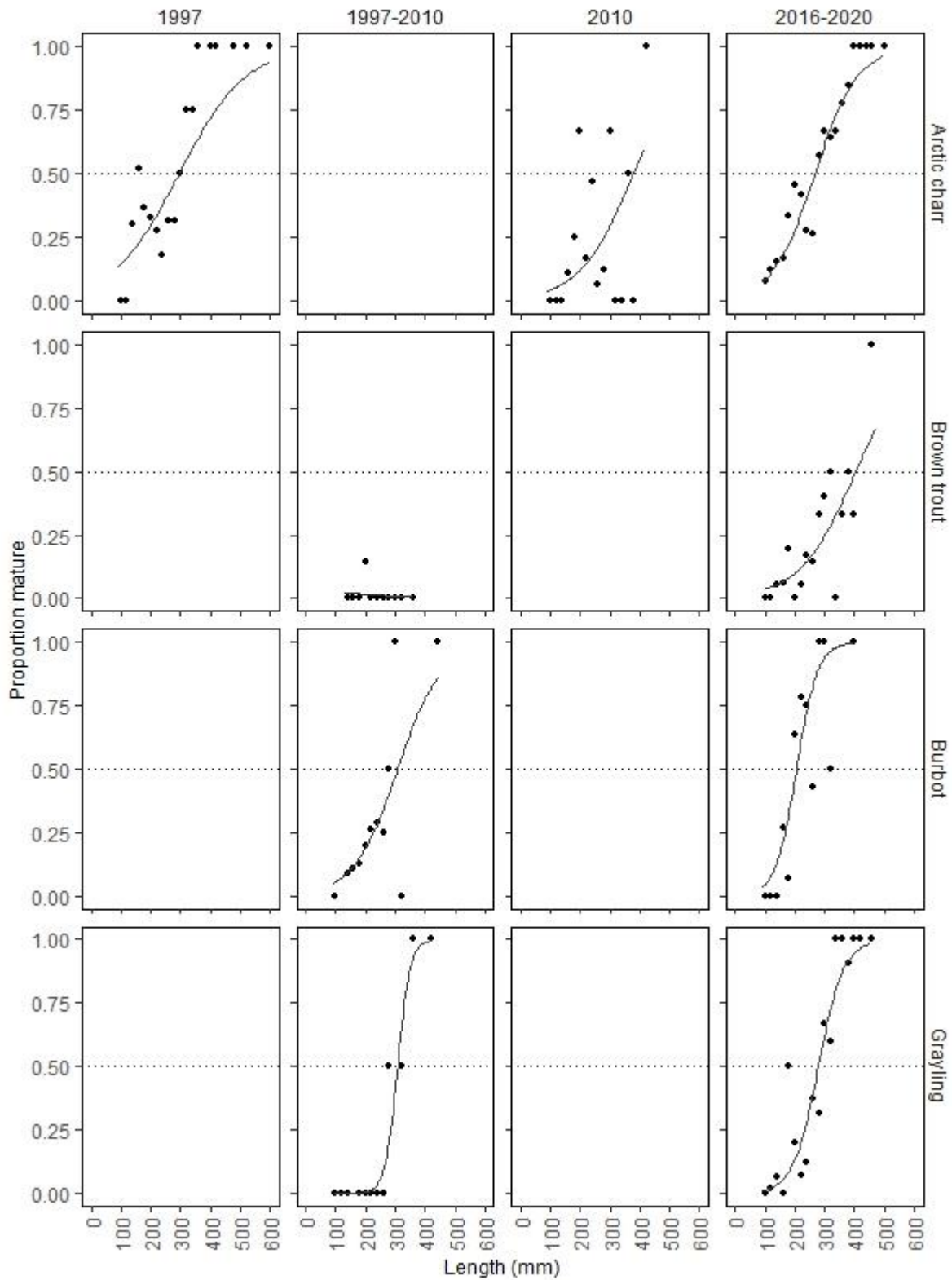
Appendix D

Proportion of mature individuals plotted against age classes (yr) with curves from logistic regression, with mature and immature individuals as binomial factors, for Arctic charr, brown trout, grayling, and burbot per period of sampling. Intercept of regression curve and dotted line indicate A_{50} .



Appendix E

Proportion of mature individuals plotted against length groups of 20 mm, with curves for logistic regression with mature and immature individuals as binomial factors, of Arctic charr, brown trout, grayling, and burbot per period of sampling. Intercept of regression curve and dotted line indicates L_{50} .



Appendix H

Age in years and length in mm \pm standard error at population 50 % maturity (A_{50} and L_{50}), for Arctic charr, brown trout, grayling, and burbot, per period of sampling. N is sample size per analysis.

Species	Period	N (A_{50})	$A_{50} \pm SE$	N (L_{50})	$L_{50} \pm SE$
Arctic charr	1997	468	5.4 \pm 0.4	495	295 \pm 20.0
	2010	112	7.4 \pm 1.4	118	379 \pm 54.9
	2016–2020	351	5.1 \pm 0.3	354	267 \pm 10.5
Brown trout	1997–2010	53	-	59	-
	2016–2020	144	9.2 \pm 2.9	145	405 \pm 55.6
Grayling	1997–2010	26	5.1 \pm 0.7	36	307 \pm 19.7
	2016–2020	221	3.9 \pm 0.2	225	278 \pm 8.6
Burbot	1997–2010	120	8.7 \pm 0.9	125	308 \pm 36.3
	2016–2020	113	4.4 \pm 0.2	113	205 \pm 7.5

