

Tonje Hornnæs

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Master's thesis in biology

Supervisor: Anders G. Finstad, Ole Kristian Berg

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Norwegian University of Science and Technology  
Faculty of Natural Sciences  
Department of Biology





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## Abstract

1. Populations of landlocked Arctic char (*Salvelinus alpinus*) living in high altitude subarctic and in Arctic lakes, as the only fish species present, are often characterised by the existence of two sympatric morphs: invertebrate feeding dwarfs with stunted growth and cannibalistic individuals reaching giant sizes. Several non-exclusive mechanisms have been suggested for controlling the recruitment of cannibalistic Arctic char: i) emergence of strong cohorts by internal control; ii) emergence of strong cohorts by external environmental variation (both in which is expected to cause pulses in dwarf and/or cannibal recruitment), by iii) early life differences in growth or by iv) genetic differences.
2. In this study I investigate the possible recruitment control by internal and external mechanisms, respectively. This is done by comparing observed size and age structures of char in standardized gillnet catches, and test for changes in these parameters within lake, across years (2002, 2009 and 2020) and within year, across lakes (11 lakes over a small area at Bear Island). A pulse recruitment is expected to show as temporal variation age distribution within lake. In the case of external environmental forcing of recruitment pulses, it is expected comparable observations of pulses in recruitment across lakes sampled the same year.
3. Size and age distribution in gillnet catches showed a bimodal pattern both among lakes and within lakes across years. There was no apparent difference in the observed age or size distribution when comparing samples between years within lake, and a lack of synchronicity in age distribution among lakes.
4. These findings do not indicate presence of recruitment pulses in char populations at Bear Island, thus they are not in accordance with the hypotheses of internal or external control mechanisms. The apparent stability of sampled char populations in this study may point towards a genetic component being important in the control and maintenance of dwarf-cannibal systems.

## Introduction

Intraspecific predation, or cannibalism, where both predator and prey belong to the same species (Claessen et al., 2004) is a widespread and important process in the biology of many species. It may influence population structure, life history, behaviour and competition for mates and resources (Polis, 1981). It is specifically through two major processes that the presence of cannibalism can affect population dynamics: (1) the decrease in density of conspecific prey through consumption, and (2) the energetic gain made by cannibals by feeding on conspecifics. It is shown that cannibals often share a resource with their conspecific prey, meaning that both predator-prey interactions and intraspecific competition can affect interactions with their prey (Claessen et al., 2000). Thus, cannibalism may have a twofold advantage for the cannibal by the direct energetic benefit from feeding on conspecifics and indirectly by reducing competition for shared resources (Claessen et al., 2000, Byström, 2006).

It is assumed that there is a maximum size of prey that the cannibals can catch due to e.g. gap limitations or the ability for prey to escape the predator (Christensen, 1996). It is therefore crucial for a cannibal to reach a size where a diet shift to prey of substantial energetic sizes is possible. Few individuals survive to these sizes, but those who do end up as one of few “giants” in the population (Claessen et al., 2004). This can lead to size dependent interactions between the cannibals and their prey.

Cannibalism occurs in many fish species (Smith and Reay, 1991), including cod (*Gadus morhua*) (Yaragina et al., 2009), Eurasian perch (*Perca fluviatilis*) (Persson et al., 2000), pike (*Esox lucius*) (Craig, 2008) and in Arctic char (*Salvelinus alpinus*) (Amundsen, 1994). Arctic char is the northern most distributed freshwater fish and is commonly found in allopatric populations, i.e. as the only fish species present, in subarctic and Arctic lakes (Klemetsen et al., 2003). These lakes are characterized by generally simple food web structure with few species present. Fish living in these low productive habitats may frequently occupy multiple trophic levels (Griffiths, 1994). Resource polymorphism and multiple life-history strategies often exist within the population (Taylor, 1999, Robinson and Parsons, 2002, Finstad and Berg, 2004, Berg et al., 2010, Amundsen, 2016). In northern Arctic char populations this frequently leads to an apparent bimodal distribution in length with an associated ontogenetic niche shift of larger individuals to cannibalism (Hammar, 2000). Both the size differences between morphs and frequency of cannibalism is shown to increase with latitude (Griffiths, 1994).

A prerequisite for such a bimodal size distribution in fish populations is the combination of (1) stagnation at the growth rate near the maximum length in the planktivorous niche and (2) an escape from the planktivorous niche by a rapid increase in the growth rate beyond this size for some individuals (Claessen et al., 2002). This may be the case for Arctic char populations as well, although in the northern lake environments plankton as a food source is often replaced by more benthic invertebrates, and often a high degree of *Chironomidae* (Svenning et al., 2007). This species is one of few insects living in Arctic environments and often appear in high concentrations making it an important food source for many insectivores including Arctic char (Finstad et al., 2006). Studies done on food choice by Arctic char on Spitsbergen (Svalbard), showed that smaller char (<150 mm) preyed upon zooplankton and chironomid larvae and pupae while the diet of larger char (>150 cm) consisted of smaller conspecifics, showing a cannibalistic behaviour all year around (Svenning et al., 2007).

This difference in diet between small and large char is reflecting contrasting life histories which is often associated with Arctic char cannibalism (Amundsen, 2016). The majority of the population are invertebrate feeders maturing early and at sizes below 150 mm (often coined as dwarfs). Restricted nutrient opportunities where most prey items available are small sized invertebrates such as chironomid larvae, causes dwarf char to remain at small sizes (Fig. 1) (Berg et al., 2010, Borgstrøm et al., 2015). However, some char feed on their dwarfed conspecifics and thus gain a higher potential to reach giant sizes (>400 mm) (Fig. 1) (Finstad et al., 2006). The cannibalistic individuals have to invest the energy in somatic growth rather than gonads to attain the minimum body length required for cannibalism, thus they often mature much later than the dwarfs (Finstad et al., 2006).





**Figure 1:** Arctic char of different lengths caught from Haussvatnet at Bear Island in 2020. The three bottom individuals are typical dwarfs, while the char at the top represent a typical cannibal. Photo: Tonje Hornnæs

The occurrence of two or more distinct char morphs in the same lake, such as dwarfs and giant cannibals, is commonly referred to as “the char problem” (Klemetsen, 2010). The underlying mechanisms controlling the emergence of multiple morphotypes remains unsolved. However, the proposed mechanisms can be structured into several non-exclusive hypotheses; i) emergence of strong cohorts by internal control; ii) emergence of strong cohorts by external environmental variation iii) early life differences in growth; iv) genetic differences.

*i) Emergence of strong cohorts by internal control*

The emergence of strong recruiting cohorts enhance the emergence of cannibals (Persson et al., 2000, Persson et al., 2004, Byström, 2006, Borgstrøm et al., 2015) by imposing competition and increased mortality on stunted adults, as well as providing a profitable recourse for a few adults to accelerate growth and reach giant sizes (Byström, 2006). Differences in year-to-year recruitment will result in some cohorts being stronger than others and thus not always providing the conditions necessary for char to enter the cannibalistic

niche. For this reason, the emergence of cannibals is expected to be frequency dependent and that an internal and underlying dynamic in the system controls the recruitment, i.e., a cannibal imposed top-down control on the dwarf part of the population (Byström, 2006). Cannibals is suggested to regulate the dwarf part of the population directly through predation, but also indirectly through causing an antipredator behaviour among dwarfs (Persson et al., 2000, Persson et al., 2004, Byström, 2006). In years with cannibal dominance the dwarfs are kept on low levels, both in number and in growth, thus the recruitment of strong cohorts is suppressed. As the dominate cannibal cohorts die out and the density of cannibals decrease, strong recruiting cohorts will emerge and provide conditions profitable for a new recruitment of some adult individuals to the cannibal niche (Persson et al., 2000, Persson et al., 2004). In this way, recruitment of both dwarfs and cannibals will occur in temporal pulses (Persson et al., 2000, Persson et al., 2004, Byström, 2006, Borgstrøm et al., 2015).

*ii) Emergence of strong cohorts by external environmental variation*

Recruitment pulses and emergence of cannibals could also be due to variation in external environmental conditions. It has been suggested that in cases where size-frequency polymorphism and a shift to cannibalism occur it is due to ontogenetic environmentally induced mechanisms, and often differences in food and growth (Svenning and Borgstrøm, 2005, Klemetsen, 2010). Every char individual has the potential to become a cannibal, it is just a result of environmental factors inducing variability in population density, alternative prey and size-differences between predator and prey (Svenning and Borgstrøm, 2005). For instance, a year with profitable melting of lake-ice in relation to hatching could lead to a strong recruiting cohort which in turn could enhance the emergence of cannibals. It is thus expected that environmentally induced mechanisms result in intermittent recruitment to the cannibal niche depending on environmental conditions (Borgstrøm and Museth, 2005, Borgstrøm et al., 2015).

*iii) Early life differences in growth*

Finstad et. al (2006) suggested that individual differences in resource availability among char in their early life stages cause some individuals to grow larger. In correlation with difference in timing of sexual maturity, this gives a possibility for some char to reach giant sizes. Already at early life stages the cannibals will have a larger growth and a delayed sexual maturity compared to dwarf individuals. According to this hypothesis, growth variation in

early life stages is a reason why some individuals becomes cannibals (Finstad et al., 2006, Florø-Larsen et al., 2016).

*iv) Genetic differences*

A high degree of genetic determination in life history choice and a strong genetic influence on cannibalistic behaviour is also suggested (Skúlason et al., 1996, Power et al., 2009). In contrast to the pulses in recruitment of cannibalistic char expected in environmentally and internally regulated populations, a more continued production of cannibals is expected in genetic determined populations, as found by Amundsen (2016). This is reflecting two contrasting temporarily stable life-history strategies within the char population (big and mature late vs. small and mature early), and possibly a genetic component causing stability in the cannibal system (Amundsen, 2016). Genetic differences between morphs have been suggested by some authors (Svenning, 1993, Amundsen et al., 1999, Gíslason et al., 1999, Janhunen et al., 2010). The evidence is, however, inconclusive and often relying on laboratory results which is difficult to extrapolate to natural settings (Svenning and Borgstrøm, 2005).

The purpose of the present study is to investigate several previously proposed mechanisms for the emergence of cannibalistic morphs in Arctic char populations. This is done by comparing observed size and age structure of Arctic char, and test for changes in these parameters within lakes over time and across lakes within year. I am going to test the following non-exclusive hypotheses:

- (1) Whether internal mechanisms in the char population cause the recruitment pulses of cannibalistic char.

In this case it is expected a temporal variation in age and growth of char within a lake due to differences in recruitment, and that removal of dominating cannibals will reduce the top-down control on the dwarf part of the population leading to strong recruiting cohorts. This hypothesis will be tested by comparing age and length structure of sampled char within lake over time.

- (2) Whether external environmental variation is controlling the temporal pattern of recruitment of cannibalistic char.

In this case it is expected that environmental conditions affect adjacent lakes in the same manner causing a similar recruiting pattern across lakes within cohort. This hypothesis will be

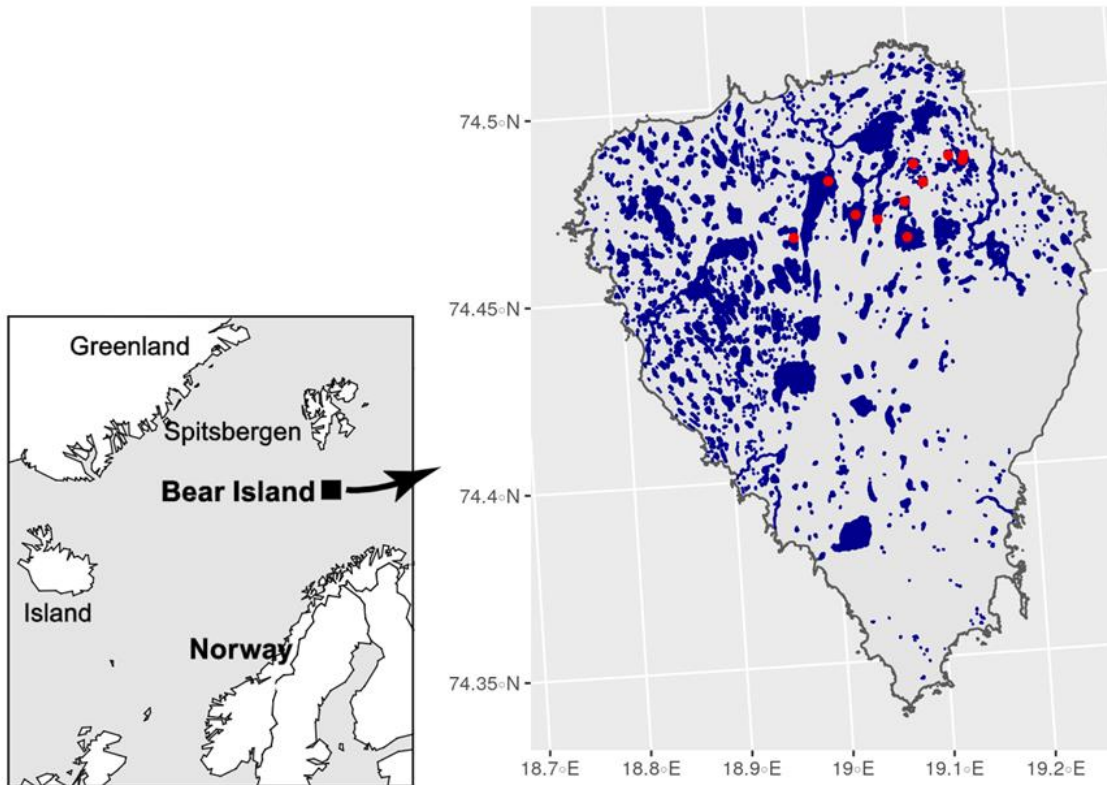
tested by comparing age distribution and modal age of char populations from different lakes sampled the same year.

In both cases I expect a temporal variable recruitment to the cannibalistic part of the population, either due to temporal differences in environmental conditions or due to year-to-year differences in strength of recruiting cohorts. External and internal mechanisms may also work together in that environmental conditions set the basis for high survival young resulting in strong recruiting cohorts which in turn will induce cannibalistic top-down controlling giants to emerge. The hypotheses differ in that I expect to see a synchronicity between lakes in a case of external control mechanisms, but less such between-lake synchronicity if internal control mechanism is dominating.

## **Study site**

### **Bear Island (nor. Bjørnøya)**

Bear Island (74.5 °N, 19.0°E) is a part of the High Arctic Archipelago of Svalbard, located in the Barents Sea approximately mid-distance from the coast of Finnmark (Norway) and the south end of Spitsbergen (Svalbard) (Fig.2). It is an isolated island stretching approximately 20 km from south to north, and 15 km from east to west, and has a total area of 178 km<sup>2</sup> (Scheie and Aarvik, 2005). The climate on Bear Island is relatively mild for an Arctic island with yearly average winter temperature of -6,6 °C, and summer temperature of 3,9 °C. Precipitation is low, on average 396 mm each year (Bilt et al., 2019). There are hundreds of lakes and ponds on Bear Island, and many of them is inhabited by Arctic char, which has an allopatric existence, meaning that it is the only fish species present in the lakes. The environmental conditions in these lakes are characterized by low temperatures all year around and few months without snow- and ice-cover. The ice-free period typically starts in May-June and lasts for only 2,5 to 3,5 months. Lakes at Bear Island are typically oligotrophic and monomictic (Klemetsen et al., 1985). They are relatively shallow, with clear water and bottom substrate generally consisting of stones, gravel, and fine sand. Mosses are usually the only macro-vegetation present. The shoreline often consists of larger boulders and gravel (Fig. 3) (Finstad and Berg, 2004). Bear Island was established as a nature reserve in August 2002 (Scheie and Aarvik, 2005), hence fishing activity on the island is negligible (Finstad and Berg, 2004). Data sampled from 11 different lakes at Bear Island was used in this study. Characteristics of sampled lakes is presented in table 1.



**Figure 2:** Sampling locations (indicated by red dots) at Bear Island 74.5 °N, 19.0°E in the Barents Sea.



**Figure 3:** Nordre Steinsjø, a typical Arctic char lake at Bear Island. A shallow lake with clear water and no higher vegetation, bottom substrate consisting of stones and fine sand and the shoreline consisting of lager boulders. Photo: Tonje Hornnæs

**Table 1:** Lake characteristics of sampled lakes. Latitude and longitude of lake centroid, surface areal (1000 m<sup>2</sup>) and maximum depth (m) of respective lakes.

Lake	Latitude	Longitude	Areal (1000m <sup>2</sup> )	Max depth (m)
Trestikkelen	74,47203	19,08772	100	4,8
Spælvatnet	74,46769	19,05973	155	2,5
Stevatnet	74,46936	19,03811	380	9,9
Lygna	74,46251	19,08806	531	20,5
Nordre Steinsjø	74,48191	19,09887	97	7,2
Søndre Steinsjø	74,47685	19,10746	65	5,6
Torstjønna	74,48333	19,15	66	4,6
Haussvatnet	74,47882	19,01297	1083	4,1
Haabethvatnet	74,482	19,14839	192	7
Olatjønna	74,48356	19,1344	44	5,5
Spongvatnet	74,4642	18,97488	214	2,3

## Materials and methods

### Sampling

Arctic char was sampled in 2002, 2009 and 2020. Sampling was conducted in altogether 11 lakes, but not all lakes were sampled all three years (Tab. 2). For some of the lakes, production estimates and otolith sizes at hatching have been described (Finstad and Berg, 2004, Berg et al., 2010, Florø-Larsen et al., 2016). In the sample-lakes, Arctic char has an allopatric existence, and the lakes were chosen because char are typically occurring in two distinct morphs: dwarfs and cannibals (Finstad and Berg, 2004, Berg et al., 2010). Char of both morphs were found in all the sampled locations.

Fish were captured using a “NORDIC” multi-mesh gillnet. This is a monofile gillnet (30 m x 1.5 m) with evenly distributed mesh sizes in every net (Appelberg et al., 1995). The net used were a slight modification of the original NORDIC series as the two smallest mesh sizes (5 and 6.25 mm) were excluded. Mesh sizes used were: 8 mm, 10 mm, 12.5 mm, 15.5 mm, 19.5 mm, 24 mm, 29 mm, 35 mm, and 45 mm. The effort varied between 10 and 120 gillnet nights in each lake per year (Tab. 1). Results from multiple fish-efforts were averaged and analysed as a single data point for a given year in the final analyses. In Lake Trestikkelen in the years 2002 and 2009 an extensive fishing was conducted in order to remove all cannibals from the lake.

Total length (mm) and mass (g) were measured within few hours after capture. The fish were dissected, and sex and maturity determined. Otoliths were sampled and stored in dry envelopes. The larger otoliths were put in small Eppendorf tubes to prevent them from breaking. The tubes were kept open so the otoliths would dry. A small piece of cotton was used to plug the tubes ensuring air access and preventing the otoliths from falling out.

From the initial material (Tab. 2) char were assigned either as dwarfs or cannibals based on size. The length-age relationship of sampled char from different lakes and years points towards a stagnation in growth around 200 mm for a large fraction of char (see Fig. 5, Result section), possibly indicating a switch to cannibalism around this size. For this reason, individuals with body length < 200 mm (total length) were assigned as dwarfs and larger individuals ( $\geq 200$  mm) were assigned as cannibals. To be sure no dwarfs were included in the cannibal fraction of the sample, upper length-limit for dwarfs was set to 200 mm (Svenning et al., 2007). The length group <200 mm most likely includes juvenile cannibalistic char, but their number is considered negligible due to population estimates of Arctic char populations showing a high ratio between dwarfs and cannibals (Finstad et al., 2001, Finstad and Berg, 2004, Berg et al., 2010, Borgstrøm et al., 2015). It is assumed that the recruitment to cannibalism reflects this number, hence the notation “dwarf” char is used for all char below 200 mm. The material for the final analysis is presented in table 2.

### **Age determination**

The age of captured individuals was determined by counting the growth-rings in their otoliths (Fig. 4). The different zones on the otolith represent the annual growth of the individuals. The middle zone is the hatching ring of the individual and the following light and dark zones represent growth in summer and winter, respectively. The length of one winter zone (dark zone) to the next represent one year of growth. Age was determined by counting the winter zones using a Leica MZ6 microscope. The otoliths were put in a black vessel to give better contrast.



**Figure 4:** Otoliths from Arctic char sampled at Bear Island in 2020. The alternating dark and light zones represent growth in winter and summer, respectively. Age of char can be determined by counting the winter zones. Left otolith is taken from a dwarf (106 mm, 8 g, 5+, sampled in Lake Trestikkelen) and right otolith is from a cannibal individual (450 mm, 672 g, 21+ years, sampled in Lake Lygna). Photo: Tonje Hornnæs

### **Statistical analyses**

In order to test the hypothesis on whether internal mechanisms control the cannibal-recruitment, differences in age-distribution, growth (expressed by the length at age relationship), modal age and probability of maturing at a specific age of the char in gillnet samples was compared between sampling years for each lake separately. I chose to compare distribution from gillnet catches instead of for example cohort strength due to issues with gillnet selectivity and low sample size in each cohort. Lakes with less than 15 datapoints per year (i.e., number of captured fish within year) were excluded from the final analysis. This left Spælvatnet, Stevatnet and Lake Lygna suitable for analysis (Tab. 2). In addition, Lake Trestikkelen was included in the analysis, despite few datapoints in 2020 (Tab. 2), to test the effect of removal of cannibals by the extensive fishing conducted in 2002 and 2009.



Differences in age distribution of char in gillnet samples between sampling years within chosen sampling lakes (i.e., Lake Trestikkelen, Spælvatnet, Stevatnet and Lake Lygna) was tested using a chi-square test. Char in gillnet catches from each sampling year and lake was divided into two length classes, char <200 mm (dwarfs) and char  $\geq$ 200 mm (cannibals) and the following statistical analyses was conducted on the different length classes separately. Differences between years in average length of dwarfs and cannibals respectively were tested with Student's t-tests. Between-year differences within lake in modal age of dwarfs and cannibals respectively were tested with a Kruskal Wallis-test. Differences in growth with time was tested for using linear regression with length (mm) as response variable and age and year of sampling as predictors. This analysis was used as an indirect measure of growth differences presuming that large differences in growth would result in differences in length at age. Age and length data were log transformed before the final analysis. All statistical analyses were conducted in R Version 3.6.1. (R Core Team, 2019). Figures were made by use of the package ggplot (Wickham, 2016). Significance was accepted at the 5% level.

In order to test the hypothesis on external environmental variation controlling the cannibal-recruitment, age structure of char in gillnet catches was compared between lakes within the same sampling year. All lakes (Tab. 1) were included in this analysis. Differences in age distribution of char sampled in different lakes within respective sampling years was tested with a chi-square test. Differences in modal age of dwarfs (char <200 mm) and cannibals (char  $\geq$ 200 mm) respectively were tested with a Kruskal Wallis test, separately.

**Table 2:** Total number of char caught with gillnets in respective sampling lakes and years, total number of gillnet-nights and number of cannibals and dwarfs in the sample.

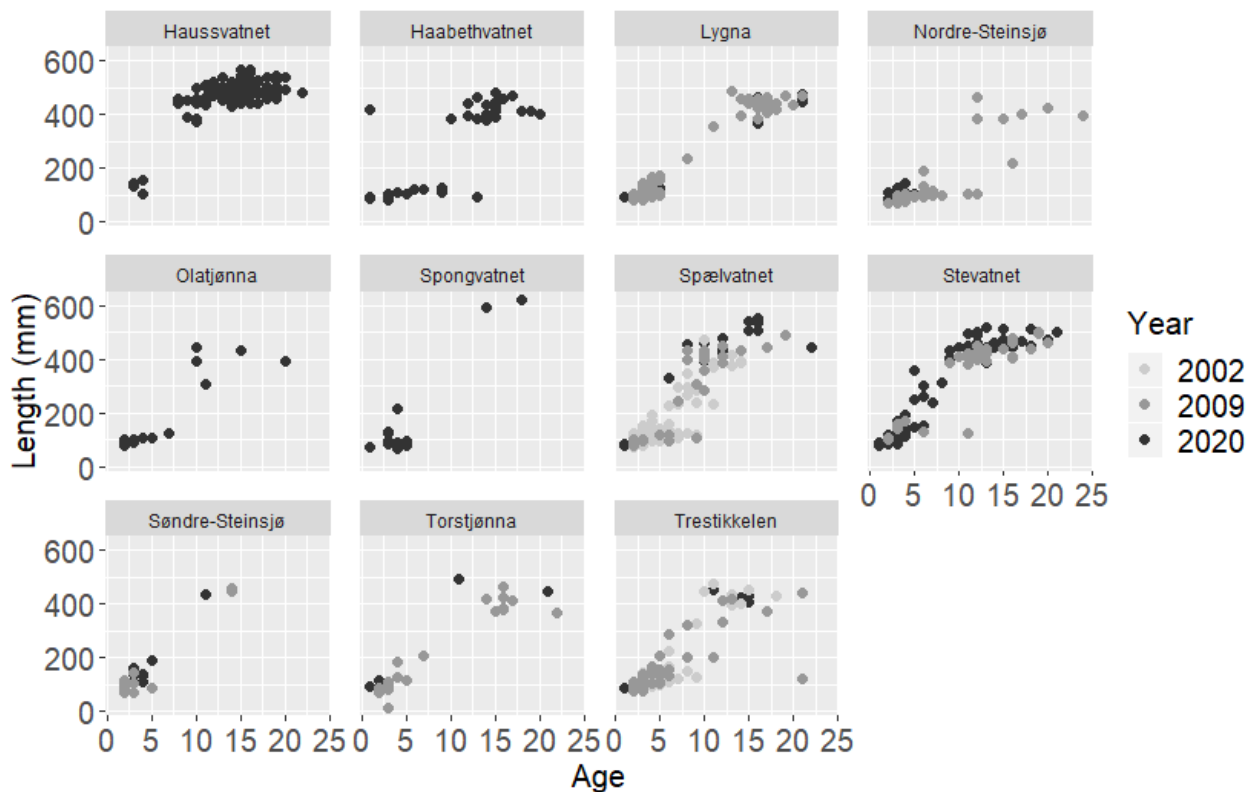
Locality and year	Number of gillnet-nights	Total number of sampled individuals	Number of sampled cannibals	Number of sampled dwarfs
Trestikkelen 2002	60	315	10	305
Trestikkelen 2009	90	76	10	66
Trestikkelen 2020	10	12	5	7
Spælvatnet 2002	120	122	18	104
Spælvatnet 2009	45	30	15	15
Spælvatnet 2020	30	38	17	21
Stevatnet 2009	15	34	27	7
Stevatnet 2020	20	79	39	40
Lygna 2009	15	70	26	44
Lygna 2020	10	16	5	11
Nordre Steinsjø 2009	45	47	7	40
Nordre Steinsjø 2020	10	14	0	14
Søndre Steinsjø 2009	45	15	3	12
Søndre Steinsjø 2020	10	11	1	10
Torstjønnå 2009	30	26	9	17
Torstjønnå 2020	10	5	2	3
Haussvatnet 2020	20	95	89	6
Haabethvatnet 2020	20	36	19	17
Olatjønnå 2020	10	18	5	13
Spongvatnet 2020	20	13	3	10

## Results

### Age and length structure overview

The length at age-relationship of char in gillnet catches points towards a stagnation in growth for a large fraction of char, while some char reached considerably larger sizes (Fig. 5). Based on a visual examination of the plot, the growth stagnation seems to occur at age up to 8+ for most char, reaching a maximum size of about 200 mm (Fig. 5). Some char-individuals, from age 10+ all the way up to 22+, reached considerably larger sizes, from 400 mm to 600 mm (Fig. 5). The difference in growth appears to occur after the age of 5+ for most populations, although in some populations there are fish of older age (10+) remaining at small sizes (<200 mm).

Dwarfs in gillnet catches from different sample lakes did not show a great divergence in length and age compared to the cannibals (Tab. 3). Average length of dwarfs varied from 97 to 134 mm, with a modal length varying from 84 to 135 mm. Their average age varied from 2 to 5 years with modal age varying from 2 to 4 years. The cannibals in gillnet catches had a greater divergence in length and age among lakes compared to the dwarfs. Average length varied from 319 to 486 mm with a modal length varying from 297 to 590 mm. Average age varied from 10 years up to 19 years, with modal age varying from 9 to 21 years (Tab. 3).

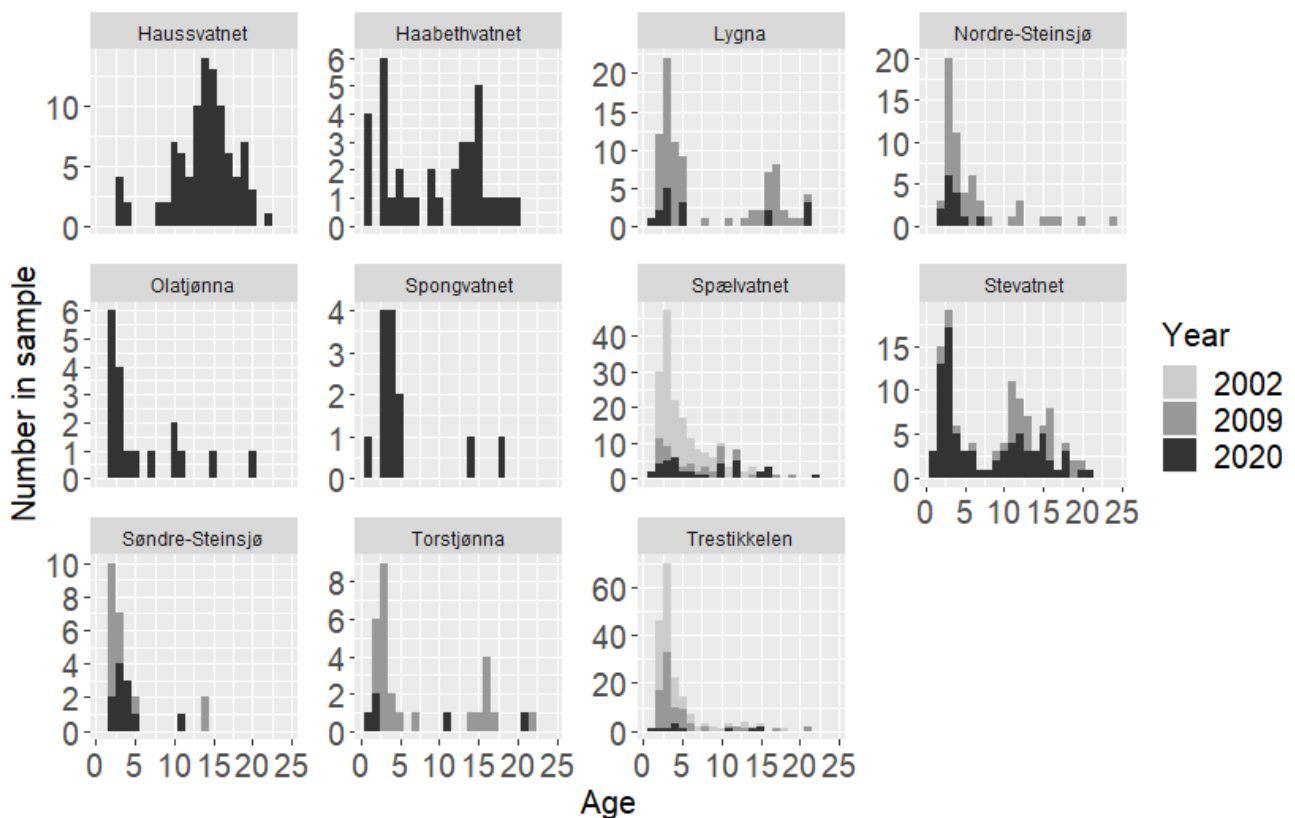


**Figure 5:** Number of Arctic char individuals from gillnet catches in different length-classes (mm) from lakes sampled in 2002 (light grey symbols), 2009 (dark grey symbols) and 2020 (black symbols).

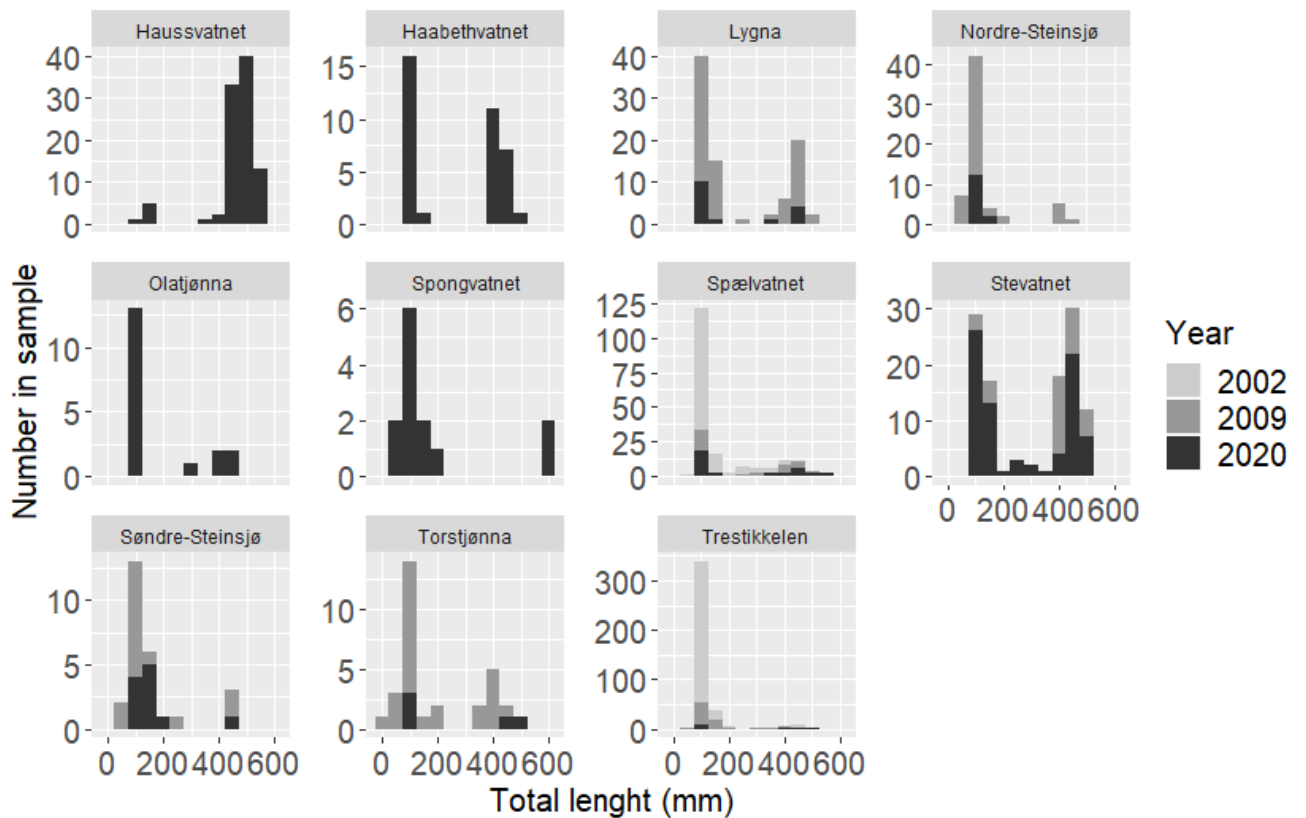
**Table 3:** Mean length (mm) and age ( $\pm$  SD), and modal length (mm) and age for Arctic char caught in gillnets in respective sampling lakes, sampling-year, and length classes (<200 and  $\geq$ 200 mm).

Length class (mm)	Year	Lake	n	Mean length [mm]	Modal length [mm]	Mean age	Modal age	
<200	2002	Trestikkelen	90	106 $\pm$ 19	104	3.2 $\pm$ 1.4	3	
	2009		65	114 $\pm$ 23	112	3.5 $\pm$ 2.4	3	
	2020		7	101 $\pm$ 12	106	3.3 $\pm$ 1.4	4	
	2002	Spælvatnet	98	107 $\pm$ 20	104	3.7 $\pm$ 1.5	3	
	2009		15	94 $\pm$ 14	95	3.5 $\pm$ 2.1	3	
	2020		21	105 $\pm$ 19	103	3.4 $\pm$ 1.5	3	
	2009	Stevatnet	7	133 $\pm$ 26	130	4.4 $\pm$ 3.2	3	
	2020		40	116 $\pm$ 26	113	2.8 $\pm$ 1.0	3	
	2009	Lygna	44	114 $\pm$ 26	106	3.3 $\pm$ 1.0	3	
	2020		11	102 $\pm$ 17	95	3.2 $\pm$ 1.3	3	
	2009	Nordre Steinsjø	36	94 $\pm$ 21	91.5	4.6 $\pm$ 2.2	4	
	2020		14	107 $\pm$ 15	104.5	3.6 $\pm$ 1.3	3	
	2009	Søndre Steinsjø	12	92 $\pm$ 23	84	2.5 $\pm$ 0.9	2	
	2020		10	134 $\pm$ 26	133.5	3.3 $\pm$ 0.9	3	
	2009	Torstjønna	16	94 $\pm$ 36	91.5	3 $\pm$ 0.8	3	
	2009		3	99 $\pm$ 14	95	1.7 $\pm$ 0.6	2	
	2020	Hausvatnet	6	134 $\pm$ 16	134.5	3.3 $\pm$ 0.5	3	
	2020		17	101 $\pm$ 15	103	4.6 $\pm$ 3.3	3	
	2020	Olatjønna	13	94 $\pm$ 13	92	3.1 $\pm$ 1.5	3	
	2020	Spongvatnet	10	92 $\pm$ 22	89.5	3.5 $\pm$ 1.2	3.5	
	$\geq$ 200	2002	Trestikkelen	10	403 $\pm$ 75	429.5	12.2 $\pm$ 3.4	13
		2009		10	320 $\pm$ 93	327.5	11.3 $\pm$ 4.9	11.5
		2020		4	427 $\pm$ 20	426	13.8 $\pm$ 1.9	14.5
		2002	Spælvatnet	18	319 $\pm$ 74	296.5	9.7 $\pm$ 2.5	9
		2009		15	393 $\pm$ 67	407	11.2 $\pm$ 3.3	10
		2020		17	452 $\pm$ 63	443	12.6 $\pm$ 3.8	12
2009		Stevatnet	27	432 $\pm$ 33	424	13.8 $\pm$ 3.0	13	
2020			39	423 $\pm$ 71	452	12.5 $\pm$ 3.0	12	
2009		Lygna	25	431 $\pm$ 50	443	16.2 $\pm$ 2.7	17	
2020			5	444 $\pm$ 45	464	19 $\pm$ 2.7	21	
2009		Nordre Steinsjø	7	381 $\pm$ 78	395	16.6 $\pm$ 4.3	16	
2020			0	-	-	-	-	
2009		Søndre Steinsjø	2	452 $\pm$ 11	452	14	14	
2020			1	433	433	11	11	
2009		Torstjønna	9	381 $\pm$ 73	386	15.4 $\pm$ 3.9	16	
2009			2	470 $\pm$ 36	469.5	16 $\pm$ 7.1	16	
2020		Hausvatnet	89	486 $\pm$ 38	486	14.5 $\pm$ 3.0	14	
2020			19	422 $\pm$ 31	413	14.1 $\pm$ 4.0	15	
2020		Olatjønna	5	394 $\pm$ 55	392	13.2 $\pm$ 4.3	11	
2020		Spongvatnet	3	475 $\pm$ 226	590	12 $\pm$ 7.2	14	

The age and length (mm) distribution of Arctic char in gillnet catches from Bear Island was in general characterised by a bimodal pattern (Fig. 6 and 7 respectively). Based on a visual examination of the plots there was an apparent higher representation of some age and length classes. There was a high representation of the age classes 1+ to 5+, and a lower, yet prominent, representation of 10+ to 15+ relative to the intermediate age classes (Fig. 6). This pattern was prominent in gillnet samples from lake Lygna, Lake Trestikkelen, Spælvatnet and in Stevatnet, but also in Nordre- and Søndre-Steinsjø, Torstjønnna and Haussvatnet (Fig. 6). In contrast, in Haussvatnet the age-classes 10+ to 20+ was seemingly more represented than the younger age-classes. Likewise, for length distribution, there was an apparent higher representation of char in the length classes 100-200 mm and 400-500 mm (Fig. 7). Both the intermediate age and length classes had a low representation relative to other classes. In Spælvatnet the intermediate classes are represented in a prominently high degree relative to the other sampling locations (Fig. 6 and 7).



**Figure 6:** Number of Arctic char individuals from gillnet catches in different age-classes from lakes sampled in 2002 (light grey bars), 2009 (dark grey bars) and 2020 (black bars)

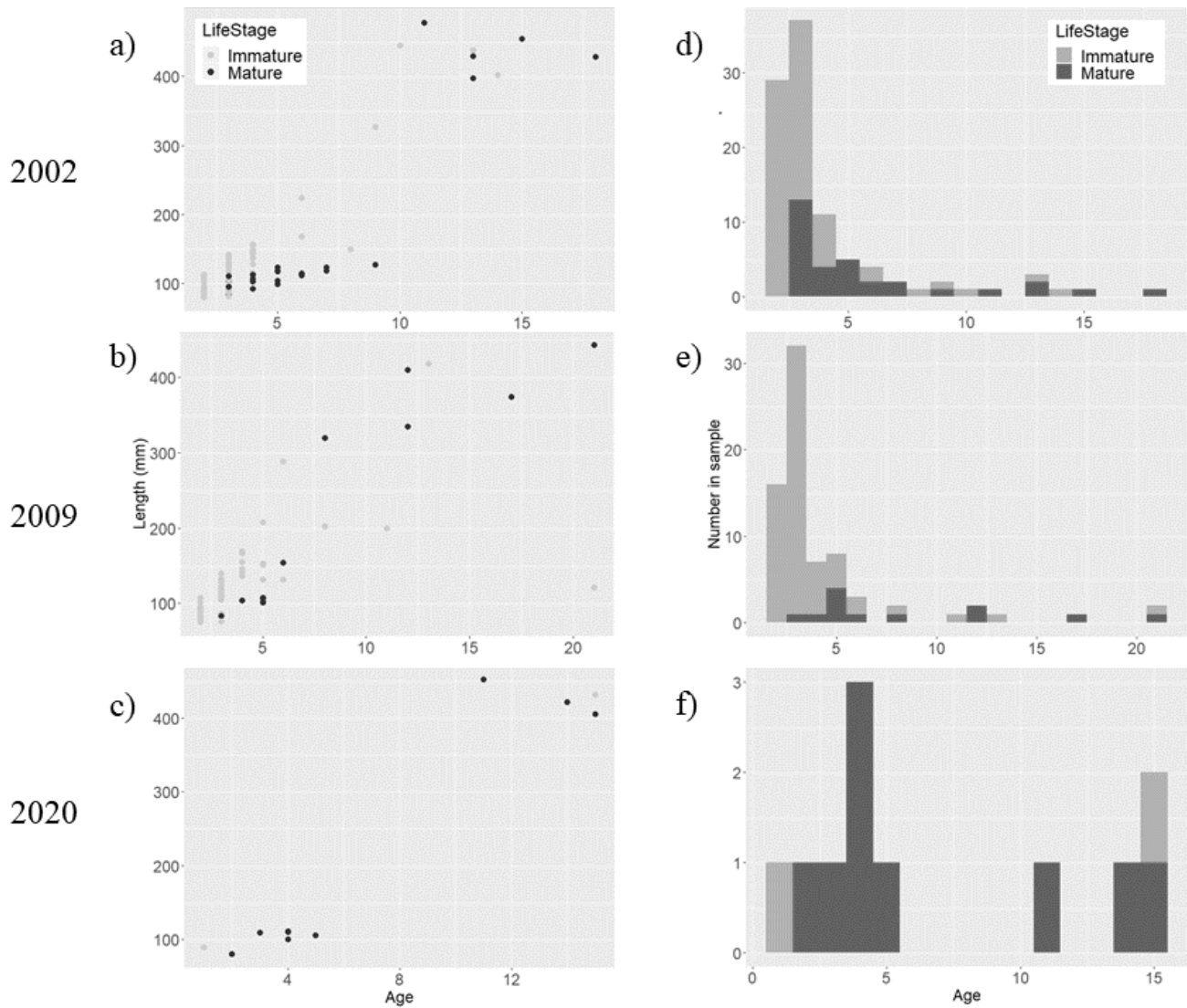


**Figure 7:** Length (mm) at age relationship for Arctic char caught in gillnets from lakes sampled in 2002 (light grey bars), 2009 (dark grey bars) and 2020 (black bars).

### **Test of internal control mechanisms: temporal age and size structure within lake**

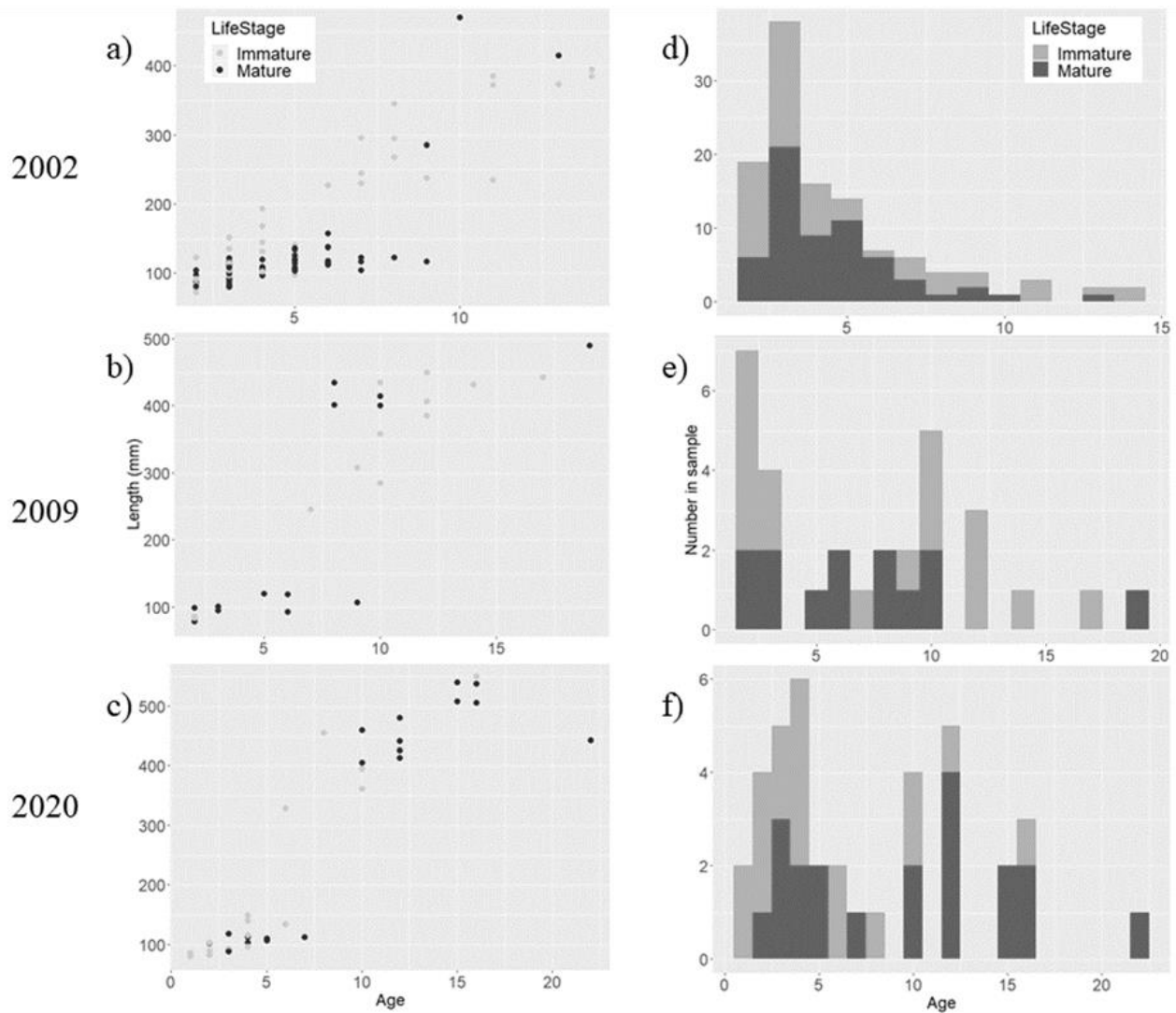
There were not any apparent strong cohorts when comparing the age and length structure of char from gillnet samples in Lake Trestikkelen across years (Fig. 8). Average length of dwarfs (<200 mm) was significantly smaller in 2002 and 2020 than in 2009 (Tab. 4). The cannibals (>200 mm) in the 2002 and 2020 samples were significantly larger in average length than cannibal char from the 2009 samples (Tab. 4). Growth of char in the sample (expressed through length at age) was significantly affected by age, but not by sampling year (Tab. 5). Further it appeared to be no difference in age distribution of char between the 2002 and 2009 samples (Tab. 6). However, there was a significant difference between the years 2009 and 2020 (Tab. 6). It appeared to be no significant difference in modal age among years, neither for dwarfs (Tab. 7) nor cannibals (Tab. 7). There was a representation of both mature and immature individuals among younger char (<7 yrs.) in samples from all years (Fig. 8). In 2002 and 2009 a higher percentage of the sample were immatures (72 % and 89 % in 2002 and 2009 respectively) while in the 2020 sample very few were immatures. However, sample sizes were small in 2020 (1 of 6 captured individuals).

There was no indication of presence of strong cohorts in Spælvatnet based on examination of the differences in age distribution and length at age relationship between years of Arctic char in the gillnet samples (Fig. 9). Average length of dwarfs (<200 mm) was significantly lower in 2009 than in 2002 and 2020 (Tab. 4). Likewise, among cannibals (>200 mm), average length of char in the 2009 sample was significantly smaller than the ones in the 2020 sample, but in contrast, had a significantly higher average length than cannibal char from the 2002 sample (Tab. 4). Length at age of both dwarfs and cannibals was dependent on age. The sample year 2020 also had a significant effect on length at age of dwarfs (Tab. 5). The age distribution of char from the 2002 sample appeared to be significantly different from the distribution in 2009, but the gillnet catches showed no significant difference between 2009 and 2020 (Tab. 6). Further, it appeared to be no significant difference in modal age among years, neither for dwarfs (Tab. 7) nor cannibals (Tab. 7). Both immature and mature individuals were represented in the gillnet catches (Fig. 9). Among young char (<7 yrs.) the distribution of matures and immatures were more even than among older char ( $\geq 7$  yrs.). Immatures largely dominated among older char in the 2002 and 2009 samples (64 and 63 % in 2002 and 2009, respectively), while in 2020 mature individuals were more represented, by a slightly higher fraction (71%).



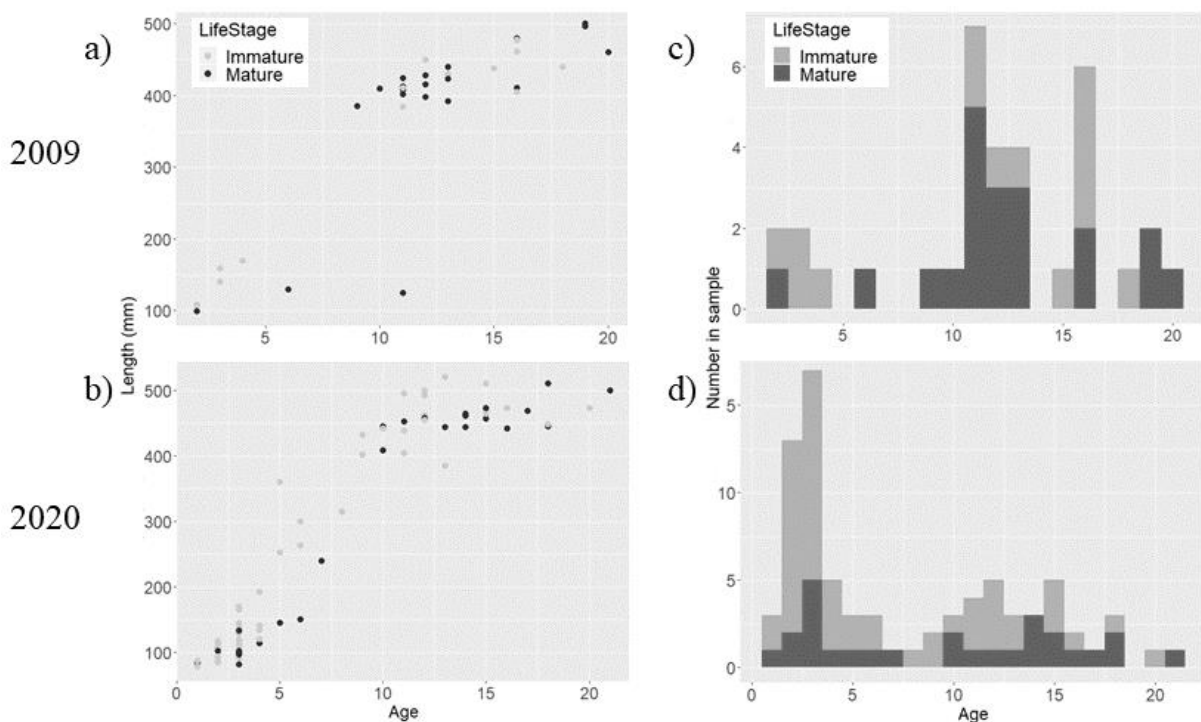
**Figure 8:** Age distribution of Arctic char caught in gillnets in Lake Trestikkelen in respective sampling years. (a-c) Length (mm) of char in different age classes. Maturity-level indicated by grey (immature) and black (mature) symbols. (d-e) Number of char in different age classes. Fraction of immature and mature individuals in each age-class is indicated by light grey and dark grey colour of the bars, respectively.



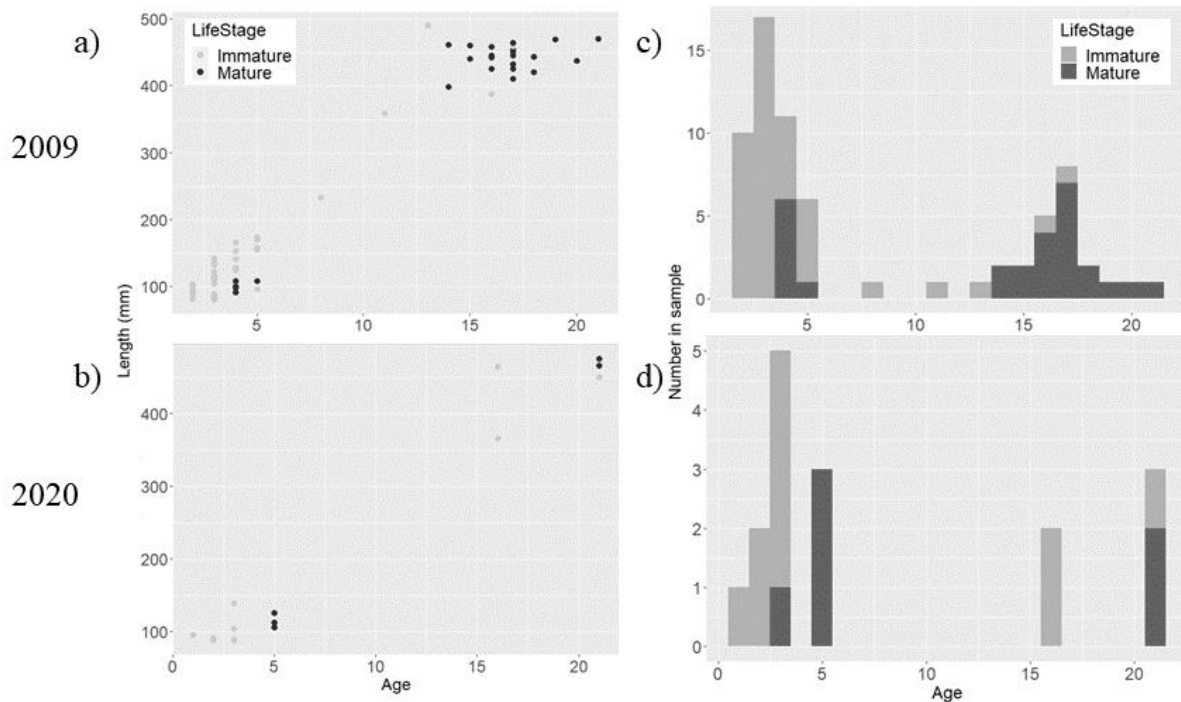


**Figure 9:** Age distribution of Arctic char caught in gillnets in Spælvatnet in respective sampling years. (a-c) Length (mm) of char in different age classes. Maturity-level indicated by grey (immature) and black (mature) symbols. (d-f) Number of char in different age classes. Fraction of immature and mature individuals in each age-class is indicated by light grey and dark grey colour of the bars, respectively.

There was a clear bimodal pattern, and no indication of strong year classes in the between years comparison of differences in age distribution and length at age relationship of char in gillnet catches from Stevatnet (Fig.10) and Lake Lygna (Fig.11). For both lakes, there was no significant difference in average length between char of the 2009 samples compared to the 2020 sample, neither for dwarf (Tab. 4) nor cannibal (Tab. 4) char. The length at age of char in the sample from Lake Lygna was significantly affected by age, but not sampling year (Tab. 5). This was also the case for cannibal char from the Stevatnet sample (Tab. 5). The length at age of dwarfs in Stevatnet was dependent on sampling year alone and also sampling year in interaction with age. Age alone had no apparent effect on length at age of dwarfs in the Stevatnet sample (Tab. 5). Further, age distribution of char in the sample from Lake Lygna does not show a significant difference between years, but there is a significant difference in age distribution of char in the Stevatnet sample (Tab. 6). Likewise, modal age revealed no significant difference in the between year comparison, neither for dwarfs (Tab. 7) nor cannibals (Tab.7).



**Figure 10:** Age distribution of Arctic char caught in gillnets in Stevatnet in respective sampling years. (a-b) Length (mm) of char in different age classes. Maturity-level indicated by grey (immature) and black (mature) symbols. (c-d) Number of char in different age classes. Fraction of immature and mature individuals in each age-class is indicated by light grey and dark grey colour of the bars, respectively.



**Figure 11:** Age distribution of Arctic char caught in gillnets in Lake Lygna in respective sampling years. (a-b) Length (mm) of char in different age classes. Maturity-level indicated by grey (immature) and black (mature) symbols. (c-d) Number of char in different age classes. Fraction of immature and mature individuals in each age-class is indicated by light grey and dark grey colour of the bars, respectively.

**Table 4:** t-values, degrees of freedom and p-values from the t-test of the between-year-comparison (2002/2009 and 2009/2020) of average length of Arctic char in different length classes (<200 and  $\geq$ 200 mm) from gillnet catches sampled in respective lakes.

Length class (mm)	Lake	2002/2009			2009/2020		
		t-value	df	p-value	t-value	df	p-value
<200	Trestikkelen	-2.21	123.08	0.029	2.44	11.63	0.032
	Spælvatnet	3.23	24.95	0.003	-1.98	33.99	0.055
	Stevatnet				1.57	8.35	0.153
	Lygna				1.93	23.28	0.066
$\geq$ 200	Trestikkelen	2.19	17.22	0.042	-3.46	10.72	0.006
	Spælvatnet	-2.97	30.78	0.006	-2.55	28.98	0.016
	Stevatnet				-0.07	57.72	0.930
	Lygna				-0.59	6.22	0.580

**Table 5:** Summary table of the analysis of differences in length (mm) at age among Arctic char in gillnet catches between years in a linear model for respective lakes and length classes (<200 and ≥200 mm). The response variable measured was size (length in mm) and the predictors were age and years (sampling year). Given are values of estimate (±SE), t-values and p-values for the intercept, between length and age (Age), between length and year (2009 and 2020) and the interaction between length and age and year (Age/2009 and Age/2020).

Lake	Length class (mm)	Predictor	Estimate (±SE)	t-value	p-value
Trestikkelen	<200	Intercept	4.37 ± 0.05	83.42	<0.001
		Age	0.25 ± 0.05	5.51	<0.001
		2009	0.01 ± 0.08	0.08	0.939
		2020	0.06 ± 0.15	0.38	0.703
		Age/2009	0.04 ± 0.07	0.66	0.511
		Age/2020	-0.09 ± 0.12	-0.70	0.486
	≥200	Intercept	4.56 ± 0.5	9.13	<0.001
		Age	0.58 ± 0.2	2.85	0.011
		2009	0.03 ± 0.6	0.06	0.954
		2020	2.17 ± 2	1.10	0.288
		Age/2009	-0.09 ± 0.2	-0.38	0.712
		Age/2020	-0.83 ± 0.8	-1.10	0.286
Spælvatnet	<200	Intercept	4.3 ± 0.05	90.22	<0.001
		Age	0.3 ± 0.04	7.97	<0.001
		2009	0.005 ± 0.1	0.05	0.961
		2020	0.1 ± 0.09	1.09	0.280
		Age/2009	-0.08 ± 0.08	-1.03	0.305
		Age/2020	-0.07 ± 0.07	-1.06	0.291
	≥200	Intercept	4.33 ± 0.3	14.10	<0.001
		Age	0.63 ± 0.1	4.63	<0.001
		2009	0.62 ± 0.5	1.34	0.186
		2020	0.95 ± 0.4	2.22	0.032
		Age/2009	-0.2 ± 0.2	-1.04	0.305
		Age/2020	-0.3 ± 0.2	-1.65	0.106
Stevatnet	<200	Intercept	4.76 ± 0.2	30.00	<0.001
		Age	0.09 ± 0.1	0.80	0.428
		2020	-0.38 ± 0.2	-2.19	0.034
		Age/2020	0.29 ± 0.1	2.19	0.034
	≥200	Intercept	5.37 ± 0.2	23.52	<0.001
		Age	0.27 ± 0.1	3.03	0.004
		2020	-0.37 ± 0.3	-1.47	0.148
		Age/2020	0.16 ± 0.1	1.63	0.108
Lygna	<200	Intercept	4.27 ± 0.1	39.38	<0.001
		Age	0.39 ± 0.1	4.27	<0.001
		2020	0.18 ± 0.2	1.02	0.314
		Age/2020	-0.24 ± 0.2	-1.56	0.124
	≥200	Intercept	4.5 ± 0.3	16.46	<0.001
		Age	0.57 ± 0.1	5.71	<0.001
		2020	0.32 ± 1.0	0.33	0.743
		Age/2020	-0.13 ± 0.33	-0.40	0.695

**Table 6:** Chi-square values, degrees of freedom and p-values from the chi-square analysis for test of difference in age distribution between years (2002/2009 and 2009/2020) among Arctic char from gillnet catches within the respective sampling lakes.

	2002/2009			2009/2020		
	Chi-square	df	p-value	Chi-square	df	p-value
Trestikkelen	17.39	16	0.361	34.38	14	0.002
Spælvatnet	46.48	14	<0.001	20.55	16	0.196
Stevatnet				34.14	20	0.025
Lygna				21.46	15	0.122

**Table 7:** H-value, degrees of freedom (in parentheses) and p-value from the Kruskal-Wallis test of the between year comparisons (2002/2009 and 2009/2020) of modal age of Arctic char in different length classes (<200 and  $\geq$ 200 mm) from gillnet catches in respective lakes.

Lake	Predictors	Estimate ( $\pm$ SE)	z-value	p-value
Trestikkelen	Intercept	-1.81 $\pm$ 0.4	-4.41	<0.001
	Age	0.25 $\pm$ 0.1	3.03	0.002
	2009	-1.15 $\pm$ 0.7	-1.62	0.105
	2020	3.61 $\pm$ 1.4	2.51	0.012
	Age/2009	-0.01 $\pm$ 0.1	-0.08	0.933
	Age/2020	-0.29 $\pm$ 0.2	-1.74	0.082
Spælvatnet	Intercept	0.30 $\pm$ 0.4	0.83	0.409
	Age	-0.04 $\pm$ 0.1	-0.63	0.529
	2009	-0.37 $\pm$ 0.8	-0.48	0.628
	2020	-1.38 $\pm$ 0.2	-1.91	0.056
	Age/2009	0.02 $\pm$ 0.1	0.15	0.878
	Age/2020	0.21 $\pm$ 0.1	2.03	0.042
Stevatnet	Intercept	-0.26 $\pm$ 0.9	-0.28	0.781
	Age	0.05 $\pm$ 0.1	0.72	0.475
	2020	-1.17 $\pm$ 1.2	-1.15	0.250
	Age/2020	0.04 $\pm$ 0.1	0.52	0.600
Lygna	Intercept	-2.82 $\pm$ 0.6	-4.87	<0.001
	Age	0.29 $\pm$ 0.1	4.85	<0.001
	2020	1.87 $\pm$ 1.0	1.91	0.057
	Age/2020	-0.24 $\pm$ 0.1	-2.61	0.009

**Test of external environmental variation as control mechanism: age structure between lakes within year**

There was a significant difference in age distribution of Arctic char in gillnet catches when comparing across lakes within the same sampling year (Tab. 8). The age distribution was different among lakes in 2009 and 2020 but there was no significant difference between char from the two lakes sampled in 2002 (Tab. 8). Modal age of both dwarfs and cannibals differed also among lakes within the same sampling year (Tab. 9). There was a significant difference in modal age of dwarfs in the 2002 and 2009 samples, but no significant difference in 2020. Modal age of cannibals differed among lakes sampled in 2009 and 2020, but there was no significant difference in modal age of cannibals between the two lakes sampled in 2002 (Tab. 9).

**Table 8:** Chi-square values, degrees of freedom and p-values from the chi-square analysis for test of difference in age distribution of Arctic char from gillnet catches between lakes within the respective sampling years. n denotes number of lakes included in the analysis.

Year	n	Chi-square	df	p-value
2002	2	14.65	13	0.330
2009	7	285.10	126	<0.001
2020	11	317.68	210	<0.001

**Table 9:** H-value, degrees of freedom and p-value from the Kruskal-Wallis test of difference in modal age of Arctic char from gillnet catches between sampling lakes within respective sampling years and length classes (<200 and ≥200 mm). n denotes number of lakes included in the analysis.

Length class (mm)	Year	n	H	df	p-value
<200	2002	2	6.31	1	0.012
	2009	7	27.76	6	<0.001
	2020	11	16.65	10	0.0824
≥200	2002	2	3.73	1	0.053
	2009	7	25.12	6	<0.001
	2020	11	20.3	9	0.016

## Discussion

There was an observed bimodality in age and length distribution of char in gillnet catches both among lakes and within lakes across years. However, there were no evident patterns in the observed age or size distribution coinciding with recruitment pulses. Further, there were no changes in observed age distribution among lakes coinciding with the hypothesis that external environmental factors play a major role in the temporal variation in population dynamics and recruitment of cannibals to the population.

The recurring observations of bimodal length and age structure in gillnet catches from Arctic and alpine Arctic char populations shown both in the current and in a number of studies e.g. Hammar (2000), is likely to be a result of methodological issues with gillnets as observational platform for interference of population size and age structure (Finstad et al., 2000, Finstad and Berg, 2004). Juveniles and smaller individuals are likely underrepresented in gillnet samples due to low activity level and antipredator behaviour. (Finstad et al., 2000, Finstad and Berg, 2004). Care should therefore be taken in direct interpretation of size and age distribution from gillnet catches. However, in this study relative changes in population structure among years and across lakes is assessed, which rests on relaxed assumptions and only presupposes that the gillnet-catches gives information about relative differences in population structure.

Catchability of fish in gillnets can differ between years due to environmental variations, such as water turbidity, bottom type, and food availability. These factors can result in changes in activity of fish (Reichard et al., 2001, Stoner, 2004, Finstad et al., 2011) and thus influence the probability of fish being caught in the nets (Finstad et al., 2000). This means that care should be taken in comparing CPUE directly among sampling periods. However, the inferences in the current study are based on comparing size and age structure, not CPUE among lakes or sampling periods. This assumes that it is not large variation in catchability among size or age classes over time or among populations. The findings of relatively stable age and size distributions among years (and lakes) does support this assumption. Furthermore, as large differences among size and age class catchability could be confused with pulse type recruitments, my main conclusions should be robust against violation of this assumption.

The observations from the current study does not support the findings of Byström (2006) and Borgstrøm et al. (2015), where strong recruiting cohorts provides a profitable resource for cannibals. The peak in abundance of young char in 2009 as well as a corresponding peak in abundance of older char in 2020 (Fig. 9e-f, 10c-d and 11c-d) could be interpreted as a

relationship between recruiting cohorts and emergence of cannibals. Particularly in combination with the lack of individuals of intermediate sizes in gillnet samples, possibly indicating a high mortality due to strong competition for resources or by suppression of older more dominant individuals, as found by Byström (2006). However, the data show no time lag in the response of cannibals to dwarf abundance with a high abundance of both young and old individuals the same year. Further, there is a synchronicity in the plots between year where abundant year-classes in 2009, for both young and older individuals, are the same in 2020. This does not coincide with the hypothesis of recruitment pulses of juveniles controlling the cannibal recruitment. Instead, this is more likely a result of gillnet selectivity, as suggested by (Finstad and Berg, 2004). This would explain the relatively similar distribution of small and large char, and the low representation of individuals of intermediate sizes. Further, the synchronicity between years is likely due to the same selective mechanisms working in all sample years.

The observed lack of between-year-differences in growth and age distribution of char in gillnet catches in this study is another finding not supporting the evidence suggested by Byström (2006) and Borgstrøm et al. (2015). Recruitment pulses and strong top-down control by cannibals can cause year-to-year changes in density of dwarfs (Byström, 2006). Because growth and maturity in fish is highly dependent on density (Fleming and Einum, 2010, Forseth et al., 2010), one would in the presence of recruitment pulses expect these parameters to change from year to year. In this study some significant differences in growth- and age patterns between years is found, but the results are inconclusive and show no prominent trends or overall differences between years. The few significant between-year-differences in growth and age distribution found in the present study cannot support the assumption of recruitment pulses and top—down control being present in the char population.

The effects after removal of cannibalistic giants in Lake Trestikkelen in 2002 and 2009 could point towards a top-down effect of cannibals on the dwarf part of the population coinciding with previous findings in both Arctic char populations (Byström, 2006, Borgstrøm et al., 2015) and other cannibal-systems (Persson et al., 2000, Persson et al., 2004). Borgstrøm et al. 2015 suggested that removal of piscivores individuals may have had an immediate effect on mortality of small char due to reduced predation pressure and thus temporarily changed the population structure towards smaller fish. The sample from Lake Trestikkelen in this study did not reveal any profound effect on population structure by removal of cannibals. However, the age distribution of char from the 2020 sample was different and dwarfs in this sample was



on average smaller, compared to previous years. Further, this difference appears to be bigger in Lake Trestikkelen than in other sampling lakes. It is possible that this is a result of difference in gillnet-catchability that can be related to low abundances of cannibals in the lake and thus an increased activity level and catchability of dwarfs. From the gillnet-samples it is impossible however, to say whether the variation in average length is caused by differences in activity level and gillnet-catchability or simply due to differences in growth that particular year.

The contrasting findings of this study and the studies by Byström (2006) and Borgstrøm et al. (2015) could be due to differences in the systems where the studies were conducted. Despite the results of this study not indicating the presence of internal mechanisms in the char populations controlling the emergence of cannibals, one should not discharge such a hypothesis. Johnson (1983) described and concluded with a remarkable stability of Arctic char populations in Arctic lakes. After severe perturbations, i.e. removal of a significant fraction of initial population by intensive gillnetting, the population returned to a state similar to the original populations structure only nine years after the last sampling was conducted (Johnson, 1983). This could possibly explain the apparent similarities between years despite extensive fishing in this study considering the long time-space between sampling years.

Another possibility is that the presence of any strong cannibal cohort is simply masked by a continuous recruitment. Once the char have reached the cannibal niche they are long lived and can persist for a long time (Hammar, 2000). If pulses of strong recruiting cohorts exist, there will probably be several such breakthroughs within the lifetime of a cannibal char, allowing new individuals to enter the cannibalistic niche. This can possibly result in stable populations with multiple coexisting cohorts of both small-sized adults and giant cannibals (Byström, 2006) and a more continuous distribution of different cohorts. This will not necessarily indicate that there are no internal control mechanism or top-down control of cannibals on dwarfs, but simply explain why no recruitment pulses were observed.

There was no apparent evidence for external environmental variation being important for the recruitment of cannibalistic char in this study, thus the findings of Svenning and Borgstrøm (2005) and Borgstrøm (2015) is not supported. This primarily based on the apparent absence of recruitment pulses in Arctic char populations, which would be expected in a case of external environmental control mechanisms, but also the apparent lack of synchronicity, i.e., no apparent similarity, in observed age structure of char when comparing samples from different lakes within year. Environmental conditions are expected to affect char populations

in all sample lakes in a similar way leading to a similarity in the patterns of age distribution and modal age between lakes. The observed difference in age distribution among lakes within year, especially in 2009 and 2020, and the difference in modal age of both dwarfs and cannibals, indicates a possible lack of environmental variation controlling the recruitment. The apparent similarity in age distribution among char in the 2002 sample could possibly indicate a synchronization by an external factor but given the sample size of only two lakes this assumption is not convincing. Likewise, modal age of dwarfs in the 2020 sample appear similar between lakes, but only with a slightly non-significant value, and cannot alone support any presence of external control mechanisms.

Despite no indication of external environmental factors being important in the control of strong recruiting year classes and cannibal emergence in this study, environmental variation among lakes may still have a large role in shaping observed differences in population structure. Environmental factors are a major cause of variation in population size of salmonid fishes (Einum and Nislow, 2010). Difference in lake morphology can possibly result in environmental factors manifesting itself in different ways in the lakes, and thus affecting the char populations differently depending on the inherent characteristic of the lake. It is suggested that differences in shapes and depths of lakes is likely causing differences in temperature and light penetration between lakes, resulting in different growth conditions for small char (Forseth et al., 2010, Borgstrøm et al., 2015). Further, larger lakes can give a possibility for a more compound way of living, than just a regular dwarf-cannibal system, and possibly support more morphological subgroups, as observed in the large Icelandic lake Thingvallavatn (Sandlund et al., 1992). This could possibly cause a higher stability in the char populations of larger lakes like Haussvatnet and Lake Lygna, making the dynamics of these populations less affected by fluctuation in environmental conditions. This assumption is further supported by the apparent similarity in age- and growth parameters of char in gillnet catches from Lake Lygna when comparing between years. Lake Lygna was the only lake with no significant values in any of the analyses (Tab. 4, 5, 6 and 7), possibly indicating a greater stability in the Lygna-population relative to other sampling lakes. The varying depths and sizes of the sample lakes in this study (Tab. 1) could be a possible explanation for the observed between-lake difference.

In conclusion, based on observed age and size structure of char in gillnet catches there was no indication of either internal or external mechanisms controlling the emergence of cannibals in the lakes at Bear Island. The main finding is no trends pointing towards the existence of

recruitment pulses in the populations, which is expected in the case of both internal and external control mechanisms. It appeared to be a relatively stable and continuous presence of larger cannibalistic char coexisting with stunted dwarfs in the Arctic char populations. A similar pattern was found by Amundsen (2016) in a char population from a subarctic lake, suggesting that life history choice of either dwarf or cannibal strategy may be determined by genetic differences. Genetic studies on Arctic char cannibal systems in subarctic Canada showed a high degree of genetic differences among dwarfs and cannibals (Power et al., 2009). Further, some degree of phenotypic plasticity, maternal effects or a combination of these may also be determining in life history choice. Phenotypic plasticity in interaction with genetic determination is commonly causing variation in life history choice in salmonid fishes (Fleming and Eium, 2010, Hutchings, 2011). A reported size difference between dwarfs and cannibals already at hatching may point towards a genetic based differentiation but does also highlight the importance of factors like maternal effects (Sinnatamby et al., 2013, Florø-Larsen et al., 2016). The key issue is therefore just how much of life history choice is under genetic control and how much is an expression of phenotypic plasticity or maternal control. Nevertheless, a genetic component in life history choice could possibly explain why there was no apparent indication of a controlling interaction between dwarfs and cannibals in this study. Although evidence of genetic differences in sympatric morphs of Arctic char exists (Klemetsen, 2010, Salisbury et al., 2018, Salisbury et al., 2020), the results in the present study is not sufficient to support the assumption of a genetic basis for dwarf and cannibal morphs in Arctic char. Further studies including molecular genetic approaches may enhance the understanding of the mechanisms controlling the emergence of cannibals in Arctic char populations.

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