



UMEÅ UNIVERSITET

# RESPONSES TO DECLINING ZOOBENTHOS ABUNDANCE

Changes over time in diet and growth of Arctic  
charr (*Salvelinus alpinus*)

Douglas Skarp

## **Abstract**

A decline in the density of zoobenthos has taken place in Lake Abiskojaure in the northern Swedish mountains between 1988 and 2019 but no response can be seen in the abundance (CPUE) of Arctic charr (*Salvelinus alpinus*) that feed mainly on benthic invertebrates. To evaluate if possible shifts in resource use of charr explain this lack of change in population abundance, stomach contents (i.e. diet) of charr between 1985 and 2020 were analyzed. Charr diets changed during the study period, with decreasing contributions to the diet of larger sized prey and increasing contribution of smaller sized prey and zooplankton. A corresponding recent decline in charr growth, size, and condition factor was observed. The proportion of large prey in diets and charr growth both show a hump-shaped relationship with time before the recent decline, indicating consumption of large prey had a positive effect on charr growth. Densities of zooplankton in the lake did not change with time, meaning increases in diet proportions are driven by something else. Declines in nitrogen and phosphorous over time may have contributed to the decline in zoobenthos densities through nutrient limitation of primary production. The results from this study suggest charr has changed diet towards smaller, less energetically efficient prey as a response to declining zoobenthos levels, and that this has had a negative effect on charr growth, size, and condition factor. Additional declines in nutrients and zoobenthos abundance may further worsen charr performance and eventually be manifested as declining charr abundance.

# Table of Contents

<b>1 Introduction</b> .....	<b>1</b>
1.1 Background .....	1
1.2 Aim .....	3
<b>2 Methods</b> .....	<b>3</b>
2.1 Collection of Data.....	3
2.2 Statistical analysis .....	4
<b>3 Results</b> .....	<b>5</b>
3.1 Proportion over time .....	5
3.2 Proportion with years grouped into periods .....	5
3.3 Weight in stomach adjusted for charr weight .....	6
3.4 Size dependency in prey use.....	7
3.5 Temperature .....	7
3.6 Charr condition, average weight, and growth estimates.....	7
3.7 Zooplankton .....	8
3.8 Water chemistry.....	8
<b>4 Discussion</b> .....	<b>8</b>
<b>5 Acknowledgements</b> .....	<b>12</b>
<b>6 References</b> .....	<b>12</b>
<b>7 Appendix</b> .....	<b>14</b>

# 1 Introduction

## 1.1 Background

Arctic charr (*Salvelinus alpinus*) has a circumpolar distribution (Klemetsen et al. 2003b; Lehtonen 1998) and is an extreme cold-water adapted fish species (Baroudy and Elliott 1994) with the lowest temperature tolerance recorded for salmonids. Charr occur at the northern most latitudes of landmass in Eurasia and North America at ~84°N, but can be found as far south as in the alps in Europe and in particularly cold lakes in Maine in eastern North America (Reist, Power, and Dempson 2012). Being a cold-water specialist, Arctic charr has an optimum feeding and growing temperature below 14.4-17.2 °C, and tend to avoid waters warmer than this (Lehtonen 1998; Larsson et al. 2005). With a stress temperature of 20-22 °C and a lethal one of 26.6 °C (Baroudy and Elliott 1994), shifts in habitat use might be necessary with warming climate and waters. The species is omnivorous and displays a large variability in diet which in some cases are related to variation in its morphology (Sandlund et al. 1992; Reist, Power, and Dempson 2012). Previous studies have shown clear feeding segregation between different life stages. The attack rate of Arctic charr on pelagic zooplankton shows a hump shaped relationship with charr size, while the attack rate on benthic macroinvertebrates increases monotonically with charr size (Byström and Andersson 2005). The diets of juvenile stages, as well as smaller morphs of the species, may depend to large extent on zooplankton and benthic invertebrates of smaller sizes. Larger individuals may feed on zooplankton, but their diets consist to a greater extent of larger macroinvertebrates (Sandlund et al. 1992; Malmquist 1992; Byström and Andersson 2005). Composition of the diet also varies substantially between different lakes, habitat use, and the time of year of the sampling (Sandlund et al. 2010). Being cold-water specialized (Klemetsen et al. 2003a; Baroudy and Elliott 1994), Arctic charr feed actively all year round, though with seasonal variation in diet (Eloranta et al. 2013).

The conditions in Arctic lakes have been undergoing change during the last decades. Concentrations of total phosphorous (TP) in lakes in northern Europe, while varying depending on local conditions, have shown signs of decline over the last decades in places like northern Sweden (Isles, Creed, and Bergström 2018; Miljödata – MVM 2020). Low levels of TP in lakes in northern Sweden also seem to coincide with years with higher than usual temperatures (Isles, Creed, and Bergström 2018). Dissolved organic nitrogen (DIN), a combination of nitric oxides (NO<sub>x</sub>) and ammonium (NH<sub>4</sub>) that is used to measure atmospheric nitrogen (N) deposition, has also been observed to decrease in lakes in northern Europe (Isles, Creed, and Bergström 2018; Karlsson et al. 2009) likely due to a reduction of NO<sub>x</sub> emissions (Lajtha and Jones 2013). How lakes respond to N deposition is strongly mediated by catchment characteristics such as vegetation cover (Hessen 2013), which has been increasing over the last three decades around Nordic Arctic lakes (Finstad et al. 2016). Further effects of increased vegetation cover in catchments, especially in combination with increased precipitation (Wit et al. 2016), is a higher input of dissolved organic materials (DOM) into waters and subsequent browning effects (Finstad et al. 2016; Isles, Creed, and Bergström 2018; Wit et al. 2016). Other than affecting lake stoichiometry by directly contributing with N and TP (Kissman et al. 2017), DOM indirectly affects N and TP concentrations by stimulating pelagic bacterial production while also limiting benthic primary production by reducing light penetration in the water column (Karlsson et al. 2009). Additionally, DOM itself contains bound phosphorous (P) and can therefore also contribute directly to changes in concentrations (Maranger and Pullin 2003). A shift towards a more mesotrophic brown lake condition with higher P levels may therefore shift the predominant source of primary production from benthic to pelagic (Vadeboncoeur et al. 2003) and change the structure and abundance of benthic communities. Reversely, a shift towards more oligotrophic conditions as can be seen in northern Sweden can change food web structures through nutrient limitation in ways that leads to declining fish production (Stockner, Rydin, and Hyenstrand 2000). Changes in community structure in food webs may in turn affect important ecosystem processes provided by benthic invertebrates such as the breaking down of organic material, sediment mixing, and nutrient cycling (Covich, Palmer, and Crowl 1999),

further reducing the contribution of benthic resources to consumers. The changes in concentrations of N and TP, and in N:TP ratios may also negatively impact grazers such as zooplankton and zoobenthos directly by dietary P-constraints which may have negative effects on the abundance of higher trophic levels such as fish (Hessen 2013). While it is clear that lake conditions are at present changing, determining what effects these changes will have on higher trophic levels is complex and requires more thorough and detailed analysis of lake systems.

A decline in benthic invertebrate density in the profundal zone (Fig 1, Miljödata – MVM 2020) has been seen in Lake Abiskojaure (lat 68.2862, long 18.5909) between 1988 and 2019. However, no decline, as one would expect, in catch per unit effort (CPUE) of Arctic charr has been seen over time, and if anything a weak positive trend is present (Fig 2, National Register of Survey test-fishing – NORS 2020). Considering the lack of any clear response in the charr population - despite declining density of their predominant food source (i.e. zoobenthos) - one can hypothesize that changes in resource use of charr have occurred to sustain stable population abundance over time. However, changes in resources might also affect the condition or growth rate (reflected in length at age) of the charr even if its abundance is the same.

Monitoring of the charr population in Lake Abiskojaure has taken place each year since 1994 by SLU Aqua with some additional fishing and monitoring being done by the Swedish Environmental Protection Agency (Naturvårdsverket) since 1981. The long-term data from these samplings in combination with its protected location in a national park make Lake Abiskojaure an excellent study system to evaluate how long-term changes in biotic and abiotic environmental conditions may affect charr resource use.

## 1.2 Aim

The purpose of this thesis was to examine how a decline in zoobenthos biomass over time affects the diet and growth rate (length at age) of Arctic charr in Lake Abiskojaure.

More specifically I hypothesize that:

- Arctic charr has changed its diet in response to declining zoobenthos biomass over the last 35 years.
- Declining zoobenthos biomass should lead to a decrease in condition factor and growth rate of charr.

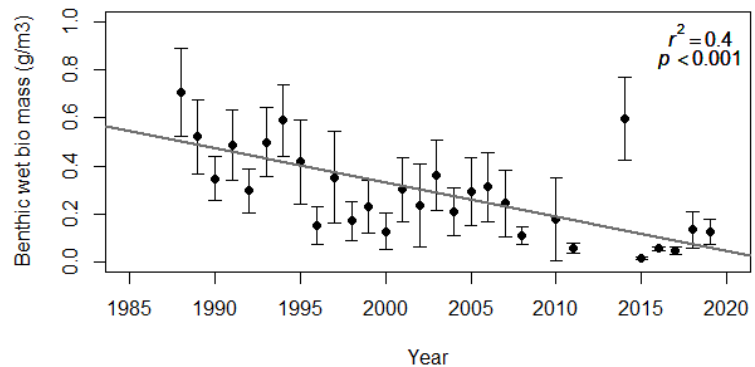


Fig 1. Wet biomass (g/m<sup>3</sup>) of benthic invertebrates over time in lake Abiskojaure in northern Sweden (Miljödata – MVM 2020). Error bars showing  $\pm 1$  SE. Samples taken at a depth of 13.5 m.

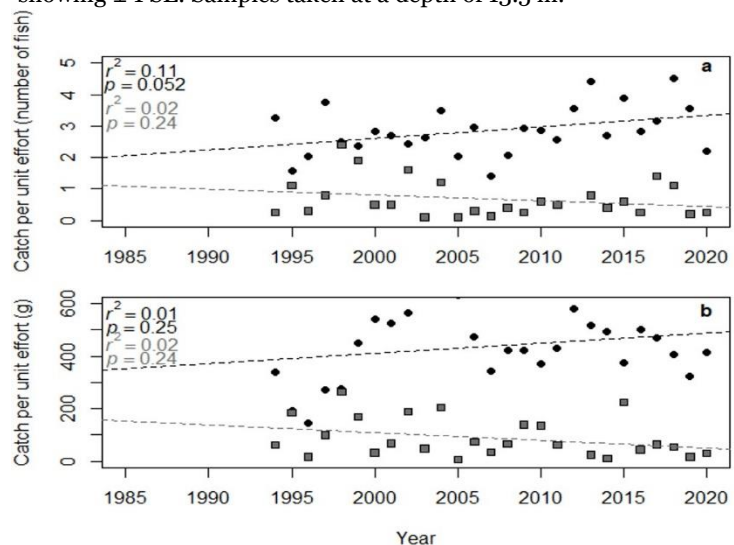


Fig 2. Catch per unit effort (catch per net) in benthic nets (circles) and pelagic nets (squares) by number of fish over time (a) and by biomass over time (b) in Abiskojaure. (National Register of Survey test-fishing – NORS 2020).

## 2 Materials and methods

### 2.1 Collection of data

The data collection was based on gill net caught Arctic charr from Lake Abiskojaure (487 m above sea level, 35 m maximum depth and 282 hectares in size) from survey gillnetting by SLU Aqua and frozen archived charr samples from the Swedish Museum of National History (NRM). During the survey gillnetting by SLU Aqua during 2015 – 2020 stomach contents were removed on site post capture and transferred directly to separate plastic containers with ~70% ethanol. Individual data on length, gonad maturity, and sex were recorded for each charr by SLU Aqua. Age was determined using otoliths. Diet samples from earlier time periods were obtained from frozen samples from NRM. Further data on charr length, weight, and age (from sample fishing 1994 – 2019) to analyze changes in charr growth, condition, and weight were made available from SLU Aqua (National Register of Survey test-fishing – NORS 2020).

Table 1. The years sampled at the Swedish Museum of Natural History and the number of individuals analyzed without empty stomachs and their average length (mm)  $\pm$  1 SD from each year.

Year	Number of individuals	Average fish length
1985	9	180 $\pm$ 12
1989	8	217 $\pm$ 81
1994	5	242 $\pm$ 57
1996	4	158 $\pm$ 106
1997	9	262 $\pm$ 13
2003	8	260 $\pm$ 30
2004	9	255 $\pm$ 13
2005	10	237 $\pm$ 106
2015	57	247 $\pm$ 103
2016	49	244 $\pm$ 102
2017	47	215 $\pm$ 91
2018	63	234 $\pm$ 92
2019	101	197 $\pm$ 73
2020	86	261 $\pm$ 86

time of the sampling by SLU to ensure no large seasonal variations in availability of different taxa zoobenthos. Samples around the apparent decline of macroinvertebrates 1994 – 1996 (Fig 1) were prioritized to examine if a shift in diets occurred in response to this decline. Second priority was to collect samples closer to 2015 to extend the timeline of data backwards from 2015 – 2020 and to get a clearer view of more recent conditions.

The stomach contents were identified in lab under a stereoscope to predetermined levels of invertebrate taxa. Up to 10 individuals of each taxa were measured for length to determine biomass using length – dry weight regression (Benke et al. 1999; Bottrell et al. 1999; Sage 1982; and other sources). If more than 10 individuals of a taxon were present in a stomach, the length of those additional individuals were assumed to be of average length of the first 10. The different taxa were then separated into a series of categories based on taxonomical similarity, phenotypical similarity, or frequency of occurrence (Table 1, appendix). Cannibalized charr in diets were assigned to category *Other* as only four instances were recorded in all samples. Although they both are zooplankton, *Eurycercus* and *Bythotrephes* were each assigned their own category due to their relatively large size, high abundance in the stomachs, and different ecological niches (*Eurycercus* being a benthic zooplankton and *Bythotrephes* being predatory on other zooplankton).

Data of benthic invertebrate densities were downloaded from SLU Miljödata – MVM (2020). Samples of invertebrates were taken from a depth of 13.5 m with an Ekman grab sampler

(surface area 250 cm<sup>2</sup>). Data on zooplankton densities were received from the Swedish environmental monitoring (Miljödata – MVM 2020), based on zooplankton collected from 0-8 m in the pelagic zone with a zooplankton net (mesh width 0,04 mm).

Air temperature data between (1985 – 2020, June – September) was obtained from Abisko Scientific Research Station (2020) and used as a proxy of water temperature development over time (Karlsson et al. 2005). Water temperature was measured only at the time of charr sampling (National Register of Survey test-fishing – NORS. 2020). From these measurements, surface temperature was highest in 2014 (15.3 °C) and lowest in 2012 (8.6 °C), with an average temperature of 12.5 °C. Bottom temperature was highest in 1994 (9.4 °C) and lowest in 1998 (5.4 °C) with an average temperature of 7.5 °C. The difference between surface and bottom water temperature was largest in 1997 (9.3 °C) and smallest in 2012 (0.6 °C), with average difference between surface and bottom temperature being 5.1 °C (NORS 2020). Most years, the lake had no clear thermocline at the time the sample fishing was performed.

Data of TP and NO<sub>x</sub>, NH<sub>4</sub> and total organic carbon (TOC) was accessed from SLU Environmental Data MVM (Miljödata – MVM 2020). DIN was calculated as the sum of NO<sub>x</sub> and NH<sub>4</sub> (Isles, Creed, and Bergström 2018).

## 2.2 Statistical analysis

In RStudio (RStudio Team 2020), proportional data from individual charr samples of each taxonomical category were arcsine-transformed and separately analyzed for correlations with time and charr length using regressions ( $\text{lm}(\text{proportion} \sim \text{year} + \text{charr length})$ ). In addition, and due to large within-year variation, yearly average proportional data were analyzed using the same model to evaluate for trends with time and charr length, to more clearly see how strong trends over time were. The models for analysis of average proportional data were stepwise optimized using AIC criteria. In addition, sample years were also separated into four groups (1985 – 1989, 1994 – 1997, 2003 – 2005, and 2015 – 2020) to evaluate for changes over time periods and mitigate the effects of one year outliers, and were analyzed with analysis of variance (ANOVA). Post hoc tests (Tukey HSD) were performed between the time periods to determine which periods differed significantly.

The dry mass of charr diets was adjusted to the weight of the charr by dividing the dry mass of each prey category in the stomach contents with the charr weight. Regression analysis was performed for total adjusted dry weight in diets and time. The same regression was also performed separately for each taxonomical category and time.

Restricting charr size to 150 – 300 mm, proportions of smaller categories (*Zooplankton* and *Eurycercus*) and larger categories (*Gammarus* and *Lepidurus*) in diets were evaluated for changes over time and charr length separately using regressions. This was done to adjust for the lack of smaller sized charr from samples 1985 – 2005.

Average yearly air temperature over time was analyzed using a linear regression to test for trends over time.

Changes in Fulton's condition factor of the charr ( $K = (W * 10^5) / L^3$ , where K = condition, W = charr weight (g), and L = charr length (mm), Ricker 1975) over time was evaluated using regressions. Additionally, changes in length over time of 2-, 3-, and 4-year old charr were evaluated with separate polynomial regressions ( $\text{lm}(\text{proportions} \sim \text{year} + \text{year}^2)$ ). Similar trends and patterns the years 2000 – 2010 in charr growth and zoobenthos wet biomass were evaluated for correlation by performing linear regressions between length at ages (2, 3, and 4 separately) and zoobenthos biomass. Trends in individual based charr weight over time was evaluated with polynomial regressions ( $\text{lm}(\text{charr weight} \sim \text{year} + \text{year}^2)$ ). Polynomial

regressions were used as higher  $r^2$ -values were given by polynomial regressions than with linear regressions.

Average zooplankton density in biovolume ( $\text{mm}^3/\text{m}^3$ ) was evaluated for changes over time with a regression analysis.

Data of DIN, TP, and DOC were evaluated separately using linear regressions to assess changes over time.

### 3 Results

#### 3.1 Proportions over time

The composition of stomach contents in Arctic charr (i.e. the proportions of various taxa) changed over the period 1985 to 2020 (Fig 3). For proportions based on individual charr prey categories, *Zooplankton*, *Bythotrephes*, *Eurycerus*, and *Diptera* increased over time, while *EPT*, *Gammarus*, and *Lepidurus* decreased ( $p < 0.05$ , Fig 3, Table 2). *Gammarus* and the category *Other* showed a positive trend with charr length, while *Zooplankton*, *Eurycerus*, and *Diptera* showed a negative trend ( $p < 0.05$ , Table 2). While trends were significant ( $p < 0.05$ ) for analysis based on individual data, adjusted  $r^2$ -values were very low and explained very little of the variation. Explanatory power increased, however, when yearly average proportions were analyzed instead. For data based on yearly means. *Zooplankton*, *Bythotrephes*, *Eurycerus*, and *Diptera* showed a positive trend with time ( $p < 0.05$ , Table 3). Data for yearly means showed stronger trends ( $r^2 = 0.27 - 0.74$ ) than data for individual charr ( $r^2 = 0.01 - 0.10$ ).

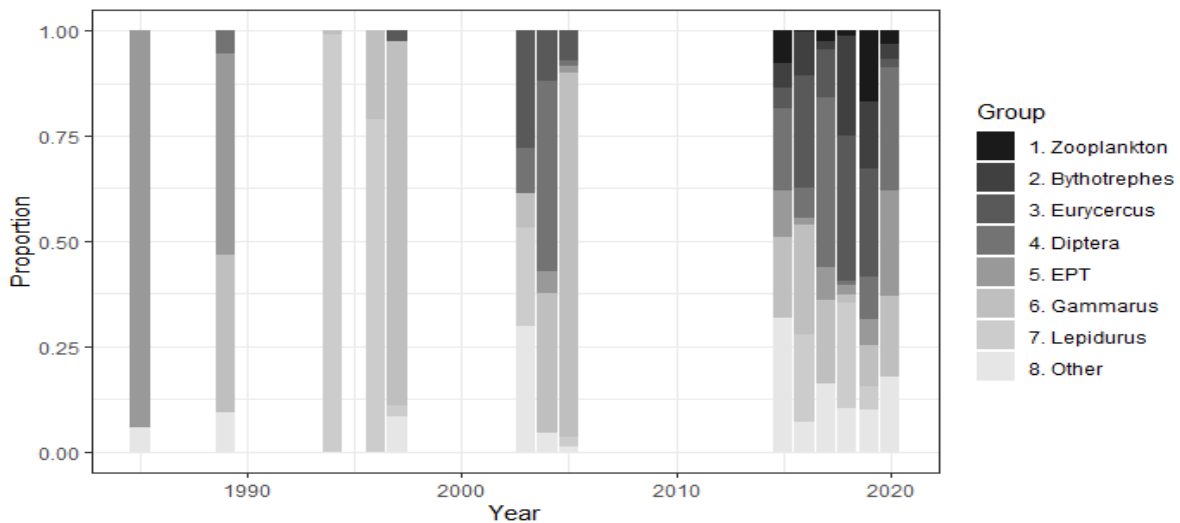


Fig 3. The average proportions of the taxonomical categories in diets each sampling year.

#### 3.2 Proportions with years grouped into periods

When grouped into four different time periods, proportions of *Eurycerus*, *EPT*, *Gammarus*, and *Lepidurus* varied between time periods (ANOVA,  $p < 0.05$ ) (Fig 4). *Eurycerus* were absent period 1 and almost absent period 2. *Zooplankton* and *Bythotrephes* were almost completely absent in frozen samples (1985 – 2005) up until period 4 where *Bythotrephes* abundance was significantly higher ( $p < 0.01$ ) but

Table 2. Results from linear models of trends in proportions of taxonomical categories in diets over time and fish length. Proportions were arcsine-transformed before analysis. Data is based on individual diet items. (+) indicates positive trend and (-) indicates negative trend.

Category	p for year	p for length	r <sup>2</sup>
1. Zooplankton	<0.01 (+)	0.08	0.02
2. Bythotrephes	<0.001 (+)	0.66	0.02
3. Eurycerus	0.002 (+)	<0.001 (-)	0.06
4. Diptera	<0.001 (+)	0.01 (-)	0.20
5. EPT	<0.001 (-)	0.89	0.05
6. Gammarus	<0.001 (-)	<0.001 (+)	0.10
7. Lepidurus	0.002 (-)	0.10	0.02
8. Other	0.12	<0.001 (+)	<0.01



Zooplankton was not. *Diptera* and the prey category *Other* did not vary significantly between the time periods.

### 3.3 Weight in stomach adjusted for charr weight

The adjusted total dry weight of stomach content of individual charr did not show any significant trend over time (Fig 5). Adjusted dry mass in diets of *EPT* ( $p = 0.03$ ,  $r^2 < 0.01$ ) and *Lepidurus* ( $p < 0.001$ ,  $r^2 = 0.04$ ) decreased with time. No other category showed significant trends with time.

Table 3. Linear models of trends in proportions of taxonomical categories in diets over time and fish length. The models presented were chosen by AIC criteria with stepwise optimization (step function in R). If the  $p$ -value is missing the factor was excluded. (\*) indicates that both factors were excluded after model optimization. If all factors were excluded, the model including only *year* was presented. Proportions were arcsine-transformed before analysis. Data is based on average proportions each year of diet items. (+) indicates positive trend and (-) indicates negative trend.

Category	$p$ for year	$p$ for length	$r^2$
1. Zooplankton	0.002 (+)	0.13	0.53
2. Bythotrephes	<0.001 (+)	0.22	0.63
3. Eurycerus	0.005 (+)	-	0.44
4. Diptera	0.03(+)	-	0.27
5. EPT	0.22 *	-	0.05
6. Gammarus	0.93 *	-	0.09
7. Lepidurus	0.46 *	-	0.03
8. Other	0.09	-	0.16

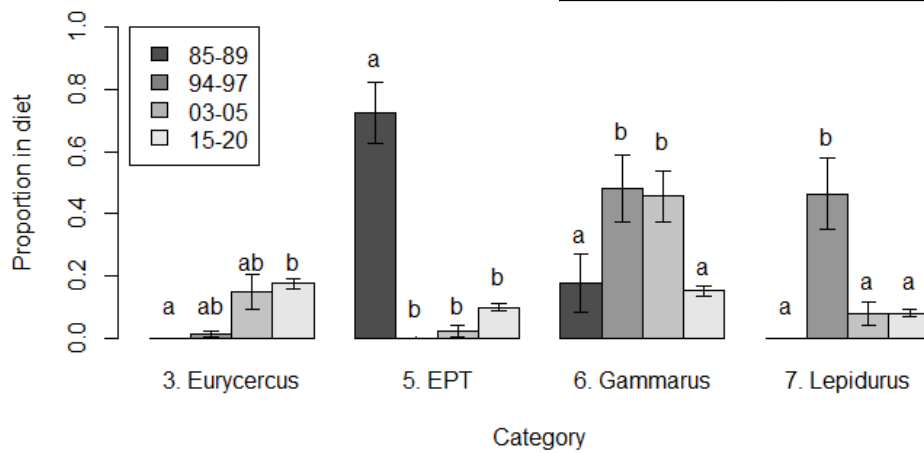


Fig 4. Proportions in diets of *Eurycerus*, *EPT*, *Gammarus*, and *Lepidurus* over time periods. Letters shared indicate no significant difference between time periods, while different letters indicate significant differences. Error bars are showing  $\pm 1$  SE.

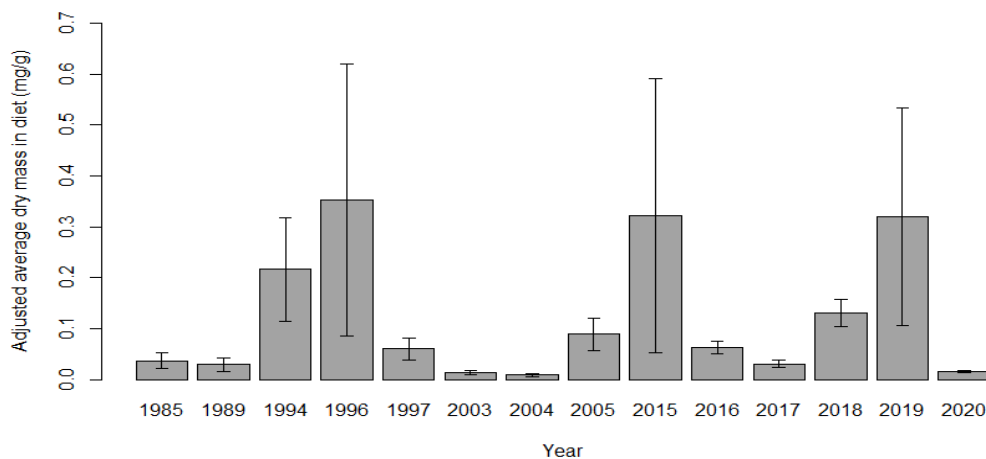


Fig 5. Average stomach content dry weight adjusted to fish weight (mg/g) over the study period (1985-2020). Error bars are showing  $\pm 1$  SE.

### 3.4 Size dependency in prey size use

Charr size was limited to 150 – 300 mm to eliminate size structure in samples differentiating between years affecting the tests. Linear regressions (using only charr diet data for sizes between 150- 300 mm) between proportions of smaller diet categories (*Zooplankton* and *Euryercus*) and time showed a positive trend ( $p < 0.01$ ,  $r^2 = 0.45$ , Fig 6a). Tests for larger diet categories (*Gammarus* and *Lepidurus*) and time showed a hump-shaped relationship ( $p < 0.001$ , Fig 6b) but no linear trend. Missing larger diet categories for 1985 may have driven this trend.

Linear regressions between proportions of smaller diet categories (*Zooplankton* and *Euryercus*) and charr length (used charr length 150-300mm) showed a negative relationship ( $p < 0.001$ ,  $r^2 = 0.06$ , Fig 7a). In contrasts no significant relationship was found between larger diet categories (*Gammarus* and *Lepidurus*) and charr length ( $p < 0.17$ , Fig 7b).

### 3.5 Temperature

Annual average air temperature during June – September increased over the years 1985 to 2020 ( $p = 0.002$ ,  $r^2 = 0.22$ , Fig 8).

### 3.6 Charr condition, average weight, and growth estimates

Charr condition varied over time between 1994 and 2019 and seemed to display a hump-shaped pattern ( $p < 0.001$ , Fig 9). The same pattern could be seen using only charr larger than 250 mm in the analysis ( $p < 0.001$ ). A corresponding pattern was present for charr weight ( $p < 0.001$ , Fig 10) with a hump-shaped relationship and a recent decline.

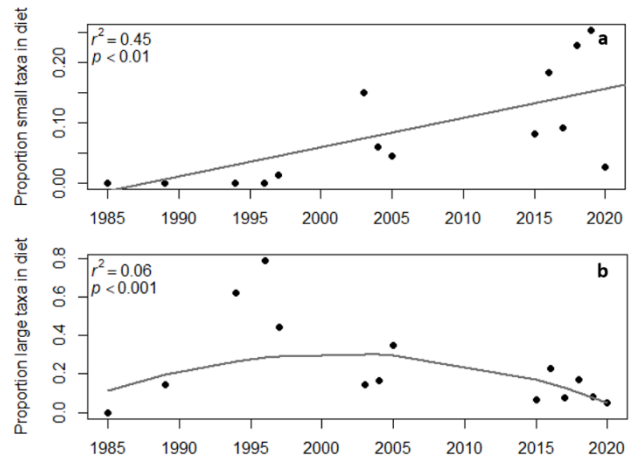


Fig 6. Proportions of small taxa (*Zooplankton* and *Euryercus*, a) and large taxa (*Gammarus* and *Lepidurus*, b) over time. Regressions were performed on only fish 150 – 300 mm. Equation used in polynomial regression was  $a+b*x+c*x^2$ .

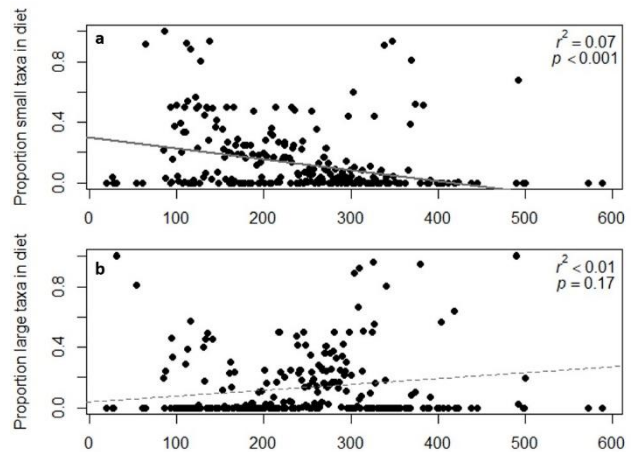


Fig 7. Proportions of small taxa (*Zooplankton* and *Euryercus*, a) and large taxa (*Gammarus* and *Lepidurus*, b) in diets of fish. Regressions were performed on only fish 150 – 300 mm.

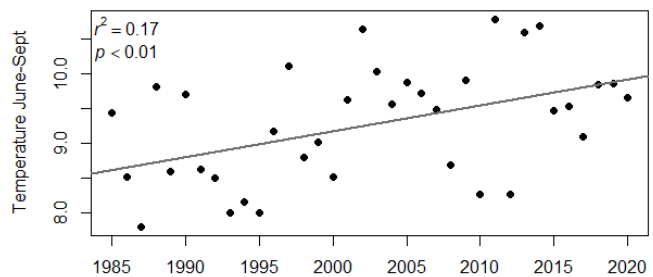


Fig 8. Average air temperature in Abisko over time during May – September between 1985 and 2020.

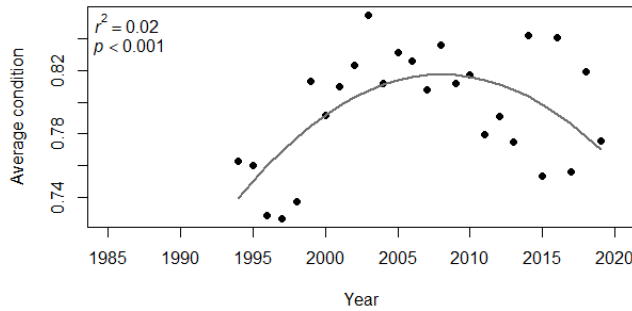


Fig 9. Polynomial regression of average fish condition factor by year. Equation used in regressions was  $a+b*x+c*x^2$ .

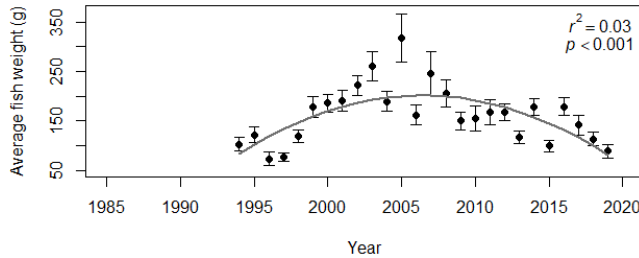


Fig 10. Fish weight over time. Points indicate average yearly fish weight. Polynomial regression is run on individual data. Error bars showing standard error. Equation used in regression was  $a+b*x+c*x^2$

Individual data on length at age 1994 – 2019 (Fig 11) for ages 2 ( $r^2 = 0.13$ ), 3 ( $r^2 = 0.21$ ), and 4 years ( $r^2 = 0.12$ ) showed significant hump-shaped relationships and a decline with time after 2005 ( $p < 0.001$  for all ages). A tendency to a corresponding hump-shaped relationship can also be seen in zoobenthos density over time during 2000 – 2010 (Fig 1), but no significant correlation between length at age and zoobenthos density during this time period was found ( $p = 0.07$  for age 2,  $p = 0.63$  for age 3,  $p = 0.35$  for age 4).

### 3.7 Zooplankton

Average zooplankton biovolume per year in  $\text{mm}^3/\text{m}^3$  did not change over time ( $p = 0.27$ , Fig 12). Analysis of log-transformed yearly means was also non-significant ( $p = 0.25$ ).

### 3.8 Water chemistry

Yearly averages of TP ( $p < 0.001$ ,  $r^2 = 0.37$ ), TOC ( $p < 0.01$ ,  $r^2 = 0.19$ ), and DIN ( $p < 0.001$ ,  $r^2 = 0.29$ ) all decreased during the time period 1988 – 2020 (Fig 13).

## 4 Discussion

The observed decline in the benthic invertebrate densities coincided as hypothesized with corresponding changes in the diets of Arctic charr in Lake Abiskojaure. Based on individual diet data, the contribution of smaller sized categories, including pelagic zooplankton

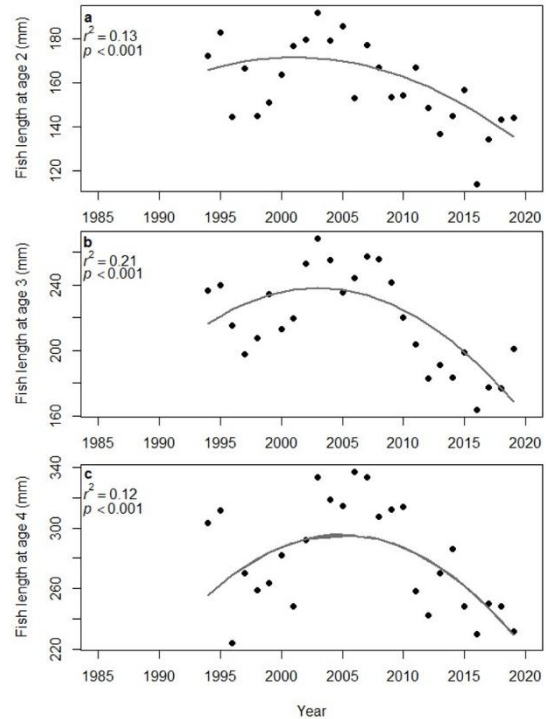


Fig 11. Polynomial regressions of average length at ages 2 (a), 3 (b), and 4 (c) over time. Equation used in regression was  $a+b*x+c*x^2$ .

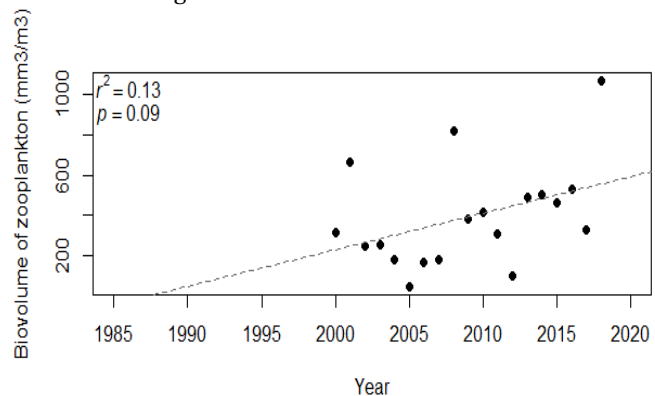


Fig 12. Total zooplankton biovolume ( $\text{mm}^3/\text{m}^3$ ) in lake Abiskojaure over time.

(*Eurycercus*, *Zooplankton*, *Bythotrephes*, *Diptera*), increased with time while generally larger sized mainly benthic prey categories (*EPT*, *Gammarus*, *Lepidurus*) decreased. The same trends for smaller prey items could be observed when analyzing data based on yearly averages, though not significantly so for larger prey. Tests omitting smaller charr (using only charr of 150 – 300 mm) showing the same trends support these analyses and suggest size structure of samples did not affect the results. Interestingly, declines of smaller diet categories and increases of larger ones in diets coincided with a decline in charr length-at-age (growth). This growth decline is in line with, and could be explained by changes in diet, as preference for larger prey items increase with charr size and is a prerequisite for high growth rates (Byström and Andersson 2005). Large prey items (categories *Gammarus* and *Lepidurus*) showed a hump-shaped with time rather than a decline when omitting smaller fish, not supporting sample size structure would have skewed the results. More importantly, omitting smaller charr from analysis still showed an increase in smaller prey items (categories *Zooplankton* and *Eurycercus*) over time, supporting that a shift towards a more zooplankton-based diet has really taken place and that charr size structure in samples has not affected this. Further, proportion of large prey items in diets did not increase with charr length when omitting smaller fish while small prey items did still decrease. Considering these results, I suggest that the seen dietary shift towards smaller sized prey and the lack of change in consumption of larger sized prey over time are real and not related to charr size.

Results from analyses of years grouped into time periods show proportions of the large prey item *Gammarus* were significantly higher in period two and three, and *Lepidurus* was significantly higher in period two. This coincides with the hump-shaped relationship that can be seen with growth for charr of ages 2, 3, and 4. The same hump-shaped relationship can also be seen in the condition factor and average charr weight over time. As the size at age and condition of charr then declines over time, so does the contribution of these two taxa to the diets. Studies of other fish species have shown a preference for larger more energetically profitable prey when given a choice (Gómez-Laplaza, Romero, and Gerlai 2019), and in a case of temporary high abundance of *Gammarus* and *Lepidurus*, charr would likely feed upon these abundant and energetically profitable resources (Gill 2003). The contribution of large prey items may thus explain the increased growth rate, condition factor, and average charr weight seen in the years 2000 – 2010. Moreover, the tendency for a hump-shape in zoobenthos density between 2000 – 2010 may explain this corresponding pattern in growth rate, but the correlation between charr growth and zoobenthos density during this time period was non-significant. Due to the decline in zoobenthos and charr growth after 2005 coinciding well with each other, and as zoobenthos is a predominant food source for charr and tied to growth rate (Byström and Andersson 2005), a correlation between them can however not be ruled out. To summarize, I suggest that a temporary increase in large energetically profitable prey during 2000 – 2010 combined with the opportunistic feeding

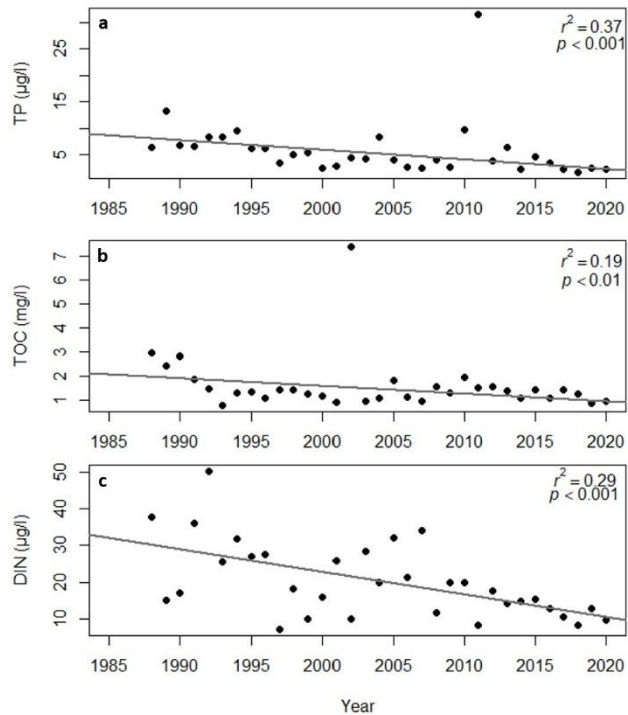


Fig 13. Total phosphorous (TP) (a), total organic carbon (TOC) (b), and dissolved organic nitrogen (DIN) (c) over time in lake Abiskojaure. Years 2012 for TP and 2002 for TOC were regarded as outliers and excluded from their respective analysis.

behavior of the Arctic charr (Power 2002) and preference towards larger prey (Gómez-Laplaza, Romero, and Gerlai 2019; Gill 2003) are likely the main cause behind the high growth and condition factor seen during the time period 2000 – 2010. Further, the subsequent recent decline in growth and condition factor is likely connected to the decline in these taxa and other zoobenthos in the lake.

There were indications that smaller prey items like *Eurycercus* and other zooplankton increased in the diets over time, with certain later years having significantly higher contribution to the overall diet of the charr. This is also supported by the analysis with years divided into periods, where proportions *Eurycercus* in diets was higher during the last period (2015 – 2020). Zooplankton abundance in the lake showed no trend of changing over time, but had noticeably higher densities during certain years than others. These outlying peaks in density during certain years do not however necessarily indicate higher density in the whole lake but might instead be the result of the sampling net passing through a dense swarm of certain taxa. *Holopedium* could be seen in the raw data as a driving factor for these peaks, making up the majority of the biovolume in peak years. The category *Zooplankton* in the diet from the older frozen samples (1985 – 2005) was almost nonexistent and the contribution of *Eurycercus* to the diet was absent before 1997. The lack of samples from smaller from early years skewing this result is unlikely considering regressions of 150 – 300 mm charr still showing an increase of *Eurycercus* and *Zooplankton* in diets over time. Changes seen in sampling methods might however have affected the results of these smaller zooplankton taxa found in diets. Different taxa of zooplankton break down in fish stomachs at different rates (Sutela and Huusko 2000) with certain taxa being completely digested after only 1.5 hours (Fossum 1983). Proportions of soft bodied taxa (like categories *Eurycercus* or *Zooplankton*) in diets may therefore vary depending on how long the nets are in the lake as well as time to freezing of sampled charr, and may actually be higher than seen in the data (Sutela and Huusko 2020). The proportion of zooplankton in diets, despite the recent increase, have however remained low throughout the study period and has never been the predominant food source for the charr. My results might thus be biased towards less digestible taxa and some variation in the data might be the result of different sampling methods. However, this bias should not have changed over the years so the results do still clearly indicate an increase in the contribution of zooplankton in the diet of charr have taken place over recent years.

The reason for the decline in zoobenthos density in the lake might stem from either increased feeding by the Arctic charr or changes in abiotic conditions. A lake without fish in proximity to Lake Abiskojaure has experienced a similar decline in zoobenthos densities over the same time period (Lake Latnjajaure, Miljödata – MVM 2020; Nilsson et al. unpublished), supporting the conclusion that it is not changes in charr feeding that have caused the observed decline in zoobenthos in Lake Abiskojaure.

Declines over time in nutrients could be a more likely cause for the declining zoobenthos. The decline in DIN was in line with other studies (Isles, Creed, and Bergström 2018; Lajtha and Jones 2013) and is likely driven by regulations on NO<sub>x</sub> emissions by industries. Emissions of NH<sub>4</sub> and TP stem mainly from agriculture (Battye et al. 1994) and vehicular combustion (Fraser and Cass 1998), both of which are scarce in proximity to Lake Abiskojaure. Though an increase of TOC, and thus also TP, would be expected to be seen with rising temperatures (Finstad et al. 2006), the effects of climate change on transport of TP to waters is relatively understudied (Isles, Creed, and Bergström 2018; Karlsson et al. 2009), and the results from these previous studies might hence not be representative for this lake as catchments characteristics can differ greatly. However, other lakes in the area have been determined N-limited (Isles, Creed, and Bergström 2018) and P-constraints could have negative indirect effects on zoobenthos populations (Hessen 2013).

A decline in pelagic primary production would lead to a subsequent decline in pelagic detritus settling in benthic habitats (Higgins and Vander Zanden 2010), and as zoobenthos are partially sustained by pelagic detritus it would also mean a decline in their resources (Docmac et al. 2017; Hayden et al. 2019). Production of periphyton on hard substrate in the benthic habitat are also linked to concentrations of TP (Vadeboncoeur et al. 2006) and would likely be reduced with declining TP inputs, further amplifying this effect. The decline in DIN and TP may therefore have contributed to the declines in zoobenthos by restricting primary production (Stockner, Rydin, and Hyenstrand 2000). In addition, increasing temperature can lead to stronger nutrient limitations for zooplankton and zoobenthos (Hessen 2013) and may indirectly affect charr populations by decreasing its food resources. Further amplifying consequences of this, increasing temperatures may also directly affect the charr by increasing their metabolic costs and hence increase resource demands (Byström et al. 2006). A shift towards pelagic habitat use could indicate higher consumption of zooplankton, and thus less of zoobenthos. However, with the CPUE in benthic and pelagic nets being unchanged over time, a shift in habitat use does not seem to have taken place during the time period of this study. Further, while air temperatures are rising the measured water temperatures were well below stress levels of charr (Baroudy and Elliott 1994) and would not either likely drive a habitat change.

I hypothesized that changes in Arctic charr diets and performance would be apparent in response to the decline in zoobenthos density. This was largely supported, as changes in diets and growth rate, together with mostly unchanging dry mass in diets fall in line with the decline seen in zoobenthos densities. Hence, my results may indicate changes in preferred prey abundance (i.e. large sized zoobenthos) being more restricting for charr performance than absolute quantity of consumed prey. However, one should keep in mind that all taxa, whether generally large or small, come in varying sizes and that empty stomachs were not taken into account in this analysis. The lack of change in charr CPUE could likely be explained by the declining zoobenthos manifesting itself as decreased growth rate and condition factor in charr rather than limiting the density of its population. One potential explanation to why the changes in resource densities did not limit the charr populations more is that the population was not as strongly limited by food densities in the past and would hence not be strongly affected at the population level by the observed changes in zoobenthos densities. Fishing could possibly have suppressive effects on the charr population and prevent them from being strongly food limited by reducing their density.

The monitoring program with gill nets is performed with the same effort each year and has been going on since 1985, usually extracting around 200 individuals annually. According to the chairman of the local Sami village Gabna (personal communication with Thomas Svonni) they do not keep records of Sami charr catch, but approximate the catch to 1000kg per year, corresponding to harvest level of 3.5 kg/ha yearly which is slightly higher the extraction of 1 – 3 kg/ha yearly seen in most Swedish mountain lakes (Hammar 2008). Increases in average charr weight can be seen in my data 1996 – 2002 during the same time as the harvest level declined according to Hammar (2008), which likely allowed charr to grow older and larger. This is followed by a time period (2006 – 2019, see Fig 10) where the average size declines, which in turn could indicate an increased fishing pressure (not verified). This scenario should normally be followed by an increase in growth of charr due to relaxed competition. However, I observed the opposite suggesting that increased fishing is not the main cause of the decline in charr size. More likely is that the decline in zoobenthos and slower growth have impacted the population structure during this time.

Cannibalism has been shown present in populations of Arctic charr in both lake and laboratory experiments (Amundsen 1994; Svenning and Borgström 2005) and may be a driver of the population dynamics in the lake. However, my diet analysis revealed only a negligible occurrence of cannibalism in charr in Lake Abiskojaure (0.003% of charr stomachs). This does not necessarily mean that cannibalism in the population has a

negligible effect as intense cannibalism during shorter time periods of small-sized victims can drastically decrease the density of smaller individuals to low levels, where then the frequency of observed cannibalism would be diminished (Claessen, de Roos, and Persson 2000). Population density of the Arctic charr may hence be regulated by something other than food density, but reductions in zoobenthos still seems to be the most plausible explanation for the observed decrease in growth, condition, and average charr weight.

In conclusion, even though no change in CPUE or consumed prey biomass mass in diets of Arctic charr was observed over time, the declining trend of zoobenthos densities in Lake Abiskojaure likely had a negative effect on average size, growth rate, and the condition factor on charr through a shift in diet towards smaller sized prey. Additional declines in zoobenthos could further negatively affect charr performance, and if accompanied by a decline in zooplankton densities due to reduced input of nutrients charr density may also decrease in the future.

## 5 Acknowledgements

I would like to first thank my supervisors Pär Byström and Karin Nilsson for the hours spent giving me feedback and helping me during this thesis. Secondly, I would like to thank everyone I met at Naturhistoriska Riskmuseet in Stockholm for being very helpful during my visit and for letting me use samples from their archive. Thirdly, I would like to thank Henrik Dahl and Gustav Linder for helping me during the sample fishing in Lake Abiskojaure during the summer of 2020 and for being fantastic company during the week there. Without these people this thesis would not have been possible.

## 6 References

- Abisko Scientific Research Station. 2020. Meteorological data from Abisko observatory, daily mean 1984-05-01 – 2020-09-30.
- Amundsen, P. -A. 1994. Piscivory and cannibalism in arctic charr. *Journal of Fish Biology* 45: sA 181-189
- Baroudy, E., and J. M. Elliott. 1994. The critical thermal limits for juvenile Arctic charr *Salvelinus alpinus*. *Journal of fish biology* 45: 6 1041-1053
- Battye, R., W. Battye, C. Overcash, and S. Fudge. 1994. Development and selection of ammonia emission factors. EPA/600/R-94/190. Final report prepared for United States Environmental Protection Agency, Office of Research and Development. USEPA Contract No. 68-D3-0034, Work Assignment 0-3
- Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society* 18(3): 308-343
- Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson, and T. Weglenska. 1976. A review of some problems in zooplankton production studies. *Norwegian Journal of Zoology* 24: 419-456
- Byström, P. and J. Andersson. 2005. Size-dependent foraging capacities and intercohort competition in an ontogenetic omnivore (Arctic char). *OIKOS* 110: 523-536
- Byström, P., J. Andersson, A. Kiessling, and L. O. Eriksson. 2006. Size and temperature dependent foraging capacities and metabolism: consequences for winter starvation mortality in fish. *OIKOS* 115:43-52.
- Claessen, D., A. M. de Roos, L. Persson. 2000. Dwarfs and giants: cannibalism and competition in size-structured populations. *The American Naturalist* 155(2) 219-237
- Covich, A. P., M. A. Palmer, and T. A. Crowl. 1999. The role of benthic invertebrate species in freshwater ecosystems. *Bioscience* 49(2): 119-127
- Docmac, F., M. Araya, I. A. Hinojasa, C. Dorador, C. Harrod. 2017. Habitat coupling writ large: pelagic-driven materials fuel benthivorous macroalgal reef fishes in an upwelling zone. *Ecology* 98(9): 2267-2272

- Eloranta, A. P., H. L. Marash, M. Rautio, and M. Power. 2013. Lipid-rich zooplankton subsidise the winter diet of benthivorous Arctic charr (*Salvelinus alpinus*) in a subarctic lake. *Freshwater Biology* 58(12): 2541-2554
- Finstad A. G., T. Andersen, S. Larsen, K. Tominaga, S. Blumentrath, H. A. de Wit, H. Tømmervik and D. O. Hessen. 2016. From greening to browning: Catchment vegetation development and reduced S-deposition promote organic carbon load on decadal time scales in Nordic lakes. *Scientific Reports* 6: 31944
- Fossum, Petter. 1983. Digestion rate of food particles in the gut of larval herring (*Clupea harengus* L.). *Fiskeridirektoratets Skrifter, Serie Havundersøkelser* 17:347-357
- Fraser, M. P. and G. R. Crass. 1998. Detection of excess ammonia emissions from in-use vehicles and the implications for fine particle control. *Environmental Science and Technology* 32: 1053-1057
- Gill, A. B. 2003. The dynamics of prey choice in fish: the importance of prey size and satiation. *The Journal of Fish Biology* 63(s1): 105-116
- Gómez-Laplaza, L. M., L. Romero, and R. Gerlai. 2019. The role of item size on choosing contrasted food quantities in angelfish (*Pterophyllum scalare*). *Scientific Reports* 9(1): 15305-12
- Hammar, J. 2008. Röding, öring, och överfisket i fjällen, biologiska förutsättningar och strategier för ett uthålligt nyttjande av fiskbestånd i fjällvatten. *Fiskeriverkets sötvattenslaboratorium* ISSN 1404-8590
- Hayden, B., C. Harrod, S. M. Thomas, A. P. Eloranta, J. -P. Myllykangas, A. Siwertsson, K. Præbel, R. Knudsen, P. A- Amundsen, and K. K. Kahilainen. 2019. From clear lakes to murky waters – tracing the functional response of high-latitude lake communities to concurrent ‘greening’ and ‘browning’. *Ecology Letters* 22(5): 807-816
- Hessen, D. O. 2013. Inorganic nitrogen deposition and its impacts on N:P-ratios and lake productivity. *Water* 5: 327-341
- Higgins, S. N., M. J. Vander Zanden. 2010. What difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems. *Ecological Monographs* 80(2): 179-196
- Isles, P. D. F., I. F. Creed, and A-K. Bergström. 2018. Recent synchronous declines in DIN:TP in Swedish lakes. *Global Biogeochemical Cycles* 32(2): 208-225
- Karlsson, J., A. Jonsson, and M. Jansson. 2005. Productivity of high-altitude lakes: climate effect inferred from altitude gradient. *Global Change Biology* 11: 710-715
- Karlsson, J., P. Byström, J. Ask, P. Ask, L. Persson, and M. Jansson. 2009. Light limitation of nutrient-poor lake ecosystems. *Nature Communications* 460(7254): 506–509
- Kissman, C. E. H., C. E. Williamson, K. C. Rose, and J. E. Saros. 2017. Nutrients associated with terrestrial dissolved organic matter drive changes in zooplankton:phytoplankton biomass ratios in an alpine lake. *Freshwater Biology* 62: 40-51
- Klemetsen, A., P. -A Amundsen, J. B. Dempson, B. Jonsson, N. Jonsson, M. G. O’Connell, E. Mortensen. 2003a. 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
- Klemetsen, A., R. Knudsen, F. J. Staldvik, and P.-A. Amundsen. 2003b. Habitat, diet and food assimilation of Arctic charr under the winter ice in two subarctic lakes. *Journal of Fish Biology* 62(5): 1082-1098
- Lajtha, K. and J. Jones. 2013. Trends in cation, nitrogen, sulfate and hydrogen ion concentrations in precipitation in the United States and Europe from 1978 to 2010: a new look at an old problem. *Biogeochemistry* 116: 303-334
- Larsson, S., T. Forseth, I. Berglund, A. J. Jensen, I. Naslund, J. M. Elliott, and B. Jonsson. 2005. Thermal adaptation of Arctic charr: experimental studies of growth in eleven charr populations from Sweden, Norway and Britain. *Freshwater Biology* 50(2): 353-368
- Lehtonen, H. 1998. Does global warming threaten the existence of Arctic charr, *Salvelinus alpinus* (Salmonidae) in northern Finland? *Italian Journal of Zoology* 65(1): 471-474
- Malmquist, H. J. 1992. Phenotype-specific feeding behaviours of two arctic charr *Salvelinus*



- alpinus* morphs. *Oecologia* 92:354-361
- Maranger, R. and M. J. Pullin. 2003. Elemental complexation by Dissolved Organic Matter in lakes: implications for Fe speciation and bioavailability of Fe and P. In: S.E.G. Findlay & R.L. Sinsabaugh (Eds), *Aquatic ecosystems: interactivity of dissolved organic matter*. Academic Press: 186-214
- Miljödata - MVM. 2020. Swedish University of Agricultural Sciences (SLU). National data host lakes and watercourses, and national data host agricultural land, <http://miljodata.slu.se/mvm/> [2020-12-02]
- Nilsson K.A., J. Nilsson, S. Belle, P. Byström, W. Goedkoop, K. Holmgren, J. Olofsson, Power, and T. Vrede. Unpublished. Long-term monitoring data from alpine lake food webs reveal responses to oligotrophication.
- National Register of Survey test-fishing – NORS. 2020. Swedish University of Agricultural Sciences, Department of Aquatic Resources. <http://www.slu.se/sjoprovfiskedatabasen> [2020-12-02].
- Power, G. 2002. Charrs, glaciations and seasonal ice. *Environmental Biology of Fishes* 64: 17-35
- Reist, J. D., M. Power, and B. Dempson. 2012. Arctic charr (*Salvelinus alpinus*): a case study of the importance of understanding biodiversity and taxonomic issues in northern fishes. *Biodiversity* 14: 1 45-56
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Department of the Environment Fisheries and Marine Services, Bulletin 191*. 116 Lisgar Street, Ottawa, Canada
- RStudio Team. 2020. RStudio: Integrated Development for R. *RStudio, PBC, Boston, MA* URL <http://www.rstudio.com/>.
- Sage, R. D. 1982. Wet and dry-weight estimates of insects and spiders based on length. *American Midland Naturalist* 108(2): 407-411
- Sandlund, O. T., K. Gunnarsson, P. M. Jónasson, B. Jonsson, T. Lindem, K. P. Magnússon, H. J. Malmquist, H. Sigurjónsdóttir, S. Skúlason, and S. S. Snorrason. 1992. The arctic charr *Salvelinus alpinus* in Thingvallavatn. *OIKOS* 64: 305-351
- Sandlund, O. T., J. Museth, T. F. Næsje, S. Rognerud, R. Skarsgård, T. Hesthagen, and R. Borgstrøm. 2010. Habitat use and diet of sympatric Arctic charr (*Salvelinus alpinus*) and whitefish (*Coregonus lavaretus*) in five lakes in southern Norway: not only interspecific population dominance? *Hydrobiologia* 650: 27-41
- SMHI: Swedish Metrological and Hydrological Institute, luftweb, 2020. <http://luftweb.smhi.se> [2020-05-05]
- Stockner, J. G., E. Rydin, and P. Hyenstrand. 2000. Cultural oligotrophication: causes and consequences for fisheries resources. *Fisheries Habitat-Perspective* 25(5): 7-14
- Sutela, T. A. Huusko. 2000. Varying resistance of zooplankton prey to digestion: implications for quantifying larval fish diets. *Transactions of the American Fisheries Society* 129: 545-551
- Svenning, M-. A., and R. Borgstrøm. 2005. Cannibalism in arctic charr: do all individuals have the same propensity to be cannibals? *Journal of Fish Biology* 66:4 957-965
- The environmental database at the Department of Aquatic Sciences and Assessment SLU. 2020. <http://www.slu.se/miljodata-MVM> [2020-04-19]
- Vadeboncoeur, Y., E. Jeppsen, M. J. Vander Zanden, H-H. Schierup, K. Christoffersen, and D. M. Lodge. 2003. From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. *Limnology and Oceanography* 48(4) 1408-1418
- Vadeboncoeur, Y., J. Kalff, K. Christoffersen, E. Jeppsen. 2006. Substratum as a driver of variation in periphyton chlorofyll and productivity in lakes. *Journal of North American Benthological Society* 25(2) 397-392
- Wit, H. A., S. Valinia, G. A. Waymenmeyer, M. N. Futter, P. Kortelainen, K. Austnes, D. O. Hessen, A. Räike, H. Laudon, and J. Vuorenmaa. 2016. Current browning of surface waters will be further promoted by wetter climate. *Environmental Science and Technology Letters* 3: 430-435

## 7 Appendix

Table 1 appendix. All taxa found during identification and the taxonomical categories they were assigned to.

Group	Taxa
Bythotrephes	Bythotrephes
Diptera	Chironomidae
Diptera	Ceratopogonidae
Diptera	Chaoborus
Diptera	Unidentified diptera
Diptera	Simuliidae
Diptera	Tipulidae
EPT	Ephemeroptera
EPT	Plecoptera
EPT	Trichoptera
Eurycercus	Eurycercus
Gammarus	Gammarus
Lepidurus	Lepidurus
Other	Bivalvia
Other	Gastropoda
Other	Arachnida
Other	Fish
Other	Fish egg
Other	Tick
Other	Coleoptera
Other	Megaloptera
Other	Notonectidae
Other	Odonata
Other	Zygoptera
Other	Hemiptera
Other	Hymenoptera
Other	Lepidoptera
Other	Terrestrial insect
Other	Hirudinea
Other	Nematoda
Other	Turbellaria
Other	Worm
Zooplankton	Bosmina
Zooplankton	Chydorus
Zooplankton	Copepoda
Zooplankton	Daphnia
Zooplankton	Holopedium
Zooplankton	Polyphemus



Institutionen för ekologi, miljö och geovetenskap (EMG)  
901 87 Umeå, Sweden  
Telefon 090-786 50 00  
Texttelefon 090-786 59 00  
[www.umu.se](http://www.umu.se)