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Impacts of water level regulation on trophic niche and growth of Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in Norwegian hydropower reservoirs

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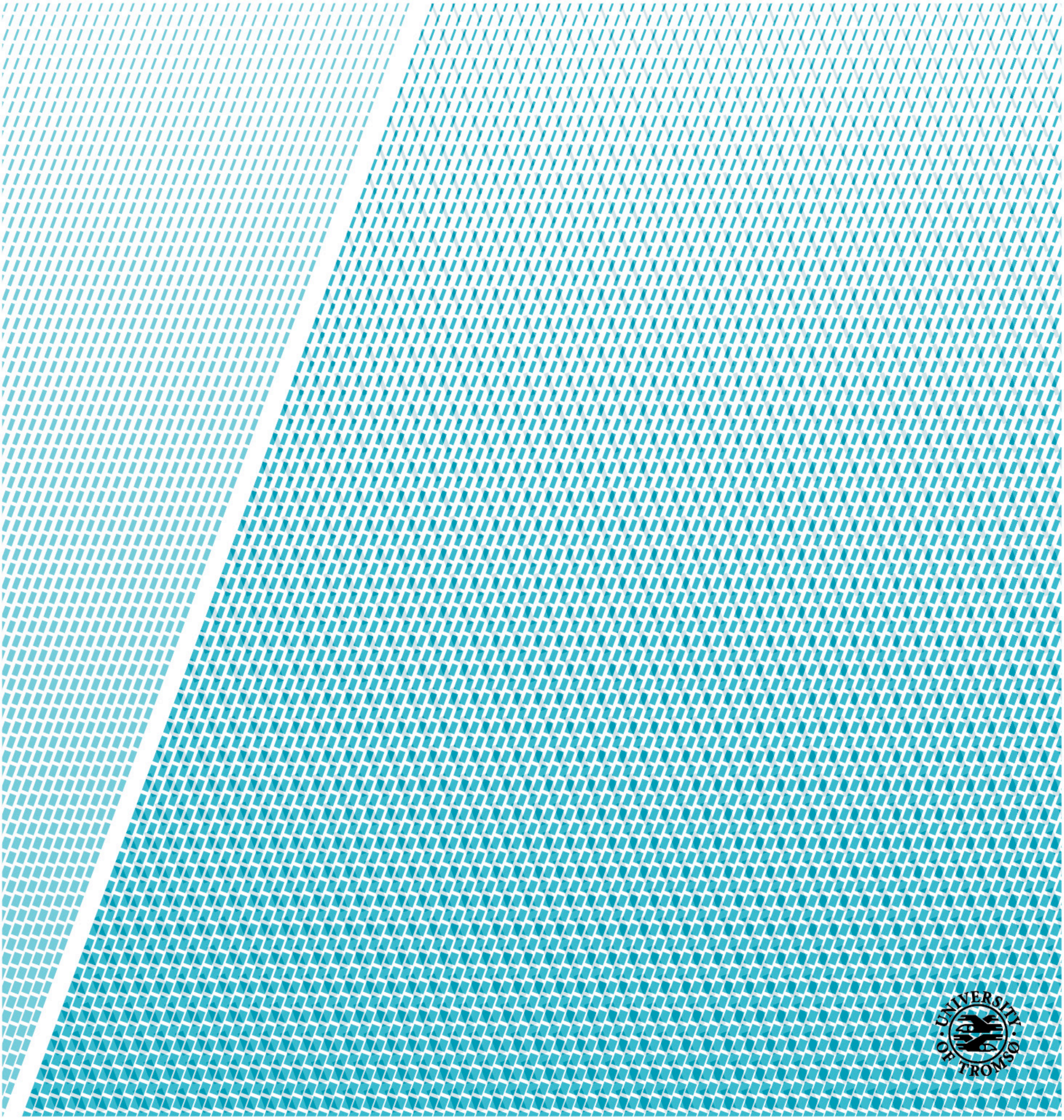
BIO-3950, Master's thesis in Biology, May 2019



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Acknowledgements

It has been a pleasure and privilege to be part of the Freshwater Ecology Group at the University of Tromsø. I have learned and grown during this journey perhaps more than ever. Thanks to the whole Freshwater Group for all the support and company.

Thanks to my great supervisors Rune and Per-Arne for all the wisdom and especially Antti for an enormous amount of guidance and support.

Thanks, Karin for the help with the otoliths, Runar and Paolo for good advises and moments at the office, Eirik for secret fishing spots, Ben and Sebastian for help and friendship, and Eva for the inspiration and help with finding this project.

Thanks to my family and Nina for the endless encouragement and support.

1 Abstract

Hydropower is among the largest renewable energy sources globally. However, it can have drastic environmental and socio-economic impacts on dammed lakes (i.e., reservoirs) and rivers where water levels are regulated due to hydropower operations. Water level regulation in hydropower reservoirs is known to be a large environmental problem, leading to changes in the abiotic conditions, which subsequently affect biological productivity and diversity and thereby may also change the trophic niche and life-history traits of top predators. Arctic charr and brown trout often coexist in subarctic lakes and hydropower reservoirs, and as top predators, they are suitable indicators for changes in the lake ecosystems. In the present study, the effects of water level regulation on trophic niche and life-history traits of Arctic charr and brown trout were studied in 14 subarctic lakes in northern Norway. Age, length, maturity, diet and stable isotope data were compared from seven regulated and seven unregulated lakes. Both charr and trout were expected to show different diet, lower littoral reliance, lower trophic position, slower growth and later maturation in regulated lakes compared to unregulated lakes. This study indicated less effect on fish predators than were expected based on previous studies of reservoir fish populations, but some expected results were also found. Charr did not show any differences in diet, trophic position or growth between the lake types. Moreover, they were found to rely more on littoral resources and to mature at a smaller size in regulated lakes than in unregulated lakes. As hypothesised, trout were found to have a different diet, lower trophic position, slower growth and higher age at maturation in regulated lakes than in unregulated lakes. However, trout also relied more on littoral resources in regulated lakes compared to unregulated lakes. The results were supported by previous studies indicating that charr with a more plastic niche can utilize alternative food and habitat resources, whereas trout are generally specialized on littoral resources and therefore suffer more from water level regulation impacts. The unaffected growth of charr in regulated lakes may result from decreased abundance in regulated lakes due to unsuccessful reproduction and increased predation on juveniles, leading to reduced intraspecific resource competition. Unexpected higher littoral reliance in regulated lakes may be linked to interspecific competitive interactions and to the effect of altitude on lake productivity. All in all, trophic niche and life-history traits of salmonids were different in regulated lakes compared to unregulated lakes. Species showed different responses to water level regulation, while possible confounding effects of the environmental factors on trophic niche and growth remain unknown.

2 Introduction

As the global need for hydropower as a renewable energy source is increasing (Solvang et al., 2014), a better understanding of its environmental impacts on lake ecosystems is needed to facilitate more sustainable hydropower development. Most of the research on the environmental effects of hydropower operations has focused on migratory fish in rivers, whereas the potential impacts on fish in reservoirs have received less attention. Reservoirs can be formed in different ways, for instance by damming a natural lake or a river or by creating a completely artificial waterbody on land. In this study, a reservoir refers to a previously natural but nowadays dammed lake. Water level regulation in hydropower reservoirs is known to be a major ecological problem and lead to changes in lake ecosystems (Baxter, 1977; Zohary & Ostrovsky, 2011). The littoral zone is the habitat most heavily impacted by water level regulation (Zohary & Ostrovsky, 2011), Changes in the abiotic conditions of the reservoir littoral zone, such as increased freezing, desiccation and erosion (Carmignani & Roy, 2017) are often reflected in the biotic communities due to cascading effects from primary production to top predators (Zohary & Ostrovsky, 2011; Carmignani & Roy, 2017; Hirsch et al., 2017). However, large-scale, comparative studies of trophic ecology and life history of salmonid fishes in hydropower reservoirs and natural lakes have been lacking. In the present study, the effects of water level regulation on trophic niche and life-history traits of Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) were examined by comparing stomach contents, stable isotope, growth and maturity data collected from regulated and unregulated subarctic lakes in northern Norway.

In many lakes, shallow littoral areas are more productive than the pelagic open water areas (Wetzel, 2001; Strayer & Findlay, 2010). The littoral zone in lakes is defined as the shallow areas where there is enough light at the bottom to enable the growth of photosynthetic benthic algae and macrophytes (Zohary & Ostrovsky, 2011). Macrophytes, invertebrates, fish and birds exploiting the littoral zone are adapted to natural water level fluctuations (Carmignani & Roy, 2017). In hydropower reservoirs, these natural water level fluctuations, associated with daily and seasonal changes in water inflows and outflows, can be heavily modified, with the water level regulation amplitude occasionally exceeding tens of meters (Zohary & Ostrovsky, 2011). In many reservoirs, the water level decreases during winter and early spring when hydropower production is most needed and most profitable due to high electricity prices.

Water level regulation typically enhances erosion along the reservoir shorelines (Baxter, 1977) and, together with wave action, it tends to transport sediments from the littoral zone down to deeper areas in the reservoir, leaving behind mainly boulders and gravel in the shallow bottom areas (Hofmann, et al., 2008; Carmignani & Roy, 2017). These changes in the abiotic conditions have been found to have negative effects on diversity and abundance of littoral macrophytes (Hellsten & Riihimäki, 1996). Macrophytes are important food and refuges for littoral invertebrates (Newman, 1991) and it is known that fluctuating water levels in reservoirs reduce abundance and diversity of littoral benthic invertebrates (Aroviita & Hämäläinen, 2008). Depleted littoral productivity means also reduced food resources for reservoir fish as some important prey taxa, such as large amphipods and snails, may disappear or become sparse (Nilsson, 1961, 1963). The regulation-induced changes in prey availability and composition are known to affect the abundance, trophic niche and growth of fish in some reservoirs (Eloranta et al., 2016, 2018). However, it remains unknown how water level regulation impacts on fish differ between reservoirs with contrasting abiotic and/or biotic characteristics, or how different salmonid fishes respond to regulation impacts.

Arctic charr (hereafter charr) and brown trout (hereafter trout) are common salmonid species in Norwegian subarctic lakes. They often coexist in the same lakes and can have various intra- and interspecific interactions (Klemetsen et al., 2003; Amundsen & Knudsen, 2009). Charr and trout predate on invertebrates and small fish, and they are often resource competitors (Langeland et al., 1991). Juvenile charr may also act as a prey for large fish, being eaten by trout or cannibalistic conspecifics (Byström, 2006; Finstad et. al., 2006). Trout is a more aggressive and territorial species, preferring shallow littoral areas, whereas charr has a more roaming behaviour and tends to be more flexible and opportunistic feeder in the littoral, pelagic and profundal zones (Nilsson, 1963, 1964; Amundsen & Knudsen, 2009). When charr and trout occur in allopatry, their food preferences are similar. They feed mostly on crustaceans, molluscs and insect larvae. However, in sympatry, the diet and feeding habitats of charr and trout often become segregated, with charr typically feeding mainly on zooplankton or small crustaceans and trout feeding on terrestrial and aquatic insects (Nilsson, 1963). Charr is often aggressively outcompeted from the littoral niche by inflexible trout and pushed towards the pelagic and profundal niche (Nilsson, 1963; Langeland et al., 1991). However, in sympatry, charr may dominate pelagic zooplankton and profundal benthic resources and thus exclude trout from these food and habitat resources (Eloranta et. al., 2013). If littoral resources are impaired due to water level regulation, fish might need to shift foraging on pelagic and profundal food resources (Eloranta et. al., 2016, Sánchez-Hernández et al., 2016). Zooplankton and small fish often become important prey items for predatory fish in reservoirs as bottom-dwelling prey tend to decrease (Nilsson, 1964; Gregersen et al., 2006). Charr is regarded to experience less impact from water level regulation due to its flexibility and ability to adapt to new conditions, whereas trout is more specialized on littoral resources and thus expected to suffer more from water level regulation (Nilsson, 1961; Hirsch et al., 2017).

The effects of water level regulation potentially change the trophic niche, which may affect several life-history traits among fish. Salmonid growth is density dependent with individuals often growing slowly in dense populations (Amundsen et. al., 2007). Hence, the growth of salmonids in hydropower reservoirs can be related to spawning success and population density. Charr typically spawn in lakes, whereas trout most often spawn in rivers and streams (Vøllestad & L'Abée-Lund, 1994; Klemetsen et. al., 2003). Water level drawdown might affect fish reproduction in reservoirs for example by preventing access to spawning grounds or by exposing eggs or juveniles to desiccation and freezing (Carmignani & Roy, 2017). Growth and size at maturation vary a lot among trout and charr populations (Klemetsen et al., 2003). Age of maturity is related to body size and thus charr and trout often delay maturation until they exceed a certain length (Jonsson & Jonsson, 1993). Therefore, the availability and quality of food is not only important for growth of reservoir salmonids, but also for their size and age at maturation and thus reproductive strategy. For trout, cold temperatures affect negatively growth and age at maturation (Jonsson et al., 1991). Previous studies have revealed that water level regulation has a negative effect on the growth of charr and trout. Runnström (1964) found reduced growth of the species following impoundment of four Swedish lakes. Correspondingly, Milbrink et al. (2011) found a dramatic long-term decrease in charr growth in nine Swedish reservoirs. However, in the study by Eloranta et al. (2016), charr showed a higher growth rate in a regulated as compared to an unregulated Norwegian lake, suggesting that the effects of water level regulation might be unpredictable and not always negative for the reservoir fish populations.

The aim of this study is to examine the impacts of water level regulation on trophic niche, growth and maturation of Arctic charr and brown trout by comparing data collected from unregulated and regulated lakes in northern Norway. Although some studies about the effects of water level regulation on charr and trout have been conducted before (for example Eloranta et al., 2016, 2018; Hirsch et al., 2017), there has been a lack of larger scale comparative studies about the potential effects on trophic niche and growth of salmonids. The present study will follow up results from previous studies by including more information from a large number of study lakes and fish individuals. In addition to regulation, other environmental factors such as lake area, altitude and fish community composition are taken into account due to their potential effects on trophic niche and growth of salmonids.

2.1 Hypotheses

The diet and reliance of charr and trout on littoral food resources are expected to differ between regulated and unregulated lakes due to impaired littoral resources associated with water level regulation. However, charr is expected to show more differences between lake types than trout, due to its better ability to switch between available food resources and habitats.

Regulated lakes are expected to be less productive and therefore to show shorter food-chain lengths than unregulated lakes. The shorter food chain is expected to be expressed as lower trophic positions of charr and trout in regulated lakes, as both species are putative top predators in the lake food webs.

Both charr and trout are expected to grow slower and mature later in regulated lakes as compared to unregulated lakes due to reduced food availability and increased physiological stress resulting from water level regulation. However, charr is expected to be less affected compared to trout due to their higher flexibility to utilize alternative habitat and food resources.

3 Material and methods

3.1 Study lakes

The dataset for this thesis was combined from multiple projects (HydroBalance: https://www.cedren.no/english/Projects/HydroBalance), and several projects at UiT), which have been carried out within recent years. The dataset consists of fish data from 14 different lakes in the subarctic northern Norway, in Troms and Nordland counties (Figure 1). Seven of the lakes are unregulated and seven are regulated hydropower reservoirs.

The surface area of the lakes ranged from 1.2 to 14 km^2 and altitude from 55 to 706 m a.s.l.. The regulation amplitude (the difference between the maximum and minimum allowed water level) in the study reservoirs ranged from 12 to 41 m. As typical for lakes in this region, they are mainly oligotrophic, dimictic and usually ice-covered from November to May/June. Typical dominating fish species for these lakes are charr and trout, but also burbot (*Lota lota*) and three-spined stickleback (*Gasterosteus aculeatus*) are found in some of the lakes (Table 1). The lake catchment areas are mainly mountainous with rocky, treeless landscapes at high altitudes and birch (*Betula pubescens)* or patchy pine (*Pinus sylvestris*) forest areas down in the valleys. There are settlements and patchy farmland in some parts of the catchment areas and some of the lakes have summer cabins along the shores.

Figure 1 – Map of the region with pinpointed study lakes (norgeskart.no).

Table 1 – Basic characteristics (surface area, altitude, regulation amplitude and fish community) of the regulated and unregulated study lakes in northern Norway

Lake	**Sampling year**	**Area (km^2)**	**Altitude (m)**	**Regulation amplitude (m)**	**Fish species**
Regulated					
Devdisjavri	2014	6.88	414	33	charr, burbot
Rihpojavri	2014	5.79	486	41	charr, trout, burbot
Govdajavri	2014	4.02	706	24	charr
Sirkelvatnet	2014	1.22	273	17	charr, trout
Jernvatnet	2014	3.62	299	34	charr, trout
Rekvatnet	2013	7.4	297	12	charr, trout
Slunkajavri	2014	6.15	531	15	trout
Mean		5.01	398	25	
Unregulated					
Takvatn	2010	14	214	0	charr, trout, stickleback
Fjellfrøsvatn	2010	5.5	125	0	charr, trout
Cazajavri	2014	1.88	723	0	charr
Josefvatn	2010	3.3	91	0	charr, trout, stickleback
Makkvatn	2013	3	117	0	charr, trout, stickleback
Skilvatn	2013	3.3	35	0	charr, trout, stickleback
Sagelvvatn	2010	5	91	0	charr, trout, stickleback
Mean		5.14	199		

3.2 Sampling

The sampling of data was conducted in August 2010, 2013 and 2014. Fish were collected using Nordic (Appelberg et al., 1995), Jensen (Jensen, 1977) and Tromsø gillnet series as well as additional single-mesh gillnets (mesh sizes of 6, 8, 26, 29, 30, 35, 36, 45 and 62 mm) (Eloranta et. al., 2013). Survey nets were set over-night in the littoral (0-9 m depth), pelagic (0-6 m below the surface) and profundal (20-40 m depth) habitats. The benthic Nordic nets were 30 m long and 1.5 m high, consisting of 12 panels with knot-to-knot mesh sizes of 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 45, and 55 mm. The pelagic Nordic nets consisted of similar panels as the benthic Nordic nets, but they were floating and 6 m high. The benthic Jensen series consisted of eight 25 m long and 1.5 m high nets with mesh sizes of 19.5, 22.5, 26, 29, 35, 40, 45, and 52 mm. The pelagic Jensen series consisted of eight 6 m high and 25 m long floating nets with mesh sizes of 12.5, 16, 19.5, 24, 29, 35, 43, and 52 mm (Eloranta et al., 2016). The Tromsø gillnet series consisted of eight panels with mesh sizes of 10, 12.5, 15, 18.5, 22, 26, 35 and 45 mm. These multi-mesh gillnets were all 40 m long, but the benthic nets were 1.5 m high and the pelagic nets were 6 m high (Eloranta et al., 2013). Benthic and pelagic prey taxa were sampled for stable isotope analysis. Littoral benthic macroinvertebrates were collected by hand picking and using a kick net with 500 µm mesh size in the shallow water (0-1 m), and benthic sledge with 500 µm mesh in the deeper littoral areas (2-6 m). Pelagic zooplankton were collected by taking several hauls with a 50-100 µm plankton net in the upper water column (Eloranta et al., 2013, 2016; Sánchez-Hernández et al., 2016).

Table 2 – Summary of sample sizes (n) and fork lengths of charr (n = 1346 in total) and trout (n = 792 in total) collected from each study lake.

	Charr				**Trout**			
	n	**Fork length (mm)**			**n**	**Fork length (mm)**		
Lake		**Mean**	**SD**	**Range**		**Mean**	**SD**	**Range**
Unregulated								
Cazajavri	74	152.7	72.8	81-526	-	-	-	-
Fjellfrosvatn	226	183.7	76.5	76-415	226	237.9	103.9	114-545
Josefvatn	126	184.1	73.0	75-380	144	181.0	59.8	77-366
Makkvattnet	71	216.3	36.4	93-260	124	202.9	45.0	103-310
Sagelvvatn	131	187.0	74.8	83-340	115	212.5	81.4	85-543
Skilvatn	145	188.5	35.7	91-328	47	192.6	43.6	123-303
Takvatn	89	213.5	72.4	82-435	102	211.9	80.5	83-634
Regulated								
Rekvatnet	82	148.9	39.2	89-270	68	167.9	40.6	85-310
Sirkelvatnet	97	190.0	45.3	85-368	38	208.6	54.5	130-337
Devdisvatn	87	212.3	62.0	105-398	-	-	-	-
Govdajavri	59	175.0	67.0	118-460	-	-	-	-
Jernvatnet	72	150.6	45.6	80-307	56	222.5	54.5	132-382
Rihpojavri	87	269.8	87.8	115-532	-	-	-	-
Slunkajavri	-	-	-	-	54	170.6	43.8	115-350

3.3 Sample preparation

Fish were identified to species, measured in fork length (± 1 mm), weighted (± 1 g) and sexed. Stage of maturity was observed from the gonads and defined in 3 levels (1 = immature, 2 = about to spawn, 3 = spawned). The stomachs were dissected, preserved in 96% ethanol and finally cut open. Stomach fullness was visually estimated in a scale ranging from empty

(0%) to full (100%). Prey items in the stomach contents were identified and sorted to species, genus or family level (Eloranta et al., 2016). The relative proportions of different prey taxa in the stomach contents were estimated according to Amundsen et al. (1996). Age determination was performed from the sagittal otoliths, which were removed, cleaned thoroughly and stored in paper envelopes. Otoliths were later submerged in distilled water and age was determined by counting the opaque zones outwards from the nucleus using a stereomicroscope (Holden & Raitt, 1974).

For stable isotope analyses, a small piece of dorsal muscle tissue was dissected from a subsample of fish and stored frozen at –20°C in Eppendorf tubes prior to subsequent preparation. Benthic and pelagic invertebrate samples for stable isotope analyses were cleaned, sorted and stored frozen at –20°C. For molluscs and trichopterans, only soft body tissue was used. Samples from fish muscle tissue and invertebrates were freeze-dried, ground to a fine powder and weighted (0.5-0.6 mg) into tin cups for the final analysis. Most stable isotope analyses were performed at the University of Jyväskylä, Finland, using a FlashEA 1112 elemental analyser connected to a Thermo Finnigan DELTA Plus Advantage Mass Spectrometer (Eloranta et al., 2013; Sánchez-Hernández et al., 2016). Most samples collected for HydroBalance project from regulated lakes were analysed at Environmental Isotope Laboratory in University of Waterloo, Canada, using a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (ThermoFinnigan, Bremen, Germany) coupled to a 4010 Elemental Analyzer (Costech International S. p. A., Milan, Italy) (Eloranta et al., 2016; Sánchez-Hernández et al., 2016).

3.4 Diet analysis

For statistical analyses, the prey taxa were divided into following prey groups: Cladocera, other zooplankton, benthic crustacean, molluscs, chironomid pupae, chironomid larvae, benthic insects, adult insects, fish and other. Cladocerans (Daphnia, Bosmina, Bythotrephes, Holopedium, Polyphemus) were separated from other zooplankton since their proportions were relatively high compared to other zooplankton species. Chironomids were divided into pupae and larvae since these life stages might be found in different habitats (Kranzfelder et al., 2015).

The stomach contents data was used to test for differences in the charr and trout diets between regulated and unregulated lakes using the non-parametric one-way analysis of similarities (ANOSIM) in the Past 3.23 software (Hammer et. al, 2001). ANOSIM provides a way to test the significant difference between two or more groups of sampling units. For a visual presentation, the relative proportions of different prey groups in charr and trout diets in regulated and unregulated were plotted in Microsoft Excel (v.14.6.9).

3.4.1 Dietary overlap

Dietary overlap between lake types and sympatric charr and trout was examined by using Schoener's similarity index (Schoener, 1970). The indices were calculated from the relative proportions of prey items in the stomach contents using the following equation:

$$\boldsymbol{\alpha = 1 - 0.5\left(\sum_{i=1}^{n} \left|P_{xi} - P_{yi}\right|\right)}$$

where α is the dietary overlap between lake type/species x and y, Pxi is the relative proportion of prey group used in lake type/by species x, Pyi is the relative proportion of prey group used in lake type/by species y, and n is the number of prey taxa or categories. The dietary overlaps are presented in a scale of 0-100% where an overlap of 60% or higher is considered to be biologically significant (Wallace, 1981).

3.4.2 Dietary niche width

Levin's B index (Levins, 1968) was used to estimate the dietary niche width of charr and trout. The index was calculated based on the relative proportions of different prey taxa in the fish stomach contents following the equation:

$$\boldsymbol{B = 1/\Sigma p_i^2}$$

where B is the calculated dietary niche width of the species or population and p_i is the proportion of prey taxa in the diet of the species or population. Levin's B values were calculated separately for charr and trout in each lake. Due to non-normality of the data (Shapiro-Wilk: $p < 0.05$) non-parametric Mann-Whitney U-test was run in Past 3.23 software to compare Levin's B values of charr and trout between lake types (regulated versus unregulated) and the two fish species.

Since fish diet is often dependent on size (Snorrason et al., 1994), to account for the apparent between-lake differences in the fish size distribution (Table 2), the dietary analyses were repeated after including only fish of fork length 100–300 mm. However, no obvious changes in the main results were observed (Table 9) and hence all individuals were retained in the reported results from stomach contents analyses.

3.4.3 Littoral reliance and trophic position estimates

Stable isotope analysis has been increasingly used in ecological studies of e.g. food-web structures and dynamics (Layman et al., 2012). Stable isotopes ratios are presented as delta values relative to the international standards for carbon and nitrogen (Vander Zanden & Rasmussen, 1999). Stable carbon isotopes ($\delta^{13}C$) can be used to trace the ultimate source of assimilated organic carbon in the fish body tissue, e.g. whether the carbon in the fish muscle tissue originates from the littoral benthic or pelagic planktonic food resources. Stable nitrogen isotopes ($\delta^{15}N$) enable to estimate the trophic position of fish in the lake food web, as $\delta^{15}N$ tends to enrich by 3-4‰ with each trophic level. Therefore, the $\delta^{15}N$ values of apex predators can also be used to estimate food chain length in a given ecosystem (Post et al., 2000).

Relative littoral reliance (LF) and trophic position (TP) estimates were calculated by comparing the carbon and nitrogen isotope values of charr and trout muscle tissue to those measured from the sampled benthic and pelagic invertebrates (Karlsson & Byström, 2005). Due to non-normality of the data (Shapiro-Wilk: $p < 0.05$) non-parametric Mann-Whitney U-test was run in Past 3.23 software to compare LF and TP estimates of charr and trout between lake types (regulated versus unregulated) and the two fish species.

3.5 Growth analysis

3.5.1 Growth

The effect of regulation on growth was tested using a linear mixed-effect model in lme4 (Bates et al., 2015) package in R 3.5.2 (R Core Team, 2018). Here, fish fork length was set as the response (predicted) variable, whereas fish age and the binomial regulation factor (1 = unregulated, 2= regulated lake) were fitted as explanatory variables (covariates) and lake was set as a random variable. Two-way interactions were included to the model, because age can be expected to have a different effect on fish length in regulated and unregulated lakes. The effects of other environmental variables on fish growth were tested by fitting lake altitude, surface area and fish community composition (1= only charr/trout, 2= charr and trout, 3= multispecies community) as additional explanatory variables into the model. The models produce outputs including coefficients for each explanatory variable, which allows detecting the effect of each variable on growth of the fish species.

3.5.2 Size and age at maturity

Fork length and age at sexual maturity was tested using a logistic regression model in FSA package (Ogle, 2013) in R 3.5.2 (R Core Team, 2018). Maturity was set as a binomial variable, with 0 referring to immature and 1 to a mature individual. Two-way interactions were included to the model, because age or fork length can be expected to have a different effect on fish maturation in regulated and unregulated lakes. The model returns a sigmoid curve from the observed values and enables to solve the proportion of matured individuals at a given fork length or age.

4 Results

4.1 Stomach contents

The diet of charr and trout was different in regulated and unregulated lakes as indicated by the low Schoener overlap indices measured between lake types (Table 3). However, only trout diet was significantly different between the lake types (Table 3). Both species had generally a broader dietary niche in regulated lakes than in unregulated lakes (Table 3). While trout had a significantly wider niche in regulated lakes than in unregulated lakes, charr did not show any significant difference.

Table 3 – Summary table presenting the niche overlap (Schoener's similarity index) and the difference in diet by analysis of variance (ANOSIM). Niche width (Levin's B index), mean littoral reliance (LF) and trophic position estimates (TP) and the difference between unregulated and regulated lakes and between charr and trout tested with Mann-Whitney U-test. Significant p-values are bolded (p<0.05).

	Charr		**Trout**		**Between species**	
	Unregulated	**Regulated**	**Unregulated**	**Regulated**	**Unregulated**	**Regulated**
Schoener	0.48		0.51		0.34	0.44
ANOSIM	p = 0.279		**p = 0.015**		**p = 0.005**	p = 0.303
Levin's B	4.98	5.13	3.57	6.25	p = 0.520	p = 0.456
Mann-Whit.	p = 0.721		**p = 0.043**			
Mean LF	0.50	0.66	0.75	0.79	**p > 0.001**	**p > 0.001**
Mann-Whit.	**p > 0.001**		**p > 0.001**			
Mean TP	3.57	3.58	3.53	3.24	p = 0.297	**p > 0.001**
Mann-Whit.	p = 0.752		**p > 0.001**			

Low Schoener indices indicate low dietary overlap between coexisting charr and trout populations in unregulated and regulated lakes, but based on ANOSIM, the differences were statistically significant only in unregulated lakes (Table 3). The highest dietary overlaps between sympatric charr and trout were found in Fjellfrosvatn, Skilvatnet and Sirkelvatnet, whereas the lowest dietary overlap was observed in Sagelvvatn (Appendix table 1). There were no significant between-species differences in dietary niche width in regulated or unregulated lakes (Table 3). Charr had on average a wider dietary niche than trout in unregulated lakes, whereas in regulated lakes the pattern was contrary. At the population level, charr had the widest dietary niche in Takvatn and the narrowest niche in Sagelvvatn, whereas trout had the widest dietary niche in Jernvatnet and the narrowest niche in Josefvatn (Appendix table 1).

Although charr diet did not show statistically significant differences between lake types (Table 3), they were feeding more on benthic crustaceans in regulated lakes than in unregulated lakes (Figure 1, Table 4). Trout fed less on adult insects and more on zooplankton in regulated lakes as compared to unregulated lakes (Figure 1, Table 4). Trout also fed more on Chironomid pupae and less on larvae in unregulated lakes than in regulated lakes.

In unregulated lakes, the diet of charr and trout was different (Figure 1, Table 3), as charr were feeding larger proportions of zooplankton and Chironomid larvae than trout (Table 4). On the other hand, trout diet consisted more of insect larvae. Charr and trout had more similar diets in regulated lakes, although trout fed more on benthic insects and charr fed in general more on Chironomids and zooplankton.

Table 4: Significant p-values from one-way ANOSIM statistics. X~y column indicates the compared groups (i.e., fish species and lake type), followed by columns showing the p-values for the tested prey groups. Blank cells indicate non-significant between-group differences (p < 0.05) in the consumption of the given prey type.

Cladoc = Cladocera, Zoopl = Zooplankton, Crust = Crustacean, Moll = Molluscs, Chir = Chironomid, Pup = Pupae, Larv = Larvae.

x-y	Cladoc.	Other zoopl.	Benthic crust.	Moll.	Chir. Pup.	Chir. Larv.	Benthic insects	Adult insects	Fish
Charr reg-charr unreg			0.024						
Trout reg-trout unreg	0.044	0.005			0.029	0.005		0.025	
Charr reg-trout reg							0.020		
Charr unreg-trout unreg	0.002					0.016	0.002	0.001	

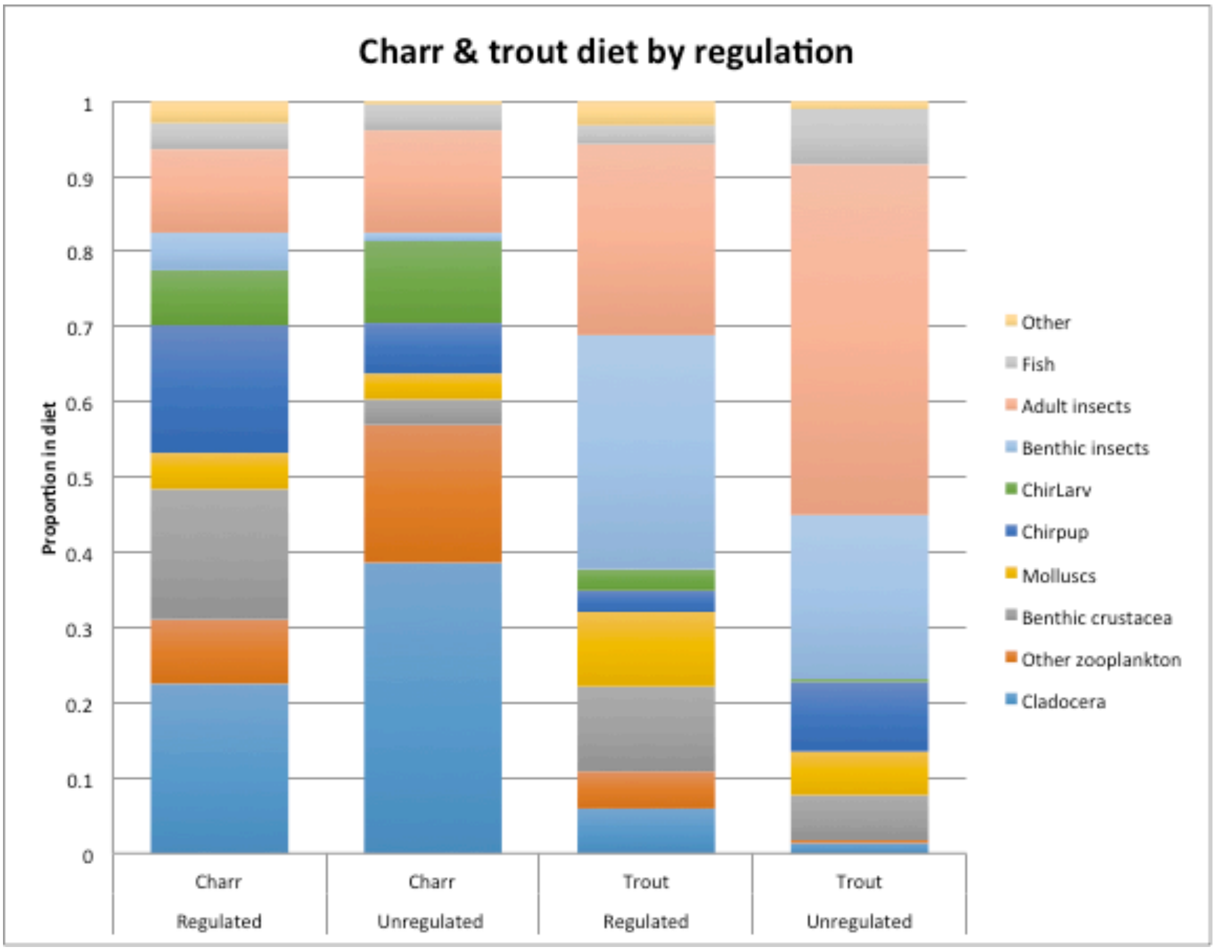


Figure 2 – Relative proportions of different prey taxa found in the stomach contents of charr and trout collected from regulated and unregulated study lakes.

4.1.1 Littoral reliance and trophic position estimates

Both charr and trout relied more on littoral carbon resources in regulated than in unregulated lakes (Table 3). Charr was generally relying less on littoral resources than trout in both lake types. Charr occupied an equal trophic position in regulated and unregulated lakes (Figure 2), whereas trout had a significantly higher (Table 3) trophic position in unregulated lakes than in regulated lakes. Charr occupied a significantly higher trophic position in regulated lakes as compared to trout, whereas in unregulated lakes, the species had more or less equal trophic positions (Table 3).

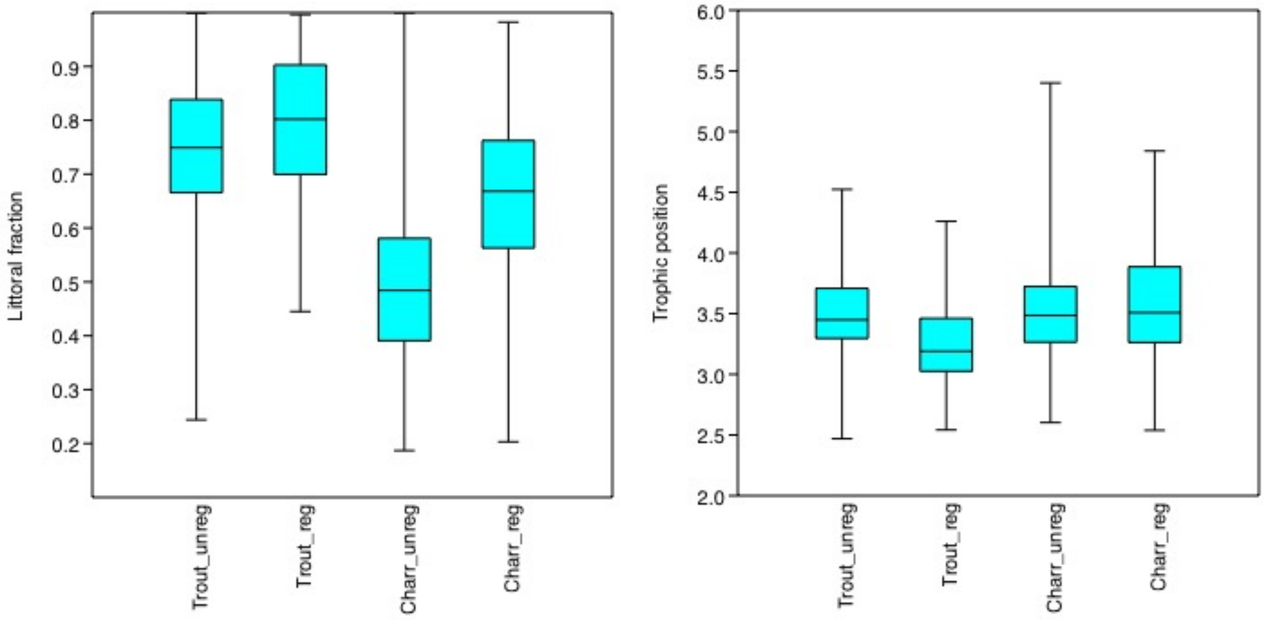


Figure 3 – Boxplots of estimated reliance on littoral carbon sources and trophic positions of trout and charr in regulated and unregulated study lakes. Blue box shows the upper and lower quartiles and the line inside the median. The littoral fraction (LF) and trophic position (TP) estimates are calculated using two-source isotopic mixing models described by Karlsson & Byström (2005). LF estimates the relative reliance of fish on littoral carbon sources compared to pelagic, whereas TP measures the relative trophic level of fish in the lake food web.

4.2 Growth

Charr did not show significant differences in growth between lake types (Table 5, Figure 3). Charr older than six years were generally larger in regulated lakes than in unregulated lakes (Appendix figure 3). However, trout was observed to grow slower in regulated lakes (Table 5, Figure 3) and trout older than 4 years were generally smaller in comparison to trout in unregulated lakes (Appendix figure 3). Other environmental factors such as fish community composition, lake altitude and area had no significant effects on the fork length of charr and trout (Table 5).

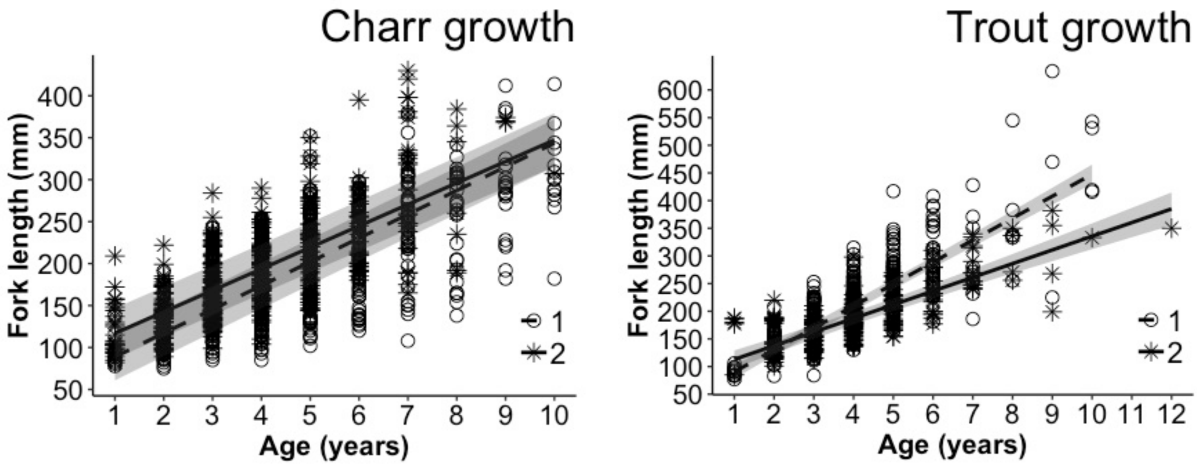


Figure 4 – Relationship between charr and trout age (years) and fork length (mm) in regulated and unregulated lakes (1=unregulated, 2=regulated). The lines represent the growth curves based on mixed-effect model predictions. Coloured shadings show the 95% confidence intervals. Note the different x- and y-axis scales in the figures.

Table 5 – Mixed-effect model output for charr and trout growth with estimates, confidence limits (Cl) and propabilities (p) for each fixed effect.

	Charr	**Fork length**		**Trout**	**Fork length**	
Predictors	***Estimates***	***Cl***	***p***	***Estimates***	***Cl***	***p***
Intercept	-24.27	-147.81 – 99.27	0.710	30.51	-24.86 – 85.87	0.304
Age	28.20	26.89 – 29.52	**<0.001**	39.78	37.27 – 42.30	**<0.001**
Regulation	40.74	-3.91 – 85.39	0.108	60.01	31.98 – 88.05	**0.001**
Fcomm	28.99	-14.04 – 72.02	0.223	8.57	-9.27 – 26.41	0.371
Altitude	0.02	-0.11 – 0.15	0.753	-0.06	-0.13 – 0.02	0.192
Area	1.22	-5.54 – 7.98	0.732	0.33	-1.80 – 2.46	0.772
Age:Regulation	-1.79	-4.08 – 0.49	0.124	-15.47	-19.82 – -11.12	**<0.001**

4.2.1 Length and age at maturity

Charr matured at a smaller size in regulated lakes than in unregulated lakes with a significant effect (p=0.006) of interaction between fork length and regulation (Figure 5, Appendix table 3). Trout matured approximately at the same size (Figure 5) in both lake types, but the age at maturity was significantly higher (p = 0.026) in regulated lakes than in unregulated lakes (Figure 5, Appendix table 3).

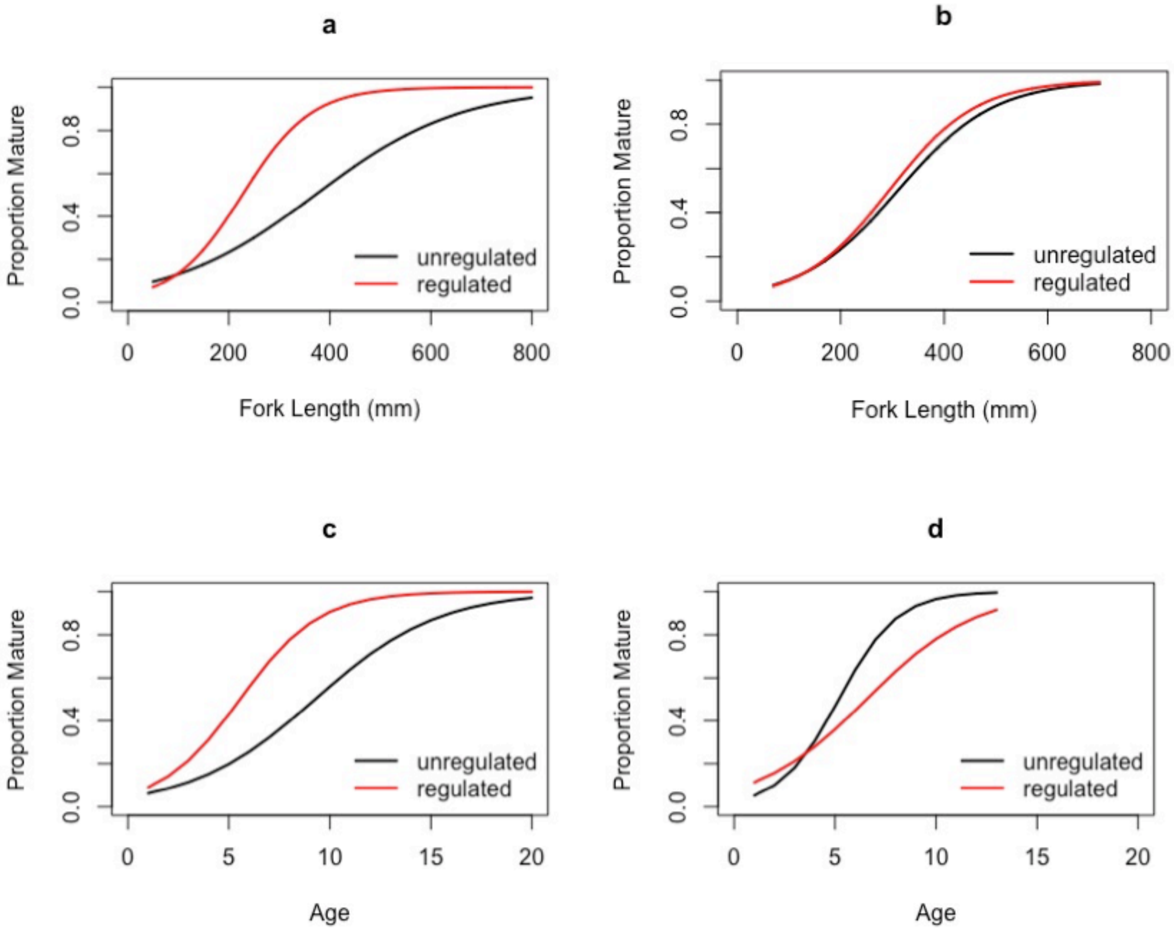


Figure 5 – Fitted logistic regression curves showing the proportion of sexually mature charr and trout as a function of fork length (mm) (a = charr, b = trout) and age (years) (c = charr, d = trout) in unregulated and regulated lakes.

5 Discussion

The present study revealed some differences in the trophic niche and growth of charr and trout between regulated and unregulated lakes. However, some of the water level regulation impacts were unexpected and apparently varied between the two fish species. Trout showed the expected slower growth and different diet in regulated lakes compared to unregulated lakes, whereas charr did not show expected differences in diet or growth. Unexpectedly, both species were relying more on littoral resources in regulated lakes than in unregulated lakes, whereas only trout showed different trophic position between lake types. Both species also showed a difference in age and size at maturation between lake types, as charr matured at a smaller size and trout at a higher age in regulated lakes than in unregulated lakes.

5.1 Trophic niche

In contrary to the hypothesis, charr diet did not differ and they occupied a similar trophic position in regulated and unregulated lakes. Furthermore, based on stable isotope data, charr relied more on littoral carbon resources in regulated than in unregulated lakes, which contrasts with earlier studies (Eloranta et al. 2016). However, the reservoirs in the present study were generally located at a higher altitude than the unregulated lakes, which may explain some of the inconsistency between this and previous studies. Milbrink et al. (2011) suggested that charr could rely more on littoral resources at high altitude reservoirs, due to lower inorganic nutrient concentrations and allochthonous subsidies in the pelagic zone compared to low altitude lakes. Based on the diet information from the present study, charr had a clear pattern of feeding large proportions of zooplankton in unregulated lakes, whereas the diet varied more between charr populations in regulated lakes. This might indicate that fish individuals in regulated lakes might be forced to specialized diets due to changes in prey availability and community compositions as well as increased intraspecific competition (Eloranta et al., 2016). Furthermore, increased water turbidity in regulated lakes may also restrict phytoplankton and zooplankton production and thus make pelagic foraging unprofitable for charr (Eloranta et al., 2016). Turbulent water may contain silt and other substances that complicate the foraging of visual feeders (Langeland et al., 1991). Charr in regulated lakes were unexpectedly found to feed more on benthic crustaceans, which are generally known to suffer from water level regulation (Nilsson, 1964). However, the main difference was caused by a large proportion (56%) of Eurycercus spp. in the diet of charr in one regulated lake (Sirkelvatnet), a species known to survive well under fluctuating water levels (Rognerud & Brabrand, 2010). The trophic position of charr did not differ between lake types, which indicates similar food chain length in regulated and unregulated charr lakes. However, fish species richness was generally higher in unregulated lakes and charr trophic position is studied to increase with fish species richness (Eloranta et al., 2015). Results indicate that charr evidently have a high dietary plasticity (Eloranta et al., 2011) and thus are able to adapt to changes in prey availability in hydropower reservoirs

Trout showed differences in diets between lake types and a generally broader dietary niche in regulated lakes. A generally broader trophic niche indicates more individual specialization for various food resources, possibly due to changed prey availability (Eloranta et. al., 2013). However, the relative littoral reliance was higher in regulated than in unregulated lakes. It could be concluded that trout, which are regarded as less flexible than charr (Amundsen & Knudsen, 2009), rely mainly on littoral prey whether the resources in the shallow areas are depleted or not. Trout and charr coexist in most of present study lakes even though charr is known to be able to dominate the less affected pelagic and profundal habitat resources (Eloranta et. al., 2013). Charr excluding trout from these habitats may be the reason for higher littoral reliance of trout in the regulated lakes. This was also supported by the stomach contents of allopatric trout in regulated Slunkajavri, where the diet of the trout population was more variable compared to other regulated lakes with sympatric fish populations. In this lake, trout also included zooplankton as prey, which were mostly utilized by charr in sympatric lakes. Based on stable isotope data, trout occupied a slightly higher trophic position in unregulated lakes, which indicates longer food chain as compared to regulated lakes. This may be explained by the presence of an intermediate consumer, i.e. three-spined stickleback, in almost all unregulated lakes, whereas in regulated lakes, this prey species was missing. Small fish are known to be an important food for trout in regulated lakes (Gregersen et al., 2006). However, stomach content data revealed more piscivory among trout populations in unregulated than in regulated lakes, yet without statistical significance. Based on stomach contents, trout and charr had distinct dietary differences in unregulated lakes, whereas in regulated lakes, the diet was more similar. It could be concluded that if littoral resources are impaired in reservoirs, charr and trout are forced to utilize more or less on the same prey groups. However, based on Schoener's indices, there were no significant dietary overlaps between any of the sympatric charr and trout populations.

5.2 Growth

Charr were, unexpectedly, not growing slower in reservoirs, but in contrast old charr (>6 years) grew better in regulated lakes than in unregulated lakes. This result contrasts previous findings by Milbrink et al. (2011), where charr in Swedish regulated lakes experienced long-term decrease in growth. A similar pattern was found by Runnström (1964), where charr experienced increased growth very soon after the impoundment, followed by a later reduction of primary and secondary production and the somatic growth of fish. However, a similar observation on growth as in the present study was made by Eloranta et al. (2016) and explained by the lower relative abundance of charr in regulated lakes. It is known that lower abundance of charr reduces intraspecific resource competition and thereby supports higher somatic growth rates of individuals (Amundsen et al., 2007). Reasons for lower abundance of charr in regulated lakes may for example be unsuccessful littoral spawning or increased predation on juvenile charr by trout or cannibalistic conspecifics. Especially if the spawning grounds and refuge areas for juveniles are exposed during periods with low water level (Carmignani & Roy, 2017). However, some charr are able to spawn in deeper habitats (Klemetsen et al., 1997), if spawning grounds in reservoirs are exposed to desiccation and freezing. All in all, charr seem to be able to feed as efficiently in both lake types despite water level regulation and thus growth rate does not differ either. However, lower abundance of charr might compensate otherwise slower growth in regulated lakes.

Trout tends to occupy a more specialized littoral niche than charr, which likely explains why trout grew slower in regulated than in unregulated lakes, as also indicated by previous studies (Runnström, 1964). Reduced growth rates of trout in reservoirs likely result from impaired littoral resources and strong interspecific resource competition with sympatric charr. Furthermore, trout growth is also known to be negatively affected by low temperatures (Klemetsen et al., 2003). The optimal temperature for trout growth is 13-15°C and 4°C is the minimum temperature that allows trout to continue growing (Langeland et al., 1991). Thus, it should be noted that most regulated lakes studied here are located at higher altitudes and potentially have colder water than the compared unregulated lakes. Although trout fork length was not affected by the lake altitude, these environmental factors should be better tested in a follow-up study. It is also obvious that during periods with low water level, the volume of the reservoir decreases and thus the relative density of fish increases, leading to stronger competitive and predatory interactions between and within fish populations. As hypothesised, trout as a littoral specialist was growing slower in regulated lakes, propably due to reduced food availability, strong intraspecific competition and possibly colder temperatures at high-altitude regulated lakes.

Maturity processes of salmonids are complicated and vary between species and populations (Klemetsen et al., 2003). Based on classical life-history theory, age and size at maturity are part of the major life-history characteristics and there is a trade-off between allocating energy to grow large or to reproduce early (Stearns, 2000). Early maturation means more small offspring and higher survival rate before the first reproduction but higher mortality of the offspring, lower growth rates and shorter lifespan. Late maturation supports higher fecundity, larger offspring and longer lifespan, but low survival rate before the first reproduction (Stearns, 1976). In the present study, charr matured generally at the same age, but at a smaller size in regulated lakes as compared to unregulated lakes. This might indicate a slower growth for charr in regulated lakes, which was not supported by other results in this study. Charr in regulated lakes might favour early maturation due to the unstable environment and higher mortality of juveniles resulting from predation and/or impaired nursery grounds exposed to low water levels. If there is a limited availability of or strong competition for littoral resources, charr may shift to a profundal niche (Sánchez-Hernández et al., 2016). Less profitable prey in the profundal zone may induce slow growth and thus smaller size at maturation. Trout matured at the same size but at a higher age in regulated than in unregulated lakes. This indicates that trout must exceed a certain length over age before sexual maturation. Ontogenetic niche shift from insectivory to piscivory often enhances trout growth to exceed the large size and high fecundity (L'Abée-Lund et. al., 2002). However, the fact that trout grew slower in regulated lakes likely explains why the species also matured at a higher age as compared to trout in unregulated lakes. The higher growth rate and lower maturation age of trout might, in turn, be associated with warmer water and shorter ice-cover period in unregulated, low-altitude lakes.

5.3 Study limitations and avenues for future research

Although the present dataset provided valuable data to compare regulated and unregulated lakes, the sampling at each lake was done only in one year and season. Hence, the data do not allow highly needed long-term or seasonal studies or before-after comparisons of regulation impacts. As mentioned earlier, most regulated lakes are located at higher altitudes than unregulated lakes. The altitude affects for example lake productivity and species richness, which both may have confounded the observed patterns of fish growth and diet. Hence, the effect of altitude and other environmental factors on reservoir fish needs more examining. Such factors are for example lake area, depth, and morphometry and fish species richness. Data of fish abundance and habitat use were not included in this study, but they could have provided interesting insights to the population and community dynamics. It should also be noted that the dataset included only two lakes with allopatric populations of charr and trout, the rest being sympatric populations. It would be best to have sufficient data from both allopatric and sympatric lakes to evaluate the role of interspecific interactions on trophic niche, growth and life history of salmonids in hydropower reservoirs.

5.4 Conclusions

As the demand for renewable energy and increased flexibility and capacity of hydropower production is increasing, the public attention and research on its potential environmental effects should increase as well. Lake ecosystems can be fragile and reflect dramatic abiotic changes, although these changes may be slow and take decades to show (Dudgeon, 2006). This study demonstrates that potential negative effects of water level regulation on biotic communities can be complex and unpredictable due to many factors. It must be noted that each lake and fish population typically have unique characteristics and therefore should be carefully examined to reliably evaluate and mitigate the local environmental and socio-economic impacts of hydropower operations. Lakes provide various ecosystem services and thus they have an important socio-economical status worldwide. It is stated in the EU Water Framework Directive 2000/60/EC (WFD) that the stage of freshwater ecosystems needs to be enhanced, which obligates us to research, understand and predict the potential harmful impacts of water level regulation on lakes and rivers. The results of this study provide valuable insights to the ecology of salmonids in reservoirs, thereby also supporting informed management and monitoring of these valuable fish populations and the ecosystems they live in.

6 References

Amundsen, P.-A., Gabler, H.-M., & Staldvik, F. J. (1996). A new approach to graphical analysis of feeding strategy from stomach contents data – modification of the Costello 1990 method. Journal of Fish Biology, 48:607–614.

Amundsen, P.-A., Knudsen, R. & Klemetsen, A. (2007), Intraspecific competition and density dependence of food consumption and growth in Arctic charr. Journal of Animal Ecology, 76:149-158.

Amundsen, P.-A. & Knudsen, R. (2009), Winter ecology of Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in a subarctic lake, Norway. Aquatic Ecology, 43:765-775.

Appelberg, M., Berger, H. M., Hesthagen, T., Kleiven, E., Kurkilahti, M., Raitaniemi, J., & Rask, M. (1995). Development and intercalibration of methods in Nordic freshwater fish monitoring. Water, Air, & Soil Pollution, 85:401–406.

Aroviita, J. & Hämäläinen, H. (2008). The impact of water-level regulation on littoral macroinvertebrate assemblages in boreal lakes, Hydrobiologia, 613:45–56.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4, Journal of Statistical Software, 67:1–48.

Baxter, R. M. (1977). Environmental Effects of Dams and Impoundments, Annual Review of Ecology and Systematics, 8:255–283.

Byström, P. (2006). Recruitment pulses induce cannibalistic giants in Arctic char. Journal of Animal Ecology, 75:434-444.

Carmignani, J. R. & Roy, A. H. (2017). Ecological impacts of winter water level drawdowns on lake littoral zones: a review, Aquatic Sciences. Springer International Publishing, 79:803–824.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. , Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A., Soto, D., Stiassny, M. L. & Sullivan, C. A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews, 81:163-182.

Eloranta, A. P., Siwertsson, A., Knudsen, R. & Amundsen, P.-A. (2011). Dietary plasticity of Arctic charr (*Salvelinus alpinus*) facilitates coexistence with competitively superior European whitefish (*Coregonus lavaretus*), Ecology of Freshwater Fish, 20:558-568.

Eloranta, A. P., Knudsen, R. & Amundsen, P.-A. (2013). Niche segregation of coexisting Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) constrains food web coupling in subarctic lakes, Freshwater Biology. 58:207–221.

Eloranta, A. P., Kahilainen, K., Amundsen, P.-A., Knudsen, R., Harrod, C. & Jones, R. (2015). Lake size and fish diversity determine resource use and trophic position of a top predator in high-latitude lakes. Ecology and Evolution. 5:1664-1675.

Eloranta, A. P., Sánchez-Hernández, J., Amundsen, P. -A., Skoglund, S., Brush, J. M., Henriksen, E. H. & Power, M. (2016). Water level regulation affects niche use of a lake top predator, Arctic charr (*Salvelinus alpinus*), Ecohydrology, 10:1–9.

Eloranta, A. P., Finstad, A., Helland, I. P., Ugedal, O. & Power, M. (2018). Hydropower impacts on reservoir fish populations are modified by environmental variation, Science of the Total Environment, 618:313–322.

Finstad, A. G., Ugedal, O. & Berg, O. K. (2006). Growing large in a low grade environment: size dependent foraging gain and niche shifts to cannibalism in Arctic char. Oikos 112:73-82

Gregersen, F., Aass, P., Vøllestad, L. A. & L'Abée-Lund, J. H. (2006). Long-term variation in diet of Arctic char, *Salvelinus alpinus*, and brown trout, *Salmo trutta*: effects of changes in fish density and food availability. Fisheries Management and Ecology, 13: 243-250.

Hammer, Ø., Harper, D.A.T., & Paul D. R. (2001). Past: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica, vol. 4, issue 1, art. 4: 9pp.

Hellsten, S., & Riihimäki, J. (1996). Effects of lake water level regulation on the dynamics of aquatic macrophytes in northern Finland. Hydrobiologia, 340:85-92.

Hirsch, P. E., Eloranta, A. P., Amundsen, P.-A., Brabrand, Å., Charmasson, J., Helland, I. P., Power, M., Sánchez-Hernández, J., Sandlund, O. T., Sauterleute, J. F., Skoglund, S., Ugedal, O. & Yang, H. (2017). .Effects of water level regulation in alpine hydropower reservoirs: an ecosystem perspective with a special emphasis on fish, Hydrobiologia, 794:287–301.

Hofmann, H., Lorke, A. & Peeters, F. (2008). Temporal scales of water-level fluctuations in lakes and their ecological implications. Hydrobiologia, 613:85–96.

Holden M.J & Raitt D.F.S. (1974). Manual of fisheries science part 2 - Methods of Resource Investigation and their Application. Food and Agriculture Organization of the United Nations, Rome, IT, pp.115.

Jensen, K. W. (1977). On the dynamics and exploitation of the population of brown trout, Salmo trutta, L., in Lake Øvre Heimdalsvatn, southern Norway. Report Institute of Freshwater Research, Drottningholm, 56:18–69.

Jonsson, B., L'Abée-Lund, J. H., Heggberget, T. G., Jensen, A. J., Johnsen, B. O., Næsje, T. F. & Sættem, L. M. (1991). Longevity, Body Size, and Growth in Anadromous Brown Trout (*Salmo trutta*), Canadian Journal of Fisheries and Aquatic Sciences, 48:1838–1845.

Jonsson, B. & Jonsson, N. (1993). Partial migration: niche shift versus sexual maturation in fishes, Reviews in Fish Biology and Fisheries, 3:348–365.

Karlsson, J. & Byström, P. (2005). Littoral energy mobilization dominates energy supply for top consumers in subarctic lakes, Limnology and Oceanography, 50:538–543.

Klemetsen, A., Amundsen, P.-A., Knudsen, R., & Hermansen, B. (1997). A profundal, winter-spawning morph of Arctic charr Salvelinus alpinus (L.) in lake Fjellfrøsvatn, northern Norway. Nordic Journal of Freshwater Research, 73:13–23

Klemetsen, A., Amundsen, P.-A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Conell, M. F. O., & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish, 12:1–59.

Kranzfelder, P., Anderson, A., Egan, A., Mazack, J., Bouchard, R., Rufer, M. & Ferrington, L. (2015). Use of Chironomidae (Diptera) Surface-Floating Pupal Exuviae as a Rapid Bioassessment Protocol for Water Bodies, *Journal of Visualized Experiments*, 101.

L'Abée-Lund, J. H., Aass, P., & Saegrov, H. (2002). Long-term variation in piscivory in a brown trout population: Effect of changes in available prey organisms. Ecology of Freshwater Fish, 11:260 –269.

Langeland, A., L'Abée-Lund, J. H., Jonsson, B. & Jonsson, N. (1991). Resource Partitioning and Niche Shift in Arctic Charr *Salvelinus alpinus* and Brown Trout *Salmo trutta*, The Journal of Animal Ecology, 60:895-912

Layman, C. A., Araujo, M. S., Boucek, R. , Hammerschlag-Peyer, C. M., Harrison, E. , Jud, Z. R., Matich, P. , Rosenblatt, A. E., Vaudo, J. J., Yeager, L. A., Post, D. M. and Bearhop, S. (2012), Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biological Reviews, 87: 545-562.

Levins, R. (1968). Evolution in changing environments: some theoretical explorations (No. 2). Princeton University Press.

Milbrink, G., Vrede, T., Tranvik, L. J., & Rydin, E. (2011). Large-scale and long-term decrease in fish growth following construction of hydroelec- tric reservoirs. Canadian Journal of Fisheries and Aquatic Sciences, 68:2137–2173.

Newman, R.M. (1991). Herbivory and detritivory on freshwater macrophytes by invertebrates: A review, Journal of the North American Benthological Society, 10:89-114.

Nilsson, N-A. (1961) The effect of water-level fluctuations on the feeding habits of trout and char in the Lakes Blåsjön and Jormsjön, North Sweden. Rep Inst. Freshw. Res. Drottningholm. 42:238-261

Nilsson, N-A. (1963) Interaction between Trout and Char in Scandinavia, Transactions of the American Fisheries Society, 92:276-285,

Nilsson, N-A. (1964) Effect of impoundment on the feeding habits of brown trout and char in Lake Ransaren (Swedish Lappland). Verh. Internat. Verein. Limnol. 15:444-452.

Ogle, D. (2013) fishR Vignette-Maturity Schedules.

Post, D. M., Pace, M. L. & Hairston, N. G. (2000). Ecosystem size determines food-chain length in lakes. *Nature.* 405:1047-1049.

R Core Team (2018). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Rognerud, S. & Brabrand, Å. (2010). HydroFish-prosjektet: Sluttrapport for undersøkelsene 2007 - 2010, *74*. Norsk institutt for vannforskning.

Runnström, S. (1964). Effects of impoundment on the growth of Salmo trutta and *Salvelinus alpinus* in Lake Ransaren (Swedish Lappland), SIL Proceedings, 1922-2010, 15:453-461.

Sánchez-Hernández, J., Eloranta, A. P., Finstad, A. G. & Amundsen, P.-A. (2016). Community structure affects trophic ontogeny in a predatory fish, *Ecology and Evolution*, 7:358–367.

Schoener, T. W. (1970). Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology, 51:408-418.

Snorrason, S. S., Skúlason, B., Jonsson, B., Malmquist, H. J., Jónasson, P, M., Sandlund, O, T. & Lindem, T. (1994). Trophic specialization in Arctic charr Salvelinus alpinus (Pisces; Salmonidae): morphological divergence and ontogenetic niche shifts, Biological Journal of the Linnean Society. Narnia, 52:1–18.

Stearns, S. (1976). Life-History Tactics: A Review of the Ideas. The Quarterly Review of Biology, 51:3-47.

Stearns, S. (2000). Life history evolution: successes, limitations, and prospects. Naturwissenschaften, 87:476-486

Solvang, E., Charmasson, J., Sauterleute, J., Harby, A., Killingtveit, Å., Egeland, H., Andersen, O., Ruud, A. & Aas, Ø. (2014). Norwegian hydropower for large-scale electricity balancing needs.

Strayer, D. L. & Findlay, S. E. G. (2010). Ecology of freshwater shore zones, Aquatic Sciences. SP Birkhäuser Verlag Basel, 72:127–163.

Vander Zanden, M.J. & Rasmussen, J.M. (1999). Primary consumer δ13C and δ15N and the trophic position of aquatic consumers, Ecology, 80:1395-1404

Vøllestad, L. A. & L'Abée-Lund, J. H. (1994). Evolution of the life history of Arctic charr *Salvelinus alpinus*, Evolutionary Ecology, 8:315–327.

Wallace, R. K. (1981). An Assessment of Diet-Overlap Indexes, Transactions of the American Fisheries Society, 110:72–76.

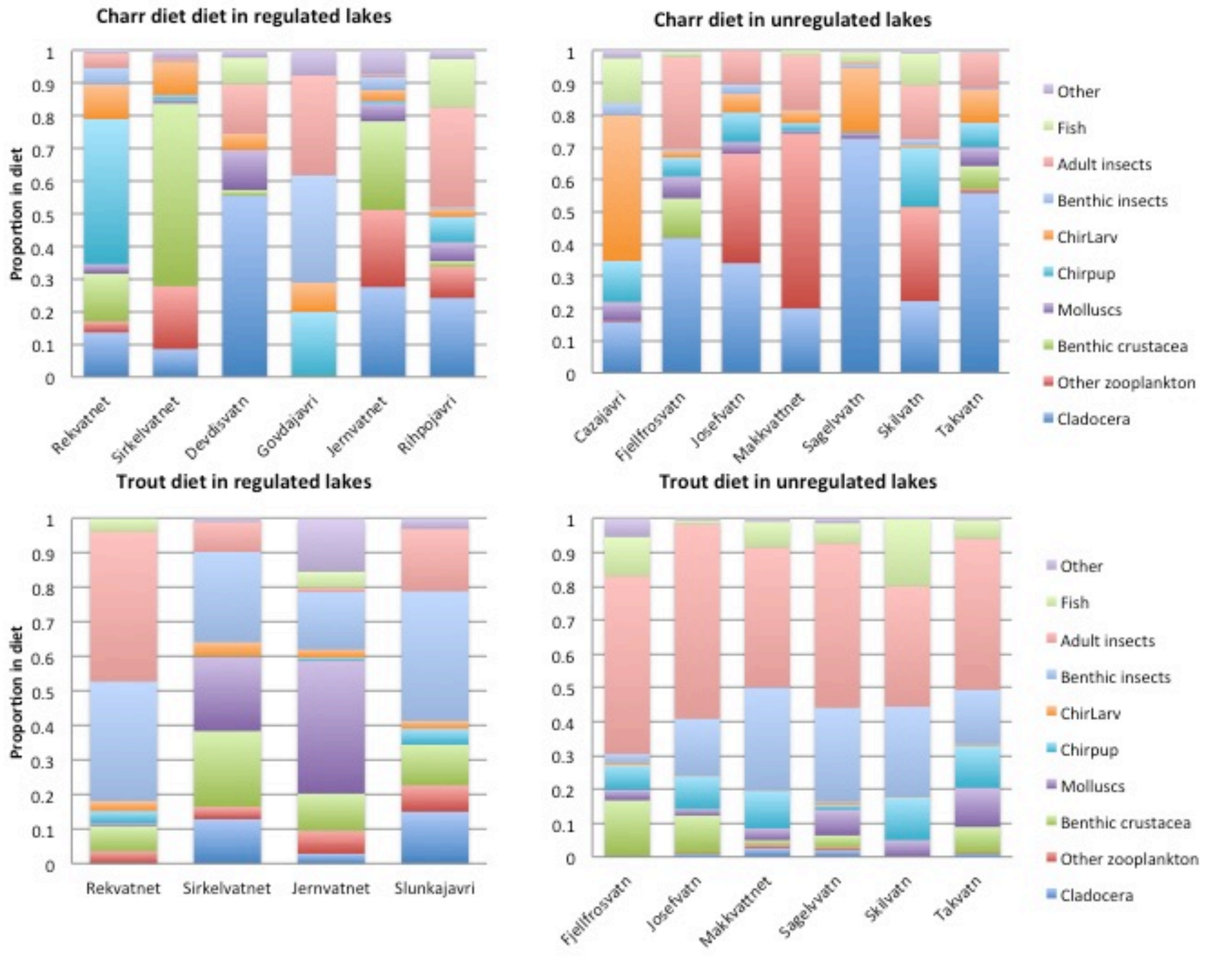
Wetzel, R. G. (2001). Limnology : lake and river ecosystems. Academic Press.

Zohary, T. & Ostrovsky, I. (2011). Ecological impacts of excessive water level fluctuations in stratified freshwater lakes, Inland Waters, 1:47–59.

7 Appendix

Appendix table 1 – Summary table of niche width (Levin's B), mean littoral reliance (LF) and trophic position (TP) estimates of as well as niche overlap (Schoener index) between charr and trout in the unregulated and regulated study lakes.

Lake	**Charr**			**Trout**			
	Levins B	**Mean LF**	**Mean TP**	**Levins B**	**Mean LF**	**Mean TP**	**Schoener between species**
Unregulated							
Cazajavri	3.68	0.81	3.81	-	-	-	-
Fjellfrosvatn	7.30	0.54	3.45	3.08	0.72	3.49	0.46
Josefvatn	3.94	0.43	3.86	2.66	0.90	-	0.25
Makkvattnet	2.92	0.39	3.24	3.90	1.24	3.26	0.24
Sagelvvatn	2.35	0.33	3.51	3.23	0.68	3.41	0.08
Skilvatn	5.84	0.57	3.64	4.39	0.88	3.99	0.41
Takvatn	8.86	0.51	3.18	4.14	0.72	3.44	0.32
Regulated							
Rekvatnet	4.08	0.75	3.32	4.09	0.90	3.03	0.26
Sirkelvatnet	2.85	0.65	3.52	6.34	0.80	3.20	0.41
Devdisvatn	4.11	0.75	3.32	-	-	-	-
Govdajavri	7.93	0.70	3.96	-	-	-	-
Jernvatnet	4.98	0.55	3.44	7.32	0.80	3.13	0.23
Rihpojavri	6.81	0.64	3.98	-	-	-	-
Slunkajavri	-	-	-	7.27	0.78	3.59	-


Charr diet diet in regulated lakes

Charr diet in unregulated lakes

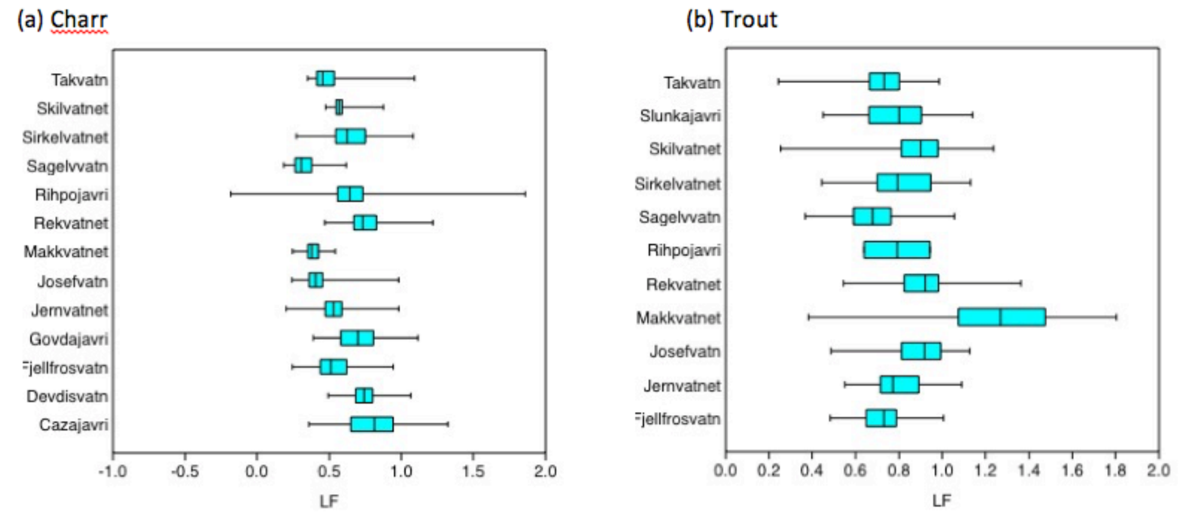
Trout diet in regulated lakes

Trout diet in unregulated lakes

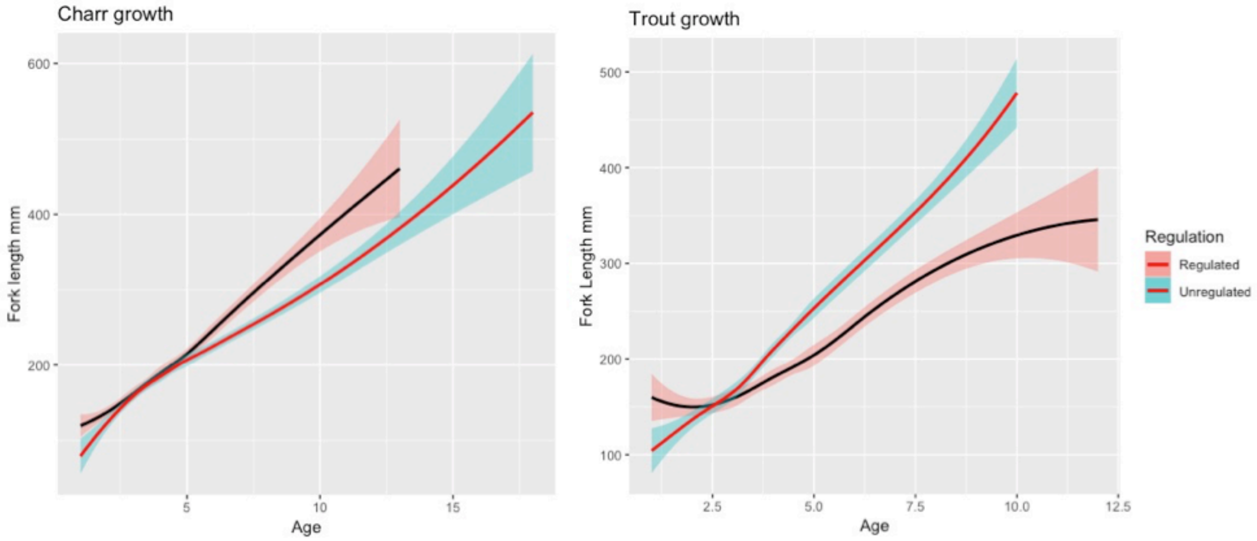
Appendix figure 1 – Relative proportions of different prey taxa found in the stomach contents of charr and trout collected from unregulated and regulated study lakes.

Appendix table 2 – Differences in diet of charr and trout in unregulated and regulated lakes based on one-way analysis of variance (ANOSIM) using limited fork length of 100-300mm.

	Unreg charr	Reg charr	Unreg trout	Reg trout
Unreg charr		p = 0.234	**p > 0.001**	**p = 0.009**
Reg charr	p = 0.234		**p = 0.002**	p = 0.422
Unreg trout	**p > 0.001**	**p = 0.002**		**p = 0.021**
Reg trout	**p = 0.009**	p = 0.422	**p = 0.021**	



Appendix figure 2 – Boxplots of estimated reliance of charr and trout on littoral carbon sources in the study lakes. Blue box shows the upper and lower quartiles and the line inside the median. The littoral fraction estimates are calculated using a two-source isotopic mixing model described by Karlsson & Byström (2005). It describes the relative reliance on littoral carbon sources compared to pelagic.



Appendix figure 3 – Relationships between age and fork length (mm) of charr and trout in regulated and unregulated lakes. Smoothened line presents the average fork length at given age interval , coloured shading showing the 95% confidence interval. Note the different x- and y-axis scales in the figures.

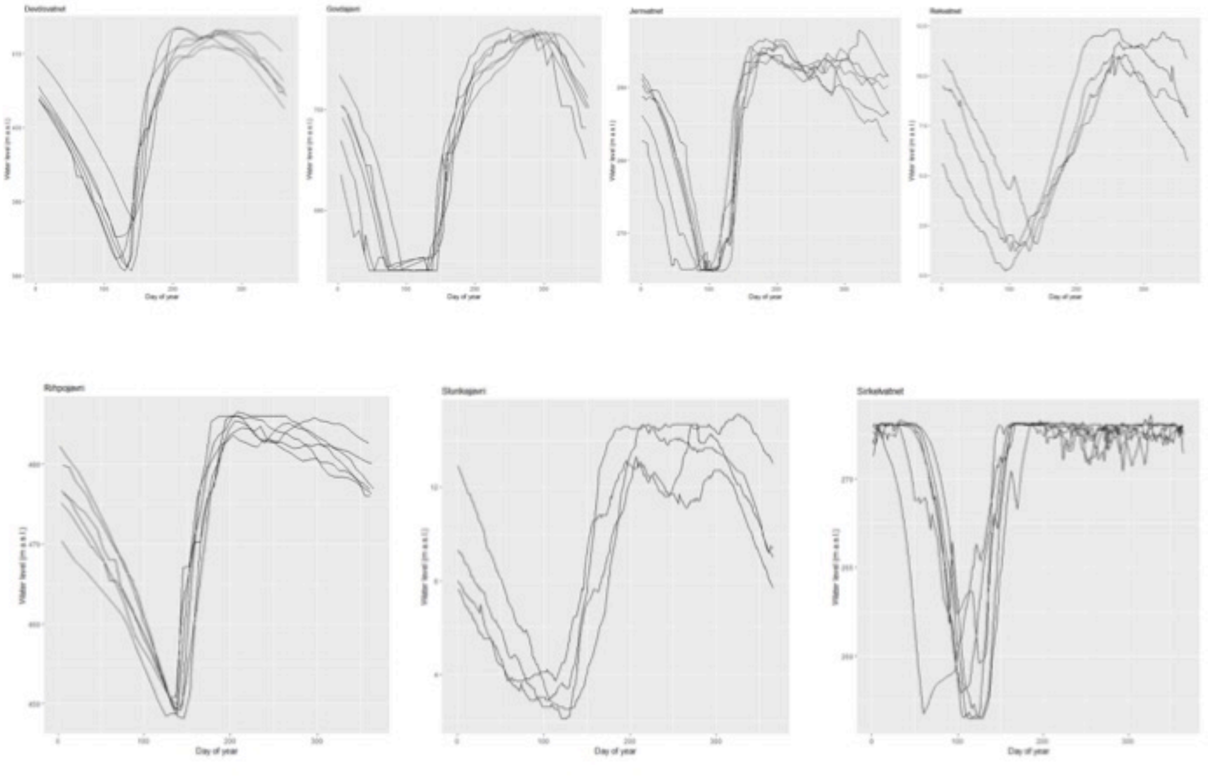
Appendix table 3a – Charr and trout maturity. The two tables show logistic regression where Maturation probability is the response variable and the predictors include either Fork length (Table 3a) or Age (Table 3b).

	Charr	**Maturity**		**Trout**	**Maturity**	
Predictors	***Odds Ratios***	***CI***	***p***	***Odds Ratios***	***CI***	***p***

Intercept	0.08	0.02–0.33	**0.001**	00.4	0.01–0.25	**0.001**
Fork length	1.01	1.00–1.01	0.062	1.01	1.00–1.02	**0.017**
Regulation	0.48	0.17–1.36	0.167	0.87	0.21–3.66	0.853
Forklength: Regulation	1.01	1.00–1.01	**0.006**	1.00	0.99–1.01	0.750

Appendix table 3b – Charr and trout maturity. The two tables show logistic regression where Maturation probability is the response variable and the predictors include either Fork length (Table 3a) or Age (Table 3b).

	Charr	**Maturity**		**Trout**	**Maturity**	
Predictors	***Odds Ratios***	***CI***	***p***	***Odds Ratios***	***CI***	***p***
Intercept	0.05	0.01–0.16	**<0.001**	00.3	0.01–0.13	**<0.001**
Age	1.39	1.08–1.79	**0.012**	2.00	1.42–2.81	**<0.017**
Regulation	1.23	0.55–2.75	0.611	3.21	1.15–8.93	**0.026**
Age:Regulation	1.20	0.99–1.45	0.059	0.72	0.58–0.91	**0.005**



Appendix figure 4 – Water level regulation during the year in study reservoirs. Water level is given as meters above the sea level (m.a.s.l.) exept in Slunkajavri and Rekvatnet, where the y-axis presents meters above the minimum allowed water level.