

Master's Thesis

**Effects of fish community composition on
ontogenetic niche shifts of Arctic charr (*Salvelinus
alpinus*) and brown trout (*Salmo trutta*) in subarctic
lakes**

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Henna Kangosjärvi: Effects of fish community composition on ontogenetic niche shifts of Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in subarctic lakes
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Food-web studies integrate both biodiversity and ecosystem function and are thus a good tool for more holistic approaches in conservation biology. In food-web studies, ontogenetic niche shifts (i.e., changes in diet and habitat use as individuals grow) by generalist predators are important factors to consider in order to understand how ecological communities are structured and what affects their functioning. By using stable isotope and stomach content analyses, I investigated how fish community composition can affect the trophic niche (i.e., diet and habitat use) of Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in nine subarctic lakes. The results indicated ontogenetic niche shifts in trophic position for both species. However, the fish community composition affected the ontogenetic niche shifts only with charr, so that trophic position of charr increased with length in charr-only fish community and decreased with length in lakes with multiple fish species. With trout, fish community did not affect the timing or direction of ontogenetic niche shifts. The results indicate how salmonid fishes with contrasting niche plasticity may show different responses to competitive and predatory interactions within lake communities. Thus, the fish community composition and ontogenetic niche shifts by native salmonid fishes are important factors to consider when developing sustainable management and protection strategies for subarctic lakes, that are increasingly subject to multiple anthropogenic threats.

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Henna Kangosjärvi: Kalayhteisön vaikutukset nieriän (*Salvelinus alpinus*) ja taimenen (*Salmo trutta*) kasvunaikaisiin ravinnonkäytön muutoksiin subarktisisissa järvissä
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Ravintoverkkotutkimukset yhdistävät biodiversiteetin sekä ekosysteemien toiminnan ja tarjoavat täten kokonaisvaltaisemman näkökulman suojelubiologiisiin tutkimuksiin. Ravintoverkkotutkimuksissa on tärkeä huomioida generalistien petojen kasvunaikaiset ravinnonkäytönmuutokset sekä niiden riippuvuus eliöyhteisön rakenteesta ja mahdolliset vaikutukset ekosysteemin toimintaan. Tutkin Pro gradu - tutkielmassani vakaiden isotooppien analyysin sekä syönnösanalyysin avulla, miten kalayhteisökoostumus vaikuttaa nieriän (*Salvelinus alpinus*) ja taimenen (*Salmo trutta*) kasvunaikaisiin ravinnonkäytön muutoksiin yhdeksässä subarktisisessa järvessä. Tulosten mukaan molemmilla lajeilla esiintyy kasvunaikaista ravinnonkäytön muutosta trofiatason suhteen. Kalayhteisö vaikutti tähän muutokseen ainoastaan nieriän kohdalla siten, että trofiataso kasvoi pituuden suhteen allopatrisessa järvessä (ainoastaan nieriää) ja laski pituuden mukaan järvissä, joissa oli useampia kalalajeja, mukaan lukien taimenta. Kalayhteisö ei vaikuttanut taimenen kasvunaikaisten ravinnonkäytönmuutosten suuntaan tai ajankohtaan. Tulokset havainnollistavat hyvin, kuinka ravinnonkäytön joustavuudeltaan eroavat lohikalat voivat reagoida eri tavoin kilpailu- ja saalistussuhteisiin järvien ravintoverkoissa. Tämän vuoksi kalayhteisökoostumus sekä alkuperäisten lohikalalajien kasvunaikaiset ravinnonkäytön muutokset tulisi huomioida subarktisten järvien suojelu- ja hoitotoimenpiteitä suunniteltaessa.

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1 INTRODUCTION

Food webs are used to describe networks of trophic interactions and fluxes of energy between species within the same ecological community. They are often described as binary, so that a link between two species either exists or not, although in nature, the interactions between species are often more complicated (Thompson et al. 2012). Traditionally, conservation biology has mainly focused on rare species rather than interaction networks and their function. However, more holistic approach focusing on the protection of ecological networks is needed to target the current conservation goals and in maintaining ecosystem integrity (Harvey et al. 2017). Food web studies integrate both biodiversity and ecosystem function, as they focus both on community and functional composition and fluxes of energy and material (Thompson et al. 2012) and are, as so, a good tool for more holistic approaches in conservation biology.

One important element of community ecology and food web studies are ontogenetic niche shifts. Ecological niches consist of both abiotic and biotic resources that the organisms use. In this thesis, ontogenetic niche shifts are referred as changes in food and/or habitat use as the body size of fish increases (Werner and Gilliam 1984). These shifts aim to maximize the fitness and lifetime reproductive output of organisms, by minimizing the ratio of mortality to growth (Werner 1986, Post 2003). In addition, ontogenetic niche shifts often support the coexistence of sympatric species that compete for shared resources (Schellekens et al. 2010, Wollrab et al. 2013). Ontogenetic niche shifts are widespread among ecological processes and central in understanding ecosystem functioning (Woodward et al. 2005, Nakazawa 2015). Studies of mechanisms behind timing and character of ontogenetic niche shifts are therefore important in improving our knowledge about how ecological communities are structured and what affects their functioning (Sánchez-Hernández et al. 2019).

Ontogenetic niche shifts can range from only few changes in resource use, to very discrete and often size-specific shifts, which are common among fish (Werner and Gilliam 1984, Sánchez-Hernández et al. 2019). Ontogenetic changes in diet or habitat of one or a few species may have widespread impacts on the whole ecosystem e.g. by altering its respiration, primary production and overall adding an extra layer of complexity to ecosystem dynamics (Werner and Gilliam 1984, Rudolf and Rasmussen 2013). The timing and extent of ontogenetic niche shifts vary between species, but also often vary among individuals within a species (Post 2003) and are determined by multiple abiotic and biotic environmental factors, such as competitive and predatory interactions (Galarowicz et al. 2006, Kimirei et al. 2013). One important factor that can limit the ontogenetic niche shifts is the gape-limitation (i.e., size of prey relative to the mouth size of the predator; Hambright et al. 1991). Gape-limited feeding has been shown to occur e.g., among subarctic populations of perch (*Perca fluviatilis*) that exhibit several ontogenetic niche shifts from zooplankton to zoobenthos and eventually to fish, with increasing size of prey items relative to the increasing body size of fish (Amundsen et al. 2003).

Lakes and their food webs are good model systems for studying food-web dynamics, as they have relatively clear boundaries and easily identifiable connections with nearby ecosystems (Vadeboncoeur et al. 2002). With simple communities and vulnerability to anthropogenic disturbances, such as damming, invasive species and climate change (Christoffersen et al. 2008, Riddle and Muir 2008, Hayden et al. 2019), subarctic lakes suit well for food web studies (Heino et al. 2020). Subarctic lakes are situated between the northern boreal zone and the Arctic (approximately between 50–70°N) and are typically clear, oligotrophic, and subject to cold temperatures and extreme seasonality (Vincent et al. 2008). They are ice-covered for most of the year and have only few dominating species, such as salmonid fishes, due to extreme conditions and difficulties in colonization (Christoffersen et al. 2008, Power et al. 2008).

Arctic charr (*Salvelinus alpinus*; hereafter charr) and brown trout (*Salmo trutta*; hereafter trout) are two abundant fish species that often coexist in subarctic lakes in

northern Europe and are both well adapted to cold and extreme environmental conditions (Svenning et al. 2007, Amundsen and Knudsen 2009). Charr is a generalist fish that has a high niche plasticity, and it typically lives in all habitats of cold oligotrophic lakes (Klemetsen et al. 2003). Although trout is also an opportunistic feeder, it is a more aggressive and territorial species that typically inhabits the shallow littoral areas of subarctic lakes (Klemetsen et al. 2003, Amundsen and Knudsen 2009).

Competition between charr and trout, or the lack of it, can have top-down impacts on lower trophic levels in subarctic lake food webs. For example, in lakes with an allopatric charr population (i.e., charr is the only fish species) that feed on littoral prey, the zooplankton community may remain relatively undisturbed (Skoglund et al. 2013). In addition, competition and predation can alter the growth and size distribution of charr and trout, since differences in body size are one of the major means by which fish species with similar niches (such as trout and charr) avoid direct competition and niche overlap. For example, charr that is often the large-sized top predator can be forced to remain at a lower trophic level and attain a smaller body size in the presence of trout (L'Abée-Lund et al. 1993, Eloranta et al. 2013a).

All these special characteristics of charr and trout make them good species for studying food-web dynamics. Generalist and highly mobile fish often show rapid responses to environmental stressors and thus they can act as the first warning signals of significant ecosystem perturbations (Bartley et al. 2019). Therefore, studies of trophic ecology and population structure of generalist charr and trout can contribute to our understanding of the natural processes and changes in cold-water subarctic lakes. The similarity of niches between charr and trout make them good species to study competitive interactions and niche segregation within relatively simple communities of subarctic lakes. In addition, both species are socio-economically important and currently facing multiple anthropogenic threats, which makes understanding their ecological interactions important for future conservation efforts (Vincent et al. 2008, Jeppesen et al. 2010, Dauwalter et al. 2019).

1.2 Research questions and hypotheses

Although the competitive interactions between charr and trout are well studied, the role of body size and ontogenetic niche shifts of charr and trout in allopatric and sympatric fish communities has received little attention despite the importance of this question in ecological interactions (e.g., Woodward et al. 2005, Sánchez-Hernández et al. 2019). Moreover, such studies of generalist charr and trout would improve our understanding of the current state of subarctic lakes, which are increasingly subjected to multiple anthropogenic threats. The aim of this MSci thesis was to investigate how fish community composition can affect the trophic niche (including ontogenetic niche shifts) and growth of charr and trout in subarctic lakes. This question was studied in nine subarctic lakes using stable isotope and stomach content analyses. Stable isotope analysis has been increasingly used in food-web studies, since it is cost efficient and accurate and it enables the assessment of main food sources assimilated over a longer period than the stomach content analysis (Post 2002, Fry 2006, Layman et al. 2012). The study lakes consisted of two allopatric lakes inhabited by only trout or charr, three sympatric lakes with charr and trout (as well as minor amounts of three-spine stickleback (*Gasterosteus aculeatus*) in two of the lakes), and four multispecies lakes with charr, trout and some other fish species, such as three-spine stickleback or burbot (*Lota lota*).

The research questions were: (1) how the lake fish community composition affects the timing and direction of ontogenetic niche shifts of charr and trout in subarctic lakes, and (2) how do these ontogenetic niche shifts affect the competition and predation between charr and trout? Based on previous studies (e.g., Klemetsen et al. 2003, Eloranta et al. 2015, Sánchez-Hernández et al. 2016), the hypotheses were that (1) charr will shift towards more pelagic food sources with increasing body size in lakes with multiple fish species, and (2) in sympatric and multispecies communities, trout will take the place of a top predator and occupy higher trophic position compared to lakes with only trout, and outcompete charr towards a lower trophic position and a less piscivorous diet.

2 MATERIALS AND METHODS

Samples of fish and the putative food sources of charr and trout were collected from nine subarctic lakes in northern Norway (Figure 1). The surface area of the lakes ranged from 0.6 to 13.3 km² and the altitude from 16 to 723 m a.s.l. (Table 1). Maximum depth ranged from 16 to 92 m. All nine lakes were either clear or very clear and oligotrophic, with total organic carbon (TOC) concentrations ranging from 0.7 to 5 mg/L and colour from 2 to <30 mg Pt/L. Lakes ranged from calcium poor (0.5 mg Ca/L) to very calcium rich lakes, such as Storvatnet with over 20 mg Ca/L. Catchment areas varied from highly mountainous areas (Čazajávri and Moskánjávri) with little vegetation to more vegetated areas with e.g. birch (*Betula pubescens*) and some agriculture patches in the lake catchment area.

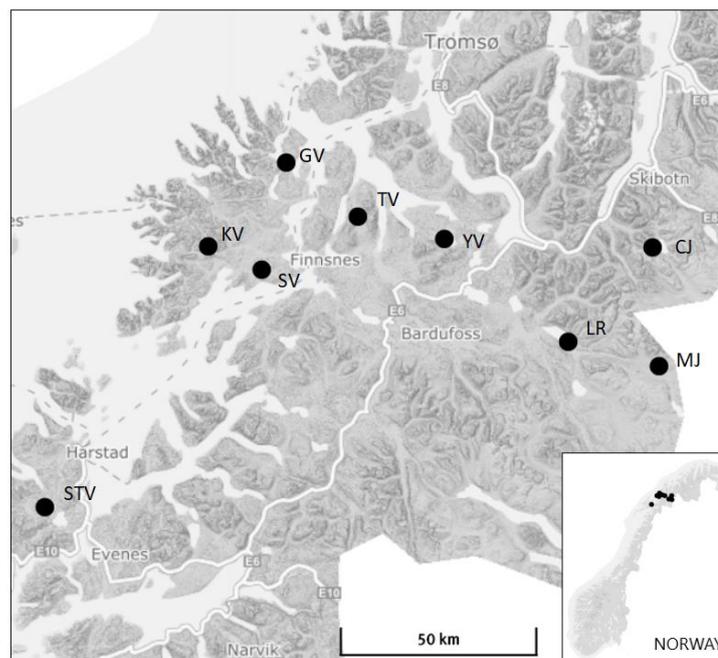


Figure 1. Map of the study lakes. Abbreviations stand for STV = Steinvatnet, KV = Kapervatn, SV = Storvatnet, GV = Geitvatnet, TV = Tårnvatnet, YV = Ytre Fiskelausvatnet, LR = Lille Rostavatn, CJ = Čazajávri and MJ = Moskánjávri. Source: norgeskart.no

The fish community composition of the study lakes varied from only charr and trout to multiple fish species (Table 1). Lille Rostavatn had the highest species diversity

2.1 Data collection

From six of the lakes, both fish and putative food source samples were collected in August 2020. Fish samples for two other lakes (Kapervatnet and Ytre Fiskelausvatnet) were collected in 2019 and putative food sources in August 2020. For Čazajávri, both fish and food source samples were collected in August 2014 (see Eloranta et al. 2016 for more details). Fish sampling was done with 1.5 m × 30 m benthic and 6.0 m × 30 m floating (pelagic) Nordic multi-mesh survey gillnets consisting of 12 panels (2.5 m each in a randomized sequence) with knot-to-knot mesh sizes of 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm (Appelberg et al. 1995). Sampling was done in varying depths and sites within each lake. Directly after collecting the nets, all fish were removed from the nets and frozen until subsequent analyses. In the laboratory, fish were identified and measured (wet mass in 0.1 g and total length in 1 mm accuracy) and sagittal otoliths were removed for subsequent age determination conducted by Norwegian colleagues. From subsamples of fish, stomachs were removed and samples of dorsal muscle tissue were dissected for subsequent stomach content (hereafter SCA) and stable isotope (hereafter SIA) analyses, respectively.

Samples of putative food sources for charr and trout included zooplankton, as well as profundal (>20 m), sublittoral (around 3–6 m) and littoral (around 0–3 m depth) benthic macroinvertebrates (hereafter benthos). From Storvatnet, no sublittoral benthos samples were collected, and no profundal benthos was collected from Geitvatnet. Zooplankton samples were collected using a plankton net (100- μ m mesh) and benthos samples with a kick-net (500- μ m mesh) and a benthic sledge (243- μ m mesh). Supplementary samples of gastropods were collected by hand from rocks in the littoral zone. In Storvatnet, an Ekman grab was used due to technical problems with the benthic sledge. All benthic samples were sieved through a 500- μ m bucket sieve to remove extra silt and detritus. In addition, biofilm was sampled by scraping small stones with a potato brush and flushing the loose epilithic algae with lake water into a 0.5 L container, followed by filtering the sample through a set of three sieves (i.e., from 200 μ m to 100 μ m to 50 μ m). All samples were stored cool

in lake water until sorting. Benthic invertebrates and zooplankton were identified to order, class or species and sorted to smaller sub-samples according to the classification. Cases of trichopteran larvae and shells of molluscs were removed and only the soft body tissues were stored for analysis. All samples were frozen at -20°C until subsequent preparation for SIA.

2.2 Data preparation and analysis

For further analyses, 420 fish samples were selected, including in total 379 charr and trout individuals of different sizes in each lake. In addition, 173 benthic and pelagic invertebrate samples were analysed, including: (1) chironomid larvae and littoral snails (*Lymanea* sp.) as littoral benthos (except for Čazajávri, where littoral benthos included Ephemeroptera, Dytiscidae, Trichoptera, Chironomidae larvae, Plecoptera, Hydrachnidae, Oligochaeta, *Diura* sp. and Tipulidae), (2) profundal chironomid larvae as profundal benthos (in Čazajávri also Hydrachnidae and *Pisidium* sp.), and (3) pelagic zooplankton, consisting from a mix of unidentified pelagic zooplankton species (table 2). Due to limited financial resources for SIA, only the biofilm samples collected from Čazajávri were analysed. All the fish chosen for SIA were also chosen for SCA and growth analyses.

Selected samples were freeze-dried for ca. 48 hours, ground to fine powder inside the sample tubes and weighed (0.500-0.600 mg) for final SIA. Stable carbon and nitrogen isotope ratios were analysed with an elemental analyser coupled to a continuous flow isotope mass spectrometer (EA+CF-SIRSM) at the Department of Biological and Environmental Science, University of Jyväskylä. Pike (*Esox lucius*) white muscle tissue was used as an internal laboratory working standard for fish and invertebrate samples and potato (*Solanum tuberosum*) leaves for biofilm with Vienna PeeDee Belemnite and atmospheric nitrogen as international references for carbon and nitrogen, respectively. Standard deviation of the internal working standard was less than 0.3 ‰ for $\delta^{13}\text{C}$ and 0.2 ‰ for $\delta^{15}\text{N}$.

Table 2. Number of charr and trout in total catch, stable isotope (SIA), stomach content (SCA) and growth analyses, as well as number of littoral benthos and pelagic zooplankton samples in SIA for each lake.

Taxon	Čazajávri	Geitvatnet	Kapervatnet	Lille Rostavatn	Moskánjávri	Steinvatnet	Storvatnet	Tårnvatnet	Ytre Fiskelausv.	Grand Total
<i>Catch</i>										
Charr	74	14	-	118	27	72	17	104	169	595
Trout	-	53	111	26	25	68	32	108	55	478
Total	74	67	111	144	52	140	49	212	224	1073
<i>SIA</i>										
Charr	74	14	-	23	20	20	17	20	20	208
Trout	-	22	30	20	20	20	19	20	20	171
Total fish	74	36	30	43	40	40	36	40	40	379
Littoral benthos	18	10	9	6	5	8	6	9	8	79
Pelagic zooplankton	7	5	5	6	6	5	6	6	7	53
Profundal benthos	9	-	3	3	5	3	3	6	5	37
<i>SCA</i>										
Charr	68	11	-	-	17	16	14	15	15	156
Trout	-	13	29	-	19	16	13	15	13	118
Total	68	24	29	-	36	32	27	30	28	274
<i>Growth analysis</i>										
Charr	74	14	-	23	20	20	17	20	19	207
Trout	-	22	30	19	20	20	18	20	19	168
Total	74	36	30	42	40	40	35	40	38	375

In recent decades, SIA has been increasingly used to study food-web structure and dynamics. Stable isotopes are different forms of the same element that have different masses depending on how many neutrons they have in the nucleus (Fry 2006). For example, carbon has two stable isotopes, ^{12}C (light) and ^{13}C (heavy). SIA is based on studying the ratio between the heavy and light isotopes of the same element. This is done by comparing the isotope ratio of the sample to the isotope ratio of an international standard. Delta values (e.g., $\delta^{15}\text{N}$) tell the ratio between heavy and light isotope between sample and the standard in ‰ following the formula

$$\delta^{\text{HX}} = [(R_{\text{sample}}/R_{\text{standard}} - 1)] \times 1000, \quad (1)$$

where $^H X$ = the heavier isotope of sample and R = the ratio between heavier and lighter isotope (Fry 2006).

The ratio of stable nitrogen isotopes ($\delta^{15}\text{N}$) can be used to study the trophic position of an organism in a food web since $\delta^{15}\text{N}$ of consumer tissue enriches by $\sim 3.4\%$ relative to the tissue of its diet during assimilation (Post 2002). Ratio of stable carbon isotopes ($\delta^{13}\text{C}$) can vary between primary producers depending on the photosynthetic pathway and/or diffusion boundary layer (Fry 2006). In lakes, littoral benthic algae typically have higher $\delta^{13}\text{C}$ values compared to pelagic phytoplankton that are exposed to high water turbulence and thus can discriminate ^{13}C (see e.g., France 1995). As the ratio of stable carbon isotopes change little in trophic transfers, the $\delta^{13}\text{C}$ values can be used to determine the relative reliance of consumers on littoral versus pelagic energy sources (Fry 2006, Layman et al. 2012).

The trophic position (hereafter TP) and the littoral reliance (hereafter LR) estimates of charr and trout were based on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, respectively, using two-source isotopic mixing models described by Post (2002):

$$LR = (\delta^{13}\text{C}_{consumer} - \delta^{13}\text{C}_{pelagic}) / (\delta^{13}\text{C}_{littoral} - \delta^{13}\text{C}_{pelagic}), \quad (2)$$

where $\delta^{13}\text{C}_{consumer}$ is the $\delta^{13}\text{C}$ value of individual fish and the $\delta^{13}\text{C}_{pelagic}$ and $\delta^{13}\text{C}_{littoral}$ are the pelagic and littoral baselines based on mean $\delta^{13}\text{C}$ values of pelagic zooplankton and littoral benthos (for most lakes, chironomid larvae and *Lymnaea* sp. snails), respectively.

$$TP = \lambda + (\delta^{15}\text{N}_{consumer} - [\delta^{15}\text{N}_{littoral} * \alpha + \delta^{15}\text{N}_{pelagic} * (1 - \alpha)]) / \Delta_n, \quad (3)$$

where α is the LR estimate of individual fish, λ is the estimated trophic level of the baseline (here 2) and Δ_n is the trophic fractionation factor of $\delta^{15}\text{N}$ (here 3.4 ‰; Post 2002).

During sampling, Kapervatnet was flooding and thus it was difficult to obtain sufficient and representative SIA samples of littoral benthic invertebrates. Therefore, littoral baseline for Kapervatnet was estimated by calculating the mean

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of littoral benthic invertebrates sampled from other lakes, and these mean values were then used in further analyses, such as when calculating the fish TP and LR estimates.

In SCA, the prey items in fish stomach contents were identified to order, family or species level using a preparation microscope. The stomach fullness of each fish was first visually estimated with a scale from 0 (empty) to 100% (extended full) after which the relative contribution (volume) of each prey taxon to the total stomach fullness was estimated (see the relative-fullness method in Amundsen and Sánchez-Hernández 2019). The SCA data was pooled to more general prey groups (Appendix 1) and plotted as stacked histograms by species and size classes (total length of <150 mm, 150–250 mm and >250 mm), lake and fish community. Lille Rostavatn was excluded from SCA since the data was not available. Pooled SCA prey groups included zooplankton (*Bythotrephes* sp., *Daphnia* sp., *Bosmina* sp., *Eurycerus* sp., *Polyphemus* sp. and unidentified zooplankton), benthic insects (chironomid larvae and pupae, trichopteran larvae and pupae, Limnephilidae, Hydrachnidae and unidentified insect larvae and pupae), terrestrial insects (Oligochaeta and Formicidae), Molluscs (*Pisidium* sp. and *Lymnaea* sp.), benthic crustaceans (*Gammarus* sp. and *Lepidurus arcticus*), fish (stickleback, burbot, charr and unidentified fish), unidentified surface insects and a group of other, unidentified prey items (Appendix 1).

Variation in TP/LR values between fish communities was tested with Tukey's HSD test. Effects of fish community on growth was tested by using generalized linear model where total length (mm) was the dependent variable and age (years), fish community (factor with three levels: allopatric, sympatric, or multispecies) and the combined (i.e., two-way interaction) effect of age and fish community were set as covariates. Ontogenetic niche shifts were statistically analysed by using generalized linear models where either TP or LR was set as the dependent variable and total length (mm), fish community (factor with three levels: allopatric, sympatric or multispecies) and the combined (i.e., two-way interaction) effect of length and fish

community were set as covariates. Statistical analyses were done in R 4.0.4 (R Core Team 2020).

3 RESULTS

In all nine lakes, charr and trout were the most abundant fish species. Other species included three-spined stickleback, burbot, grayling (*Thymallus thymallus*), minnow (*Phoxinus phoxinus*), and Atlantic salmon (*Salmo salar*). Total length of trout varied from 74 mm to 580 mm and of charr from 47 mm to 570 mm. Moskánjávri had the largest charr and trout individuals and in average, charr were biggest in Moskánjávri and trout in Storstvatnet, with Moskánjávri as close second (Figure 2).

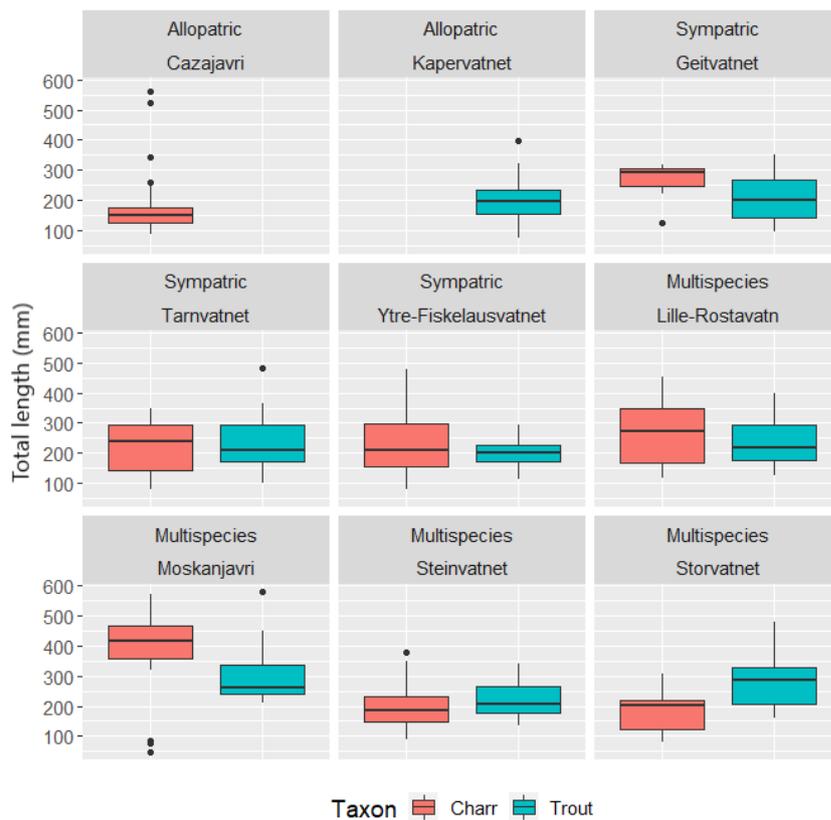


Figure 2. Total length (mm) of charr and trout, with median, 1st and 3rd quartiles and largest/smallest value at 1.5*IQR from the quartiles marked by line, hinges, and whisker, respectively. Outliers are marked by dots. Lakes are grouped by fish communities.

Age had a significant positive effect on total length of both charr (GLM: $F_{5,192} = 148.8$, $R^2_{adj.} = 0.79$, $p < 0.001$) and trout ($F_{5,153} = 169.6$, $R^2_{adj.} = 0.84$, $p < 0.001$). However, fish community did not affect the growth of trout, as the fish community and age did not show a statistically significant interaction with the total length of fish (Table 3). With charr, there was a significant two-way interaction between age and fish community, indicating that the charr growth was affected by fish community, being highest in the multispecies lakes (Table 3, Figure 3).

Table 3. Summary of the generalized linear models explaining the variation in the total length (mm) of charr and trout as a function of fish age (years) and lake fish community. Statistically significant parameters ($p < 0.05$) are marked in bold. Intercept can be interpreted as the model baseline, defining the expected value of the predicted variable (total length) at the covariate values of zero (i.e., Age = 0 & Fish community = Allopatric).

Species	Parameter	Estimate	SE	<i>t</i>	p
Charr	Intercept	52.36	16.17	3.24	0.001
	Age	21.50	3.22	6.69	<0.001
	Sympatric	25.98	22.44	1.16	0.248
	Multispecies	-20.32	20.29	-1.00	0.318
	Age x Sympatric	6.85	4.14	1.66	0.099
	Age x Multispecies	18.49	3.77	4.90	<0.001
Trout	Intercept	38.67	16.19	2.39	0.018
	Age	40.47	3.71	10.92	<0.001
	Sympatric	15.76	19.89	0.79	0.429
	Multispecies	17.72	19.35	0.92	0.361
	Age x Sympatric	-4.28	4.43	-0.97	0.336
	Age x Multispecies	0.47	4.22	0.11	0.911

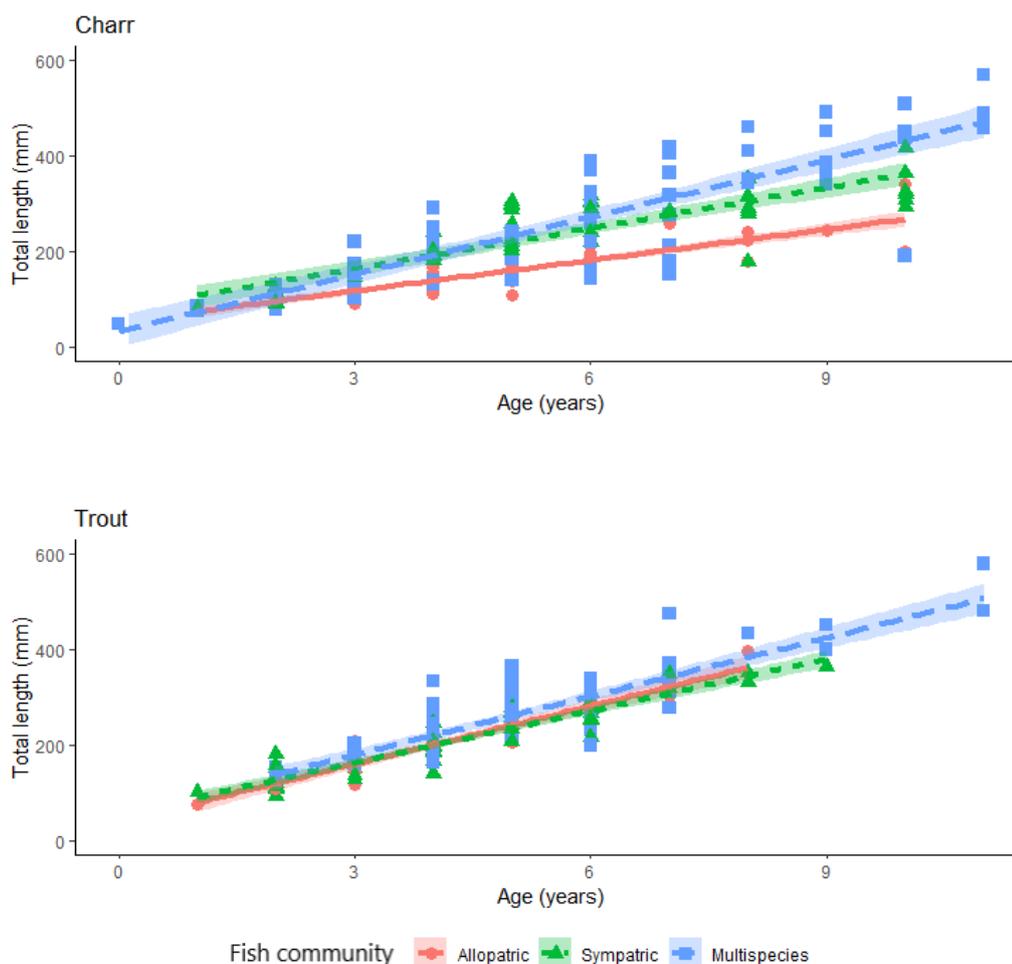


Figure 3. Relationship between the total length (mm) and age (years) of charr and trout in different fish community categories with the 95% confidence intervals for the predicted total lengths.

For all the lakes, pelagic zooplankton had lower $\delta^{13}\text{C}$ values than littoral benthos (Figure 4). In most lakes, the $\delta^{13}\text{C}$ values of profundal benthos were somewhere between the values of littoral benthos and pelagic zooplankton, whereas the $\delta^{15}\text{N}$ values were often higher. In Čazajávri, the profundal benthos $\delta^{13}\text{C}$ values were much higher than in other lakes. The mean $\delta^{15}\text{N}$ values of charr and trout were consistently higher than those of invertebrates. Charr had in general lower $\delta^{13}\text{C}$ values, indicating more pelagic trophic niche compared to coexisting trout, which had higher $\delta^{13}\text{C}$ values (Figure 4). In most lakes, both trout and charr had similar trophic positions (similar $\delta^{15}\text{N}$ values), except in Geitvatnet, where trout had on average higher trophic position and charr seemed to be specialized to pelagic

zooplanktivorous niche and thus showed exceptionally small individual variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Sticklebacks seemed to have in general a littoral benthivorous diet (low $\delta^{15}\text{N}$ and high $\delta^{13}\text{C}$ values) and burbot had similar trophic niche with charr and trout.

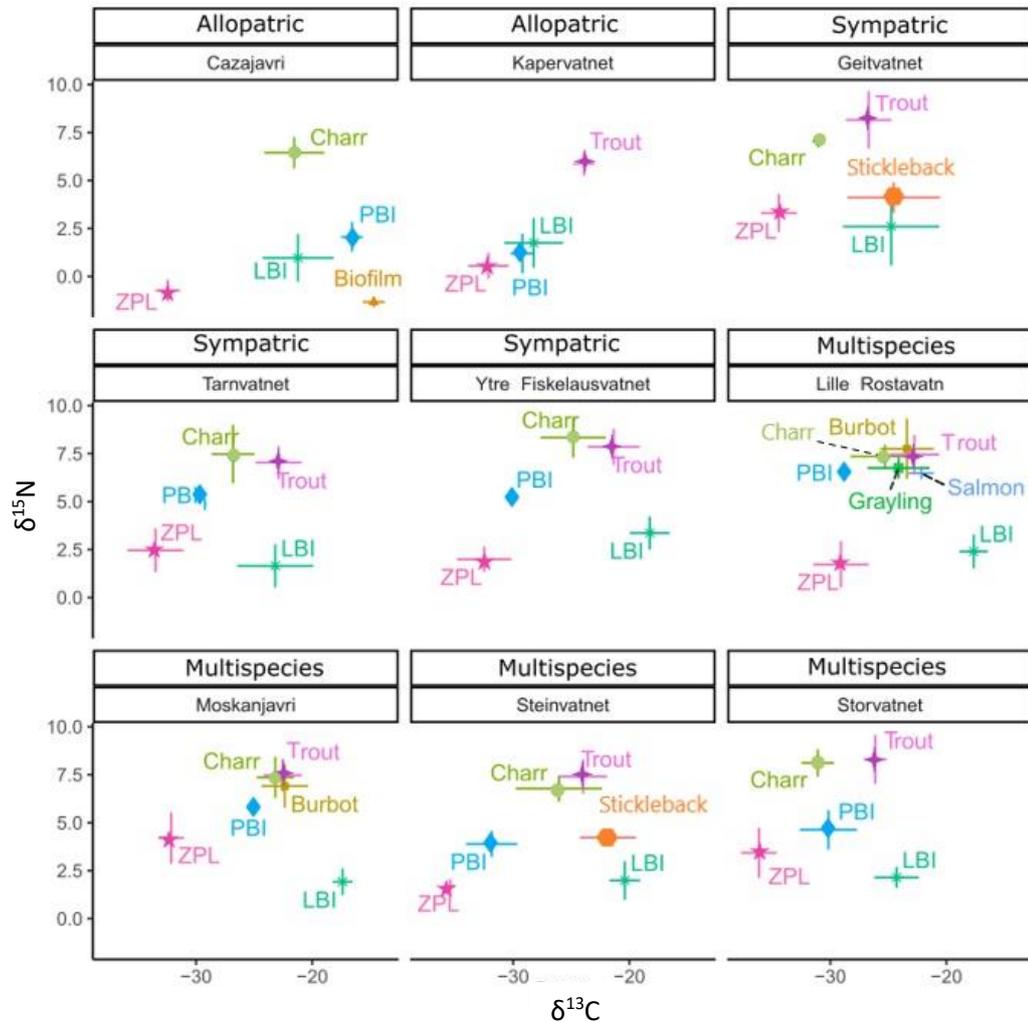


Figure 4. Stable isotope biplots representing mean \pm SD $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of littoral, pelagic and profundal invertebrates and of different fish species. Abbreviations are PBI = profundal benthos, LBI = littoral benthos and ZPL = pelagic zooplankton.

Contrary to LR, there was evidence for a significant ontogenetic shift in TP with increasing length for both charr (GLM: $F_{5,201} = 7.03$, $R^2_{\text{adj.}} = 0.13$, $p < 0.001$) and trout ($F_{5,156} = 26.18$, $R^2_{\text{adj.}} = 0.44$, $p < 0.001$) (Table 4, Figure 5). For charr, TP decreased in multispecies lakes and increased in the allopatric lake, whereas there were no

significant ontogenetic shifts in TP in sympatric communities. For trout, TP increased in all communities with length, but there was no significant combined effect of fish community and length and the increase was similar in all the communities. The highest mean values of TP were observed for charr in the allopatric lake and for trout in the multispecies communities (Table 5, Figure 6).

Table 4. Summary of the generalized linear models explaining the variation in trophic position (TP) and littoral reliance (LR) of charr and trout as a function of fish total length and lake fish community. Statistically significant parameters ($p < 0.05$) are marked in bold. Intercept can be interpreted as the model baseline, defining the expected value of the predicted variable (i.e., LR or TP) at the covariate values of zero (i.e., Total length = 0 & Fish community = Allopatric).

Species	Parameter	Estimate	SE	<i>t</i>	p
<i>Trophic position (TP)</i>					
Charr	Intercept	3.75	0.04	103.30	<0.001
	Sympatric	-0.24	0.05	-4.62	<0.001
	Multispecies	-0.26	0.05	-5.43	<0.001
	Length	0.19	0.04	5.32	<0.001
	Sympatric x Length	-0.10	0.06	-1.78	0.077
	Multispecies x Length	-0.22	0.04	-5.07	<0.001
Trout	Intercept	3.29	0.05	67.43	<0.001
	Sympatric	0.26	0.06	4.37	<0.001
	Multispecies	0.23	0.06	3.94	<0.001
	Length	0.17	0.07	2.50	0.013
	Sympatric x Length	0.13	0.08	1.61	0.109
	Multispecies x Length	0.04	0.07	0.58	0.563
<i>Littoral reliance (LR)</i>					
Charr	Intercept	0.96	0.03	31.92	<0.001
	Sympatric	-0.43	0.04	-9.96	<0.001
	Multispecies	-0.48	0.04	-12.17	<0.001
	Length	0.00	0.03	-0.14	0.888
	Sympatric x Length	0.01	0.05	0.19	0.852
	Multispecies x Length	0.05	0.04	1.48	0.139
Trout	Intercept	0.75	0.03	21.57	<0.001
	Sympatric	0.13	0.04	3.11	0.002
	Multispecies	-0.06	0.04	-1.42	0.158
	Length	0.01	0.05	0.12	0.903
	Sympatric x Length	0.04	0.06	0.64	0.521
	Multispecies x Length	0.01	0.05	0.25	0.806

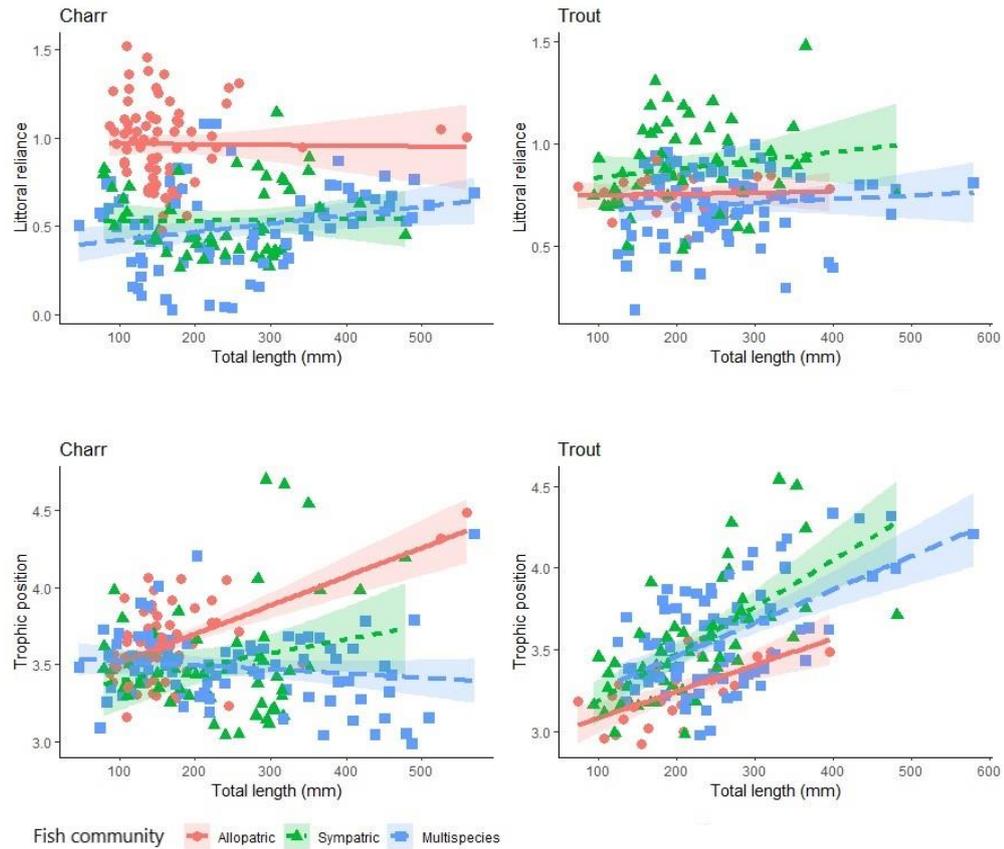


Figure 5. Relationships between littoral reliance (LR) and trophic position (TP) and the total length of charr and trout in different fish community categories with the 95% confidence intervals for the predicted LR and TP estimates.

Table 5. Summary of Tukey's HSD test comparing the trophic position (TP) and littoral reliance (LR) estimates of charr and trout between different fish community categories. Statistically significant differences ($p < 0.05$) are marked in bold.

Species	Comparison	Difference	lwr 95% CI	upr 95% CI	p
<i>Trophic position (TP)</i>					
Charr	Sympatric-Allopatric	-0.12	-0.24	0.00	0.047
	Multispecies-Allopatric	-0.16	-0.27	-0.05	0.002
	Multispecies-Sympatric	-0.04	-0.16	0.08	0.735
Trout	Sympatric-Allopatric	0.27	0.10	0.44	<0.001
	Multispecies-Allopatric	0.33	0.17	0.49	<0.001
	Multispecies-Sympatric	0.06	-0.07	0.19	0.550
<i>Littoral reliance (LR)</i>					
Charr	Sympatric-Allopatric	-0.43	-0.53	-0.34	<0.001
	Multispecies-Allopatric	-0.47	-0.55	-0.39	<0.001
	Multispecies-Sympatric	-0.04	-0.13	0.06	0.623
Trout	Sympatric-Allopatric	0.13	0.03	0.23	0.005
	Multispecies-Allopatric	-0.05	-0.14	0.04	0.390
	Multispecies-Sympatric	-0.18	-0.26	-0.11	<0.001

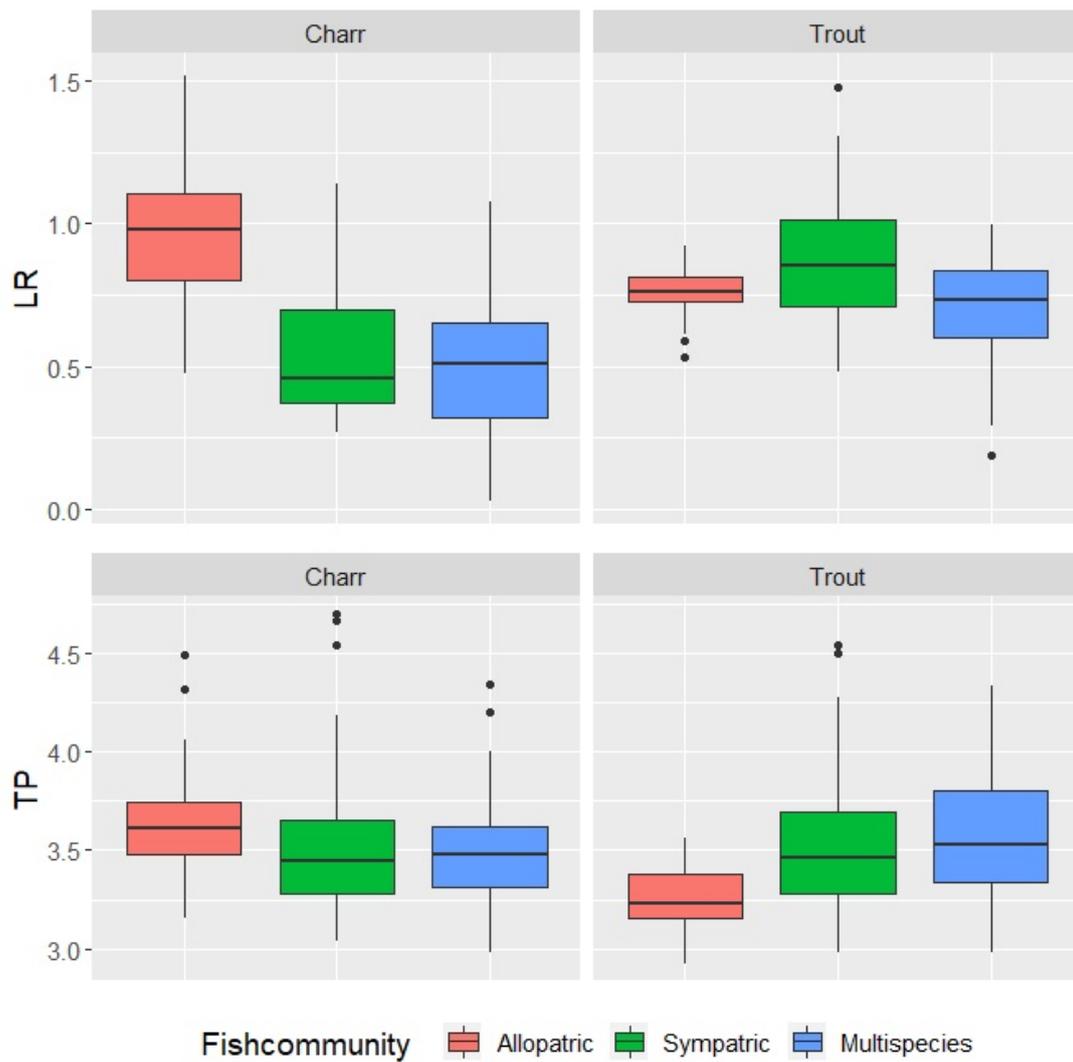


Figure 6. Littoral reliance (LR) and trophic position (TP) of charr and trout in different fish community categories, with median, 1st and 3rd quartiles and largest/smallest value at 1.5*IQR from the quartiles marked by line, hinges, and whisker, respectively. Outliers are marked by dots.

Stomach content analysis showed variation between diets of charr and trout and between fish communities and lakes (Figure 7). Trout seemed to feed more on littoral food sources than charr, such as benthic crustaceans, insect larvae and pupae, molluscs, and surface insects. Trout also shifted towards a more piscivorous diet in multispecies lakes and with increasing size. In many sympatric and multispecies lakes, charr fed mainly on zooplankton and had only little fish or surface insects in the diet. Allopatric charr fed mainly on benthic insects, zooplankton, and bigger individuals also on small conspecifics.

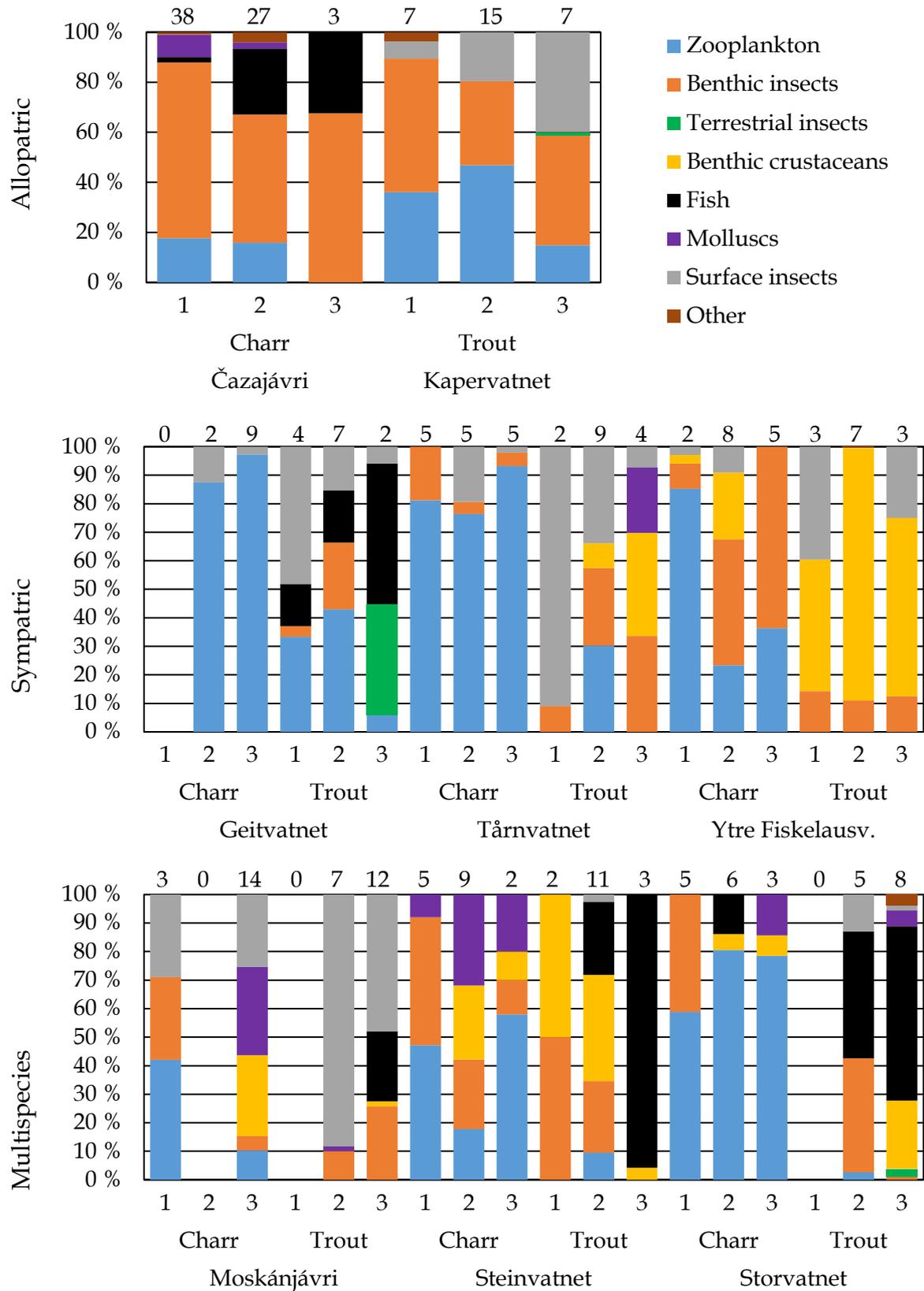


Figure 7. Stomach contents of charr and trout in different size classes (1 = <150 mm, 2 = 150–250 mm, 3 = >250 mm) in allopatric, sympatric, and multispecies lakes. Numbers above the columns indicate the number of fish analysed for SCA in each size class.

4 DISCUSSION

This study found clear differences between charr and trout in response to fish community composition. Fish community affected the ontogenetic niche shifts only with charr, so that trophic position (TP) increased with length in the allopatric lake and decreased with length in multispecies communities. In trout, TP increased with length, but fish community did not affect the timing or direction of these changes. This is contradictory to an earlier study by Sánchez-Hernández et al. (2016) which suggested that piscivory (which correlates positively with TP) would be supported by increasing abundance of prey fish species. However, it should be noted that the positive trend between piscivory and abundance of fish species in their study was not statistically significant. On the other hand, based on the present SCA results, the prevalence of trout piscivory did seem to increase with increasing abundance of fish species, especially when small-sized prey fish (stickleback) was present. Since the temporal resolution of these two methods varies (SIA tells the more long-term assimilated diet and SCA the most recent), the results could indicate that sticklebacks are more important prey item for short term, but trout does not rely on them enough over a longer time to reveal clear differences in SIA results.

Fish community affected the growth of charr but not of trout, with charr growing faster in multispecies lakes. The exceptionally fast growing charr population of multispecies lake Moskánjávri most likely partly explains this, as the growth of charr was much higher in this lake compared to the others (Appendix 3). Growth of charr in Moskánjávri was most probably supported by the abundance of high-quality invertebrate prey, such as *Gammarus* sp. and *Lepidurus arcticus* (Appendix 1), which contain good quality fatty acids and can support the growth of charr both in summer and winter (Eloranta et al. 2013b).

Based on the SIA results, charr had the highest littoral reliance (LR) estimates in the allopatric fish community, which partly confirmed the hypothesis that charr would shift towards more pelagic food sources (such as zooplankton) in sympatric and multispecies communities. Correspondingly, the SCA results showed a shift

towards more planktivorous diet in sympatric and multispecies communities. However, there seemed to be no evident shift towards more pelagic food sources with increasing body size (i.e., ontogenetic niche shifts) which contradicted the hypothesis. These results are supported by earlier studies showing that in allopatry charr prefers the littoral habitat and food resources, but often shifts to a more pelagic or profundal trophic niche when coexisting with a sympatric competitor species such as trout or whitefish (*Coregonus lavaretus*) (Eloranta et al. 2011, 2013, Sandlund et al. 2016). The present results confirmed the hypothesis that in sympatric and multispecies communities, trout will take the place of a top predator (higher TP) and outcompete charr from littoral areas towards more pelagic and profundal food resources and a lower trophic position.

In the allopatric community, charr seemed to feed mostly on benthic invertebrates (such as chironomid larvae) and shifted towards cannibalism with increasing body size. This is also supported by earlier studies showing that in allopatric communities with no other small-sized fish to prey on, charr can become cannibalistic and start to prey on smaller conspecifics (Byström 2006, Finstad et al. 2006, Eloranta et al. 2010). In sympatric and multispecies lakes, charr did not shift to cannibalism or to substantial piscivorous foraging on other prey fishes like trout did. Instead, charr seemed to feed mostly on pelagic zooplankton or benthic invertebrates, which were mostly profundal chironomid larvae (Appendix 1). This is most probably due to increased competition, because charr is a more generalist and flexible feeder and thus the more aggressive and littoral-oriented trout can force it to shift to a more pelagic trophic niche (Klemetsen et al. 2003, Eloranta et al. 2013a). Trout is more visually oriented feeder compared to charr, so it relies more heavily on littoral habitat and diet, where there is sufficient light for successful benthivorous and piscivorous predation (Langeland et al. 1991, Helland et al. 2011).

Based on the results and earlier literature, sympatric charr and trout often segregate by their diets and habitat use to avoid negative competitive interactions (Eloranta et al. 2013a). Earlier studies suggest that ontogenetic dietary and habitat shifts are common for both charr and trout due to intra- and interspecific competition, and

the niche shifts depend on the availability of prey items, such as small fish (Klemetsen et al. 2003, Amundsen et al. 2008, Eloranta et al. 2010, Sánchez-Hernández et al. 2016). These findings are also confirmed by the present results that showed evident ontogenetic niche shifts in the TP for both charr and trout. For trout, the TP increased with body size in all communities whereas for charr, the intraspecific competition seemed to cause more drastic ontogenetic niche shifts towards cannibalism, whereas the presence of small fish (e.g., stickleback) did not affect the charr niche shifts, as the TP decreased in multispecies lakes. Earlier studies have shown similar ontogenetic niche shifts in allopatric populations, where adults often feed on larger benthic invertebrates and small conspecifics in the littoral zone and force juveniles to utilize profundal or pelagic food and habitat resources (Klemetsen et al. 1985, L'Abée-Lund et al. 1993). The decrease in TP of charr in multispecies lakes is contradictory to an earlier study by Eloranta et al. (2015), which showed increasing TP and piscivorous diet of charr with increasing species richness in 17 subarctic lakes. On the contrary, the results of the present study indicate that interspecific competition with trout seemed to force the ontogenetic niche shift of charr to take other routes in sympatric and multispecies lakes.

One important feature within ontogenetic niche shifts is the mixed competition-predation interaction (Werner and Gilliam 1984), where juvenile stages of a larger predator species compete with individuals of a smaller species that will eventually become prey as the individuals of the larger species grow. For example, in many sympatric trout and charr communities, trout may simultaneously compete with and prey on charr (Persson et al. 2013, Sánchez-Hernández et al. 2016). However, such mixed competition-predation interactions were not present in study lakes of this thesis. Earlier studies show that for trout, the presence of intermediate consumer (such as stickleback) facilitates the shift towards piscivory more than the presence of mixed competitor-prey fish species (charr) (Sánchez-Hernández et al. 2016). This could explain why for trout, there seemed to be no shift towards piscivory in sympatric lakes if sticklebacks were not abundantly present. Intermediate consumers, such as stickleback, may serve as an important stepping-stone for trout and charr to shift towards piscivory by filling in prey size gap

between prey invertebrates and larger sized prey fish (Eloranta et al. 2015, Sánchez-Hernández et al. 2016). However, based on the results, the presence of stickleback did not always mean that trout would shift towards piscivory. For example, in Ytre Fiskelausvatnet trout mainly fed on *Gammarus* sp. amphipods (Appendix 1) although stickleback was present in the lake. This could indicate that a shift towards piscivory might not be a profitable feeding strategy for trout and charr in subarctic lakes where high-quality invertebrate prey resources are more available than e.g. sticklebacks. For example, crustaceans (e.g., pelagic zooplankton and epibenthic amphipods) can serve as an excellent prey item for trout and charr in subarctic lakes, as they contain high amounts of good fatty acids that can support the growth, maturation and overwintering of salmonids (Eloranta et al. 2013b).

Some weaknesses of this thesis include the relatively small number of SIA and SCA samples as well as limited number of study lakes. In addition, the grouping of lakes into fish communities proved challenging, as there was only one lake with solely trout and charr (Tårnvatnet) and the distinction between sympatric and multispecies lakes was not always clear to determine. To better understand and estimate how ontogenetic niche shifts of charr and trout might be affected by the fish community composition, a wider range of lakes with more varying fish community compositions and especially more replicates of allopatric charr and trout lakes should be included. It is also good to keep in mind that linear models might not be the best in estimating the ontogenetic niche shifts, as there might be some non-linear relationships that cannot be detected with linear models (such as seen in e.g., Ytre Fiskelausvatnet; Appendix 2). Moreover, besides TP, results mainly focused on comparing the littoral vs. pelagic energy sources (littoral reliance), which does not detect profundal food sources that have been proven to be important especially for charr in some subarctic lakes (Amundsen et al. 2008, Knudsen et al. 2016). In addition to the effects of fish community, the effects of abiotic characteristics of lakes (such as climate, morphometry and water quality) should be considered in future studies, as there could be some strong interactions between lake abiotic characteristics and the ontogenetic niche shifts of subarctic salmonid fish (as shown e.g., in Eloranta et al. 2015). However, in this thesis it was

not possible to estimate the effects of abiotic characteristics (e.g., altitude, area, colour and TOC) due to limited number of study lakes and non-normal distribution of the variables (Appendix 4).

Limnologists have traditionally focused on pelagic food-web compartments (Vadeboncoeur et al. 2002) but, based on the present results as well as earlier studies (e.g., Klemetsen et al. 2003, Amundsen et al. 2008, Eloranta et al. 2010, Knudsen et al. 2016), littoral and profundal resources are often more important for subarctic salmonid species. More holistic studies considering the pelagic, profundal and littoral food sources of salmonids are thus needed to better understand the structure and functioning of subarctic lake food webs more accurately. A larger scale food web modelling study to better estimate the ontogenetic niche shifts of trout and charr in subarctic lakes with contrasting biotic and abiotic characteristics could accomplish this.

Understanding the functioning and structure of subarctic lake food webs is important, since they are faced with multiple anthropogenic threats such as damming, invasive species and climate change (Christoffersen et al. 2008, Riddle and Muir 2008, Hayden et al. 2019). For example, in the future, more southern species could invade more northern lakes and trout could disperse to habitats currently dominated by charr (e.g., Helland et al. 2011, Hayden et al. 2017, Svenning et al. 2021). Based on the results as well as earlier studies, this could lead to a decrease in the presence and abundance of piscivorous/cannibalistic charr, since in lakes with competitive species, charr is less piscivorous compared to allopatric communities (Klemetsen et al. 2003, Eloranta et al. 2013a). In addition, the shortening of ice-covered period and increasing allochthonous runoff can also have a cascading effect on the competition between trout and charr, since trout is a more visually oriented feeder whereas charr is often competitively stronger in winter and under poor light conditions (Helland et al. 2011, Ulvan et al. 2011). These are just few examples on how changes in the lake fish community composition or abiotic characteristics, caused by anthropogenic disturbances, can alter the structure and functioning of subarctic food webs. More research on the current state of subarctic

lakes and their food webs is thus needed to better develop sustainable management and protection strategies (Heino et al. 2009, 2020).

In conclusion, fish community composition in the present study lakes seemed to affect the ontogenetic niche shifts of charr but not of trout, so that in general charr shifted towards more piscivorous diet in allopatry but remained at a lower trophic position and pelagic niche when coexisting with trout. Combined with earlier studies, these results illustrate how salmonid fishes with contrasting niche plasticity may show different responses to competitive and predatory interactions within lake communities. Thus, the fish community composition and ontogenetic niche shifts by native salmonid fishes are important factors to consider when evaluating potential population- and community-level responses and developing sustainable management and protection strategies for subarctic lakes that are increasingly subject to multiple anthropogenic threats and under rapid environmental changes. More research is needed to better understand the current state of these lakes and the status of their socio-economically valuable salmonid fish species.

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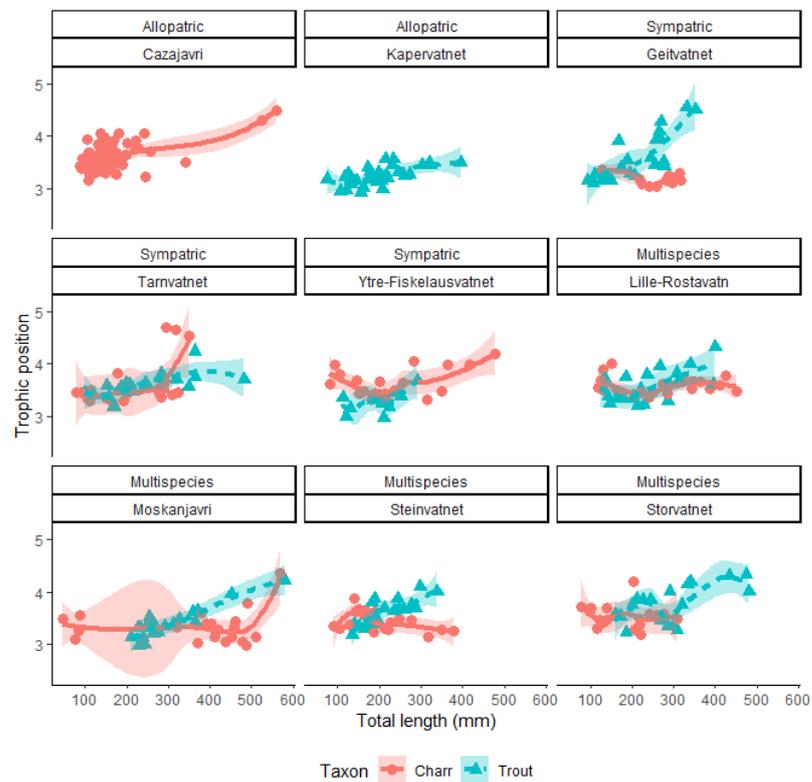
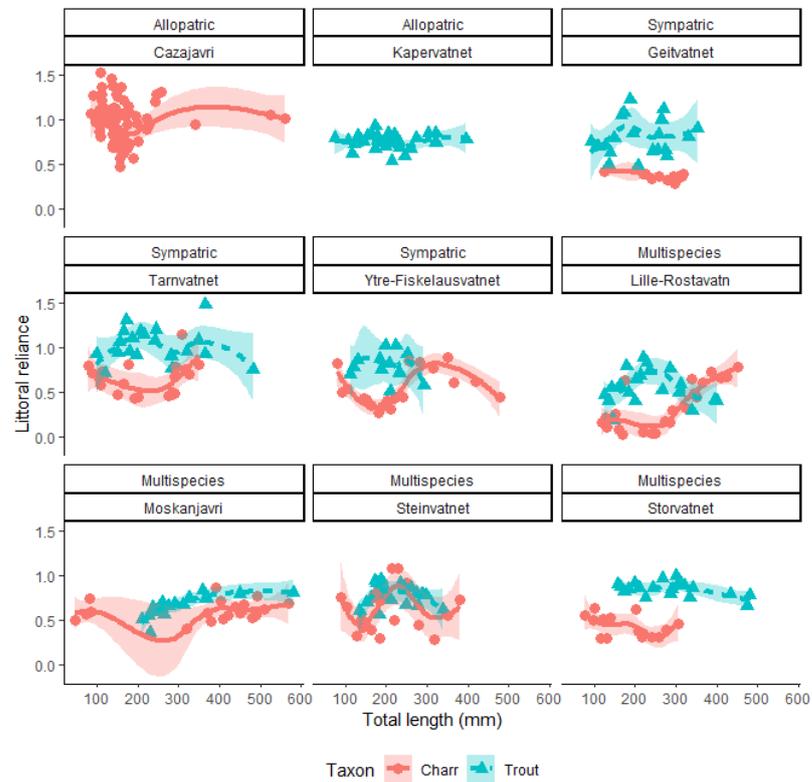
APPENDIX 1. DETAILED STOMACH CONTENT DATA BY TOTAL SUMS OF ESTIMATED PREY PROPORTIONS

Fish community		Allopatric				Sympatric				Multispecies							
Lake		CJ		KV		GV		TV		YV		MJ		STV		SV	
Group	Taxon	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T
Surface insect	Surface insect	2	213	23	186	32	257	4	13	131	535		1				38
Zooplankton	<i>Bythotrephes</i>		244	5	53	38	3	5		9		37	7	12	3		
	<i>Daphnia</i>		24	477	176			2		2		149	3	192	1		
	<i>Bosmina</i>	438				15	23	2				18		41	1		
	<i>Eurycercus</i>		2			115	8	165		1							
	<i>Polyphemus</i>																2
	<i>U/I zooplankton</i>	1															
Benthic insect	Chironomidae larvae	1253	153			62	3	8	2	1	1	9	25				
	Trichoptera larvae		133		6	11	147	15	45	53	75	56	123	1	5		
	U/I insect larvae		8		2		12	4		5					7	4	
	Limnephilidae	96															
	Chironomidae pupae	352	155					12	15	8	45	5	1	7	5		
	Trichoptera pupae		12			5	5	4		3	45			2	6		
	U/I insect pupae								15								
	Hydrachnidae	6															
Terrestrial insect	Oligochaeta				65												5
	Formicidae		2		1												
Molluscs	<i>Pisidium</i>	16						1		47	5	26					
	<i>Lymnaea</i>							15		46		16		1	1		
Benthic crustacea	<i>Gammarus</i> sp.							78	95	467	78	1	88	215	15	43	
	<i>Lepidurus arcticus</i>										7						
Fish	U/I fish				179												
	3-spined-stickleback												33	25	23		
	Burbot											138					
	Charr	384															
Other	U/I small eggs		19														7
	U/I insect								2								
	U/I rest	62															

CJ = Čazajávri, KV = Kapervatn, GV = Geitvatnet, TV = Tårnvatnet, YV = Ytre Fiskelausvatnet, MJ = Moskánjávri, STV = Steinvatnet, SV = Storvatnet

C = charr, T = trout

APPENDIX 2. LITTORAL RELIANCE AND TROPHIC POSITION AGAINST THE TOTAL LENGTH OF CHARR AND TROUT



APPENDIX 3. GROWTH OF CHARR AND TROUT BY LAKES

