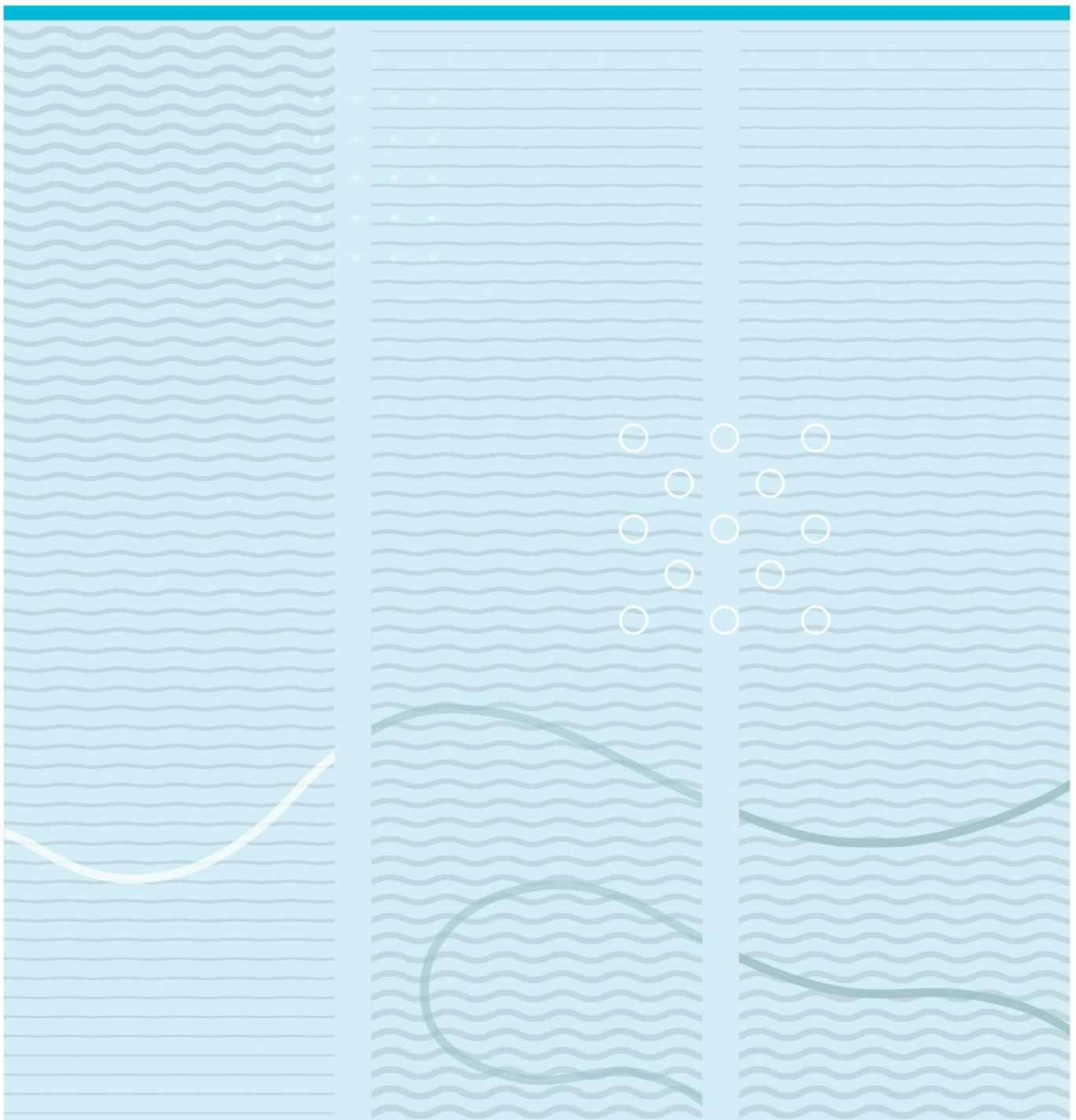


Mathias Leithe Haukø

Variation in macro parasites within and between three fish species in Lake Norsjø, southern Norway



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This thesis is worth 60 study points

Abstract

Interspecific competition among fish in multispecies lakes is an important factor for choice of habitat and feeding by the different species. Feeding and habitat use also seem to affect abundance, prevalence, and diversity of parasites within and between fish species. In addition, bioaccumulation of trophic transmitted parasites leads to increased parasite abundance in larger and older fish. In this study, variation in parasite abundance and diversity between and within Arctic charr *Salvelinus alpinus*, whitefish *Coregonus lavaretus* and perch *Perca fluviatilis* were investigated.

In 2018, 75 Arctic charr, 50 whitefish and 75 perch were caught with gillnets in three locations over three seasons (spring, summer, fall) in Lake Norsjø, a large and deep oligotrophic lowland lake in southern-eastern Norway. Macro endo and ecto parasites were sampled and determined. In fish, length and weight were measured, sex and age determinate, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures were analysed to reveal organic carbon source (habitat use) and trophic position, respectively. Generalized linear mixed effect models were used to investigate effects on total parasite abundance and generalized least squares to analyse effects on trophic position and habitat use within and between the three fish species.

Significant difference in parasite abundance, trophic position and habitat use were revealed between the three investigated fish species. Arctic charr exhibited profundal habitat use, highest average trophic position, highest parasite abundance and highest parasite diversity. Whitefish were revealed to have a pelagic-littoral habitat use, the lowest average trophic position, and the largest range in trophic position in addition to the second highest parasite diversity and abundance. Perch had the lowest range in trophic positions and the highest diversity in habitat use. In addition, had perch the lowest abundance and diversity of parasites. Fish length was the most important factor for parasite abundance in Arctic charr and whitefish and the second most important in perch after season. Dietary breadth, trophic position and fish size were most important for the total parasite abundance and diversity of parasites in the three investigated fish species. In addition a segregation in parasite fauna were related to habitat use.

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Mathias Leithe Haukø

1. Introduction

As freshwater food webs have been investigated since the first food webs were described in the 1880's, significant knowledge exists despite high diversity among these ecosystems (Thompson et al., 2012). In many food webs omnivory has complicated the understanding of communities (Pimm & Lawton, 1978; Polis & Strong, 1996), as omnivory in fish has complexed the understanding of freshwater food webs (Vadas, 1990). In freshwater ecosystems with sympatric fish populations, predation and competition are two important drivers for the community structure, besides variation in number of species, species abundance and habitat use (Jackson et al., 2001) which may complicate the understanding of food web structures also within aquatic ecosystems.

In multiple lakes in Scandinavia Arctic charr *Salvelinus alpinus* (Linnaeus, 1758), whitefish *Coregonus lavaretus* (Linnaeus, 1758), and perch *Perca fluviatilis* (Linnaeus, 1758) are living sympatric (Borgstrøm & Hansen, 2000). Arctic charr is well known to occur in different morphs that can vary in size, habitat use and feeding behaviour. Arctic charr can feed on zooplankton and zoobenthos regardless of size, in addition to be piscivore when reaching a certain, larger size (Amundsen, 1994; Hooker et al., 2016; Jonsson & Jonsson, 2001; Klemetsen, 2010; Skoglund et al., 2015). Despite the plasticity in feeding, Arctic charr is documented to be a weak competitor in multispecies lakes, and often use the deeper parts of lakes where the interspecific competition decreases, but also the nutrient supply often is poorer (Klemetsen et al., 2003; Sandlund et al., 2016; Sandlund et al., 2010). Whitefish is a species well known for polymorphism, with morphs adapted to different habitat and feeding patterns, but primarily with planktivore and benthivore dominated populations (Amundsen et al., 2004; Præbel et al., 2013). Thus, due to their plasticity both Arctic charr and whitefish exhibit large variations in diet and habitat use. Perch on the other hand, has a narrower feeding behaviour basically linked to ontogenetic diet shifts. This means they are being planktivorous as very young and small, benthivorous as at intermediate age and size, before ending up as piscivorous when they reaches the length of approximately 20 cm, however some variations in feeding between lakes are revealed (Amundsen et al., 2003; Mittelbach & Persson, 1998; Persson, 1983; Pethon, 2005; Svanbäck & Eklöv, 2002). When Arctic charr, whitefish and perch coexist it is reported that whitefish and Arctic charr exhibits overlapping pelagic niches with

zooplankton dominated dietary, while perch use littoral habitats with zoobenthos and later fish as main prey in large and deep Norwegian lakes (Sandlund et al., 2016).

To assess habitat use and trophic position in freshwater ecosystems, stable isotope analyses of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are often used. Organic carbon sources derived from different habitats of a lake is revealed with $\delta^{13}\text{C}$ analysis. Vander Zanden and Rasmussen (1999) reported significant difference in $\delta^{13}\text{C}$ signatures between organic carbon formed in profundal, pelagic and littoral habitats within lake systems, i.e., -30.5 ‰, -28.4 ‰ and -23.8 ‰, respectively. Further, $\delta^{15}\text{N}$ analysis is used for trophic position estimates of organisms (DeNiro & Epstein, 1978; Fry & Sherr, 1989; Post, 2002; Vander Zanden & Rasmussen, 1999). According to Post (2002), there is an $\delta^{15}\text{N}$ enrichment of ≈ 3.4 ‰ per trophic level in aquatic food webs, which is an estimated value often used in the scientific literature. Thus, measurements of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ can be used to describe two important factors when describing aquatic ecosystems.

Regarding trophic positions, bioaccumulating compounds like persistent organic pollutants or heavy metals are normally found in higher concentrations in fish feeding on higher trophic levels, as these compounds biomagnify up in the food web (Barni et al., 2016; Pourang, 1995). Also, trophic transmitted parasites are documented to accumulate in fish over time as the parasite transmission often is linked to feeding by the host (Poulin & Leung, 2011; Valtonen et al., 2010). Further has the variation in parasite communities among freshwater fish been linked to segregation in both habitat use and trophic position between and within different fish species (Knudsen et al., 2008; Knudsen et al., 2014). This is likely because trophic transmitted parasites have multiple ways to transmit to a fish, through intermediate hosts such as zoobenthos, zooplankton, and fish, but those linkages can be complex (Lafferty et al., 2006; Woo et al., 2006). However, as fish size seems to be important for the parasite abundance in fish (Bell & Burt, 1991; E. H. Henriksen et al., 2019; Timi et al., 2011), we might expect large fish at higher trophic positions (Romanuk et al., 2011) to have a higher parasite abundance than smaller fish at lower trophic positions.

In this study, Arctic charr, whitefish and perch were caught at three locations and three seasons in 2018 in Lake Norsjø, a big lake in South-Eastern Norway. Fish size (length and weight), age, sex, abundance of macro parasites, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were analysed in the fish material. By this data, difference in total parasite abundance, habitat use, and trophic position were revealed and causes for the variation further discussed. The main goal was to test the hypothesis that parasite abundance, and type of parasites, likely is linked to factors as size, age, trophic position, and habitat use of the three fish species. In addition information about possible seasonal variations in parasite abundance, and parasite species were wanted to be obtained.

2. Methods

2.1. Study area

Fish sampling was done at three locations in Lake Norsjø, located in Vestfold & Telemark County, South-Sastern Norway (Figure 1). Lake Norsjø (15 m a.s.l.) is a large lowland lake with a surface area of 55.1 km² and a lake volume of 5.1 km³ (Vann-Nett, 2020). Maximum depth in Lake Norsjø is 171 m with a middle depth of 87 m. The catchment area is 10 382 km², and water mainly drains into the lake through three main rivers in the northern parts of the lake. All the three rivers are draining from high mountain areas in northern parts of Vestfold and Telemark County. Lake Norsjø is regulated for electrical power production, but the regulation is small (0.15 m; LRW=15.15 m, HRW=15.3 m; Vann-Nett, 2020). The lake have been classified as an oligotrophic lake, with minor ecological or chemical impacts from the surrounding agricultural areas (Solheim et al., 2016).

In Lake Norsjø, 13 fish species are identified (Jensen, 1954): Arctic charr, whitefish, perch, Northern pike *Esox lucius* (Linnaeus, 1758), brown trout *Salmo trutta* (Linnaeus, 1758), Atlantic salmon *Salmo salar* (Linnaeus, 1758), European smelt *Osmerus eperlanus* (Linnaeus, 1758), European eel *Anguilla anguilla* (Linnaeus, 1758), Crucian carp *Carassius carassius* (Linnaeus, 1758), river lamprey *Lampetra fluviatilis* (Linnaeus, 1758), Eurasian minnow *Phoxinus phoxinus* (Linnaeus, 1758), tench *Tinca tinca* (Linnaeus, 1758), and three spined stickleback *Gasterosteus aculeatus* (Linnaeus, 1758). Both Arctic charr and whitefish have been suggested to exist in different morphs in Lake Norsjø (Jensen, 1954).

2.2. Field sampling

In 2018, fish were sampled over the three seasons spring (late May), summer (late July) and fall (mid-September) at three different locations, North, Mid and South in Lake Norsjø (Figure 1). The sampling was done by two previous master's students at the University of South-Eastern Norway (Dolven, 2020; A.-C. Henriksen, 2019). Fish were caught by bottom

gill nets, where two series containing eight 1,5x25 m gillnets, varying in mesh size from 13.5-45.0 mm, were set at each location every time. The nets were sat from the shore and towards the deepest point in the area, fishing in depths from about 2 m to 40-60 m. The nets were fishing for approximately for 24 hours each, every time.

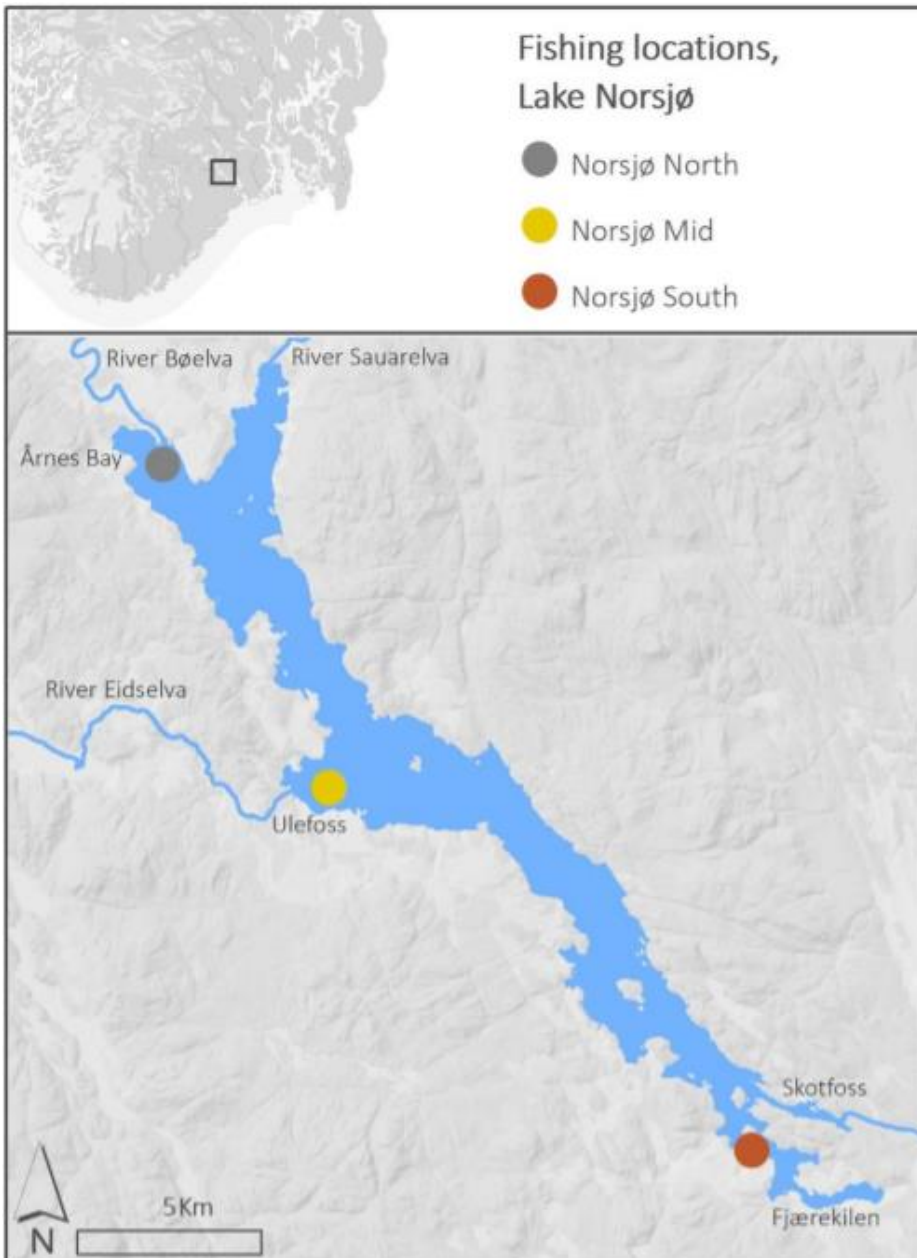


Figure 1. Locations in Lake Norsjø where fish sampling were done in three seasons in 2018. Figure is used with permission from A.-C. Henriksen (2019).

Ectoparasites were collected in field after the fish were taken out of the gillnets and stored in 96% ethanol for later investigation. Fish weight was measured with a digital weight to the nearest gram, while fish length was measured with a ruler to the nearest millimetre. Subsequently the fish were frozen individually in unique marked plastic bags until later examination in laboratory.

The fish used in this study is a subsample of 75 Arctic charr, 75 perch and 50 whitefish of the total catch from 2018. The subsampling was done using the random number generator in Microsoft Excel (Microsoft-Corporation, 2018). The number of individuals of each species were selected to a certain degree represent the distribution of total catches, with most perch (n=258) and Arctic charr (n=173), and less whitefish (n=101). The total number of 200 fishes were selected due to limited economy for stable isotope analyses.

2.3. Laboratory work

All fish have in advance been investigated for ecto and endo macro parasite by the same master students as did the fish sampling (Dolven, 2020; A.-C. Henriksen, 2019) which identified the parasites to the lowest phylogenetic level as possible based on “naked eye” and microscopy.

For this study, otoliths from the 200 fish were sampled for age determination. The otoliths were divided using a scalpel and burned over a propane stove. Opaque winter zones were counted in a stereo microscope at 40 x magnification to determine the age of the fish.

Further, approximately 2 g of muscle tissue from each individual fish was sampled from the area below the dorsal fin and freeze-dried for 24 hours in a Heto LyoLab 3000 (Heto-Holten A/S, Allerød, Danmark). The freeze-dried tissue were then grounded to fine powder with a mortar, and approximately 20 µg of dried fish powder from each sample was placed in separate tin capsules and sent to the IFE (Norwegian Institute for Energy Technology) for stable isotope analysis. At IFE, the following procedure were done to determine the stable isotope values: Samples were combusted with O₂ and Cr₂O₃ at

1700 °C, in a NCS 2500 elemental analyzer (Thermo Fisher Scientific, Waltham, MA, USA). At 650 °C in a Cu oven, NO_x was reduced to N₂. Further, H₂O was removed in a Mg (ClO₄) chemical trap before separation of N₂ and CO₂ on a 2 m poraplot Q GC column (Agilent J&W, Santa Clara, CA, USA). To determine δ¹³C, δ¹⁵N and the C/N ratio, N₂ and CO₂ were directly injected on-line to a DeltaXP plus isotope ratio mass spectrometer (IRMS) (Thermo Fisher Scientific, Waltham, MA, USA). The reference standards for the stable nitrogen and carbon isotopes are atmospheric nitrogen and Pee Dee Belemnite limestone, respectively (Gröning, 2004).

2.4. Data analysis

Two pooled groups of parasites containing multiple species were made in advance of the analysis. Copepod transmitted parasites were pooled by the species *Eubothrium salvelini* (Schrank, 1790), *Proteocephalus* sp., *Dibothriocephalus dendriticus* (Nitzsch, 1824) Lühe, 1899, *Dibothriocephalus ditremus* (Creplin, 1825) Lühe, 1899, and *Triaenophorus nodulosus* (Pallas, 1781) as they all transmit to the fish by copepods. In addition, *D. dendriticus*, *D. ditremus* and *T. nodulosus* were pooled as plerocercoids larvae of cestodes (referred to as plerocercoids) since they share the same characteristics in the fish (Halvorsen & Andersen, 1984). Both copepod transmitted parasites and plerocercoids will be counted in as own groups in addition to the species. Despite the parasites were described to different phylogenetic levels they will be referred to as species, further copepod transmitted parasites and plerocercoids will be referred to as groups. For each parasite species in addition to the two groups abundance and prevalence were calculated (Bush et al., 1997). Prevalence and abundance for the total parasite burden in each fish were additionally calculated and included in the statistical analysis.

The mean, median, standard deviation and range were calculated for the numerical variables length, weight, age, δ¹⁵N and δ¹³C. Difference in trophic position between the species was calculated by dividing the difference in the average δ¹⁵N signatures by 3.4, assuming an δ¹⁵N enrichment of 3.4 ‰ per trophic level (Post, 2002). The same method

was used to calculate the difference in trophic position within the species, by dividing the range in $\delta^{15}\text{N}$ by 3.4.

All data handling and statistical analysis were done in Microsoft Excel and R studio (Microsoft-Corporation, 2018; R-Core-Team, 2019) and all figures were made with the ggplot2 package in R studio (Wickham, 2016). For the statistical analysis two different methods were used. In analysis with total parasite abundance as response variable GLMM (generalized linear mixed effect models) were used, and for the models with stable isotopes as response variables GLS (generalized least squares) were used. All reported models were checked to not include zero within the 95% confidence interval, as they would be considered as uninformative (Arnold, 2010).

Total parasite abundance (GLMM)

Due to high zero inflation in the parasite data, the GLMMs were made in the glmmTMB package in R studio (Magnusson et al., 2017). For analysis of effects on total parasite abundance four models were made: One for the whole dataset containing all fish species, and one for each of the three fish species, all four models with total parasite abundance as response variable. The numeric explanatory variables in the global models were length, weight, age, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$. Categorical variables were sex (two factor: male, female), season (three factor: spring, summer, fall) and location (three factor: North, South, Mid). In the model for the whole dataset also the categorical variable species (three factor: Arctic charr, whitefish, perch) were added. The models were corrected for zero inflation setting the *ziformula* to zero, and a negative binomial distribution fit were selected (Brooks et al., 2017).

The validity of the models were inspected visually by plotting the simulated residuals using the *SimulateResiduals* function in the DHARMA-package in R studio (Hartig, 2019). Further, the best models were selected by simplifying the global model by selecting the best fitting explanatory variables to the given data using the dredge function in the MuMin package in R studio (Barton, 2020). When dredging models, the best models were selected using Akaike information criterion AIC (Hurvich & Tsai, 1993) and for the model selection output, only models with $\Delta\text{AIC}<2$ were included. The simplified models with

$\Delta AIC = 0$ were considered as the best for the given data, hence reported. Validity of the best fitted models was again inspected by plotting the simulated residuals before reported. The GLMM model selection tables are shown in Appendix 2.

Stable isotopes (GLS)

Due to heterogeneity in the isotope data, GLS was selected as method for the analysis with stable isotopes as response variables (Zuur et al., 2009). The models were made with the *nmle* package in R studio using the GLS function with maximum likelihood fit in the model selection process (Pinheiro et al., 2021; Zuur et al., 2009).

Two models for each of the three fish species and two models for the whole data (all species in one data set) were made. For each of the four data sets one model with $\delta^{15}\text{N}$ and one with $\delta^{13}\text{C}$ as response variables were made, in total eight models. The numeric explanatory variables used were length, weight, age, and the stable isotope that was not used as response variable in the respective model (i.e., $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$). Categorical explanatory variables were sex (male, female), location (North, South, Mid), and season (spring, summer, fall). In the two models for the whole dataset categorical variable species (Arctic charr, whitefish, perch) were added. Since the effects on total parasite abundance were analysed in separate models including zero inflation correction, the parasite abundance were not included in the GLS analyses.

For all eight GLS analysis the process of model fitting and selection were the same: First, a null model for the overall mean ($y \sim 1$) for the response variable ($\delta^{15}\text{N}$ or $\delta^{13}\text{C}$) were made. Further, alternative models were made by adding one explanatory variable in a model with the same response variable as the null model, this was done with all explanatory variables. Model selections were done by ANOVA to compare the fit of the null model and the alternative models (Zuur et al., 2009). If the ANOVA gave a significant p-value ($p < 0.05$), the alternative model was considered as better fitting for the given data than the null model, thus retained. For models with unequal amount of data in response variables and explanatory variables, the model with lowest AIC was used to determine the best fitted model (Hurvich & Tsai, 1993), as the p-value in the ANOVA were not available. See complete model selection tables in Appendix 3-10.

If there was more than one alternative model better than the null model after the model selection the model with lowest AIC was considered as the best model for the given data, thus selected as the final model (Hurvich & Tsai, 1993). Final models with correlation in the residuals were remade with one-way exponential variance for the explanatory variable, further used as final model (Zuur et al., 2009). All final models were remade with restricted maximum likelihood and were visually inspected and verified by plotting fitted values vs standardized residuals, and normal distribution of residuals were checked in qq-plots. Only the final models with lowest AIC-value for each response variable of each data set were reported as they were most certain to explain effects for the given data.

3. Results

The Arctic charr (n=75), whitefish (n=50) and perch (n=75) used in this study were caught in all three seasons (spring, summer, fall), whitefish and perch were caught in all three sites (North, Mid, South), and Arctic charr only caught at site North and Mid locations (Appendix 1). For all three species both male and female fish were caught.

3.1. Descriptive statistics

The average length measured in Arctic charr, whitefish and perch were 272.5 ± 62.9 mm, 279.2 ± 47.4 mm and 212.2 ± 55.1 mm, respectively (Table 1). The highest average weight was measured in Arctic charr with 231.2 ± 188.3 g, followed by whitefish with 198.7 ± 120.0 g and perch with 141.3 ± 141.3 g. Arctic charr also had the highest average age, 11.9 ± 6.7 years, while whitefish and perch had a lower average age with 4.9 ± 2.1 and 4.2 ± 1.7 years, respectively. Highest average $\delta^{15}\text{N}$ signature was measured in Arctic charr, 11.6 ± 1.84 ‰, followed by perch 9.0 ± 1.5 ‰, and whitefish 8.0 ± 2.3 ‰. Perch exhibited the less depleted $\delta^{13}\text{C}$ signature -24.9 ± 2.5 ‰, than whitefish -28.3 ± 2.3 ‰ and Arctic charr -29.4 ± 1.1 ‰ (Table 1).

Arctic charr exhibited the highest average trophic position of the three species, 0.8 higher than perch and 1.0 higher than whitefish. Whitefish exhibited the largest individual range in trophic positions by 2.6, followed by Arctic charr, 2.4, and perch, 2.0.

Table 1. Mean, median, standard deviation (SD) and range of length (mm), weight (g), age (years) $\delta^{15}\text{N}$ (‰) and $\delta^{13}\text{C}$ (‰) in the three species Arctic charr (n=75), whitefish (n=50) and perch (n=75) caught in Lake Norsjø, 2018.

Species	Variable	Mean	Median	SD	Range
Arctic charr	Length (mm)	272.5	259.0	62.9	153.0-438.0
	Weight (g)	231.2	170.0	188.3	28.0-981.0
	Age (years)	11.9	10.0	6.7	4.0-31.0
	$\delta^{15}\text{N}$ (‰)	11.6	11.6	1.84	6.6-14.8
	$\delta^{13}\text{C}$ (‰)	-29.4	-29.5	1.1	-32.1- -27.1
Whitefish	Length (mm)	279.2	282.5	47.4	186.0-440.0
	Weight (g)	198.7	177.0	120.0	47.0-757.0
	Age (years)	4.9	4.5	2.1	2.0-9.0
	$\delta^{15}\text{N}$ (‰)	8.0	8.3	2.3	3.6-12.3
	$\delta^{13}\text{C}$ (‰)	-28.3	-28.6	2.3	-31.3- -21.8
Perch	Length (mm)	212.2	197.0	55.1	112.0-356.0
	Weight (g)	141.3	83.0	141.3	13.0-633.0
	Age (years)	4.2	4.0	1.7	1.0-10.0
	$\delta^{15}\text{N}$ (‰)	9.0	9.2	1.5	5.6-12.2
	$\delta^{13}\text{C}$ (‰)	-24.9	-25.1	2.5	-29.6 - -19.3

Arctic charr had the highest diversity of parasites with nine different species and the highest average abundance by 24.9 ± 22.7 (Table 2). In whitefish, seven different parasite species were found, with an average total abundance of 5.7 ± 13.1 . Five different species of parasites were found in perch, with an average total abundance of 4.9 ± 6.9 . In Arctic charr copepod transmitted parasites and plerocercoid exhibited highest prevalence by 99 %. In both whitefish and perch acanthocephala exhibited the highest prevalence, 36 % and 79 %, respectively (Table 2).

Table 2. Prevalence (%) and mean abundance (\pm standard deviation) of each parasite species/groups found in the three fish species Arctic charr ($n=75$), whitefish ($n=50$) and perch ($n=75$) caught in Lake Norsjø in 2018.

Parasite group/species	Prevalence (%) & mean Abundance \pm SD					
	Arctic charr		Whitefish		Perch	
Acanthocephala	3	0.0 ± 0.3	36	4.4 ± 11.9	79	4.7 ± 6.8
Copepod transmitted	99	24.9 ± 22.5	28	0.7 ± 2.0	12	0.2 ± 0.5
Plerocercoids	99	22.0 ± 20.4	4	0.0 ± 0.2	7	0.1 ± 0.4
<i>Argulus Coregoni</i>	1	0.0 ± 0.1	20	0.4 ± 1.0	—	—
Cysts (Plerocercoids)	93	20.2 ± 19.8	—	—	—	—
<i>Dibothriocephalus dendriticus</i>	25	0.3 ± 0.5	—	—	—	—
<i>Dibothriocephalus ditremus</i>	43	1.0 ± 1.5	—	—	—	—
<i>Dibothriocephalus</i> spp.	—	—	4	0.0 ± 0.2	4	0.1 ± 0.3
<i>Eubothrium salvelini</i>	68	2.6 ± 4.4	—	—	—	—
<i>Eubothrium</i> sp.	—	—	—	—	3	0.0 ± 0.3
Nematoda	—	—	2	0.0 ± 0.1	—	—
<i>Proteocephalus</i> sp.	7	0.3 ± 1.4	24	0.7 ± 2.0	4	0.1 ± 0.4
<i>Salmincola edwardsii</i>	16	0.2 ± 0.4	—	—	—	—
<i>Salmincola</i> sp.	—	—	12	0.1 ± 0.4	—	—
Trematoda	—	—	2	0.1 ± 0.4	—	—
<i>Triaenophorus nodulosus</i>	36	0.6 ± 1.2	—	—	4	0.0 ± 0.2
Total	99	24.9 ± 22.7	66	5.7 ± 13.1	80	4.9 ± 6.9

3.2. Statistical analysis

Total parasite abundance (GLMM)

For the whole data set, the variation in total parasite abundance between the species were the most significant ($p < 0.05$; Table 3). Arctic charr had the highest parasite abundance, followed by whitefish and perch (Table 2). A significant effect of $\delta^{13}\text{C}$ on the total parasite abundance were revealed, with the parasite amount increased with decreasing $\delta^{13}\text{C}$ signatures. There also were significant higher abundance of parasite in spring ($p = 0.028$) and summer ($p = 0.032$) than fall. There was also an almost significant trend of increasing parasite abundance with increasing weight ($p = 0.050$), but not fully significant, i.e., $p < 0.05$ (Table 3).

Table 3. GLMM output of modelling total parasite abundance vs selected variables fish species, season, $\delta^{13}\text{C}$ (‰) signatures and weight (g) for the whole dataset of fish caught in Lake Norsjø in 2018.

Variable	Estimate	Std. error	z-value	p-value
Intercept	5.347	1.440	3.714	<0.005
Species Perch	-1.911	0.340	-5.628	<0.005
Species Whitefish	-1.750	0.301	-5.811	<0.005
Season spring	0.500	0.227	2.199	0.028
Season summer	0.490	0.490	0.228	0.032
$\delta^{13}\text{C}$	0.102	0.048	2.145	0.032
Weight	0.001	0.001	1.192	0.050

In the model for total parasite abundance in Arctic charr, age and length were the two variables left in the final model after model selections. Only length had a significant positive effect on total parasite abundance ($p = 0.008$; Table 4), where a higher abundance in longer fish were revealed (Figure 2).

Table 4: GLMM output of modelling effects of total parasite abundance vs selected variables age (years) and length (mm) in Arctic charr ($n=75$) caught in Lake Norsjø, 2018.

Variable	Estimate	Std. error	z-value	p-value
Intercept	1.238	0.522	0.237	0.018
Age	0.002	0.023	0.094	0.926
Length	0.006	0.003	2.661	0.008

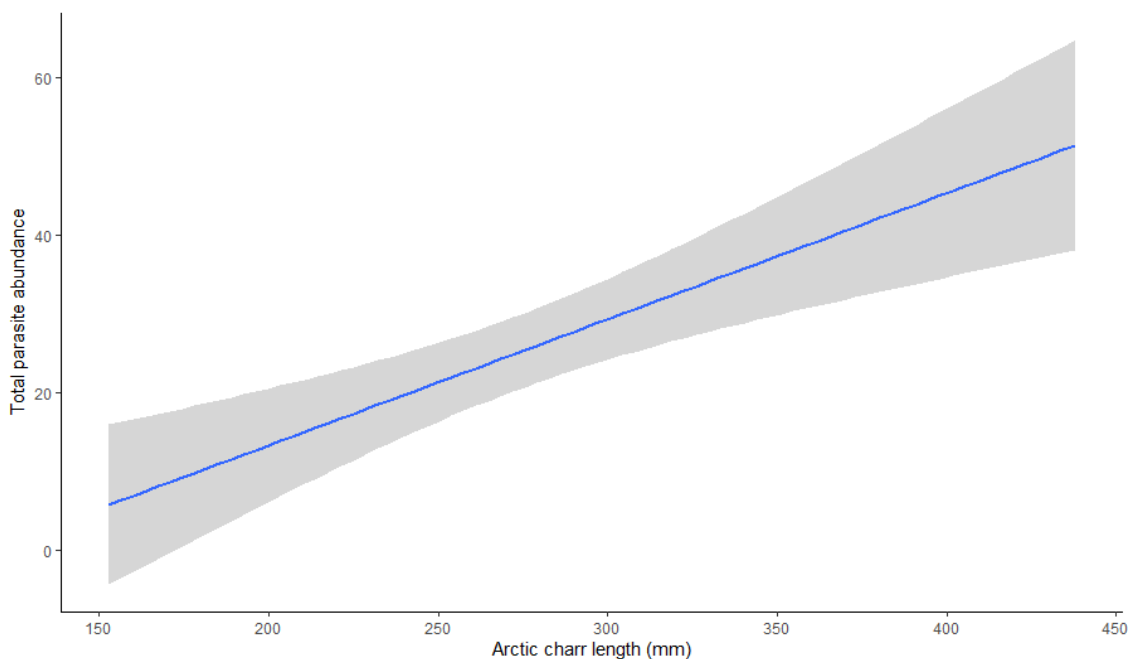


Figure 2. The significant effect of length on total parasite abundance in Arctic charr ($n=75$) caught in Lake Norsjø, 2018. Grey areas: 95% confidence interval.

In whitefish, both length and spring season had significant effects on the total parasite abundance (Table 5). Length was the most significant effect, revealing increased parasite abundance in larger individuals ($p<0.005$; Figure 3). Regarding season, only spring season had a significant effect ($p=0.013$) on total abundance of parasites in whitefish with more parasites in spring than summer and fall (Table 5). The catch in spring, summer and fall were 21, 19, and 10, respectively (Appendix 1).

Table 5. GLMM output of modelling effects of total parasite abundance vs selected variables season and length (mm) in whitefish (n=50) caught in Lake Norsjø, 2018.

Variable	Estimate	Std. error	z-value	p-value
Intercept	-8.818	2.270	-3.884	<0.005
Season spring	1.628	0.652	2.496	0.013
Season summer	0.521	0.669	0.779	0.436
Length	0.033	0.007	4.507	<0.005

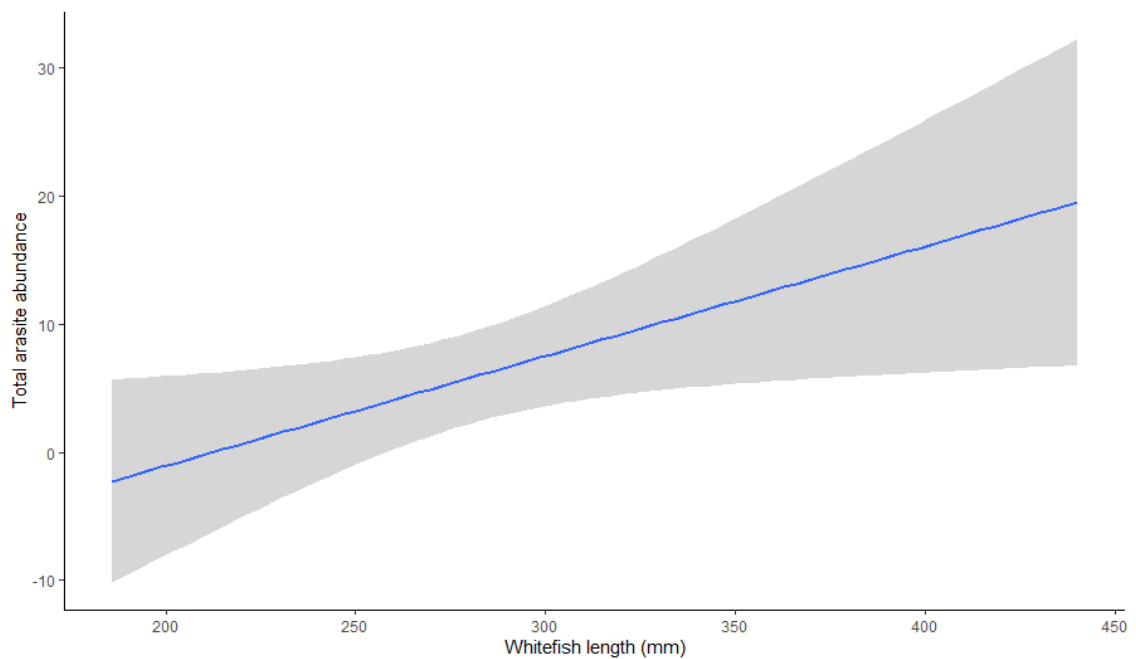


Figure 3. The significant effect of length on total parasite amount in whitefish (n=50) caught in Lake Norsjø in 2018. Grey area: 95 % confidence interval.

In perch, season exhibited most significant effect (spring: $p=0.002$, summer: $p<0.005$) on total parasite abundance (Table 6), where highest parasite abundance in summer and spring, with lowest in fall were revealed (Figure 4). The number of perch incorporated in the model was 28, 26 and 21 in spring, summer, and fall, respectively (Appendix 1). The size variables length and weight were also left in the selected model, with only effect of length as significant ($p=0.008$; Table 6; Figure 5) while the effect of weight was not significant ($p=0.085$; table 6).

Table 6: GLMM output of modelling effects of total parasite abundance vs selected variables season, length (mm), and weight (g) in perch (n=75) caught in Lake Norsjø, 2018.

Variable	Estimate	Std. error	z-value	p-value
Intercept	-2.800	1.080	-2.510	0.0121
Season spring	1.076	0.348	3.094	0.002
Season summer	1.511	0.363	4.165	<0.005
Length	0.016	0.006	2.672	0.008
Weight	-0.004	0.002	-1.723	0.085

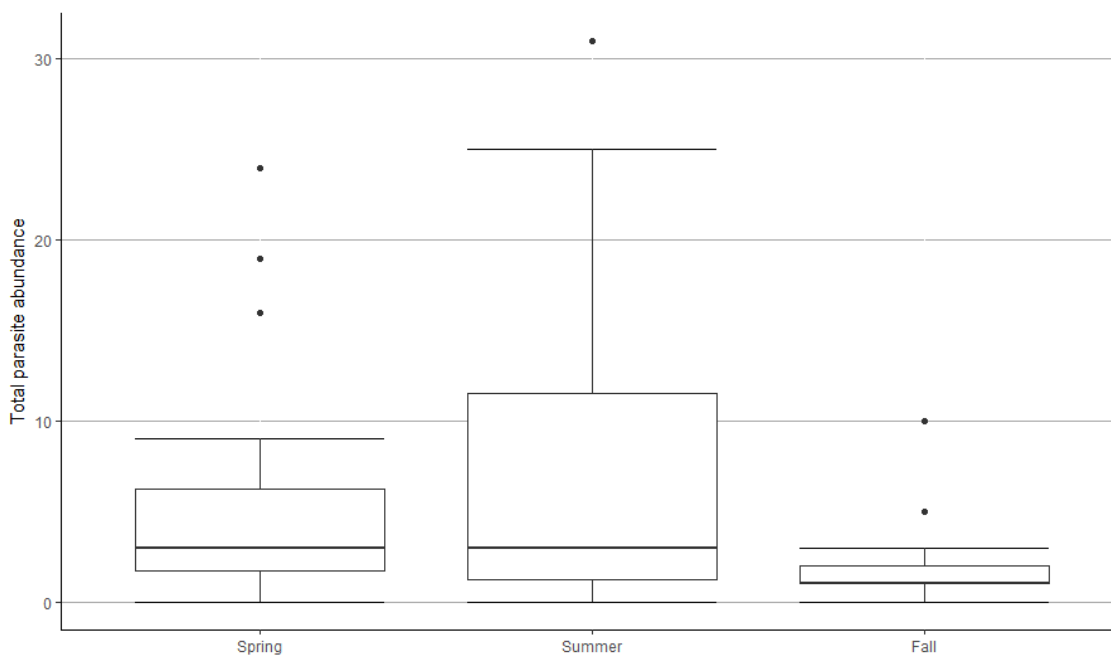


Figure 4. The total parasite abundance in perch (n=75) caught in spring, summer and fall in Lake Norsjø in 2018. The number of perch caught per season was 28 in spring, 26 in summer, and 21 in the fall

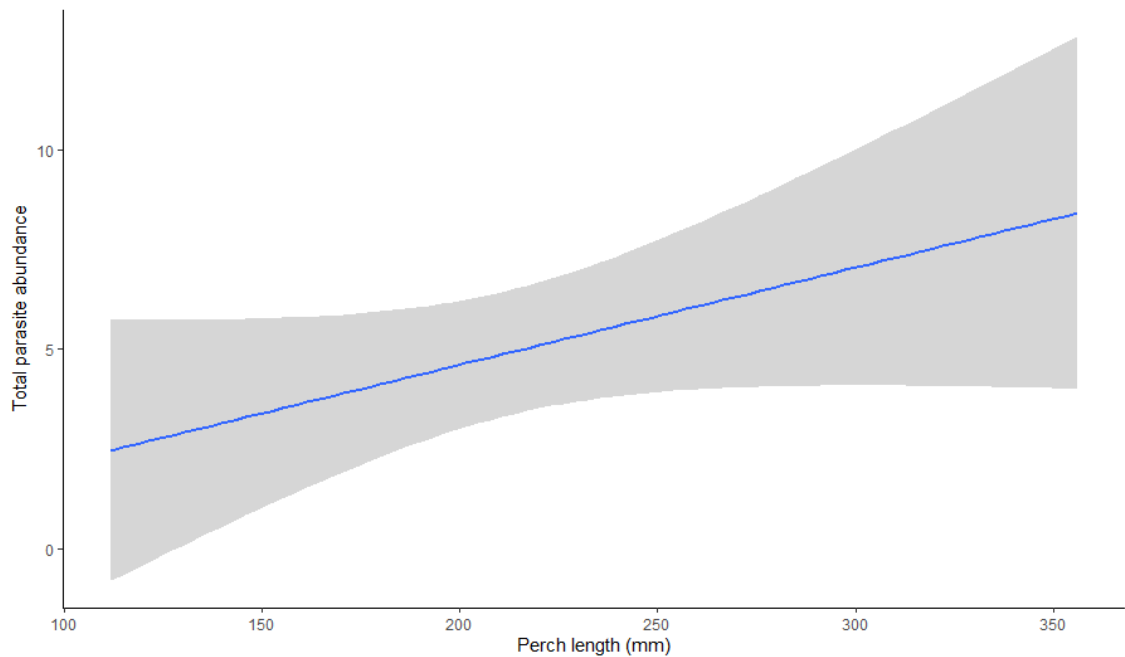


Figure 5. The significant effect of length on the total parasite abundance in perch ($n=75$) caught in Lake Norsjø, 2018. Grey field: 95 % confidence interval.

Stable isotopes (GLS)

Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ exhibited significant differences between the three fish species ($p<0.005$), which means significant difference in both trophic level ($\delta^{15}\text{N}$) and habitat use ($\delta^{13}\text{C}$) between Arctic charr, whitefish and perch (Table 7; Figure 8).

Table 7. GLS final model output modelling effects of $\delta^{15}\text{N}$ (‰) and $\delta^{13}\text{C}$ (‰) vs fish species Arctic charr ($n=75$) whitefish ($n=50$) and perch ($n=75$) caught in Lake Norsjø in 2018.

Response v.	Parameter	Value	Std. error	t-value	p-value
$\delta^{15}\text{N}$	Intercept	11.547	0.214	54.054	<0.005
	Perch	-2.532	0.302	-8.382	<0.005
	Whitefish	-3.512	0.338	-10.398	<0.005
$\delta^{13}\text{C}$	Intercept	-29.436	0.233	-126.249	<0.005
	Perch	4.533	0.330	13.748	<0.005
	Whitefish	1.157	0.369	3.138	<0.005

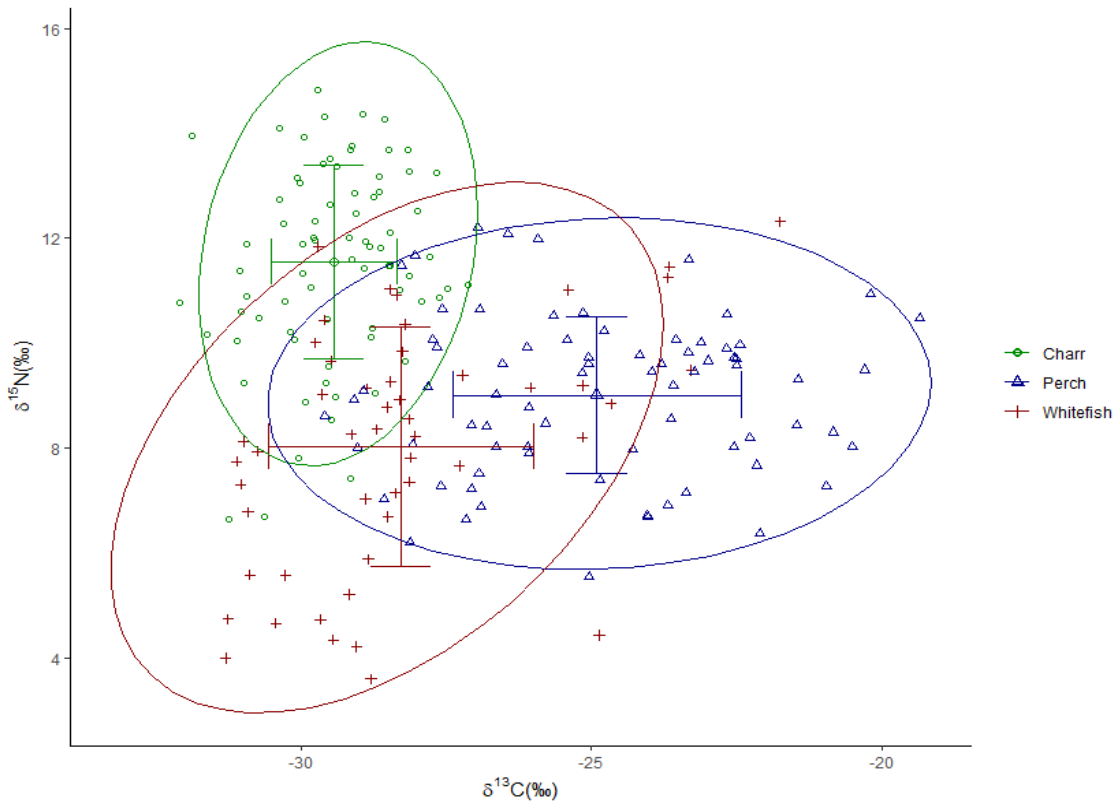


Figure 6: Biplot of mean \pm standard deviation for $\delta^{13}\text{C}$ ‰ and $\delta^{15}\text{N}$ ‰ in Arctic charr (Charr; $n=75$; $\delta^{13}\text{C}$: -29.4 ± 1.1 ‰, $\delta^{15}\text{N}$: 11.6 ± 1.8 ‰), perch ($n=75$; $\delta^{13}\text{C}$: -28.3 ± 2.3 ‰, $\delta^{15}\text{N}$: 8.0 ± 2.3 ‰) and whitefish ($n=50$; $\delta^{13}\text{C}$: -24.9 ± 2.5 ‰, $\delta^{15}\text{N}$: 9.0 ± 1.5 ‰) caught in Lake Norsjø in 2018. Single points represent each individual fish.

In Arctic charr, age showed the most significant and positive effect ($p=0.025$) on the $\delta^{15}\text{N}$ values, revealing increased trophic position by older fish (Table 8; Figure 7). Regarding $\delta^{13}\text{C}$, age was left as explanatory variable in the final model, but no significance was detected ($p=0.272$; Table 8).

Table 8. GLS final model output of modelling effects $\delta^{15}\text{N}$ (‰) and $\delta^{13}\text{C}$ (‰) vs age (years) in Arctic charr ($n=75$) from Lake Norsjø in 2018. Significance was only detected in $\delta^{15}\text{N}$ vs age.

Response v.	Parameter	Value	Std. error	t-value	p-value
$\delta^{15}\text{N}$	Intercept	10.705	0.434	24.651	<0.005
	Age	0.072	0.032	2.287	0.025
$\delta^{13}\text{C}$	Intercept	-29.667	0.261	-113.595	<0.005
	Age	0.021	0.019	1.105	0.272

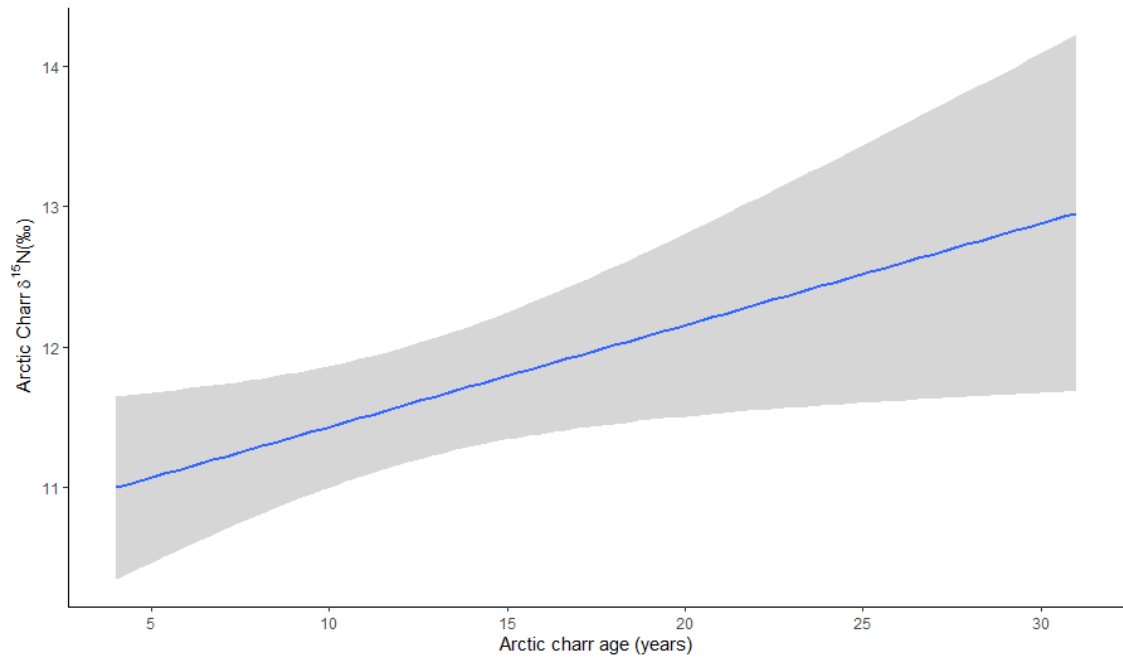


Figure 7. The significant effect of age (years) on $\delta^{15}N$ (‰) in Arctic charr ($n=75$) caught in Lake Norsjø in 2018. Grey field: 95 % confidence interval.

In whitefish, $\delta^{13}C$ exhibited the most significant and positive effect on the $\delta^{15}N$ signatures (Table 9; Figure 8). In addition, fish weight was significantly and positive correlated with the $\delta^{13}C$ signature (Table 9; Figure 8).

Table 9. GLS final model output of modelling effects on $\delta^{15}N$ (‰) vs $\delta^{13}C$ (‰) and $\delta^{13}C$ (‰) vs weight (g) in whitefish ($n=50$) caught in Lake Norsjø, 2018.

Response v.	Parameter	Value	Std. error	t-value	p-value
$\delta^{15}N$	Intercept	21.392	3.424	6.647	<0.005
	$\delta^{13}C$	0.472	0.121	3.888	<0.005
$\delta^{13}C$	Intercept	-31.251	0.395	-79.175	<0.005
	Weight	0.015	0.002	8.882	<0.005

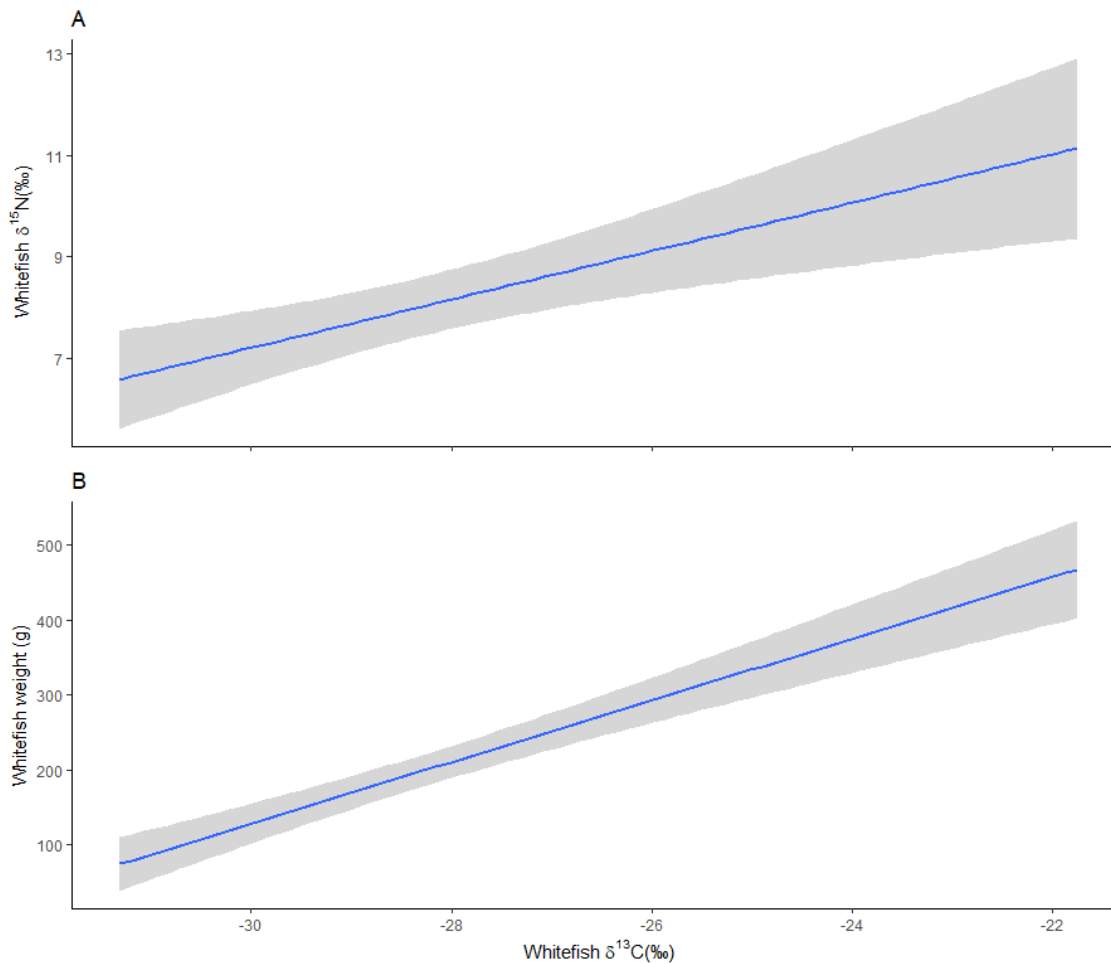


Figure 8. The significant effects of $\delta^{13}\text{C}$ (‰) on $\delta^{15}\text{N}$ (‰) (A) and fish weight (B) in whitefish ($n=50$) caught in Lake Norsjø, 2018. Grey areas: 95 % confidence interval.

In perch, increased length exhibited significant ($p<0.005$) and negative correlation with $\delta^{13}\text{C}$ values (Table 10; Figure 9). Sex was left as the explanatory variable in the final model for $\delta^{15}\text{N}$, but no significant effect was detected ($p=0.107$; Table 10).

Table 10. GLS final model output of modelling $\delta^{15}\text{N}$ (‰) vs sex and $\delta^{13}\text{C}$ (‰) vs length (mm) in perch ($n=75$) from Lake Norsjø in 2018. Significance was only detected in $\delta^{13}\text{C}$ vs length.

Response v.	Parameter	Value	Std. error	t-value	p-value
$\delta^{15}\text{N}$	Intercept	9.210	0.211	43.749	<0.005
	Sex	-0.584	0.365	-1.603	0.107
$\delta^{13}\text{C}$	Intercept	-21.775	0.927	-23.498	<0.005
	Length	-0.015	0.004	-4.127	<0.005

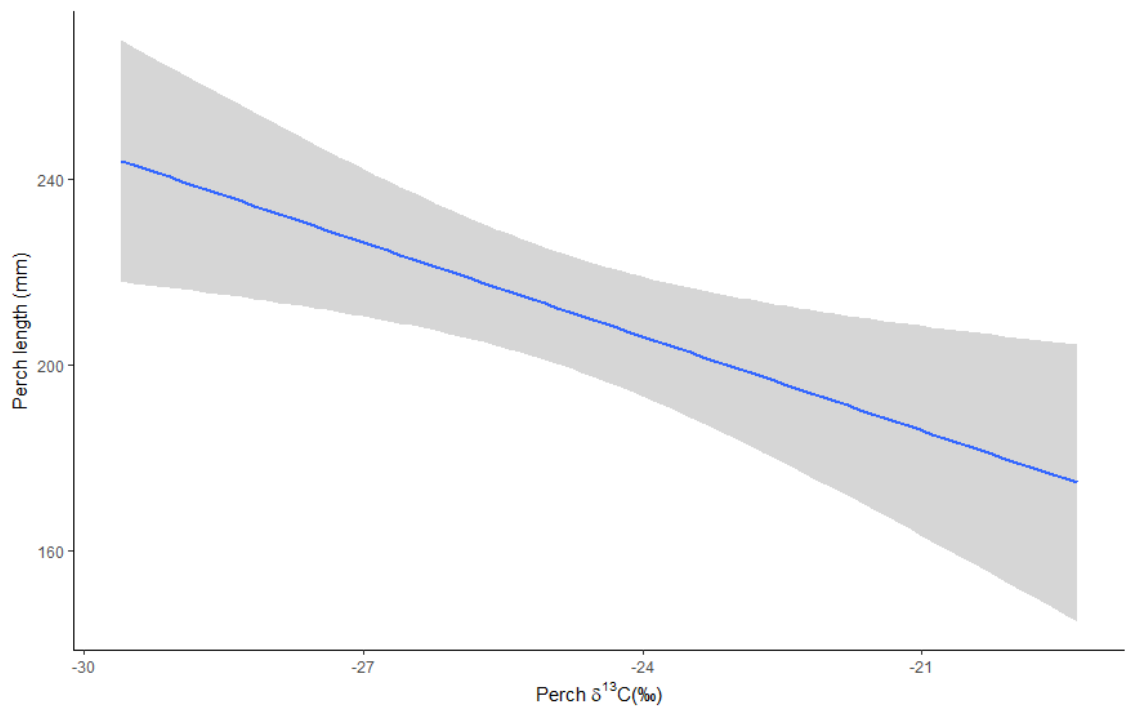


Figure 9. The significant effect of length (mm) on $\delta^{13}\text{C}$ (‰) in perch ($n=75$) caught in Lake Norsjø in 2018, Gray area: 95% confidence interval.

4. Discussion

Arctic charr, whitefish and perch caught in Lake Norsjø in 2018 exhibited significant differences in parasite abundance, habitat use and trophic position (Table 3 & 7). Perch and whitefish had $\delta^{13}\text{C}$ signatures linking them to diets deriving from littoral and pelagic habitats in the lake, with whitefish with the most pelagic derived diet and perch with the most littoral derived diet. The $\delta^{13}\text{C}$ signatures in Arctic charr, which was the most depleted, mirrored a profundal derived diet. Based on the average $\delta^{15}\text{N}$ signatures, Arctic charr exhibited the highest trophic position among the three fish species, 0.8 trophic position over perch and 1.0 over whitefish. Regarding average parasite abundance, Arctic charr exhibited the highest abundance and diversity, followed by whitefish and perch (Table 2). Further, highest prevalence of parasites were also detected in Arctic charr, with second highest in perch and lowest in whitefish.

In addition to the significant difference in parasite abundance between the three fish species, a significant higher abundance was revealed in relation to increased fish length for all three species. Fish length was the most significant parameter regarding total parasite abundance in Arctic charr and whitefish, and the second most significant in perch (Figure 2, 3 & 5). Earlier work on the same fish species focusing on abundance by different parasite species, have reported similar increased abundance by fish size and age (Dolven, 2020; A.-C. Henriksen, 2019; Olk et al., 2020). Age and size are often correlated in fish, including the fish used in this study (Appendix 11), and shows similar effects on infection of trophic transmitted parasites (Pacala & Dobson, 1988; Poulin, 2000). However, a higher parasite abundance with increased body size has been reported in several studies (Bell & Burt, 1991; E. H. Henriksen et al., 2019; Poulin, 2000; Timi et al., 2011). This can be a consequence of larger fish are larger and more available habitats for the parasites (Poulin, 1995; Poulin & Leung, 2011), in addition to higher feeding rates on larger prey by large fish, with subsequent increased exposure for trophic transmitted parasites (Poulin, 1997). In whitefish, perch and for the whole data material a significant seasonal variation in total parasite abundance were revealed (Table 3, 5 & 6). Perch caught in spring and summer had significant higher parasite abundance than fish caught in fall (Figure 4), and whitefish caught in spring had significant higher abundance of parasite than fish caught in summer and fall. The most prevalent and abundant parasite in both perch and

whitefish were acanthocephalan (Table 2) which have a one-season life cycle and recruits to the fish in the spring (Nickol, 2006), and likely explain the seasonal variation in parasite abundance observed in this study. Additionally, a significant effect of increased parasite abundance in fish with more depleted $\delta^{13}\text{C}$ signatures were revealed in analysis for the whole data material (Table 3). This is likely a consequence of most of the fish were caught in the pelagic and profundal habitats of the lake (Figure 6).

The lowest range and average $\delta^{13}\text{C}$ signatures among the three fish species were revealed in Arctic charr (Table 1), with a diet deriving from the pelagic-profundal habitats of the lake. No significant effects on $\delta^{13}\text{C}$ by the measured parameters were revealed, which can reflect a homogeneity in habitat use by Arctic charr caught in this study (Table 8). Similar habitat use by Arctic charr as detected in this study have been reported in multispecies lakes where Arctic charr, perch and whitefish coexist (Sandlund et al., 2013; Sandlund et al., 2010). This is likely due to the weak ability of Arctic charr to compete with other species for habitats and food resources and therefore is “squeezed” to deeper, colder, and more nutrient poor parts of the lakes (Klemetsen et al., 2003; Sandlund et al., 2016; Sandlund et al., 2010), which have results in small deep-water morphs in several lakes (Klemetsen, 2010).

Despite the narrow habitat use, Arctic charr exhibited the highest average trophic position (highest $\delta^{15}\text{N}$ signatures) by the three fish species (Table 1), in addition to an individual range of 2.4 trophic positions, similar as reported in this lake earlier (Lydersen & Moreno, 2016; Olk et al., 2016). Arctic charr is reported to be piscivorous at certain size and potentially become a top predator in both sympatric and allopatric lakes, hence found on a high trophic position (Amundsen, 1994; Kahilainen et al., 2019; L'Abée - Lund et al., 1992; Svenning & Borgstrøm, 2005). In this present study, a significant increase in trophic position by age was revealed in Arctic charr (Figure 7). Age and size in fish is very often positively correlated in fish, included the Arctic charr in this study (Appendix 11). By this, old, large individuals may feed on higher (piscivore) trophic positions while smaller and younger individuals feeds on lower trophic positions, i.e., zoobenthos and zooplankton (Borgstrøm & Hansen, 2000; Romanuk et al., 2011). Despite this, some profundal Arctic charr morphs are reported to be smaller and have a slower growth rate

than the more pelagic and littoral individuals (Klemetsen, 2010; Klemetsen et al., 1997). However, Olk et al. (2016) reported all size classes of Arctic charr in Lake Norsjø feeding on invertebrates in addition to a piscivore diet by fish at lengths over 140 mm. Further, the highest diversity, prevalence and abundance of parasites were revealed in Arctic charr among the three fish species. This, in addition to high the range and average in trophic positions indicates a large breadth and a plasticity in dietary by Arctic charr in Lake Norsjø (Eloranta et al., 2011; Knudsen et al., 2004; Locke et al., 2014). In this present study, copepod transmitted parasites were the most abundant parasites and detected in 99 % of the examined Arctic charr (Table 2), despite small numbers of copepods in stomach analysis of Arctic charr from Lake Norsjø (Olk et al., 2016). This can be a result of biomagnification over time although the feeding rates on copepods were low (Poulin & Leung, 2011; Valtonen et al., 2010). Furthermore, some parasites are reported to change the behaviour of its copepod host (Poulin et al., 1992) which leads to fish selectively feed on the infected copepods, hence high infection in the fish by those parasites despite a low copepod diet.

Whitefish exhibited lowest average but the highest range in trophic positions among the three fish species (Table 1). Also, a large range in habitat use among whitefish were revealed with $\delta^{13}\text{C}$ signatures derived from the profundals to the littorals, with average signatures from the pelagic habitats. Significant relations by habitat use ($\delta^{13}\text{C}$) on trophic position ($\delta^{15}\text{N}$) and fish length were detected in whitefish (Figure 8). This indicates large whitefish on high trophic position were feeding in the littoral habitats, while smaller fish on lower trophic positions used the pelagic and profundal habitats. Jensen (1954) reported a potentially existence of three different whitefish morphs in Lake Norsjø, “stream whitefish” (strømsik), “winter whitefish” (vintersik) and “littoral whitefish” (grunnsik), differing in size, habitat use, and spawning time and area. Littoral whitefish was reported to be the largest morph, while winter whitefish was a smaller individuals using the deeper and more pelagic habitats of the lake. Thus, fish size related to habitat use among whitefish found in this present study are like what Jensen (1954) reported, similar results are also reported by Lydersen and Moreno (2016). The well documented polymorphism in whitefish within multiple Scandinavian lakes makes it reasonable to

assume polymorphism by whitefish in a large diverse lake as Lake Norsjø (Amundsen et al., 2004; Eloranta et al., 2011; Schluter, 1996).

The high polymorphism in whitefish leads to a large plasticity in feeding behaviour (Borgstrøm & Hansen, 1987; Pethon, 2005). In Lake Norsjø, Jensen (1954) reported whitefish only feeding on invertebrates, while Olk et al. (2016) reported whitefish feeding on micro and macro invertebrates, in addition to some individuals with a piscivorous dietary in the winter and spring season. 66 % of the whitefish in this study were infected by parasites (Table 2) where acanthocephalan was the most abundant and prevalent (36 %), transmitted to the fish by amphipods, ostracods, isopods, and fish (Nickol, 2006). Further, copepod transmitted parasites exhibited second highest abundance and prevalence (28 %) in whitefish. The difference in prevalence of copepod transmitted parasite and acanthocephala compared with the total prevalence (66 %) indicates a segregation in parasite fauna among the collected whitefish. Acanthocephalan were probably most abundant in the littoral whitefish feeding on both zoobenthos and fish, while pelagic whitefish most likely had a zooplanktivore diet, thus were more infected by copepod transmitted parasites (Knudsen et al., 2003).

The second highest average trophic position among the three fish species was revealed in perch, which also exhibited the lowest individual range by 2 trophic positions (Figure 6). No significant effects on $\delta^{15}\text{N}$ signatures (trophic position) among the measured variables were detected, which can mirror a small variation in diet among the perch. Mean and median length in perch were close to 200mm (Table 1), a length where perch usually exhibits ontogenetic dietary shifts from benthivore dominated to piscivore dominated diet. However, dietary shifts and feeding by perch are depended on available food resources and competition, thus can vary between and within lakes (Borgstrøm & Hansen, 1987; Borgstrøm & Hansen, 2000; Mittelbach & Persson, 1998; Persson, 1983; Pethon, 2005). Perch in this study were found to feed on an average trophic position 0.8 below Arctic charr, but 0.2 over whitefish. Average trophic position in perch can reflect a zoobenthos dominated diet compared with Arctic charr being piscivorous and whitefish being planktivorous and benthivorous. A zoobenthos dominated dietary in perch were also supported by the almost dominating parasite abundance and prevalence of

acanthocephalan (79 %; Table 2), which transmits by amphipods, isopods, ostracods in addition to some transmission by fish (Nickol, 2006).

Even if a narrow range in feeding were revealed in perch, it exhibited highest individual range of habitat use ($\delta^{13}\text{C}$) among the three fish species (Table 1). Perch used habitats from the extreme littoral to the pelagic, with average $\delta^{13}\text{C}$ signature deriving from the littorals. A significant relation in length to $\delta^{13}\text{C}$ signatures were revealed in perch, indicating larger fish being more pelagic, and smaller individuals being littoral (Table 10; Figure 9). Sandlund et al. (2013) reports and discuss that the upper parts of the pelagic habitats as profitable habitats for small zooplanktivore individuals, where large perch also were observed. On the other hand, Svanbäck and Eklöv (2002) reported that large perch were feeding on both zooplankton and fish in the pelagic, while littoral perch were mainly feeding on zoobenthos. Further, Olk et al. (2020) reported that oldest, largest perch to exhibit highest abundance of copepod transmitted parasites in Lake Norsjø. This indicates that large and old pelagic perch were feeding on zooplankton in Lake Norsjø, hence got infected by copepod transmitted parasites. Furthermore, the littoral perch were probably mainly feeding on zoobenthos, thus got infected by of acanthocephala. However, habitat use and feeding by perch seems to be complex to study and is determined by multiple factors such as vegetation in the littoral zone, size classes of perch, prey-predator interactions with other species and even the morphology of the perch (Bean & Winfield, 1995; Diehl, 1993; Eklöv, 1997; Hjelm et al., 2000).

It is worth to mention that the baseline correction with primary consumers for the stable isotope analyses were not included in this study. Vander Zanden and Rasmussen (1999) reports $\delta^{15}\text{N}$ signatures in primary consumers in deep profundal and extreme littoral habitats to differ, with lowest signatures in the littorals. Further, Lydersen and Moreno (2016) reported similar results in trophic position and habitat use among Arctic charr, whitefish and perch from Lake Norsjø with base line correction by primary consumers included. After all, the results in this present study are likely giving a correct picture of relative trophic position between the three investigated fish species.

5. Conclusion

Arctic charr, whitefish and perch from Lake Norsjø, 2018 exhibited a significant difference in trophic position, habitat use and abundance of macro parasites. Arctic charr exhibited a profundal habitat use and a high trophic position. Whitefish had a wide range in both trophic position and habitat use, indicating a polymorphism within the lake. Perch had a narrow range of trophic position and used habitats from the extreme littoral to the pelagic.

The highest prevalence, abundance and diversity of parasites were detected in Arctic charr. This were linked to the high trophic position and high dietary breadth revealed in Arctic charr, despite narrow use of habitats. Whitefish had the lowest total prevalence, but second highest total abundance of parasites by the three fish species, in addition to second highest diversity of parasites. Whitefish likely had a segregation in parasite fauna related to difference in feeding between what seems to be a littoral benthivore and a more pelagic zooplanktivore morph. Perch had the lowest abundance of parasites and lowest diversity of parasites. Further, perch exhibited higher trophic position and had a higher total prevalence of macro parasites than whitefish. The parasite fauna in perch were almost dominated by acanthocephala, which indicates a zoobenthos and fish dominating diet. In addition, some zooplankton feeding by larger pelagic perch were detected.

By this, large individuals with high dietary breadth on high trophic position seems to be the fish that is most exposed to macro parasites in Lake Norsjø. In addition, trophic position and feeding habitat seem to be important for the diet by the fish, which to a certain degree determine what parasites they get infected by. For further studies, a frequently sampling through the whole year to detect seasonal variation would be preferable. Additionally, investigation of stomach content to relate the parasites to in situ feeding to even get a better picture of omnivory and host-parasite linkages.

6. References

- Amundsen, P.-A. (1994). Piscivory and cannibalism in Arctic charr. *Journal of Fish Biology*, 45, 181-189.
- Amundsen, P.-A., Bøhn, T., Popova, O. A., Staldivik, F. J., Reshetnikov, Y. S., Kashulin, N. A., & Lukin, A. A. (2003). Ontogenetic niche shifts and resource partitioning in a subarctic piscivore fish guild. *Hydrobiologia*, 497(1-3), 109-119.
- Amundsen, P.-A., Knudsen, R., Klemetsen, A., & Kristoffersen, R. (2004). Resource competition and interactive segregation between sympatric whitefish morphs. *Annales Zoologici Fennici* (pp. 301-307).
- Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *The Journal of Wildlife Management*, 74(6), 1175-1178.
- Barni, M. F. S., Ondarza, P. M., Gonzalez, M., Da Cuña, R., Meijide, F., Grosman, F., . . . Miglioranza, K. S. (2016). Persistent organic pollutants (POPs) in fish with different feeding habits inhabiting a shallow lake ecosystem. *Science of the Total Environment*, 550, 900-909.
- Barton, K. (2020). Package "MuMin". 1.43.17, 75. Retrieved from <https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf>.
- Bean, C., & Winfield, I. (1995). Habitat use and activity patterns of roach (*Rutilus rutilus* (L.)), rudd (*Scardinius erythrophthalmus* (L.)), perch (*Perca fluviatilis* L.) and pike (*Esox lucius* L.) in the laboratory: the role of predation threat and structural complexity. *Ecology of Freshwater Fish*, 4(1), 37-46.
- Bell, G., & Burt, A. (1991). The comparative biology of parasite species diversity: internal helminths of freshwater fish. *The Journal of Animal Ecology*, 1047-1064.
- Borgstrøm, R., & Hansen, L. P. (1987). Fisk i ferskvann: Økologi og ressursforvaltning. (Oslo): *Landbruksforlaget*.
- Borgstrøm, R., & Hansen, L. P. (2000). Fisk i ferskvann : et samspill mellom bestander, miljø og forvaltning (2. utg. ed.). Oslo: *Landbruksforlaget*.
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., . . . Bolker, B. M. (2017). Modeling zero-inflated count data with glmmTMB. *BioRxiv*, 132753.

- Bush, A. O., Lafferty, K. D., Lotz, J. M., & Shostak, A. W. (1997). Parasitology meets ecology on its own terms: Margolis et al. revisited. *The Journal of parasitology*, 575-583.
- DeNiro, M. J., & Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et cosmochimica acta*, 42(5), 495-506.
- Diehl, S. (1993). Effects of habitat structure on resource availability, diet and growth of benthivorous perch, *Perca fluviatilis*. *Oikos*, 403-414.
- Dolven, S. I. (2020). Macroparasite investigations of European perch (*Perca fluviatilis*) and European whitefish (*Coregonus lavaretus*) in Lake Norsjø, South-Eastern Norway. (*Master's thesis, University of Southeastern Norway*).
- Eklöv, P. (1997). Effects of habitat complexity and prey abundance on the spatial and temporal distributions of perch (*Perca fluviatilis*) and pike (*Esox lucius*). *Canadian journal of fisheries and aquatic sciences*, 54(7), 1520-1531.
- 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(4), 558-568.
- Fry, B., & Sherr, E. B. (1989). $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. In *Stable isotopes in ecological research* (pp. 196-229): Springer.
- Gröning, M. (2004). International stable isotope reference materials. In *Handbook of stable isotope analytical techniques* (pp. 874-906): Elsevier.
- Halvorsen, O., & Andersen, K. (1984). The ecological interaction between arctic charr, *Salvelinus alpinus* (L.), and the plerocercoid stage of *Diphyllbothrium ditremum*. *Journal of Fish Biology*, 25(3), 305-316.
- Hartig, F. (2019). DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. *R package version 0.2, 4*.
- Henriksen, A.-C. (2019). Seasonal and spatial variation in the macroparasite fauna of Arctic charr (*Salvelinus alpinus* L.) in Lake Norsjø, South-Eastern Norway. (*Master's thesis, University of South-Eastern Norway*).

- Henriksen, E. H., Smalås, A., Strøm, J. F., & Knudsen, R. (2019). The association between parasite infection and growth rates in Arctic charr: do fast growing fish have more parasites? *Hydrobiologia*, *840*(1), 261-270.
- Hjelm, J., Persson, L., & Christensen, B. (2000). Growth, morphological variation and ontogenetic niche shifts in perch (*Perca fluviatilis*) in relation to resource availability. *Oecologia*, *122*(2), 190-199.
- Hooker, O., Barry, J., Van Leeuwen, T., Lyle, A., Newton, J., Cunningham, P., & Adams, C. (2016). Morphological, ecological and behavioural differentiation of sympatric profundal and pelagic Arctic charr (*Salvelinus alpinus*) in Loch Dughail Scotland. *Hydrobiologia*, *783*(1), 209-221.
- Hurvich, C. M., & Tsai, C. L. (1993). A corrected Akaike information criterion for vector autoregressive model selection. *Journal of time series analysis*, *14*(3), 271-279.
- Jackson, D. A., Peres-Neto, P. R., & Olden, J. D. (2001). What controls who is where in freshwater fish communities the roles of biotic, abiotic, and spatial factors. *Canadian journal of fisheries and aquatic sciences*, *58*(1), 157-170.
- Jensen, K. W. (1954). Fisk og fiske i Norsjø.
- Jonsson, B., & Jonsson, N. (2001). Polymorphism and speciation in Arctic charr. *Journal of Fish Biology*, *58*(3), 605-638.
- Kahilainen, K. K., Thomas, S., Harrod, C., Hayden, B., & Eloranta, A. (2019). Trophic ecology of piscivorous Arctic charr (*Salvelinus alpinus* (L.)) in subarctic lakes with contrasting food-web structures. *Hydrobiologia*, *840*(1), 227-243.
- Klemetsen, A. (2010). The charr problem revisited: exceptional phenotypic plasticity promotes ecological speciation in postglacial lakes. *Freshwater Reviews*, *3*(1), 49-74.
- Klemetsen, A., Amundsen, P., 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., Jonsson, B., Jonsson, N., O'connell, M., & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish*, *12*(1), 1-59.

- Knudsen, R., Amundsen, P.-A., Nilsen, R., Kristoffersen, R., & Klemetsen, A. (2008). Food borne parasites as indicators of trophic segregation between Arctic charr and brown trout. *Environmental Biology of Fishes*, *83*(1), 107-116.
- Knudsen, R., Amundsen, P. A., & Klemetsen. (2003). Inter - and intra - morph patterns in helminth communities of sympatric whitefish morphs. *Journal of Fish Biology*, *62*(4), 847-859.
- Knudsen, R., Curtis, M. A., & Kristoffersen, R. (2004). Aggregation of helminths: the role of feeding behavior of fish hosts. *Journal of Parasitology*, *90*(1), 1-7.
- Knudsen, R., Siwertsson, A., Adams, C. E., Newton, J., & Amundsen, P. A. (2014). Similar patterns of individual niche use are revealed by different time - integrated trophic tracers (stable isotopes and parasites). *Ecology of Freshwater Fish*, *23*(2), 259-268.
- L'Abée - Lund, J., Langeland, A., & Sægrov, H. (1992). Piscivory by brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.) in Norwegian lakes. *Journal of Fish Biology*, *41*(1), 91-101.
- Lafferty, K. D., Dobson, A. P., & Kuris, A. M. (2006). Parasites dominate food web links. *Proceedings of the National Academy of Sciences*, *103*(30), 11211-11216.
- Locke, S. A., Marcogliese, D. J., & Valtonen, E. T. (2014). Vulnerability and diet breadth predict larval and adult parasite diversity in fish of the Bothnian Bay. *Oecologia*, *174*(1), 253-262.
- Lydersen, E., & Moreno, C. E. (2016). Variations in feeding habitats and mercury levels in fish from Lake Norsjø, Southern Norway. *Vann*, *51*, 381-404.
- Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., . . . Brooks, M. M. (2017). Package 'glmmTMB'. *R Package Version 0.2. 0*.
- Microsoft-Corporation. (2018). Microsoft Excel. Retrieved from <https://office.microsoft.com/excel>
- Mittelbach, G. G., & Persson, L. (1998). The ontogeny of piscivory and its ecological consequences. *Canadian journal of fisheries and aquatic sciences*, *55*(6), 1454-1465.
- Nickol, B. B. (2006). Phylum Acanthocephala In P. T. K. Woo (Ed.), *Fish diseases and disorders, Volume 1: Protozoan and Metazoan infections* (Vol. 1, pp. 800).

- Olk, T. R., Henriksen, A.-C., Dolven, S. I., Haukø, M. L., Lydersen, E., & Mo, T. A. (2020). Factors determining parasite abundance in European perch, *Perca fluviatilis*, European whitefish, *Coregonus lavaretus*, and Arctic charr, *Salvelinus alpinus*, in an oligotrophic lake, southern Norway. *Fauna norvegica*, 40, 109-129.
- Olk, T. R., Karlsson, T., Lydersen, E., & Økelsrud, A. (2016). Seasonal variations in the use of profundal habitat among freshwater fishes in Lake Norsjø, Southern Norway, and subsequent effects on fish mercury concentrations. *Environments*, 3(4), 29.
- Pacala, S., & Dobson, A. (1988). The relation between the number of parasites/host and host age: population dynamic causes and maximum likelihood estimation. *Parasitology*, 96 (1), 197-210.
- Persson, L. (1983). Food consumption and competition between age classes in a perch *Perca fluviatilis* population in a shallow eutrophic lake. *Oikos*, 197-207.
- Pethon, P. (2005). Aschehougs store fiskebok [Aschehougs guide to fishes]. In: Oslo: Aschehoug.
- Pimm, S., & Lawton, J. H. (1978). On feeding on more than one trophic level. *Nature*, 275(5680), 542-544.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & Maintainer, R. (2021). Package 'nlme'. *Linear and nonlinear mixed effects models, version, 3.1-152*(1). Retrieved from <https://cran.r-project.org/web/packages/nlme/nlme.pdf>.
- Polis, G. A., & Strong, D. R. (1996). Food web complexity and community dynamics. *The American Naturalist*, 147(5), 813-846.
- Post, D. M. (2002). Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, 83(3), 703-718.
- Poulin, R. (1995). Phylogeny, Ecology, and the Richness of Parasite Communities in Vertebrates: Ecological Archives M065-001. *Ecological Monographs*, 65(3), 283-302.
- Poulin, R. (1997). Species richness of parasite assemblages: evolution and patterns. *Annual review of Ecology and Systematics*, 28(1), 341-358.

- Poulin, R. (2000). Variation in the intraspecific relationship between fish length and intensity of parasitic infection: biological and statistical causes. *Journal of Fish Biology*, 56(1), 123-137.
- Poulin, R., Curtis, M., & Rau, M. (1992). Effects of *Eubothrium salvelini* (Cestoda) on the behaviour of *Cyclops vernalis* (Copepoda) and its susceptibility to fish predators. *Parasitology*, 105(2), 265-271.
- Poulin, R., & Leung, T. (2011). Body size, trophic level, and the use of fish as transmission routes by parasites. *Oecologia*, 166(3), 731-738.
- Pourang, N. (1995). Heavy metal bioaccumulation in different tissues of two fish species with regards to their feeding habits and trophic levels. *Environmental Monitoring and Assessment*, 35(3), 207-219.
- Præbel, K., Knudsen, R., Siwertsson, A., Karhunen, M., Kahilainen, K. K., Ovaskainen, O., . . . Amundsen, P. A. (2013). Ecological speciation in postglacial European whitefish: rapid adaptive radiations into the littoral, pelagic, and profundal lake habitats. *Ecology and evolution*, 3(15), 4970-4986.
- R-Core-Team. (2019). R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Romanuk, T. N., Hayward, A., & Hutchings, J. A. (2011). Trophic level scales positively with body size in fishes. *Global Ecology and Biogeography*, 20(2), 231-240.
- Sandlund, O. T., Eloranta, A. P., Borgstrøm, R., Hesthagen, T., Johnsen, S. I., Museth, J., & Rognerud, S. (2016). The trophic niche of Arctic charr in large southern Scandinavian lakes is determined by fish community and lake morphometry. *Hydrobiologia*, 783(1), 117-130.
- Sandlund, O. T., Haugerud, E., Rognerud, S., & Borgstrøm, R. (2013). Arctic charr (*Salvelinus alpinus*) squeezed in a complex fish community dominated by perch (*Perca fluviatilis*). *Fauna norvegica*, 33, 1-11.
- Sandlund, O. T., Museth, J., Næsje, T. F., Rognerud, S., Saksgård, R., Hesthagen, T., & Borgstrøm, R. (2010). Habitat use and diet of sympatric Arctic charr (*Salvelinus alpinus*) and whitefish (*Coregonus lavaretus*) in five lakes in southern Norway: not only interspecific population dominance? *Hydrobiologia*, 650(1), 27-41.

- Schluter, D. (1996). Ecological speciation in postglacial fishes. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 351(1341), 807-814.
- Skoglund, S., Siwertsson, A., Amundsen, P. A., & Knudsen, R. (2015). Morphological divergence between three Arctic charr morphs—the significance of the deep - water environment. *Ecology and evolution*, 5(15), 3114-3129.
- Solheim, A. L., Schartau, A. K., Bongard, T., Bækkelie, K. A. E., Edvardsen, H., Jensen, T., . . . Sandlund, O. T. (2016). ØKOSTOR: Økosystemovervåking av store innsjøer 2015. Utprøving av metodikk for overvåking og klassifisering av økologisk tilstand iht vannforskriften. *NIVA-rapport*.
- Svanbäck, R., & Eklöv, P. (2002). Effects of habitat and food resources on morphology and ontogenetic growth trajectories in perch. *Oecologia*, 131(1), 61-70.
- Svenning, M. A., & Borgstrøm, R. (2005). Cannibalism in Arctic charr: do all individuals have the same propensity to be cannibals? *Journal of Fish Biology*, 66(4), 957-965.
- Thompson, R. M., Dunne, J. A., & Woodward, G. (2012). Freshwater food webs: towards a more fundamental understanding of biodiversity and community dynamics. *Freshwater Biology*, 57(7), 1329-1341.
- Timi, J., Rossin, M., Alarcos, A., Braicovich, P., Cantatore, D., & Lanfranchi, A. (2011). Fish trophic level and the similarity of non-specific larval parasite assemblages. *International journal for parasitology*, 41(3-4), 309-316.
- Vadas, R. L. (1990). The importance of omnivory and predator regulation of prey in freshwater fish assemblages of North America. *Environmental Biology of Fishes*, 27(4), 285-302.
- Valtonen, E., Marcogliese, D. J., & Julkunen, M. (2010). Vertebrate diets derived from trophically transmitted fish parasites in the Bothnian Bay. *Oecologia*, 162(1), 139.
- Vander Zanden, M. J., & Rasmussen, J. B. (1999). Primary consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and the trophic position of aquatic consumers. *Ecology*, 1395-1404.
- Vann-Nett. (2020). Norsjø. Retrieved from <https://www.vann-nett.no/portal/#/waterbody/016-6-L>
- Wickham, H. (2016). ggplot2: elegant graphics for data analysis: *springer*.

Woo, P. T., Leatherland, J. F., & Bruno, D. W. (2006). *Fish diseases and disorders* (Vol. 3): CABI.

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*: Springer Science & Business Media.

7. Appendix

Appendix1

Seasonal and location distribution of selected Arctic charr, whitefish and perch used in this present study. The samples are randomly selected of a total catch of 173 Arctic charr, 101 whitefish and 258 perch collected over three seasons in three location in Lake Norsjø in 2018.

	Location			Season			Total Sample
	North	Mid	South	Spring	Summer	Fall	
Arctic charr	39	36	0	20	25	30	75
Whitefish	33	10	7	21	19	10	50
Perch	22	28	25	28	26	21	75

Appendix 2

Model selection tables after simplifying the global models using the dredge function in R. The global models were GLMMs for the whole data set (all data), Arctic charr, whitefish and perch data with total amount of parasites as response variable, the selection table only include models with $\Delta AIC < 2$ and is ranked with the best model on top. The top model ($\Delta AIC = 0$) are the models reported in the result chapter in the study.

Data: All data

Model nr	AIC	ΔAIC	Weight	Included explanatory variables
96	1288.9	0.00	0.308	Age, Season, Sex, Species, $\delta^{13}C$, Weight
92	1289.1	0.22	0.276	Age, Season, Species, $\delta^{13}C$, Weight
94	1290.2	1.32	0.159	Age, Sex, Species, $\delta^{13}C$, Weight
32	1290.5	1.66	0.134	Age, Season, Sex, Species, $\delta^{13}C$
30	1290.7	1.85	0.122	Age, Sex, Species, $\delta^{13}C$

Data: Arctic charr data

Model nr	AIC	ΔAIC	Weight	Included explanatory variables
34	612.7	0.00	0.424	Age, Length
38	614.1	1.35	0.216	Age, Sex, Length
50	614.3	1.58	0.192	Age, $\delta^{15}N$, Length
42	614.6	1.85	0.168	Age, $\delta^{13}C$, Length

Data: Whitefish data

Model nr	AIC	ΔAIC	Weight	Included explanatory variables
40	233.0	0.00	0.140	Age, Season, Sex, Length
36	233.1	0.09	0.134	Age, Season, Length
32	233.5	0.43	0.113	Age, Season, Sex, $\delta^{13}C$, $\delta^{15}N$
56	234.2	1.18	0.077	Age, Season, Sex, $\delta^{15}N$, Length
104	234.3	1.29	0.074	Age, Season, Sex, Length, Weight
12	234.4	1.34	0.072	Age, Season, $\delta^{13}C$
16	234.7	1.62	0.062	Age, Season, Sex, $\delta^{13}C$
30	234.8	1.81	0.057	Age, Sex, $\delta^{13}C$, $\delta^{15}N$
34	234.8	1.81	0.057	Age, Length
68	234.9	1.91	0.054	Age, Season, Weight
101	234.9	1.91	0.054	Sex, Length, Weight
102	234.9	1.91	0.054	Age, Sex, Length, Weight
72	235.0	1.94	0.053	Age, Season, Sex, Weight

Data: Perch data

Model nr	AIC	ΔAIC	Weight	Included explanatory variables
99	389.3	0.00	0.226	Season, Length, Weight
35	389.7	0.47	0.178	Season, Length
51	390.0	0.71	0.159	Season, $\delta^{15}N$, Length
115	390.3	1.06	0.133	Season, $\delta^{15}N$, Length, Weight
100	390.3	1.08	0.132	Age, Season, Length, Weight
4	391.2	1.89	0.088	Age, Season
103	391.2	1.95	0.085	Season, Sex, Length

Appendix 3-10

GLS model selection tables for the model for the whole data set (3 & 4) and each species (5-10). The model selection is done with ANOVA test and AIC value-ranking. Only models with lowest AIC are reported in the result chapter in the study.

3 All data with $\delta^{15}\text{N}\sim 1$ as null model			
Variable	AIC	Anova p-value	Rank
Species	818.62	<0.001	1
Age	849.26	NA	2
Location	901.98	<0.001	3
Weight	903.49	<0.001	4
Length	904.89	0.001	5
* $\delta^{13}\text{C}$	911.72	0.061	6
*Sex	913.19	0.154	7
Null model ($\delta^{15}\text{N}$)	913.25	NA	8
Season	914.41	0.245	9

*The models with $\delta^{13}\text{C}$ and Sex as explanatory variables had lower AIC than the null model, but were not significant in the ANOVA test

4 All data with $\delta^{13}\text{C}\sim 1$ as null model			
Variable	AIC	Anova p-value	Rank
Species	853.64	<0.001	1
Location	962.78	<0.001	2
Age	962.12	NA	4
Length	975.06	<0.001	3
*Weight	988.28	0.055	5
* $\delta^{15}\text{N}$	988.46	0.613	6
Null model ($\delta^{13}\text{C}$)	989.96	NA	7
Sex	989.99	0.161	8
Season	991.53	0.297	9

*The models for $\delta^{15}\text{N}$ and Weight as explanatory variables had lower AIC than the null model, but were not significant in the ANOVA test

5 Arctic charr data with $\delta^{15}\text{N}\sim 1$ as null model			
Variable	AIC	p-value	Rank
Age	299.60	NA	1
<i>Null model ($\delta^{15}\text{N}$)</i>	307.44	NA	2
$\delta^{13}\text{C}$	306.16	0.070	3
Length	307.36	0.149	4
Weight	307.49	0.163	5
Sex	309.04	0.527	6
Location	309.42	0.908	7
Season	311.00	0.804	8

6 Arctic charr with $\delta^{13}\text{C}\sim 1$ as null model			
Variable	AIC	Anova p-value	Rank
*Age	224.34	NA	1
* $\delta^{15}\text{N}$	226.44	0.070	2
<i>Null model ($\delta^{13}\text{C}$)</i>	227.73	NA	3
Location	228.56	0.280	4
Length	228.57	0.282	5
Weight	229.59	0.712	6
Sex	229.61	0.724	7
Season	230.64	0.580	8

*The models with Age and $\delta^{15}\text{N}$ as explanatory variable had lower AIC than the null model. The $\delta^{15}\text{N}$ model were not significant, and the model with Age did not show significant results

7 Whitefish with $\delta^{15}\text{N}\sim 1$ as null model			
Variable	AIC	Anova p-value	Rank
$\delta^{13}\text{C}$	216.73	<0.001	1
Weight	217.95	<0.001	2
Length	220.15	0.002	3
Age	220.65	0.003	4
Sex	221.29	0.004	5
<i>Null model ($\delta^{15}\text{N}$)</i>	227.51	NA	6
Location	229.25	0.323	7
Season	230.06	0.485	8

8 Whitefish with $\delta^{13}\text{C}\sim 1$ as response variable			
Variable	AIC	Anova p-value	Rank
Weight	181.76	<0.001	1
Length	189.80	<0.001	2
$\delta^{15}\text{N}$	216.81	<0.001	3
Season	220.07	0.003	4
Age	222.25	0.007	5
Sex	223.49	0.014	6
<i>Null model ($\delta^{13}\text{C}$)</i>	227.59	NA	7
Location	231.06	0.766	8

9 Perch with $\delta^{15}\text{N}\sim 1$ as null model			
Variable	AIC	Anova p-value	Rank
*Sex	276.48	0.107	1
Null model $\delta^{15}\text{N}$	277.07	NA	2
Location	277.47	0.165	3
Season	278.20	0.238	4
Age	278.32	0.382	5
Length	278.58	0.484	6
$\delta^{13}\text{C}$	279.00	0.785	7
Weight	279.06	0.897	8

*The model with sex as explanatory variable had lower AIC than the null model but were not significant in the ANOVA test

10 Perch with $\delta^{13}\text{C}\sim 1$ as null model			
Variable	AIC	Anova p-value	Rank
Length	347.52	0.007	1
Weight	348.15	0.009	2
*Location	351.89	0.081	3
*Age	352.17	0.098	4
Null model ($\delta^{13}\text{C}$)	352.91	NA	5
$\delta^{15}\text{N}$	354.80	0.785	6
Sex	354.85	0.791	7
Season	355.37	0.467	8

*Model with Location and Age as explanatory variables had lower AIC than the null model, but were not significant in the ANOVA test.

Appendix 11

Length (dashed blue lines) and weight (solid red lines) in relation to age in Arctic charr ($n=75$), whitefish ($n=50$) and perch ($n=75$) caught in Lake Norsjø, 2018. Grey areas: 95% confidence intervals

