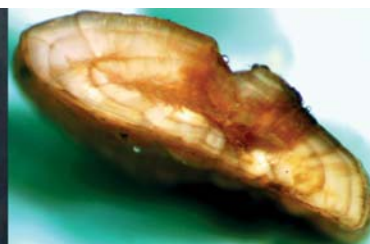
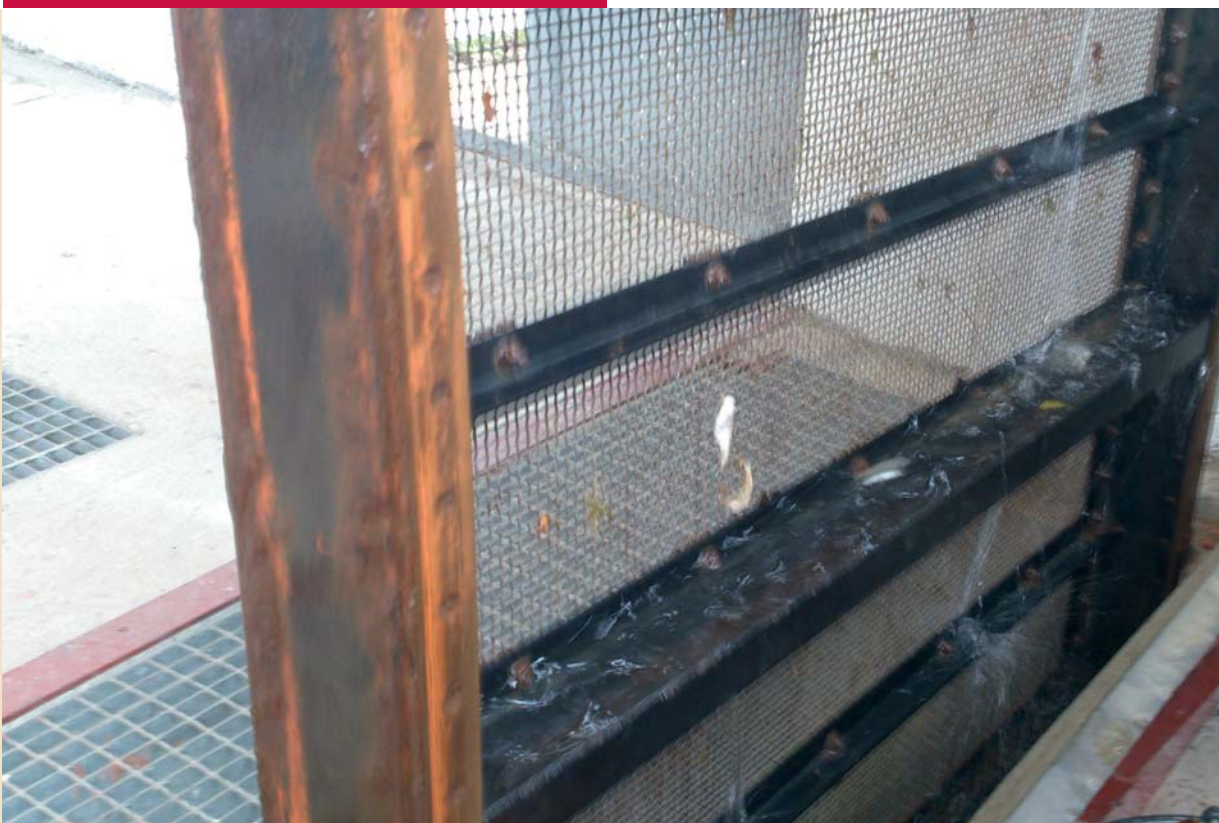


Master Thesis

Tom Robin Olk & Tobias Karlsson

Seasonal variations in the use
of profundal habitat among
freshwater fishes in Lake Norsjø,
southern Norway, and subsequent
effects on fish mercury concentrations



Telemark University College

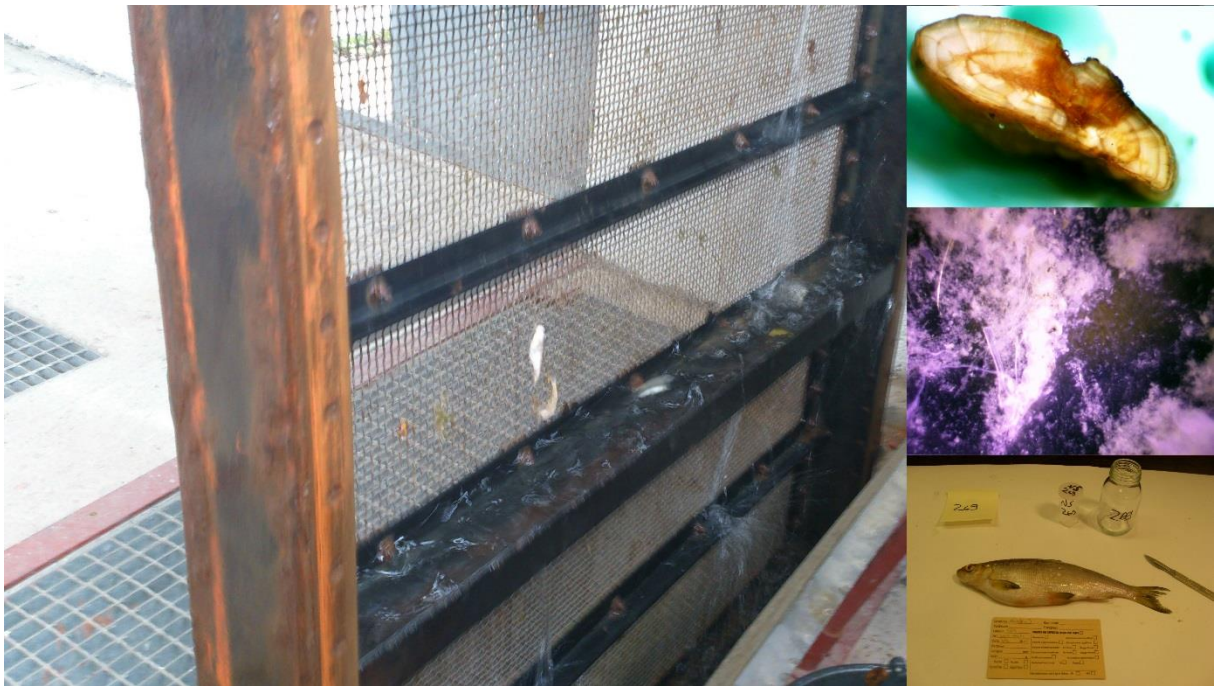
Faculty of Arts and Sciences

Master's Thesis in Environmental and Health Studies

Tom Robin Olk & Tobias Karlsson

Seasonal variations in the use of profundal habitat among freshwater fishes in Lake Norsjø, southern Norway, and subsequent effects on fish mercury concentrations.

2015



Telemark University College
Faculty of Art and Sciences
Department of Environmental and Health Studies
Hallvard Eikas plass
3800 Bø i Telemark

<http://www.hit.no>

© 2015 Tom Robin Olk & Tobias Karlsson

Seasonal variations in the use of profundal habitat among freshwater fishes in Lake Norsjø, southern Norway, and subsequent effects on fish mercury concentrations.

by

Tom Robin Olk and Tobias Karlsson

ABSTRACT

This study is based on monthly sampling of fish from an industrial water intake, located at the bottom of Lake Norsjø, at a depth of 50 m, during one year (2014). By this sampling strategy, we have obtained unique information about the seasonal use of the profundal habitat among > 15 fish species present in the lake. However, besides a very few individuals of perch (*Perca fluviatilis*, n = 4) and one individual of Northern pike (*Esox lucius*) and brown trout (*Salmo trutta* L.), respectively, only Arctic char (*Salvelinus alpinus*), European smelt (*Osmerus eperlanus*) and whitefish (*Coregonus lavaretus*) were caught. While A. char was present in the profundal habitat all year, E. smelt were only absent in June, and whitefish was primarily present during the winter, December-March. The main reasons for searching to this poor, cold and dark habitat, are primarily predator avoidance, interspecific competition, hatching and subsequent feeding on row. The various use of the profundal habitat among fish species, have primarily been linked to age, length and weight, stomach analyses and stable isotope signatures, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, in fish muscle. By also comparing the number of gill rakers (NGR) in whitefish caught by gill nets in a nearby littoral area, we revealed two morphs of whitefish, a profundal morph (NGR = 26.5 ± 0.4) and a littoral morph (NGR = 32.0 ± 0.6). The varying degree of habitat use (profundal, pelagic, littoral) among fish species and morphs, has further been shown to have implication for the mercury (Hg) concentration in fish, as baseline Hg and fish growth differ between different lake habitats. Accordingly, these factors, besides the more classical factors as trophic position and age, are essential for Hg concentration in fish.

Keywords: Freshwater fish, profundal habitat, Hg, Tot-Hg, Stable isotopes, Biomagnification, *Salvelinus alpinus*, *Coregonus lavaretus*, *Osmerus eperlanus*

INTRODUCTION

In the environment, mercury (Hg) is a widespread contaminant of concern. It is a pollutant with long-range transport from source regions to remote areas in the world (AMAP, 2011, Ranneklev et al., 2009). Most Hg in the atmosphere in Scandinavia has its origin in industrial activity in central Europe (Ranneklev et al., 2009). There are both natural and anthropogenic sources of Hg. The oceans are considered the greatest natural source of Hg to the atmosphere. Ocean waters are usually supersaturated with Hg^0 , and thus continuously emit this gaseous elemental form of Hg into the atmosphere (Morel et al., 1998). Other natural sources are biomass combustion, such as forest fires, and volcanoes (Mason and Sheu, 2002, Pirrone et al., 2010). Since the beginning industrial age, Hg concentrations in the surface layers of the ocean and in the atmosphere have tripled (Mason et al., 1994, Lamborg et al., 2002, Mason et al., 2012). The main anthropogenic source of Hg is fossil fuel combustion, for instance of coal, which stands for 35-45% of the total anthropogenic Hg emissions (Pacyna et al., 2010, Pirrone et al., 2010). Other anthropogenic sources are mining activity and chemical processes, for example the production of batteries.

Approximately 95% of total Hg in the atmosphere is in the elemental state Hg^0 (Fitzgerald and Lamborg, 2004). It oxidises to cationic Hg(II) , a form of Hg which easily bonds to aerosols and particles, and is subsequently deposited on land and water by wet and dry deposition (Mason and Sheu, 2002). Reemission to the atmosphere occurs by reduction from Hg(II) to Hg^0 by biota (Barkay et al., 2003) or photochemical processes (Amyot et al., 1994).

Hg compounds can be toxic in aquatic environments. The toxicity of Hg depends on the chemical form (Clarkson, 1998). Particularly methyl-Hg (MeHg), which is produced from inorganic forms of Hg in aquatic ecosystems, is a toxic Hg species. Methylation happens primarily in aquatic environments, especially under anaerobic conditions (Gilmour and Riedel, 1995, Hollweg et al., 2010, Macalady et al., 2000, Lehnher et al., 2012). In freshwater, there are different sources of MeHg, like anoxic hypolimnetic lake water (Eckley et al., 2005, Eckley and Hintelmann, 2006), bottom sediments (Gilmour and Riedel, 1995), periphyton biofilms (Gilmour and Riedel, 1995, Desrosiers et al., 2006), and moss mats (St Louis et al., 2004, Yu et al., 2010). A result of the transfer of MeHg through the food web is, that Hg bioaccumulates (increase of contaminant compared to environment) and biomagnifies in the food web. As a

result, predators at the top of an aquatic food chain can have Hg concentration millions of times higher than observed in the surrounding waters (Kidd et al., 2012). This can lead to fish and fish-eating wildlife reaching toxic concentrations of Hg (Watras et al., 1998). MeHg is a potent neurotoxin (WHO, 1989, WHO, 1990, Boening, 2000), and symptoms of poisoning in humans can be numbness in hands and feet, loss of fine motor skills, memory loss, blindness (Takeuchi et al., 1962), speech disorder, loss of muscle control and negative effects on the cardiovascular system and immune system (Mergler et al., 2007).

The greatest increase of MeHg concentration is not biomagnification between trophic levels. Instead, it is from abiotic materials, such as water and sediments, to the base of the food web (Fitzgerald et al., 2007, Pickhardt and Fisher, 2007). At higher trophic levels, most of the Hg is MeHg (Morel et al., 1998), because it accumulates at higher rates (Lavoie, 2013). The proportion of MeHg/TotHg increase from about 10 % in the water, 15 % in phytoplankton, 30 % in zooplankton and 95 % in fish (Watras and Bloom, 1992). To confirm biomagnification from one trophic level to another, a correlation between the stable isotope ratio of nitrogen ($\delta^{15}\text{N}$) and Hg is used (Cabana and Rasmussen, 1994, Atwell et al., 1998). There are ecological factors that control the Hg concentrations in the biota, such as food chain length, habitat selection, foraging behaviour (Loseto et al., 2008, Swanson and Kidd, 2010, St Louis et al., 2011). Cold temperatures, low productivity and acidic condition can indirectly increase Hg by reducing growth rates (Greenfield et al., 2001, Essington and Houser, 2003).

Stable isotope ratio analyses of carbon $\text{C}^{13}/\text{C}^{12}$ and nitrogen $\text{N}^{15}/\text{N}^{14}$ is a highly valuable tool to trace the energy flow ($\delta^{13}\text{C}$) and trophic position ($\delta^{15}\text{N}$) in food webs (Peterson and Fry, 1987, Cabana and Rasmussen, 1996, Post, 2002). The different stable isotopes have differences in the ability to form chemical bonds, which leads to different isotopic values. The lighter isotopes react more readily, but the heavier form stronger bonds (Hoefs, 2013). The ratio of isotope enrichment change slightly about 0.4 ‰ for $\delta^{13}\text{C}$ between trophic levels, and it is used to characterise dietary carbon sources derived from primary producers (Post, 2002). For $\delta^{15}\text{N}$, an enrichment of 3.4 ‰ per trophic level is estimated (Minagawa and Wada, 1984, Post, 2002). Various other effects determine the Hg concentration in fish as well, for instance feeding habitat. There are studies that show patterns that pelagic feeding fish have higher values of Hg in their tissues than littoral feeding fish at a similar trophic position (Power et al., 2002, Gorski et al., 2003, Stewart et al., 2008), and studies with no variation in Hg at similar

trophic positions (Chumchal and Hambright, 2009). A study of Gorski et al. (2003) shows that there are among-lake variations that reflect habitat use within a species such as northern pike (*Esox Lucius*) that are on the same trophic position in the food chain, but rely on different prey in the food web. Pike feeding on fish that had a pelagic-based food had higher values of Hg than pike feeding on fish that had benthic-based food.

This study examines Hg concentration and stable isotope signatures in fish in a bay (Fjærekilen) of Lake Norsjø, which is among the twenty largest lakes in Norway. The collected fish were trapped in an industrial scale water intake tunnel ($\approx 15 \text{ m}^3 \text{ s}^{-1}$) when passing by. Trapped fish were sampled weekly, and our investigations rely on one sample from each month during a one-year period. Arctic char (*Salvelinus alpinus*), European smelt (*Osmerus eperlanus*) and whitefish (*Coregonus lavaretus*) were the most abundant species caught. As the water intake tunnel is located at the bottom of the bay at approximately 50 m depth, this investigation is a unique study of fish species and strains/morphs “seeking out” this hypolimnetic habitat during a year. It was generally hypothesised, that biomagnification along the food chain is pronounced in all species. Horizontal variations in food web structure, such as feeding habitat and prey species, or competition and resource limitation were linked to effects on Hg-concentrations and stable isotope ratios. Additionally, potential seasonal variations were investigated.

MATERIAL AND METHODS

Site description

Lake Norsjø (59.29' N, 9.36' E) is a large (55.24 km²), deep (middle depth = 87 m, maximal depth = 171 m) and oligotrophic lake (Holtan, 1968, Miljødirektoratet, 2015) located in Telemark county in southeast Norway. This study has been performed in Fjærekilen, which is a bay at the southern end of Lake Norsjø. This basin extends parallel to the discharge at Skotfoss (Figure 1).

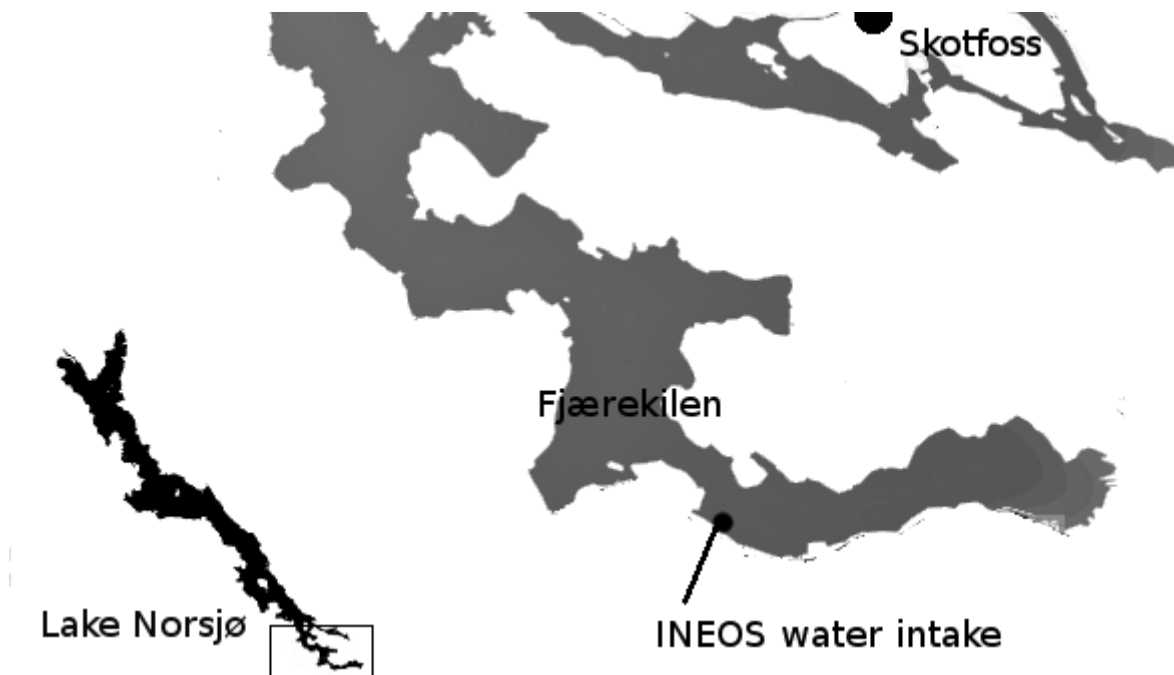


Figure 1. Map of Fjærekilen, the investigated bay in Lake Norsjø.

Sampling

The fish used in this study were acquired at the INEOS (petrochemical company) water intake in Fjærekilen, which is located at a depth \approx 50 m, 60 to 80 m off the shore. The fish were caught continuously at a grate, preventing fish being artificially transferred to the brackish fjord, Frierfjorden, where INEOS is located. Fish was retrieved weekly by INEOS industry workers and our fish was sampled between February 2014 and January 2015 on the following dates: 04.02.2014, 04.03.2014, 29.04.2014, 27.05.2014, 01.07.2014, 19.08.2014, 23.09.2014, 28.10.2014, 02.12.2014 and 13.01.2015. The fish were frozen when collected by INEOS industry workers, and the accumulated catch of each week was stored in plastic bags. Additionally, fresh fish were acquired on the sampling dates named above. All fish were frozen

in plastic bags sorted by sampling date and stored in a freezer ($\leq 20^{\circ}\text{C}$) at Telemark University College until analysed. The littoral whitefish were caught by gill nets (16 – 52 mm mash size) set perpendicular out from to the shore at a depth between 1-5 m on September 9, 2012.

General analysis

The collected fish were sorted, and approximately 20 individuals of each species were analysed each month. Total length of each fish were determined to the closest millimetre in a measuring cone, and weight was determined to the closest gram on a scale model Philips HR2393. The otoliths were removed, and subsequently burned over a propane torch before being sectioned transversally for later age determination under a stereomicroscope at a magnification of 48x. Each fish was opened for inspection of sex and maturity.

Stomach content analysis

Stomach samples were taken from approximately five fish of each species each month. The stomachs were preserved in 70% ethanol in glass bottles prior to analysis. Stomach content was identified under a stereomicroscope at a magnification of 48x to the closest taxa using a taxonomic key (Raastad and Olsen, 1999), and each items occurrence was estimated in volume percent. For littoral whitefish, all available stomach samples were investigated.

Preparation of muscle fillet samples

About 2 g of muscle fillet were removed from the dorsal side of each fish under the dorsal fin. The samples were weighted on a scale type Kern 442-43 at a precision to 0.1 g, before freeze-dried in a Heto Lyolab 3000 freeze-drier for at least 14 hours at a temperature $\leq 30^{\circ}\text{C}$. The drying process was aided by an infrared lamp. Dried samples were weighted on a Sartorius AX124 scale with a precision to 0.0001 g. The dried samples were ground and homogenised using an agate pestle and a mortar.

Stable isotope analysis

Up to 15 fish of each species each month were selected for stable isotope analysis, covering the largest possible variety in age, length and weight. Between 1.0 and 1.4 mg of the selected, freeze-dried samples were weighted on a Sartorius AX124 scale, and stored in tin capsules of the types Elemental Microanalysis D1006 (6 x 4 mm) and Elemental Microanalysis D1008 (8 x 5 mm). The capsules were sent to the Norwegian Institute for Energy Technology (Institutt for

Energiteknikk, IFE) for stable isotope analysis. Results were delivered in the delta (δ) notation, which is measured in per mil (‰) deviation from a standard material, and calculated according to the following formula:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = ([R_{\text{sample}}/R_{\text{standard}}] - 1) * 1000,$$

where R represents the ratio of the heavier isotope ^{13}C or ^{15}N to the lighter ^{12}C or ^{14}N (Vander Zanden and Rasmussen, 1999, Eagles-Smith et al., 2008). As standard material, Pee Dee belemnite limestone is used to calculate $\delta^{13}\text{C}$ (Craig, 1957), and atmospheric nitrogen is used for $\delta^{15}\text{N}$.

Hg Analysis

Freeze-dried dorsal muscle fillet samples were also used for determination of Hg-content in fish. Approximately 20 mg were used for each sample, weighted in on a Sartorius AX124 scale (precision: 0.0001g). Total Hg was analysed by a Lumex Hg-analyser type Pyro-915 (Lumex Instruments, St. Petersburg, FL. USA), and two replicates were analysed for each sample. Measurements were repeated if both replicates deviated with more than 10%. The equipment was calibrated using a standard sample of tuna (European Reference Material, ERM-CE 464), which was used as control after each 20th fish. Hg-content was estimated to be the average of the two replicate samples, and concentrations were transformed to resemble wet weight (ww.) concentrations by the following formula: $[\text{Hg}]_{\text{dry weight}} * \text{dry weight} / \text{ww}$.

This was done, because most nations are using wet weight concentrations of Hg in fish, in their monitoring programs, and consumption advice guidelines.

Gill rakers

The gill rakers of whitefish were counted on the outermost gill ark for each fish. A stereomicroscope of 48x magnification was used to count gill rakers.

Data analysis

Fulton's condition factor (Fulton, 1904, Goede and Barton, 1990, Smolders et al., 2005) was calculated for each fish of the species Arctic char and whitefish using the following formula:

$$K_f = \frac{W * 100}{L^3}$$

where W is the weight of the fish (g), and L is the total length (cm). All Hg-concentrations were logarithmically transformed to match normal distributions and linear relationships with $\delta^{15}\text{N}$. Descriptive statistics were calculated for age, length, weight, K_f (except *E. smelt*), $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and [Hg] for each species using Microsoft Excel (Microsoft, 2013). The relationships between K_f , $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and $\ln[\text{Hg}]$ for each population were tested for correlation using Pearson's product moment or Spearman ranks depending on the distribution of the raw data in the statistical program R (R Core Team, 2014). In addition, length was correlated to $\delta^{13}\text{C}$ to discover ontogenetic habitat shifts. $\ln[\text{Hg}]$ was correlated to age and length. For each pair of variables, which is significantly correlated, a linear regression was calculated using Microsoft Excel (Microsoft, 2013) and R (R Core Team, 2014). Post hoc tests for normal distribution and homoscedasticity were conducted on the residuals. Differences in age, length, weight, condition, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\ln[\text{Hg}]$ and gill raker counts between profundal and littoral whitefish were tested using Welch's two sample t-test or Mann-Whitney-Wilcoxon tests in R (R Core Team, 2014) depending on the fit of the data to a normal distribution. In addition, differences in growth were accounted for by comparing the length of 3-year old whitefish, using a Welch's two sample t-test, and logistic regressions. Growth was also estimated for the other fish species. For all tests a standard significance level of $\alpha = 0.05$ has been used, and near significance was noted at a p-value between 0.05 and 0.10.

The arithmetic mean volume percentage of each diet item was calculated for each population, including all fish with at least one identified stomach content item. Additionally, prey was grouped in primary consumer- and secondary consumer-invertebrates and fish based material. The occurrence of each group has been correlated to fish length using Pearson's product moment or Spearman ranks in R (R Core Team, 2014). The prey taxa have also been grouped in profundal, littoral, pelagic and fish based items. A. char individuals were grouped by total length, above and below 140 mm, and average diet overlap was estimated using Schoener's similarity index (Schoener, 1970), which is calculated using the following formula:

$$D = 100 - 0.5 \sum (|p_i - q_i|),$$

where p is the average volume percent of one type of prey in the first group of fish, and q is the average volume percent of the same item in the other group of fish. Diets are considered to overlap significantly if D exceeds 60 % (Wallace, 1981).

Sampled Fish

Totally, 471 fish were sampled in the water intake at a depth of ≈ 50 m in Fjærekilen, a bay south in Lake Norsjø. The most abundant species A. char ($n = 191$) and E. smelt ($n = 158$) were present in the catch during all seasons, while profundal whitefish ($n = 117$) were mainly caught between December and March (Figure 2). Perch (*Perca fluviatilis*) ($n = 4$) and Northern pike ($n = 1$) were only sporadically present, and accordingly insufficient data was available for further analysis of these two species. In addition littoral whitefish ($n = 20$), caught by gillnets in September 2012, has been used for comparison of littoral and profundal whitefish.

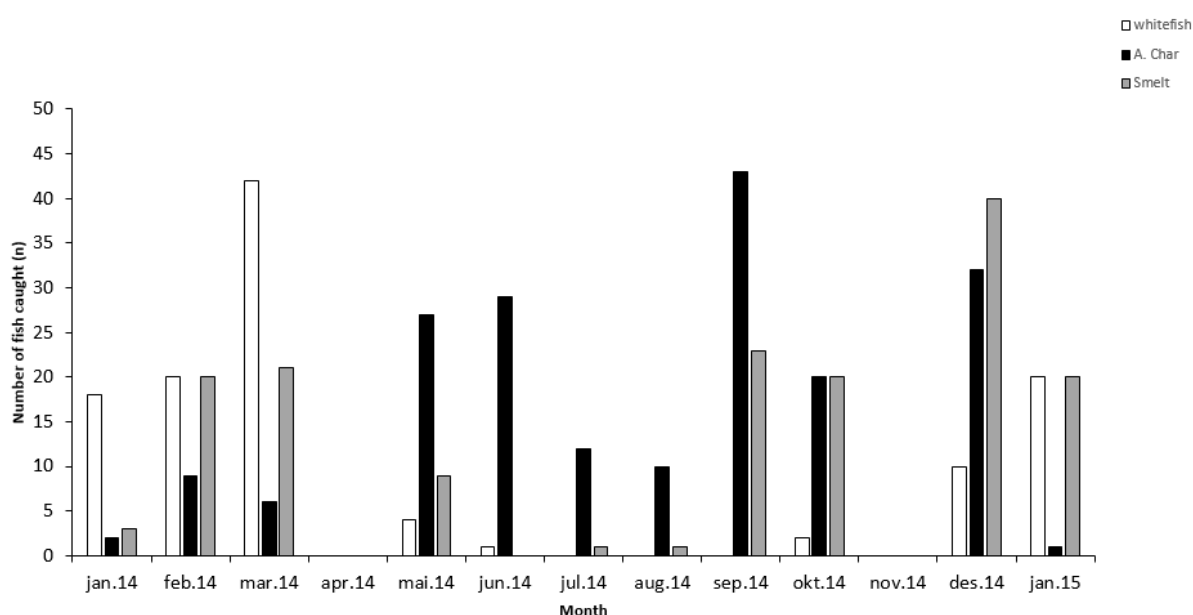


Figure 2. Seasonal variations in the number of profundal whitefish, A. char and E. smelt sampled from the water intake at 50 m depth in Southern Lake Norsjø.

RESULTS

Age and size distribution

A. char ($n = 191$) varied in age from 2 to 26 years (Table 1), with an average age of 8 ± 4 years ($n = 185$). The individuals' length varied from 71 to 283 mm, with an average of 132 ± 45 mm ($n = 191$), while average weight was 28 ± 38 g ($n = 190$), varying from 3 g to 211 g. Average condition factor (K_f) was 0.86 ± 0.32 , with large individual variations from 0.48 to 1.80.

Table 1. Descriptive statistics for the variables age, length, weight, K_f , $\delta^{13}C$, $\delta^{15}N$ and Hg in Arctic char, European smelt, profundal whitefish (W.fish P) and littoral whitefish (W.fish L).

Variable	Species	n	Median	Mean \pm SD	Min	Max	Max-Min
Age (yr)	A. char	185	7	8 ± 4	2	26	24
	E. smelt	156	2	2 ± 1	1	8	7
	W.fish P	117	4	5 ± 3	1	17	16
	W.fish L	20	3.5	4 ± 3	1	13	12
Length (mm)	A. char	191	118	132 ± 45	71	283	212
	E. smelt	158	98	99 ± 6	83	115	32
	W.fish P	117	252	247 ± 33	115	310	195
	W.fish L	20	276	286 ± 55	219	470	251
Weight (g)	A. char	190	14	28 ± 38	3	211	208
	E. smelt	158	4	4 ± 1	1	13	12
	W.fish P	117	131	128 ± 43	10	265	255
	W.fish L	20	176	239 ± 211	96	1065	969
$\delta^{15}N$ (‰)	A. char	90	12.05	11.75 ± 1.20	6.86	13.51	6.65
	E. smelt	103	10.17	10.39 ± 0.97	7.64	13.6	5.96
	W.fish P	76	8.35	8.60 ± 1.25	6.39	12.63	6.24
	W.fish L	20	8.56	8.63 ± 0.77	7.54	11.14	3.6
$\delta^{13}C$ (‰)	A. char	90	-29.20	-29.69 ± 1.45	-34.74	-27.79	6.95
	E. smelt	103	-29.07	-29.13 ± 0.55	-32.38	-27.6	4.78
	W.fish P	76	-29.14	-29.12 ± 0.49	-30.21	-27.61	2.60
	W.fish L	20	-26.34	-26.19 ± 2.04	-28.88	-23.07	5.81
Hg (ppm ww)	A. char	180	0.14	0.22 ± 0.22	0.06	1.5	1.44
	E. smelt	156	0.19	0.21 ± 0.08	0.06	0.54	0.48
	W.fish P	117	0.19	0.21 ± 0.09	0.05	0.49	0.44
	W.fish L	20	0.11	0.12 ± 0.05	0.04	0.28	0.24

E. smelt ($n = 158$) varied in age from 1 to 8 years (Table 1), while the average age was 2 ± 1 years ($n = 156$). The length varied from 83 to 115 mm with an average of 99 ± 6 mm ($n = 158$), while average weight was 4 ± 1 g ranging from 1 to 13 g.

Profundal whitefish ($n = 117$) varied in age from 1 to 17 years, with an average age of 5 ± 3 years (Table 1). Fish length varied from 115 to 310 mm, with average length of 247 ± 33 mm. Average weight was 128 ± 43 g, ranging from 10 to 265 g. The condition factor (K_f) of profundal whitefish ranged from 0.58 to 1.22, with an average K_f of 0.81 ± 0.11 .

Littoral whitefish ($n = 20$) were only caught by gillnets in September. The fish were between 2 and 13 years old, with an average age of 4 ± 3 years (Table 1). Fish length varied from 219 to

470 mm, with an average of 286 ± 55 mm. Average weight was 239 ± 211 g, ranging from 96 to 1065 g. The condition factor (K_f) ranged from 0.71 to 1.09, with an average K_f of 0.88 ± 0.10 .

Use of profundal habitat

A. char were present in the profundal habitat the whole year, but with highest occurrence in September and December (Figure 2). A. char differed seasonally in age (Figure 3), as the oldest fish on average, were caught in January and February. The largest variety in age was present in June where all age groups except the youngest fish (< 4 years) were present. All other months, the majority of the fish caught were between 5 and 10 ten years old.

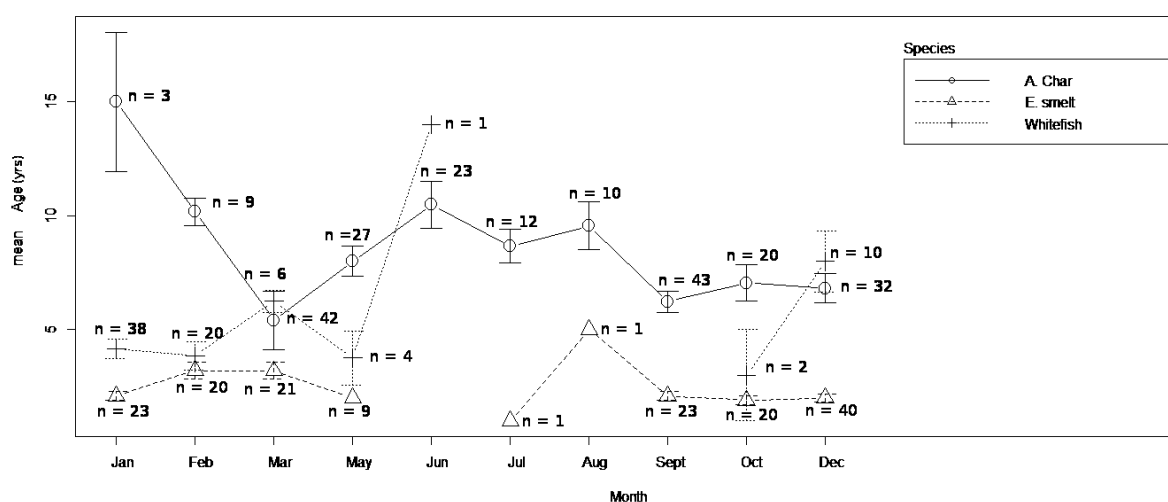


Figure 3. Seasonal variations in age (mean \pm SD) of A. char, E. smelt and profundal whitefish, trapped in the water intake at 50 m depth in Fjærkilen, southern Lake Norsjø.

E. smelt were also present all year, except June, with highest occurrence in December. Their age varied marginally between months (Figure 3), but largest age variations were revealed in February and March, where slightly older fish were caught.

Profundal whitefish were primarily caught between December and March (Figure 2), and highest average age where present in the December catch (Figure 3). This whitefish, caught at 50 m depth, differed significantly from the whitefish caught by gillnets in the littoral zone. Gill raker numbers in profundal whitefish (average: 26.5 ± 0.4) were significantly lower than in littoral whitefish (average: 32.0 ± 0.6), and length, weight and K_f were all significantly lower in the profundal whitefish than in littoral whitefish (Table A3). Length at the age of 3 differed

near significantly between the whitefish populations ($p=0.067$) (Figure 4). Despite so, the Hg concentrations were significantly higher in the profundal population, even though they did not differ significantly regarding $\delta^{15}\text{N}$ signatures. On the other hand, profundal whitefish had significantly more depleted $\delta^{13}\text{C}$ signatures than littoral whitefish.

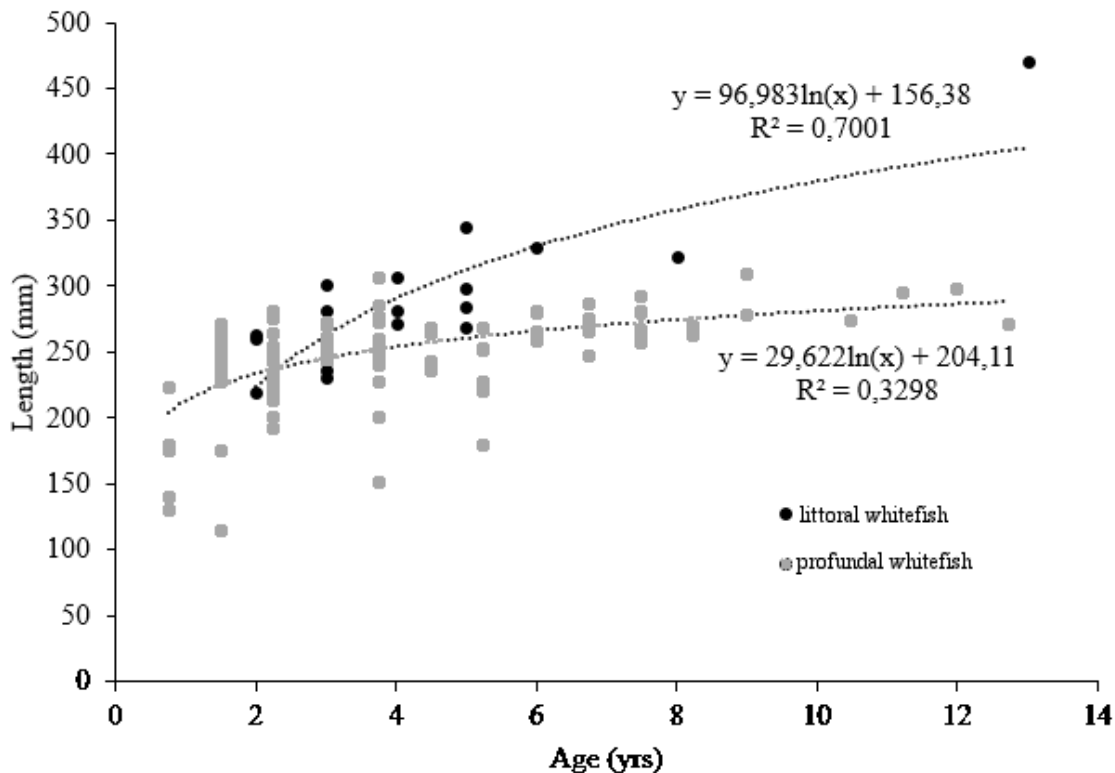


Figure 4. Logistic regressions for growth patterns of littoral and profundal whitefish.

Stomach content –diet

Benthic invertebrates

Chironomidae sp. were found in the stomachs of all species and populations, and contributed to the diet with 43.9, 24.7, 25.9 and 0.8 Vol-% for *A. char* ($n = 41$), *E. smelt* ($n = 31$), profundal ($n = 22$) and littoral ($n = 12$) whitefish, respectively. In *E. smelt*, *Chironomidae sp.* were only found between August and December.

Pisidium sp. were found in *A. char* (2.1 Vol-%), profundal whitefish (15.6 Vol-%) and littoral whitefish (5.4 Vol-%), but not in *E. smelt*. Ostracods were found in *A. char* restricted to the period between August and February (0.8 Vol-%), and they were continuously present in *E.*

smelt (9.0 Vol-%) and profundal whitefish (3.6 Vol-%). *Phryganea grandis* were only found in A. char, exclusively from March to June (5.4 Vol-%).

Caddisflies (*Trichoptera*) were only found in E. smelt (1.9 Vol-%) and littoral whitefish (1.7 Vol-%), while *Asellus aquaticus* was only found in profundal and littoral whitefish, contributing with 1.8 Vol-% and 4.2 Vol-% respectively. Other items, such as insect imagoes (4.2 Vol-%), *Hydracarina sp.* (0.4 Vol-%), *Lymnea sp.* (1.8 Vol-%), *Gyraulus sp.* (12.1 Vol-%), other gastropods (8.3 Vol-%) and remains of vegetation (0.3 Vol-%), were only found in littoral whitefish.

Pelagic invertebrates

Copepods were found in all investigated fish species, and constituted 11.7, 47.7, 8.2 and 0.8 Vol-% in A. char, E. smelt, profundal and littoral whitefish, respectively. In A. char, copepods were a seasonal item, only found from August to February. Cladocerans, i.e. *Daphnia sp.* were only found in E. smelt (5.3 Vol-%).

Fish and other items

Fish occurred in the stomach samples of A. char (19.5 Vol-%), profundal whitefish (21.4 Vol-%) and littoral whitefish (4.2 Vol-%). Regarding profundal whitefish, fish were only found between January and May. Fish roe were seasonally present in all three fish species, primarily in September and February in A. char (5.7 Vol-%), and in December and January in E. smelt (7.7 Vol-%) and profundal whitefish (9.1 Vol-%). In littoral whitefish, which were only sampled in September, 17.9 Vol-% of the stomach content was roe. In profundal whitefish, an ant was found (1.8 Vol-%), while unidentified remains constituted 10.9, 3.7, 12.6 and 37.9 Vol-% in A. char, E. smelt, profundal and littoral whitefish, respectively.

Stomach content in Arctic char below and above 140 mm of length

The largest A. char, individuals > 140 mm (n = 20), consumed less *Chironomidae sp.*, *Pisidium sp.* and copepods, but more roe than smaller individuals, < 140 mm (n = 21). Additionally, the largest individuals consumed fish (\approx 40 Vol-%). The Schoener's similarity index (Schoener, 1970), indicated, no significant overlap in the diets of A. char above and below 140 mm of length (D = 51 %).

Stable isotope signatures and Hg in fish

A. char exhibited average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of $-29.69 \pm 1.45 \text{ ‰}$ and $11.75 \pm 1.20 \text{ ‰}$ ($n = 90$), respectively (Table 1). The individual variations in $\delta^{13}\text{C}$ ranged from -34.74 ‰ to -27.79 ‰ , while the corresponding variations in $\delta^{15}\text{N}$ were from 6.86 ‰ to 13.51 ‰ . The range in $\delta^{15}\text{N}$ by 6.65 ‰ , indicates an individual variation in trophic position by almost 2 trophic levels ($\Delta = 1.96$) within the group of A. char caught, assuming a $\delta^{15}\text{N}$ enrichment of 3.4 ‰ per trophic level (Δ), as estimated by Minagawa and Wada (1984) and Post (2002).

The average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures in E. smelt were $-29.13 \pm 0.55 \text{ ‰}$ and $10.39 \pm 0.97 \text{ ‰}$ ($n = 103$), respectively, with individual variations in $\delta^{13}\text{C}$ from -32.38 to -27.60 ‰ , and from 7.64 ‰ to 13.60 ‰ regarding $\delta^{15}\text{N}$. The range in $\delta^{15}\text{N}$ by 5.96 ‰ , indicates an individual variation in trophic level (Δ) by 1.75Δ within the group of E. smelt caught.

Profundal whitefish had average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of $-29.12 \pm 0.49 \text{ ‰}$ and $8.60 \pm 1.25 \text{ ‰}$ ($n = 76$), respectively. While individual $\delta^{13}\text{C}$ signatures ranged from -30.21 to -27.61 ‰ , the $\delta^{15}\text{N}$ signatures varied from 6.39 to 12.63 ‰ . The range in $\delta^{15}\text{N}$ by 6.24 ‰ , indicates an individual variation in trophic level (Δ) by 1.84Δ for the profundal whitefish caught. Littoral whitefish had average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of $-26.19 \pm 2.04 \text{ ‰}$ and $8.63 \pm 0.77 \text{ ‰}$, ($n = 20$), respectively, with individual variations in $\delta^{13}\text{C}$ from -28.88 to -23.07 ‰ and from 7.54 to 11.14 ‰ regarding $\delta^{15}\text{N}$. The variation in $\delta^{15}\text{N}$ by 3.60 ‰ , indicates variations in trophic position (Δ) by 1.06Δ among the littoral whitefish caught.

Tot-Hg in A. char varied from 0.06 ppm to 1.50 ppm (Table 1), with an average concentration of 0.22 ± 0.22 ppm ($n = 180$), while E. smelt varied between 0.06 and 0.54 ppm, with an average of 0.21 ± 0.08 ppm ($n = 156$). While Tot-Hg in profundal whitefish varied from 0.05 to 0.49 ppm, with an average of 0.21 ± 0.09 ppm ($n = 117$), Tot-Hg in littoral whitefish varied from 0.04 to 0.28 ppm, with an average of 0.12 ± 0.05 ppm ($n = 20$).

Important parameter correlations

Logistic regressions between age and length were significant and positive in all populations investigated (Table A2). Age was also significantly, positively correlated with $\text{Ln}[\text{Hg}]$ in fish in all investigated species (Table A1), including the two whitefish morphs. Length was also significantly, positively correlated with $\text{Ln}[\text{Hg}]$ in fish, except for the littoral whitefish

population, a population primarily represented by adult individuals varying in length from 210 to 410 mm and with minor variations in trophic level ($\Delta\lambda = 1.06$). The correlation between $\delta^{15}\text{N}$ and $\text{Ln}[\text{Hg}]$ was significant in E. smelt and profundal whitefish, and near significant ($p = 0.051$) in A. char. Additionally, K_f was significantly, negatively correlated with $\text{Ln}[\text{Hg}]$ in littoral whitefish, but not in any of the other populations investigated (Table A1). The littoral whitefish were also the only population with significant, positive linear regressions between length and $\delta^{13}\text{C}$ ($p < 0.001$) and between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($p = 0.014$, Table A2).

The average volume percent of primary consumer-invertebrates in stomach samples was significantly, negatively correlated to fish length in A. char, or opposite, significantly positively correlated to the average volume percent of fish in stomach samples.

DISCUSSION

Age and size distribution

Borgstrøm and Saltveit (1981) investigated the size distribution and occurrence of all fish species caught in the water intake from 1979 until spring 1981. In general, the size distributions were similar to the fish caught in this study. Average weight for A. char between 1979 and 1981 was about 100 g (Borgstrøm and Saltveit, 1981), which is higher than the average weight found in 2014 ($28 \pm 38\text{g}$). Mature E. smelt caught in Bøelva, a tributary to Lake Norsjø, varied in length between 85 and 135 mm, and the weight was between 3 and 12 g (Borgstrøm and Saltveit, 1981). In this study, length of E. smelt varied between 83 and 115 mm, and weight varied between 1 and 13 g. For profundal whitefish, an average weight of 150 g was assumed by Borgstrøm and Saltveit (1981), which is close to the average found in this study ($128 \pm 43\text{g}$). In addition, littoral whitefish were caught by gill nets by Borgstrøm (1974), of which most had a length between 290 and 340 mm and a weight about 300 g, which is similar to the majority of littoral whitefish caught in this study (Length: $286 \pm 55\text{ mm}$; Weight: $239 \pm 211\text{ g}$). In addition, one littoral whitefish with a length of 470 mm and a weight of 1065 g was caught in this study. The presence of large littoral whitefish was also confirmed by Borgstrøm (1974), as some whitefish were around 500 mm and between 1100 and 1200 g. Littoral whitefish exhibit high growth rates in Lake Norsjø, especially the first two summers (Borgstrøm, 1974), which is confirmed in this study, as individual whitefish, larger than 200 mm, were found to be 2+ years old.

Use of profundal habitat

The different species caught in the water intake at 50 m depth, i.e. the profundal area of the lake, occurred in individual patterns. Similar to investigation from the same water intake made 35 years ago by Borgstrøm and Saltveit (1981). A. char were present in this profundal area all year but showed seasonal variations in presence and age and size distribution. While the highest presence of A. char occurred during autumn, the oldest fish were present in January and February. E. smelt were also found all year, but fewer individuals during summer, also reported by Borgstrøm and Saltveit (1981). E. smelt is an important prey for piscivorous fishes in the lake, primarily brown trout (*Salmo trutta L.*), and therefore the population exhibits diurnal vertical migration patterns, feeding in the epilimneon during night, and staying close to the bottom during daytime (Nellbring, 1989, Horppila et al., 2000). However, predator avoidance is likely to be most pronounced during the growth season, which exhibits low numbers of E. smelt outside the water intake at 50 m depth. It is therefore more plausible that E. smelt utilises the profundal habitat for feeding, when zooplankton is scarce.

Profundal whitefish were caught between October and May in this study, analogous to the observations made by Borgstrøm and Saltveit (1981), who reported the highest catches of whitefish in January and February (200 – 300 individuals per week), with decreasing numbers during spring and no whitefish during summer. In a gill net survey by Borgstrøm (1974), whitefish were only caught in the depth interval 25 – 50 m in Lake Norsjø during the spawning season. Thus, profundal whitefish only seems to occur at this depth of the lake during spawning. Jensen (1954) proposed that there were likely to be three whitefish morphs, spawning in different areas at different times, in Lake Norsjø, which are littoral whitefish, stream whitefish and winter whitefish. Winter whitefish spawns in deep areas (15 – 70 m) during January and February, and is equivalent to the profundal whitefish caught at a depth of 50 m during winter in this study.

European whitefish is the most diverse Coregonid species (Svårdson, 1979, Bernatchez, 2004, Hudson et al., 2007), which exploits littoral, pelagic and profundal niches (Kahilainen et al., 2003, Kahilainen et al., 2004, Kahilainen et al., 2005). The different morphs, observed in Scandinavia, have evolved by adaptive radiation, and phenotypes are usually linked to foraging traits (Schluter, 1996, Clabaut et al., 2007). One example, used in this study, is the number of gill rakers, which is a highly heritable trait that is widely used to characterise

whitefish morphs (Svårdson, 1979, Rogers and Bernatchez, 2007). The whitefish in Lake Norsjø differed significantly in gill raker count, pointing out that they belong to separate populations. The profundal population, with an average gill raker count of 26.5 ± 0.4 , matches best to what is described as large sparsely rakered whitefish, which has 25 ± 0.3 gill rakers on average, according to material revised by Harrod et al. (2010). This is the ancestral morph, which has diverged into pelagic and benthic morphs (Østbye et al., 2005, Østbye et al., 2006). Preferably, these whitefish would consume zooplankton (Heikinheimo et al., 2000), which is a part of the diet of profundal whitefish in Lake Norsjø. In competition with other morphs and fish species, as they are in Lake Norsjø, large sparsely rakered whitefish show character displacement (Harrod et al., 2010), as they are more generalistic, thus driven to exploit less favourable niches (Werner and Hall, 1979). In competition with more densely rakered whitefish, large sparsely rakered whitefish are often driven to sub-littoral habitats (Harrod et al., 2010) like the profundal whitefish in Lake Norsjø. Similar age distributions in both populations combined with higher weight, length and condition factor in littoral whitefish support the hypothesis that profundal whitefish are outside their preferred niche. Littoral whitefish at the age of 3 are near significantly larger than profundal whitefish at the same age, the mean length at the age of 3 is 257 and 235 mm for littoral and profundal whitefish respectively. The lower growth rates in profundal whitefish may be a result of lower availability of food, however, as profundal and littoral whitefish are distinct morphs, they may be caused by genetic differences.

The littoral whitefish in Lake Norsjø, which has an average gill raker count of 32 ± 0.6 , most likely belongs to the densely rakered morph, which has an average gill raker number around 34 ± 0.1 (Harrod et al., 2010). The densely rakered morph mainly feeds on zooplankton (Amundsen et al., 2004) like smaller littoral whitefish in Lake Norsjø. In addition, densely rakered morphs consume epibenthic prey (Kahilainen and Lehtonen, 2002), which larger littoral individuals in Lake Norsjø do according to the littoral carbon signatures and gut content analysis.

Stable isotope signatures and Hg in fish

A. char exhibited the most depleted $\delta^{13}\text{C}$ signature range (-34.74 - -27.79 ‰) among the fish species investigated. Compared with Vander Zanden and Rasmussen (1999), based on 14 oligotrophic lakes in Canada, this $\delta^{13}\text{C}$ signature range represents profundal (average = -30.5 ‰) to pelagic (average = -28.4 ‰) habitat. As A. char is the weaker competitor in an

asymmetric competition with whitefish (Nilsson, 1967, Amundsen et al., 2010), *A. char* is forced to occupy the less favourable profundal niche (Borgstrøm and Saltveit, 1981, Degerman et al., 2001, Sandlund et al., 2013). The highest average $\delta^{15}\text{N}$ signature ($11.75 \pm 1.20 \text{ ‰}$) and the largest $\delta^{15}\text{N}$ range ($6.65 - 13.51 \text{ ‰}$) of *A. char* are results of a predominantly profundal-based diet, as primary consumers in profundal habitats normally have higher $\delta^{15}\text{N}$ signatures compared to pelagic and littoral primary consumers (Vander Zanden and Rasmussen, 1999). In addition, larger *A. char* in Lake Norsjø ($> 140 \text{ mm}$) often are piscivorous. The differences in prey choice between small and large *A. char* are revealed in the $\delta^{15}\text{N}$ variations, which span over 2 trophic levels, assuming a difference in $\delta^{15}\text{N}$ of 3.4 ‰ per trophic level (Minagawa and Wada, 1984, Post, 2002). Similar to *A. char*, the average $\delta^{13}\text{C}$ signature in *E. smelt* ($-29.13 \pm 0.55 \text{ ‰}$) and $\delta^{13}\text{C}$ range ($-32.38 - -27.60 \text{ ‰}$) indicates a combined profundal-pelagic diet, also for this species. This was also supported by the stomach analyses, as both profundal and pelagic prey items were present. However, stomach samples of *E. smelt* in Lake Norsjø revealed, that they predominantly fed on zooplankton, especially copepods. Regarding the interpretation of $\delta^{13}\text{C}$ signatures in *E. smelt*, it is important to be aware of the temporal variations in stable isotope (SI) ratios of short lived and small animals (Toda and Wada, 1990, Gu et al., 1994, Yoshioka et al., 1994, Cabana and Rasmussen, 1996). Accordingly, periodical $\delta^{13}\text{C}$ signature depletion in zooplankton can reach values similar to profundal organisms (e.g. Grey and Jones, 2001), thus the profundal diet content may be overestimated in SI analysis. The $\delta^{15}\text{N}$ signatures in *E. smelt* span over 1.75 trophic levels. This may arise, as *E. smelt* consumes zooplankton at low trophic levels and omnivorous benthic animals like *Chironomidae sp.* at higher trophic levels. Vander Zanden and Rasmussen (1999) also found different baseline $\delta^{15}\text{N}$ values for profundal (average = 5.2 ‰) and pelagic (average = 3.1 ‰) prey, which may increase the variability of $\delta^{15}\text{N}$ in *E. smelt* in Lake Norsjø. Profundal whitefish exhibited $\delta^{13}\text{C}$ signatures ($-30.21 - -27.61 \text{ ‰}$) and $\delta^{15}\text{N}$ signatures ($6.39 - 12.63 \text{ ‰}$) very similar to those in *E. smelt*. The variability of SI signatures relies on the variation of pelagic and profundal prey items, and the span in $\delta^{15}\text{N}$ of 1.84 trophic levels indicates a certain degree of piscivory in some profundal whitefish individuals. The most deviant SI signatures were found in littoral whitefish. The variation in $\delta^{13}\text{C}$ signatures from -28.88 to -23.07 ‰ (average: $-26.19 \pm 2.04 \text{ ‰}$), resembled a mixture of pelagic (average = -28.4 ‰) and littoral (average = -23.8 ‰) food items, according to Vander Zanden and Rasmussen (1999). The small range in $\delta^{15}\text{N}$ signatures is explained by the small sample size ($n = 20$) and the absence of sub-adult

individuals. Despite so, according to the $\delta^{15}\text{N}$ signatures *per se*, littoral whitefish appeared on the lowest trophic level among the investigated fish species, and beside invertebrates, only roe was found in their stomachs. However, the generally lower $\delta^{15}\text{N}$ signatures found in littoral whitefish are likely to be a habitat effect: Vander Zanden and Rasmussen (1999) have shown, that littoral primary consumers create lower baseline levels for $\delta^{15}\text{N}$ (average = 1.6 ‰) compared to pelagic (average = 3.1 ‰) or profundal (average = 5.2 ‰) primary consumers.

The significantly higher concentration of Hg found in profundal whitefish compared with littoral whitefish might be a result of different MeHg loads as a result of various physiochemical *in situ* conditions for MeHg formations between profundal, pelagic and littoral habitats in the lake. Thus, higher Hg levels in profundal whitefish might be a result of generally higher MeHg baselines in the profundal zone as reported by Lavoie et al. (2010). Stafford et al. (2003) found a positive correlation between Hg in biota (lake trout (*Salvelinus namaycush*) and invertebrates) and lake depth, highlighting water depth as another possible explanation or underlying factor. In addition, several explanatory biological factors may also be decisive for the habitat variation in Hg in biota. Algal bloom dilution (ABD), which means that MeHg is distributed among a larger biomass of algae during the growth season (Pickhardt et al., 2002, Pickhardt et al., 2005), and somatic growth dilution (SGD), which means that organisms add new biomass at higher rates than MeHg (Thomann, 1989, Verta, 1990, Ward et al., 2010, Lepak et al., 2012), will of course vary depending on productivity and trophic status of lakes or lake habitats. As both factors are reported to be important for temporary/seasonal variations in Hg in biota, they accordingly should be important explanatory factors for the differences in Hg between profundal and littoral biota. Despite both ABD and SGD being different processes, they occur simultaneously in an ecosystem, leaving them impossible to separate quantitatively without laboratory procedures (Foe and Louie, 2014). Another biological factor regarding Hg-variations in biota, is the possibility of starvation, as A. char (permanently) and profundal whitefish (temporary) are forced to occupy the less energetically favourable profundal niche. Starvation is earlier assumed to be an explanatory factor for elevated Hg in fish (Hobson et al., 1993), and ABD/SGD was confirmed by negative correlations between K_f and Hg-concentrations in striped bass (*Morone saxatilis*, Cizdziel et al., 2002) and Northern pike (Olsson, 1976). K_f is also significantly, negatively correlated to $\ln[\text{Hg}]$ in littoral whitefish in this study. Contrary to Hg in fish, the $\delta^{15}\text{N}$ signatures were not significantly different

between the two populations of whitefish. As the exact reasons remain unclear, there are effects influencing $\delta^{15}\text{N}$ in both directions. Baselines for $\delta^{15}\text{N}$ are higher in the profundal zone (Vander Zanden and Rasmussen, 1999), and $\delta^{15}\text{N}$ can additionally be enriched, when animals are starving (Waterlow, 1968, Waterlow et al., 1978, Gannes et al., 1998), which are both factors leading to increased $\delta^{15}\text{N}$ in profundal biota as profundal whitefish. On the other hand, littoral whitefish are larger, and may feed on higher trophic levels, and thus a trophic level based $\delta^{15}\text{N}$ signature enrichment may occur.

Hg concentrations and biomagnification rates differ between species in Lake Norsjø, as Hg concentrations are dependent on habitat (Lavoie et al., 2010, Eagles-Smith et al., 2008), trophic position (Eagles-Smith et al., 2008), age (Stafford et al., 2003, Eagles-Smith et al., 2008), and total length (Huckabee et al., 1979, Driscoll et al., 1994, Cizdziel et al., 2002, Stafford et al., 2003, Eagles-Smith et al., 2008). The lowest Hg concentrations were found in littoral whitefish, which ranged from 0.04 to 0.28 ppm ww. with an average at 0.12 ± 0.05 ppm ww. The logarithmically transformed Hg concentrations were only linear dependent on age, and this relationship featured the lowest intercept and the lowest slope of all species in this study. As littoral whitefish appear to have high growth rates, this could be a result of SGD (Thomann, 1989). The low intercepts may be explained by lower Hg baselines, as Hg is reported to be positively related to depth (Stafford et al., 2003). The habitat effect may also be part of the explanation for the similar average Hg concentrations of all other species, which are 0.22 ± 0.22 , 0.21 ± 0.08 and 0.21 ± 0.09 for A. char, E. smelt and profundal whitefish respectively. A. char exhibits the largest range of Hg concentrations from 0.06 to 1.50 ppm ww. The median concentration of 0.14 ppm ww. is low compared to profundal whitefish and E. smelt, which both have a median concentration at 0.19 ppm ww., however, the maximum concentration in A. char is the highest measured concentration in this study. The low concentrations reflect a majority of small and young fish caught, while A. char has the highest potential of magnifying Hg due to high maximum age (Klemetsen et al., 2003), profundal habitat (Stafford et al., 2003) and poor condition (Cizdziel et al., 2002). Hg concentrations are similar in profundal whitefish and E. smelt, while profundal whitefish grows larger than E. smelt in Lake Norsjø. Profundal whitefish spawn by the water intake during winter (Borgstrøm and Saltveit, 1981), but they may have access to prey from shallow depths in the summer, which contains lower amounts of Hg (Stafford et al., 2003). In this study, one ant has been

found in the stomachs of profundal whitefish, proving at least occasional access to terrestrial prey. Contrary to profundal whitefish, E. smelt is not shown to ingest potential lower Hg prey. Additionally, the largest E. smelt caught in this study, which had a total length of 115 mm, was only two years old. This indicates a stagnation in growth, as no E. smelt over 2 years old exceeded a length of 115 mm. E. smelt matures at 2 – 4 years of age (Jonsson, 2006), and reduced growth rates or stagnation in growth are often a consequence of maturation (Garnås, 1979). That means that Hg is not diluted efficiently by growth in adult E. smelt, which results in high Hg concentrations compared to fish of the same size of other species.

Important parameter correlations

Hg concentrations are reported to increase with age and size (Stafford et al., 2003, Eagles-Smith et al., 2008), which is found in all populations in this study except for littoral whitefish. The littoral whitefish population, however, is represented by adult individuals with little variation in trophic level, where this effect may not be pronounced in the data. Analogously, the correlation between $\delta^{15}\text{N}$ and $\text{Ln}[\text{Hg}]$ was not significant for littoral whitefish. Contrary, E. smelt and profundal whitefish exhibited a significant, positive correlation between $\delta^{15}\text{N}$ and $\text{Ln}[\text{Hg}]$, and this correlation was near significant in A. char ($p = 0.051$), which confirms the general hypothesis, that Hg biomagnifies (Cabana and Rasmussen, 1994, Atwell et al., 1998, Watras et al., 1998, Eagles-Smith et al., 2008, Lavoie, 2013) for E. smelt and profundal whitefish.

Length and $\delta^{13}\text{C}$, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were only significantly, positively correlated in littoral whitefish, indicating an ontogenetic diet and habitat shift in this population. A whitefish morph, similar in gill raker count, from Lake Paadar (Finland), the large densely rakered whitefish, consumes zooplankton in early life stages, before the diet shifts towards surface insects (Kahilainen et al., 2014). A similar shift in diet matches the distribution of $\delta^{13}\text{C}$ in littoral whitefish, which varies between a rather pelagic value of -28.88‰ and a littoral value of -23.07‰ (Vander Zanden and Rasmussen, 1999), with smaller and younger fish towards the pelagic end and older fish towards the littoral end of the scale. This hypothesis could not be entirely confirmed by stomach samples, as mainly littoral prey, and only 0.8 Vol-% copepods as pelagic prey, were found in littoral whitefish. However, littoral whitefish were only caught on one day, leaving the stomach samples as a mere identification of possible prey (Vinson and Budy, 2011).

An ontogenetic diet shift can also be observed in the stomach samples of A. char. The diet shifts from predominantly *Chironomidae* sp., some pelagic prey such as copepods, and other items like *Phryganea grandis* and roe to a diet mainly based on fish, *Chironomidae* sp., *Phryganea grandis* and roe. The ontogenetic diet shift in A. char, which have invertebrate consumption and cannibalism as different stages in the same life history strategy, has been proposed by e.g. Finstad et al. (2006). Another explanation for the differences in the two groups is a dimorphism with invertebrate eating dwarfs and cannibalistic giants (Hammar, 2000), which could persist permanently (Svenning and Borgstrøm, 1995). Parker and Johnson (1991), for example, have observed phenological differences between A. char morphs such as different numbers of gill rakers. However, molecular techniques have only revealed slight genetic differences at first (Hindar et al., 1986, Snorrason et al., 1989, Danzmann et al., 1991, Hartley et al., 1992), and different phenotypes are rather a result of genetic and environmental components in combination (Nordeng, 1983, Nordeng et al., 1989). More recently, evidence for larger genetic differences in A. char was found, especially if different populations inhabit different niches (Westgaard et al., 2004, Adams et al., 2007, Gomez-Uchida et al., 2008, Power et al., 2009, Conejeros et al., 2014, May-McNally et al., 2015). Further investigations in Lake Norsjø are necessary in order to determine, whether A. char undergoes an ontogenetic diet shift, or if there are two different life history strategies. For this purpose, differences in gill raker counts could be examined.

CONCLUSION

All investigated populations, except A. char, appeared to be in a similar state as in previous studies, though direct comparability was compromised as sampling methods differed. Temporal and spatial distributions remained unchanged. A. char is the weaker competitor compared to whitefish, thus occupies the profundal zone all year, while profundal whitefish spawns on banks in the profundal zone in January-February. European smelt migrates vertically during the day, and utilises the profundal zone to avoid predation and for feeding.

The hypothesised increase in Hg-concentrations with increasing $\delta^{15}\text{N}$ was confirmed for profundal whitefish and E. smelt. Additionally, several horizontal effects determining Hg-concentrations such as growth dilution and habitat effects were found. In interspecific

comparisons, habitat, condition and choice of prey are important factors determining Hg-concentrations.

ACKNOWLEDGEMENTS

We thank E. Lydersen (TUC) for guidance, inspiration, instructions in field and laboratory work and revision, and A. Økelsrud (TUC) for guidance and instructions in field and laboratory work. We thank B. Steen (TUC) and K. Brekke Li (TUC) for laboratory assistance and F. Bergan (TUC), H. Parker (TUC) and J. Heggenes (TUC) for assisting our field work, especially the age determination of fish. We are grateful for assistance with fish sampling by J. Ellingsen (INEOS) and comments on the manuscript from J. G. Brynjulvsrud.

LITERATURE

- ADAMS, C., FRASER, D., WILSON, A. J., ALEXANDER, G., FERGUSON, M. M. & SKÚLASON, S. 2007. Patterns of phenotypic and genetic variability show hidden diversity in Scottish Arctic charr. *Ecology of Freshwater Fish*, 16, 78 - 86.
- AMAP, A. 2011. assessment 2011: mercury in the Arctic. *Arctic Monitoring and Assessment Programme (AMAP)*, Oslo, Norway, 193.
- AMUNDSEN, P.-A., KNUDSEN, R. & BRYHNI, H. T. 2010. Niche use and resource partitioning of Arctic charr, European whitefish and grayling in a subarctic lake. *Hydrobiologia*, 650, 3 - 14.
- AMUNDSEN, P.-A., KNUDSEN, R., KLEMETSEN, A. & KRISTOFFERSON, R. 2004. Resource competition and interactive segregation between sympatric whitefish morphs. *Annales Zoologici Fennici*, 41, 301 - 307.
- AMYOT, M., MIERLE, G., LEAN, D. R. S. & MCQUEEN, D. J. 1994. SUNLIGHT-INDUCED FORMATION OF DISSOLVED GASEOUS MERCURY IN LAKE WATERS. *Environmental Science & Technology*, 28, 2366-2371.
- ATWELL, L., HOBSON, K. A. & WELCH, H. E. 1998. Biomagnification and bioaccumulation of mercury in an arctic marine food web: insights from stable nitrogen isotope analysis. *Canadian Journal of Fisheries and Aquatic Science*, 55, 1114 - 1121.
- BARKAY, T., MILLER, S. M. & SUMMERS, A. O. 2003. Bacterial mercury resistance from atoms to ecosystems. *Fems Microbiology Reviews*, 27, 355-384.
- BERNATCHEZ, L. 2004. Ecological theory of adaptive radiation. An empirical assessment from Coregonine fishes (Salmonilores). In: STEARNS, A. P. H. S. C. (ed.) *Evolution Illustrated: Salmon and Their Relatives*. Oxford: Oxford University Press.
- BOENING, D. W. 2000. Ecological effects, transport, and fate of mercury: a general review. *Chemosphere*, 40, 1335-1351.
- BORGSTRØM, R. 1974. Oppsamlingskjønn for Norsjø m.v. Ovenforliggende regulerings virkning på fiskebestander og utøvelsen av fisket. Oslo: Rapp. Lab. Ferskv. Økol. Innlandsfiske.
- BORGSTRØM, R. & SALTVEIT, S. J. 1981. En vurdering av fisketap gjennom tappetunnelene fra nedre Norsjø til Rafnes og Porsgrunn fabrikker. Ås: Institutt for naturforvaltning, NLH.

- CABANA, G. & RASMUSSEN, J. B. 1994. Modeling food-chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature*, 372, 255 - 257.
- CABANA, G. & RASMUSSEN, J. B. 1996. Comparison of aquatic food chains using nitrogen isotopes. *Proceedings of the National Academy of Sciences (USA)*, 93, 10844 - 10847.
- CHUMCHAL, M. M. & HAMBRIGHT, K. D. 2009. ECOLOGICAL FACTORS REGULATING MERCURY CONTAMINATION OF FISH FROM CADDO LAKE, TEXAS, USA. *Environmental Toxicology and Chemistry*, 28, 962-972.
- CIZDZIEL, J. V., HINNERS, T. A., POLLARD, J. E., HEITHMAR, E. M. & CROSS, C. L. 2002. Mercury Concentrations in Fish from Lake Mead, USA, Related to Fish Size, Condition, Trophic Level, Location and Consumption Risk. *Arch. Environ. Contam. Toxicol.*, 43, 309 - 317.
- CLABAUT, C., BUNJE, P. M. E., SALZBURGER, W. & MEYER, A. 2007. Geometric morphometric analyses provide evidence for the adaptive character of the Tanganykan chichlid fish radiations. *Evolution*, 61, 560 - 578.
- CLARKSON, T. W. 1998. Human toxicology of mercury. *The Journal of trace elements in experimental medicine*, 11, 303-317.
- CONEJEROS, P., PHAN, A., POWER, M., O'CONNELL, M., ALEKSEYEV, S., SALINAS, I. & DIXON, B. 2014. Differentiation of sympatric Arctic char morphotypes using major histocompatibility class II genes. *Transaction of the American Fisheries Society*, 143, 586 - 594.
- CRAIG, H. 1957. Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of carbon dioxide. *Geochimica Cosmochimica Acta*, 12, 133 - 149.
- DANZMANN, R. G., FERGUSON, M. M., SKÚLASON, S. S. & NOAKES, D. L. G. 1991. Mitochondrial DNA diversity among four sympatric morphs of Arctic charr, *Salvelinus alpinus* L., from Thingvallavatn, Iceland. *Journal of Fish Biology*, 39, 649 - 659.
- DEGERMAN, E., HAMMAR, J., NYBERG, P. & SVARDSON, G. 2001. Human impact on the fish diversity in the four largest lakes of Sweden. *Ambio.*, 30.
- DESROSIERS, M., PLANAS, D. & MUCCI, A. 2006. Mercury methylation in the epilithon of boreal shield aquatic ecosystems. *Environmental Science & Technology*, 40, 1540-1546.
- DRISCOLL, C. T., YAN, C., SCHOFIELD, C. L., MUNSON, R. & HOLSAPPLE, J. 1994. The mercury cycle and fish in the Adirondack lakes. *Environ. Sci. Tech.*, 28, 136 - 143.

- EAGLES-SMITH, C. A., SUCHANEK, T. H., COLWELL, A. E. & ANDERSON, N. L. 2008. Mercury trophic transfer in a eutrophic lake: the importance of habitat-specific foraging. *Ecol Appl*, 18, A196-212.
- ECKLEY, C. S. & HINTELMANN, H. 2006. Determination of mercury methylation potentials in the water column of lakes across Canada. *Science of The Total Environment*, 368, 111-125.
- ECKLEY, C. S., WATRAS, C. J., HINTELMANN, H., MORRISON, K., KENT, A. D. & REGNELL, O. 2005. Mercury methylation in the hypolimnetic waters of lakes with and without connection to wetlands in northern Wisconsin. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 400-411.
- ESSINGTON, T. E. & HOUSER, J. N. 2003. The effect of whole-lake nutrient enrichment on mercury concentration in age-1 yellow perch. *Transactions of the American Fisheries Society*, 132, 57-68.
- FINSTAD, A. G., UGEDAL, O. & BERG, O. K. 2006. Growing large in a low grade environment: size dependent foraging gain and niche shifts to cannibalism in Arctic char. *Oikos*, 112, 73 - 82.
- FITZGERALD, W. & LAMBORG, C. 2004. Atmospheric cycling and chemistry of mercury. *Environmental geochemistry*, 9, 107-148.
- FITZGERALD, W. F., LAMBORG, C. H. & HAMMERSCHMIDT, C. R. 2007. Marine biogeochemical cycling of mercury. *Chemical Reviews*, 107, 641-662.
- FOE, C. & LOUIE, S. 2014. Appendix A: Importance of Primary and Secondary Production in Controlling Fish Tissue Mercury Concentrations.
- FULTON, T. W. 1904. The rate of growth of fishes.
- GANNES, L. Z., MARTINEZ DEL RIO, C. & KOCH, P. 1998. Natural Abundance Variations in Stable Isotopes and Their Potential Uses in Animal Physiological Ecology. *Comp. Biochem. Physiol.*, 119A, 725 - 737.
- GARNÅS, E. 1979. Krøkle (*Osmerus eperlanus* (L)) i Nordfjorden. *Tyrifjordundersøkelsen 1970 - 1986*. Oslo: Direktoratet for vilt og ferskvannsfisk.
- GILMOUR, C. C. & RIEDEL, G. S. 1995. MEASUREMENT OF HG METHYLATION IN SEDIMENTS USING HIGH SPECIFIC-ACTIVITY HG-203 AND AMBIENT INCUBATION. *Water Air and Soil Pollution*, 80, 747-756.

- GOEDE, R. W. & BARTON, B. A. 1990. Organismis indices and an autopsy-based assessment as indicators of health and condition of fish. *Am. Fish. Soc. Symp.*, 8, 93 - 108.
- GOMEZ-UCHIDA, D., DUNPHY, K. P., O'CONNELL, M. F. & RUZZANTE, D. E. 2008. Genetic divergence between sympatric Arctic charr *Salvelinus alpinus* morphs in Gander Lake, Newfoundland: roles of migration and unequal effective population sizes. *Journal of Fish Biology*, 73, 2040 - 2057.
- GORSKI, P. R., CLECKNER, L. B., HURLEY, J. P., SIERSZEN, M. E. & ARMSTRONG, D. E. 2003. Factors affecting enhanced mercury bioaccumulation in inland lakes of Isle Royale National Park, USA. *Science of the Total Environment*, 304, 327-348.
- GREENFIELD, B. K., HRABIK, T. R., HARVEY, C. J. & CARPENTER, S. R. 2001. Predicting mercury levels in yellow perch: use of water chemistry, trophic ecology, and spatial traits. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 1419-1429.
- GREY, J. & JONES, R. I. 2001. Seasonal changes in the importance of the source of organic matter to the diet of zooplankton in Loch Ness, as indicated by stable isotope analysis. *Limnol. Oceanogr.*, 46, 505 - 513.
- GU, B., SCHELL, D. M. & ALEXANDER, V. 1994. Stable carbon and nitrogen isotopic analysis of the plankton food web in a subarctic lake. *Canadian Journal of Fisheries and Aquatic Sciences*, 51, 1338 - 1344.
- HAMMAR, J. 2000. Cannibals and parasites: conflicting regulators of bimodality in high latitude Arctic char, *Salvelinus alpinus*. *Oikos*, 88, 33 - 47.
- HARROD, C., MALLELA, J. & KAHILAINEN, K. K. 2010. Phenotype-environment correlations in a putative whitefish adaptive radiation. *Journal of Animal Ecology*, 79, 1057 - 1068.
- HARTLEY, S. E., MCGOWAN, C., GREER, R. B. & WALKER, A. F. 1992. The genetics of sympatric Arctic charr [*Salvelinus alpinus* (L.)] populations from Loch Rannoch, Scotland. *Journal of Fish Biology*, 41, 1021 - 1031.
- HEIKINHEIMO, O., MIINALAINEN, M. & PELTONEN, H. 2000. Diet, growth and competitive abilities of sympatric whitefish forms in a dense introduced population: results of stocking experiment. *Journal of Fish Biology*, 57, 808 - 827.
- HINDAR, K., RYMAN, N. & STAHL, G. 1986. Genetic differentiation among local populations and morphotypes of Arctic charr, *Salvelinus alpinus*. *Biological Journal of the Linnean Society*, 27, 269 - 285.

- HOBSON, K. A., ALISAUSKAS, R. T. & CLARK, R. G. 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analysis of diet. *Condor*, 95, 388 - 394.
- HOEFS, J. 2013. *Stable isotope geochemistry*, Springer Science & Business Media.
- HOLLWEG, T. A., GILMOUR, C. C. & MASON, R. P. 2010. Mercury and methylmercury cycling in sediments of the mid-Atlantic continental shelf and slope. *Limnology and Oceanography*, 55, 2703-2722.
- HOLTAN, H. 1968. Norsjø: en limnologisk undersøkelse utført i 1967.
- HORPPILA, J., MALINEN, T., NURMINEN, L., TALLBERG, P. & VINNI, M. 2000. A metalimnetic oxygen minimum indirectly contributing to the low biomass of cladocerans in Lake Hiidenvesi - a diurnal study on the refuge effect. *Hydrobiologia*, 436, 81 - 90.
- HUCKABEE, J. W., ELWOOD, J. W. & HILDEBRAND, S. G. 1979. Accumulation of mercury in freshwater biota. In: NRIAGU, J. O. (ed.) *Biogeochemistry of mercury in the environment*. New York: Elsevier/North-Holland Biomedical Press.
- HUDSON, A. G., VOULANTHEN, P., MÜLLER, R. & SEEHAUSEN, O. 2007. Review: The geography of speciation and adaptive radiation of Coregonines. *Advances in Limnology*, 60, 111 - 146.
- JENSEN, K.W., 1954. Fish and fisheries in Lake Norsjø, 68 pp (In Norwegian).
- JONSSON, B. 2006. *Fisker*, Oslo, Cappelens Naturhåndbøker.
- KAHILAINEN, K., ALAJÄRVI, E. & LEHTONEN, H. 2005. Planktivory and diet-overlap of densely rakered whitefish (*Coregonus lavaretus* (L.)) in a subarctic lake. *Ecology of Freshwater Fish*, 14, 50 - 58.
- KAHILAINEN, K. & LEHTONEN, H. 2002. Habitat use and growth of three sympatric forms of European whitefish, *Coregonus lavaretus* (L.), in the subarctic Lake Muddusjärvi. *Archiv für Hydrobiologie Special Issues Advanced Limnology*, 57, 277 - 290.
- KAHILAINEN, K., LEHTONEN, H. & KÖNÖNEN, K. 2003. Consequence of habitat segregation to growth rate of two sparsely rakered whitefish (*Coregonus lavaretus* (L.)) forms in a subarctic lake. *Ecology of Freshwater Fish*, 12, 275 - 285.
- KAHILAINEN, K., MALINEN, T., TUOMAALA, A. & LEHTONEN, H. 2004. Diel and seasonal habitat and food segregation of three sympatric *Coregonus lavaretus* forms in a subarctic lake. *Journal of Fish Biology*, 64, 418 - 434.

- KAHILAINEN, K. K., PATTERSON, W. P., SONNINEN, E., HARROD, C. & KILJUNEN, M. 2014. Adaptive Radiation along a Thermal Gradient: Preliminary Results of Habitat Use and Respiration Rate Divergence among whitefish morphs. *PLoS ONE*, 9.
- KIDD, K., CLAYDEN, M. & JARDINE, T. 2012. Bioaccumulation and biomagnification of mercury through food webs. *Environmental chemistry and toxicology of mercury*. Wiley, Hoboken, 455-499.
- KLEMETSEN, A., AMUNDSEN, P.-A., DEMPSON, J. B., JONSSON, B., JONSSON, N., O'CONNELL, M. F. & 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.
- LAMBORG, C. H., FITZGERALD, W. F., O'DONNELL, J. & TORGENSEN, T. 2002. A non-steady-state compartmental model of global-scale mercury biogeochemistry with interhemispheric atmospheric gradients. *Geochimica Et Cosmochimica Acta*, 66, 1105-1118.
- LAVOIE, R. A., HEBERT, C. E., RAIL, J.-F., BRAUNE, B. M., YUMVIHOZE, E., HILL, L. G. & LEAN, D. R. S. 2010. Trophic structure and mercury distribution in a Gulf of St. Lawrence (Canada) food web using stable isotope analysis. *Sci. Total Environ.*, 408, 5529 - 5539.
- LAVOIE, R. A., JARDINE, T.D., CHUMCHAL, M.M., KIDD, K.A. & CAMPBELL, L.M. 2013. Biomagnification of Mercury in Aquatic food webs: A Worldwide Meta-Analysis. *Environ. Sci. Tech.*, 47, 13385 - 13394.
- LEHNHERR, I., ST LOUIS, V. L. & KIRK, J. L. 2012. Methylmercury Cycling in High Arctic Wetland Ponds: Controls on Sedimentary Production. *Environmental Science & Technology*, 46, 10523-10531.
- LEPAK, J. M., KINZLI, K.-D., FETHERMAN, E. R., PATE, W. M., HANSEN, A. G., GARDUNIO, E. I., CATHCART, C. N., STACY, W. L., UNDERWOOD, Z. E., BRANDT, M. M., MYRICK, C. A. & JOHNSON, B. M. 2012. Manipulation of growth to reduce mercury concentrations in sport fish on a whole-system scale. *Canadian Journal of Fisheries and Aquatic Sciences*, 69, 122-135.
- LOSETO, L. L., STERN, G. A., DEIBEL, D., CONNELLY, T. L., PROKOPOWICZ, A., LEAN, D. R. S., FORTIER, L. & FERGUSON, S. H. 2008. Linking mercury exposure to habitat and feeding behaviour in Beaufort Sea beluga whales. *Journal of Marine Systems*, 74, 1012-1024.

- MACALADY, J. L., MACK, E. E., NELSON, D. C. & SCOW, K. M. 2000. Sediment microbial community structure and mercury methylation in mercury-polluted Clear Lake, California. *Applied and Environmental Microbiology*, 66, 1479-1488.
- MASON, R. P., CHOI, A. L., FITZGERALD, W. F., HAMMERSCHMIDT, C. R., LAMBORG, C. H., SOERENSEN, A. L. & SUNDERLAND, E. M. 2012. Mercury biogeochemical cycling in the ocean and policy implications. *Environmental Research*, 119, 101-117.
- MASON, R. P., FITZGERALD, W. F. & MOREL, F. M. M. 1994. THE BIOGEOCHEMICAL CYCLING OF ELEMENTAL MERCURY - ANTHROPOGENIC INFLUENCES. *Geochimica Et Cosmochimica Acta*, 58, 3191-3198.
- MASON, R. P. & SHEU, G. R. 2002. Role of the ocean in the global mercury cycle. *Global Biogeochemical Cycles*, 16.
- MAY-MCNALLY, S. L., QUINN, T. P., WOODS, P. J. & TAYLOR, E. B. 2015. Evidence for genetic distinction among sympatric ecotypes of Arctic char (*Salvelinus alpinus*) in southwestern Alaskan lakes. *Ecology of Freshwater Fish*, 24, 562 - 574.
- MERGLER, D., ANDERSON, H. A., CHAN, L. H. M., MAHAFFEY, K. R., MURRAY, M., SAKAMOTO, M. & STERN, A. H. 2007. Methylmercury exposure and health effects in humans: A worldwide concern. *Ambio*, 36, 3-11.
- MICROSOFT 2013. Microsoft Excel. Redmond, Washington: Microsoft.
- MILJØDIREKTORATET. 2015. *Vann-nett* [Online]. Available: <http://www.vann-nett.no/portal/water?waterbodyID=016-6-L>.
- MINAGAWA, M. & WADA, E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochimica Cosmochimica Acta*, 48, 1135 - 1140.
- MOREL, F. M. M., KREPIEL, A. M. L. & AMYOT, M. 1998. The chemical cycle and bioaccumulation of mercury. *Annu. Rev. Ecol. Syst.*, 29, 543 - 566.
- NELLBRING, S. 1989. The ecology of smelts (genus *Osmerus*): a literature review. *Nordic Journal of Freshwater Research*, 65, 116 - 145.
- NILSSON, N. A. 1967. Interactive segregation between fish species. In: GERKING, S. D. (ed.) *The biological basis of freshwater fish production*. Oxford (UK): Blackwell Scientific.
- NORDENG, H. 1983. Solution to the 'Char Problem' based on Arctic char (*Salvelinus alpinus*) in Norway. *Canadian Journal of Fisheries and Aquatic Science*, 40, 1372 - 1387.

- NORDENG, H., BRATLAND, P. & SKURDAL, J. 1989. Patterns of smolt transformation in the resident fraction on anadromous Arctic charr *Salvelinus alpinus*; genetic and environmental influence. In: H. KAWANABE, F. Y. D. L. G. N. (ed.) *Biology of charrs and Masu salmon*. Japan: Kyoto University.
- OLSSON, M. 1976. Mercury level as a function of size and age in northern pike 1 and 5 years after the mercury ban in Sweden. *Royal Swed. Acad. Sci.*, 5, 73 - 76.
- PACYNA, E. G., PACYNA, J. M., SUNDSETH, K., MUNTHER, J., KINDBOM, K., WILSON, S., STEENHUISEN, F. & MAXSON, P. 2010. Global emission of mercury to the atmosphere from anthropogenic sources in 2005 and projections to 2020. *Atmospheric Environment*, 44, 2487-2499.
- PARKER, H. H. & JOHNSON, L. 1991. Population structure, ecological segregation and reproduction in non-anadromous Arctic charr, *Salvelinus alpinus* (L.), in four unexploited lakes in the Canadian high Arctic. *Journal of Fish Biology*, 38, 123 - 147.
- PETERSON, B. J. & FRY, B. 1987. STABLE ISOTOPES IN ECOSYSTEM STUDIES. *Annual Review of Ecology and Systematics*, 18, 293-320.
- PICKHARDT, P. C. & FISHER, N. S. 2007. Accumulation of inorganic and methylmercury by freshwater phytoplankton in two contrasting water bodies. *Environmental Science & Technology*, 41, 125-131.
- PICKHARDT, P. C., FOLT, C. L., CHEN, C. Y., KLAUE, B. & BLUM, J. D. 2002. Algal blooms reduce the uptake of toxic methylmercury in freshwater food webs. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 4419-4423.
- PICKHARDT, P. C., FOLT, C. L., CHEN, C. Y., KLAUE, B. & BLUM, J. D. 2005. Impacts of zooplankton composition and algal enrichment on the accumulation of mercury in an experimental freshwater food web. *Science of the Total Environment*, 339, 89-101.
- PIRRONE, N., CINNIRELLA, S., FENG, X., FINKELMAN, R., FRIEDLI, H., LEANER, J., MASON, R., MUKHERJEE, A., STRACHER, G. & STREETS, D. 2010. Global mercury emissions to the atmosphere from anthropogenic and natural sources. *Atmospheric Chemistry and Physics*, 10, 5951-5964.
- POST, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, 83, 703 - 718.

- POWER, M., KLEIN, G. M., GUIGUER, K. & KWAN, M. K. H. 2002. Mercury accumulation in the fish community of a sub-Arctic lake in relation to trophic position and carbon sources. *Journal of Applied Ecology*, 39, 819-830.
- POWER, M., POWER, G., REIST, J. D. & BAJNO, R. 2009. Ecological and genetic differentiation among the Arctic charr of Lake Aigueau, Northern Québec. *Ecology of Freshwater Fish*, 18, 445 - 460.
- R CORE TEAM 2014. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.
- RAASTAD, J. E. & OLSEN, L.-H. 1999. *Insekter og småkryp i vann og vassdrag*, Oslo, Aschehougs Naturbøker.
- RANNEKLEV, S., DE WIT, H., JENSSEN, M., SKJELKVÅLE, B. L. & SKJELKVÅLE, B. L. P. M. 2009. An assessment of Hg in the freshwater aquatic environment related to long-range transported air pollution in Europe and North America.
- ROGERS, S. M. & BERNATCHEZ, L. 2007. The genetic architecture of ecological speciation and the association with signatures of selection in natural lake whitefish (*Coregonus* sp Salmonidae) Species pairs. *Molecular Biology and Evolution*, 24, 1423 - 1438.
- 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.
- SCHLUTER, D. 1996. Ecological speciation in postglacial fishes. *Philosophical transactions of the Royal Society B*, 351, 807 - 814.
- SCHOENER, T. W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology*, 51, 408 - 418.
- SMOLDERS, R., DE COEN, W. & BLUST, R. 2005. Integrative measures of toxicant exposure in Zebra fish (*Danio rerio*) at different levels of biological organization. In: OSTRANDER, G. K. (ed.) *Techniques in Aquatic Toxicology*. Boca Raton, Florida: CRC Press.
- SNORRASON, S. S., SKÚLASON, S., SANDLUND, O. T., MALMQUIST, H. J., JONSSON, B. & JONASSON, P. M. 1989. Shape polymorphism in Arctic charr, *Salvelinus alpinus*, in Thingvallavatn, Iceland. In: H. KAWANABE, F. Y. D. L. G. N. (ed.) *Biology of charr and Masu salmon*. Japan: Kyoto University.
- ST LOUIS, V. L., DEROCHER, A. E., STIRLING, I., GRAYDON, J. A., LEE, C., JOCKSCH, E., RICHARDSON, E., GHORPADE, S., KWAN, A. K., KIRK, J. L., LEHNHERR, I. & SWANSON,

- H. K. 2011. Differences in Mercury Bioaccumulation between Polar Bears (*Ursus maritimus*) from the Canadian high- and sub-Arctic. *Environmental Science & Technology*, 45, 5922-5928.
- ST LOUIS, V. L., RUDD, J. W. M., KELLY, C. A., BODALY, R. A., PATERSON, M. J., BEATY, K. G., HESSLEIN, R. H., HEYES, A. & MAJEWSKI, A. R. 2004. The rise and fall of mercury methylation in an experimental reservoir. *Environmental Science & Technology*, 38, 1348-1358.
- STAFFORD, C. P., HANSEN, B. & STANFORD, J. A. 2003. Mercury in Fishes and their Diet items from Flathead Lake, Montana. *Transaction of the American Fisheries Society*, 133, 349 - 357.
- STEWART, A. R., SAIKI, M. K., KUWABARA, J. S., ALPERS, C. N., MARVIN-DIPASQUALE, M. & KRABBENHOFT, D. P. 2008. Influence of plankton mercury dynamics and trophic pathways on mercury concentrations of top predator fish of a mining-impacted reservoir. *Canadian Journal of Fisheries and Aquatic Sciences*, 65, 2351-2366.
- SVENNING, M. A. & BORGSTRØM, R. 1995. Population structure in landlocked Spitzbergen Arctic char. Sustained by cannibalism? *Nord. J. Freshwater Res.*, 71, 424 - 431.
- SVÄRDSON, G. 1979. Speciation of Scandinavian Coregonus. *Report of the Institute of Freshwater Research Drottningholm*, 57, 1 - 95.
- SWANSON, H. K. & KIDD, K. A. 2010. Mercury Concentrations in Arctic Food Fishes Reflect the Presence of Anadromous Arctic Charr (*Salvelinus alpinus*), Species, and Life History. *Environmental Science & Technology*, 44, 3286-3292.
- TAKEUCHI, T., MORIKAWA, N., MATSUMOTO, H. & SHIRAISHI, Y. 1962. A pathological study of Minamata disease in Japan. *Acta Neuropathologica*, 2, 40-57.
- THOMANN, R. V. 1989. Bioaccumulation model of organic chemical distribution in aquatic food chains. *Environmental Science and Technology*, 23, 699 - 707.
- TODA, H. & WADA, E. 1990. Use of $^{15}\text{N}/^{14}\text{N}$ ratios to evaluate the food source of the mysid, *Neomysis internedia* Czeriawsky, in a eutrophic lake in Japan. *Hydrobiologia*, 194, 85 - 90.
- 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*, 80, 1395 - 1404.
- VERTA, M. 1990. CHANGES IN FISH MERCURY CONCENTRATIONS IN AN INTENSIVELY FISHED LAKE. *Canadian Journal of Fisheries and Aquatic Sciences*, 47, 1888-1897.

- VINSON, M. R. & BUDY, P. 2011. Sources of variability and comparability between salmonid stomach contents and isotopic analyses: study design lessons and recommendations. *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 137 - 151.
- WALLACE, R. K. 1981. An Assessment of diet overlap indices. *Transaction of the American Fisheries Society*, 110, 72 - 76.
- WARD, D. M., NISLOW, K. H. & FOLT, C. L. 2010. Bioaccumulation syndrome: identifying factors that make some stream food webs prone to elevated mercury bioaccumulation. In: OSTFELD, R. S. & SCHLESINGER, W. H. (eds.) *Year in Ecology and Conservation Biology 2010*.
- WATERLOW, J. C. 1968. The adaption of protein metabolism to low protein intake. In: R.A. MCCANCE, E. M. W. (ed.) *Calorie and Protein Deficiencies*. Boston: Little, Brown and Company.
- WATERLOW, J. C., GARLICK, P. J. & MILLWARD, D. J. 1978. *Protein turnover in Mammalian Tissues and in the Whole Body*, North-Holland, Oxford.
- WATRAS, C. J., BACK, R. C., HALVORSEN, S., HUDSON, R. J. M., MORRISON, K. A. & WENTE, S. P. 1998. Bioaccumulation of mercury in pelagic freshwater food webs. *Science of The Total Environment*, 219, 183-208.
- WATRAS, C. J. & BLOOM, N. S. 1992. Mercury and methylmercury, in individual zooplankton: Implications for bioaccumulation. *Limnology and Oceanography*, 37, 1313-1318.
- WERNER, E. E. & HALL, D. J. 1979. Foraging efficiency and habitat switching in competing sunfishes. *Ecology*, 60, 256 - 264.
- WESTGAARD, J. I., KLEMETSEN, A. & KNUDSEN, R. 2004. Genetic differences between two sympatric morphs of Arctic charr confirmed by microsatellite DNA. *Journal of Fish Biology*, 65, 1185 - 1191.
- WHO 1989. Mercury - Environmental aspects. *Environmental Health Criteria 86*. Geneva.
- WHO 1990. Methylmercury. *Environmental Health Criteria 101*. Geneva.
- YOSHIOKA, T., WADA, E. & HAYASHI, H. 1994. A stable isotope study on seasonal food web dynamics in a eutrophic lake. *Ecology*, 75, 835 - 846.
- YU, R.-Q., ADATTO, I., MONTESDEOCA, M. R., DRISCOLL, C. T., HINES, M. E. & BARKAY, T. 2010. Mercury methylation in Sphagnum moss mats and its association with sulfate-reducing bacteria in an acidic Adirondack forest lake wetland. *Fems Microbiology Ecology*, 74, 655-668.

- ØSTBYE, K., AMUNDSEN, P.-A., BERNATCHEZ, L., KLEMETSEN, A., KNUDSEN, R., KRISTOFFERSEN, R., NAESJE, T. F. & HINDAR, K. 2006. Parallel evolution of ecomorphological traits in the European whitefish *Coregonus lavaretus* (L.) species complex during postglacial times. *Molecular Ecology*, 15, 3983 - 4001.
- ØSTBYE, K., BERNATCHEZ, L., NAESJE, T. F., HIMBERG, K. J. M. & HINDAR, K. 2005. Evolutionary history of the European whitefish *Coregonus lavaretus* (L.) species complex as inferred from mtDNA phylogeography and gill raker numbers. *Molecular Ecology*, 14, 4371 - 4387.

APPENDIX 1 – TABLES AND FIGURES

Table A1. Correlations for Arctic char, European smelt, profundal whitefish (W.fish P) and littoral whitefish (W.fish L).

Species	Variable	Variable	Test	S/t	ρ/cor	df	p
A. char	Age	Length	Spearman ranks	36299.9	0.653	-	< 0.001
A. char	Age	ln[Hg]	Spearman ranks	386470.8	0.567	-	< 0.001
A. char	Length	ln[Hg]	Spearman ranks	42612.54	0.959	-	< 0.001
A. char	K	$\delta^{13}\text{C}$	Spearman ranks	101983.7	0.161	-	0.131
A. char	K	ln[Hg]	Spearman ranks	361694	0.011	-	0.890
A. char	K	$\delta^{15}\text{N}$	Spearman ranks	156876	-0.291	-	0.005
A. char	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Spearman ranks	137081.1	-0.128	-	0.228
A. char	$\delta^{13}\text{C}$	ln[Hg]	Spearman ranks	96570.99	0.022	-	0.841
A. char	$\delta^{13}\text{C}$	Length	Spearman ranks	79679.77	0.344	-	< 0.001
A. char	$\delta^{15}\text{N}$	ln[Hg]	Spearman ranks	77690.89	0.213	-	0.051
A. char	Length	Primary	Spearman ranks	17373.34	-0.514	-	< 0.001
A. char	Length	Fish	Spearman ranks	6639.837	0.422	-	0.006
E. smelt	Age	Length	Spearman ranks	336239.2	0.469	-	< 0.001
E. smelt	Age	ln[Hg]	Spearman ranks	226465.2	0.464	-	< 0.001
E. smelt	Length	ln[Hg]	Pearson's Product moment	3.875	0.298	154	< 0.001
E. smelt	Length	$\delta^{13}\text{C}$	Spearman ranks	192492.2	-0.057	-	0.567
E. smelt	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Spearman ranks	226584.2	-0.244	-	0.013
E. smelt	$\delta^{13}\text{C}$	ln[Hg]	Spearman ranks	203200.5	-0.184	-	0.066
E. smelt	$\delta^{15}\text{N}$	ln[Hg]	Spearman ranks	127203.4	0.259	-	0.009
W.fish P	Age	Length	Spearman ranks	113621.9	0.574	-	< 0.001
W.fish P	Age	ln[Hg]	Spearman ranks	83105.54	0.689	-	< 0.001
W.fish P	Length	ln[Hg]	Spearman ranks	62227.24	0.767	-	< 0.001
W.fish P	K	ln[Hg]	Pearson's Product moment	-1.774	-0.164	115	0.078
W.fish P	K	$\delta^{13}\text{C}$	Pearson's Product moment	-1.624	-0.186	74	0.109
W.fish P	K	$\delta^{15}\text{N}$	Pearson's Product moment	0.9753	0.113	74	0.333
W.fish P	Length	$\delta^{13}\text{C}$	Spearman ranks	84403.69	-0.154	-	0.185
W.fish P	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Pearson's Product moment	-0.8179	-0.095	74	0.416
W.fish P	$\delta^{13}\text{C}$	ln[Hg]	Pearson's Product moment	-1.3697	-0.157	74	0.175
W.fish P	$\delta^{15}\text{N}$	ln[Hg]	Pearson's Product moment	apr.71	0.492	74	< 0.001
W.fish L	Age	Length	Spearman ranks	291.7	0.781	-	< 0.001
W.fish L	Age	ln[Hg]	Spearman ranks	453.75	0.659	-	0.002
W.fish L	Length	ln[Hg]	Pearson's Product moment	0.7253	0.169	18	0.480
W.fish L	K	$\delta^{13}\text{C}$	Pearson's Product moment	feb.88	0.515	18	0.020
W.fish L	K	ln[Hg]	Pearson's Product moment	-2.7996	-0.551	18	0.012
W.fish L	K	$\delta^{15}\text{N}$	Pearson's Product moment	0.9584	0.220	18	0.351
W.fish L	Length	$\delta^{13}\text{C}$	Pearson's Product moment	4.0862	0.694	18	< 0.001
W.fish L	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Pearson's Product moment	feb.57	0.542	18	0.014
W.fish L	$\delta^{13}\text{C}$	ln[Hg]	Pearson's Product moment	-1.3514	-0.304	18	0.200
W.fish L	$\delta^{15}\text{N}$	ln[Hg]	Pearson's Product moment	0.2158	0.051	18	0.832

Table A2. Significant linear regressions in Arctic char, European smelt, profundal whitefish (W.fish P) and littoral whitefish (W.fish L).

Species	Regression		Slope	Intersept	R ²	F	df	p
A. char	Ln(Age) vs Length		59.34	16.98	0,44	144.8	1,183	< 0.001
E. smelt			5.62	94.94	0.21	40.18	1,154	< 0.001
W.fish P			29.62	204.11	0.33	56.6	1,115	< 0.001
W.fish L			96.98	156.38	0.70	42.01	1,18	< 0.001
A. char	Age vs Ln[Hg]		0.098	-2.61	0.37	101.3	1,173	< 0.001
E. smelt			0.123	-1.88	0.21	41.0	1,152	< 0.001
W.fish P			0.086	-2.10	0.42	82.4	1,115	< 0.001
W.fish L			0.073	-2.51	0.20	4.5	1,18	0.047
A. char	Length vs Ln[Hg]		0.011	-3.26	0.53	197.1	1,178	< 0.001
E. smelt			0.017	-3.25	0.09	15.0	1,154	< 0.001
W.fish P			0.010	-4.03	0.50	115.1	1,115	< 0.001
W.fish L			22.27	335.21	0.03	0.526	1,18	0.478
A. char	$\delta^{15}\text{N}$ vs Ln[Hg]		0.360	12.355	0.045	3.908	1,82	0.051
E. smelt			0.0744	-2.3344	0.04288	4.44	1,99	0.038
W.fish P			0.1846	-3.2908	0.2425	23.69	1,74	< 0.001
W.fish L			0.095	8.834	0.003	0.047	1,18	0.832

Table A3. Comparison between littoral and profundal whitefish.

Variable	Profundal Whitefish	Littoral Whitefish	Test	W/t	df	p
Gill raker	26.5	32	Welch's two-sampled t-test	7.528	28	< 0.001
Length	252	276	Mann-Whitney-Wilcoxon	1725.5	-	< 0.001
Length at age 3	235	257	Welch's two-sampled t-test	2.0535	10	0.067
Weight	131	176	Mann-Whitney-Wilcoxon	1804	-	< 0.001
K	0.81	0.88	Welch's two-sampled t-test	2.9668	27	0.006
Age	4.0	3.5	Mann-Whitney-Wilcoxon	1006	-	0.312
$\delta^{13}\text{C}$	-29.14	-26.34	Mann-Whitney-Wilcoxon	1457.5	-	< 0.001
$\delta^{15}\text{N}$	8.60	8.63	Welch's two-sampled t-test	0.0988	49	0.922
Ln[Hg]	-1.65	-2.19	Welch's two-sampled t-test	5.4215	27	< 0.001