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Mercury in fish from a subarctic watercourse and its relation to trophic ecology

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Abstract

Mercury (Hg) contamination in aquatic ecosystems is a serious concern because it can bioaccumulate and biomagnify to harmful concentrations within a food web and consequently end up in humans that eat polluted fish. The Pasvik watercourse, located in the border area between Norway, Finland and Russia, is strongly affected by the emissions of heavy metals from nearby Russian metallurgic smelters. In this study, the feeding ecology of the fish species present in Pasvik watercourse is examined. Further, Hg contamination in relation to their position in the trophic network and their distance from the local pollution sources is explored. Seven fish species (including three different morphotypes of whitefish, vendace, perch, pike, burbot, brown trout and grayling) were collected from two lakes in the Pasvik watercourse. Lake Vaggatem is located 40 km upstream from the main smelters and Lake Skrukkebukta 16 km downstream. Analyzes of stomach contents, habitat use and stable isotope signatures ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) revealed similar food web structures in the two study lakes, especially in respect to the piscivorous species. However, some trophic differences were evident between the lakes for vendace and two of the whitefish morphs seemingly caused by a more pronounced dominance and ecological effect of the invasive vendace in Vaggatem. In Skrukkebukta, there were significant differences in Hg concentrations between the littoral feeding LSR whitefish and the pelagic foraging DR whitefish. This was not evident in Vaggatem, probably due to the vendace dominance in the pelagic zone of this lake, resulting in a habitat relegation of DR whitefish from the pelagic to the littoral, and a more various diet also including benthic prey for this morphotype. The piscivorous species had higher Hg concentrations than the invertebrate feeders and the concentrations increased with size for the piscivores and for vendace. Pike, perch, vendace and the profundal feeding SSR whitefish had significantly higher Hg concentrations in Skrukkebukta. In addition, the downstream Lake Skrukkebukta showed a significantly higher biomagnification rate than in Vaggatem. It is plausible that the nearby smelters contributed to the significantly higher Hg concentrations in fish from Lake Skrukkebukta. However, the differences in feeding ecology also seems to play an important role. The invasive vendace has restructured the food web to a larger extent in the upstream Lake Vaggatem, which consequently may affect the transfer of Hg in the food web.

1 Introduction

Mercury (Hg) is a major environmental pollutant (Park & Zheng, 2012) included on Norway's priority list of hazardous substances (Christensen et al., 2015). It is a potent neurotoxin that can bioaccumulate and biomagnify in food webs, making it a significant public and ecological health concern (Driscoll et al., 2007; AMAP, 2011). Hg also occurs naturally (Boening, 2000) and can be released to the environment through weathering of rocks, emissions from volcanos or by volatilization from the oceans (Boening, 2000; Park & Zheng, 2012). Anthropogenic Hg originates from burning fuels and other raw materials, or through intentional extraction of the metal for use in industry, agriculture and medicines (AMAP, 2011; Park & Zheng, 2012). Post-industrialization, the Hg emissions from human activities have increased dramatically (AMAP, 2011). While emissions in Europe and North America peaked circa 1990, emissions in Asia have continued to increase (AMAP, 2011).

Hg in the environment (water, sediments and atmosphere) occurs in several chemical forms, both inorganic and organic. One of the most toxic forms of Hg is methyl Hg, MeHg (CH₃Hg), which easily bioaccumulates in organisms (AMAP, 2011). MeHg is produced through methylation of inorganic Hg, which occurs in wetlands and sediments in watersheds, coastal zones and in the upper ocean (Boening, 2000; Driscoll et al., 2013). Both inorganic Hg and MeHg can be assimilated by biota at the lowest levels of food chains, such as phytoplankton, benthic algae and bacteria, but only MeHg biomagnifies (AMAP, 2011). Hg concentrations increase with age (bioaccumulation) and with trophic position (biomagnification) as organisms retain the contaminants their food sources contain, with top predators and older and larger fish typically having the highest Hg concentrations (AMAP, 1998; Boening, 2000; Eagles-Smith et al., 2008).

Predicting the resulting Hg burden in higher trophic-level species is complex since the diet of a particular species can vary over time and space through ontogenetic habitat and/or dietary shifts, or via changes in prey availability (Liu et al., 2011). Karimi et al. (2016) found that pelagic zooplankton generally had higher Hg concentrations than most nearshore benthic invertebrates, resulting in fish with a pelagic diet having higher Hg concentrations than fish relying on benthic prey, a finding that has been supported by several other fish studies (e.g., Power et al., 2002; Karimi et al., 2016; Kahilainen et al., 2017). Benthic invertebrates may also often be of higher quality due to higher caloric content, which will result in a somatic

growth dilution of Hg for the fish that are feeding in this habitat (Karimi et al., 2016). Therefore, both horizontal (habitat) and vertical (trophic) food web structure influence Hg concentrations in fish tissue. One common way to investigate these trophic relationships among biota is the use of stable isotopes of carbon and nitrogen which provide a time-integrated view of diet and trophic position (Power et al., 2002).

Long-range transported contaminants are common in the Arctic (e.g., Sandanger et al., 2013), but local sources of atmospheric emissions and wastewater discharges are also present (Amundsen et al., 2011). The border area of Norway and Russia is heavily affected by these kinds of anthropogenic disturbances and has received considerable attention due to the metallurgical industry on the Russian side of the border. Particularly elevated concentrations of sulfur dioxide (SO₂) and heavy metals have been detected from the two nickel industries in the area (Sandanger et al., 2013). One of them, the Nikel smelters, drains directly into the Pasvik watercourse, the principal freshwater body in the region. UiT The Arctic University of Norway has conducted long-term ecological studies in the Pasvik watercourse since 1991, including examining trends in fish mercury levels (Amundsen et al., 1997; Amundsen, 2015; Amundsen et al., 2019) Preliminary findings indicate that the amount of mercury in fish has increased from 1991 to 2013 (Amundsen, 2015). The contamination levels in fish generally increased with trophic level, with higher amounts of mercury in predatory species than in coregonids. Similarly, the levels of mercury increased with fish size for pike (*Esox lucius*), perch (*Perca fluviatilis*), burbot (*Lota lota*), brown trout (*Salmo trutta*) and vendace (*Coregonus albula*), whereas a similar pattern was not evident for the three whitefish morphs (*Coregonus lavaretus*) present in the watercourse.

The aim of the present study is to enhance the knowledge and understanding of how the feeding ecology of fish in the Pasvik watercourse, their position in the trophic network and their distance from the local pollution sources may impact their Hg contaminations. Two lake localities are explored; Vaggatem and Skrukkebukta, located in the upper and lower parts of the watercourse, respectively. Skrukkebukta is situated downstream, and closer to the Nikel smelters, but previous studies have revealed no significant differences in Hg contaminations in fish between the two lakes (Amundsen et al., 2015; Christensen et al., 2020). The present study firstly addresses any differences in the vertical and horizontal food web structure of the dominant fish species in the watercourse from analyses of habitat use, diet and stable isotope signatures ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$), assessing variations within and between the two lakes. Secondly,

the study explores whether Hg concentrations differ between trophic levels, body size and/or habitats used by the fish, and investigates any differences in fish Hg concentrations between the two localities. Finally, the biomagnification rates in the two lakes are estimated and contrasted to provide a better picture of the biomagnification dynamics of Hg concentrations for the fish species in each lake. Specifically, the study addresses the following hypotheses:

[1] Food web structure as represented by the isotopic range of basal food resources, trophic level, habitat choice and diet are similar for the fish communities in the two lakes.

[2] Piscivorous fish have higher Hg concentrations than invertebrate feeders, while whitefish relying on benthic food sources have lower Hg concentrations than planktonic feeding coregonids. For the piscivores, the Hg concentrations increase with increasing fish size.

[3] There are no significant differences in the Hg concentrations of conspecific fish between Vaggatem and Skrukkebukta.

[4] The biomagnification rate of Hg is similar in the two lakes due to the similar food web structures.

2 Materials and methods

2.1 Study area

The Pasvik watercourse (69° N, 30° E; Figure 1) originates from Lake Inari in Finland, runs north into Russia and then forms the border between Norway and Russia for approximately 120 km, before it drains into the Barents Sea (Amundsen et al., 2011). The Norwegian-Russian part of the watercourse has a total area of 142 km² (Bøhn & Amundsen, 1998). The catchment area of the watercourse is large with an area of 21 000 km², mostly in Finland, with about 5 % located in Norway (Amundsen et al., 2011; Tervo et al., 2018). There are seven water impoundments (hydropower reservoirs) in the watercourse between Lake Inari and the Barents Sea. Thus most rapids and waterfalls have disappeared, and today the river system consists primarily of lakes and reservoirs with a mean annual water flow of approximately 175 m³/s at the outlet (Amundsen et al., 2011).

The lakes and reservoirs are ice-free from May/beginning of June to the end of October/early November. The lakes and reservoirs are dimictic and oligotrophic with some humic tributary systems (Amundsen et al., 1997, 1999). Secchi depth ranges from 2 to 6 m (Bøhn et al., 2008). The geology in the region is dominated by bedrock, mainly gneiss and the surrounding landscape is dominated by birch (*Betula* sp.) and pinewood (*Pinus sylvestris*) forests with significant areas of *Sphagnum* bogs (Bøhn et al., 2008). The annual mean air temperature is -0.3°C, and minimum and maximum monthly mean temperatures are -13.5°C (February) and +14.0°C (July), respectively (Amundsen et al., 2009). The mean annual precipitation in the area is 358 mm (Amundsen et al., 1997), but in recent decades there has been demonstrated an increase in both precipitation and temperatures due to climate change (Amundsen, 2015).

The soils in the Pasvik watershed are naturally rich in metals and minerals, with ores having a high content of heavy metals like nickel (Ni) and copper (Cu) in addition to sulfur (S) (Sandanger et al., 2013). About 5 kilometers from the Norwegian border in the Russian town of Nikel, a smelter has been refining nickel since the 1930's (Berglen et al., 2018; Sandanger et al., 2013). In Zapolyarny, located 30 km from Nikel and approximately 15 km from the Norwegian border, there is a briquetting facility. Both industries emit large quantities of sulfur dioxide (SO₂) and metals such as nickel and copper, particulate matter (PM), water vapor, mercury (Hg) and nitrogen oxides (NO_x) (Sandanger et al., 2013). In addition, large quantities of metals are discharged into local water bodies through wastewater and runoff

from the smelters and slag piles (Amundsen et al., 1997; Dauvalter et al., 2011). As elsewhere in the Arctic, deposition of long-range transported contaminants is a concern (Berglen et al., 2018), and heavy metals such as mercury (Hg) can be supplied to the freshwater system via atmospheric deposition within the catchment area (Dauvalter & Rognerud, 2001). Both catchment soils and wetlands are important sources of Hg due to the production and storage of methyl Hg (MeHg) that can be transported to surrounding waters (Rudd, 1995).

The sampling for the study was conducted in two of the lakes in the Pasvik watercourse: Vaggatem and Skrukkebukta. Vaggatem is located about 40 km upstream of the Nickel smelters (Terentjev et al., 2015) and consists of two connected lake sites (see Figure 1): Ruskebukta (69°12' N 29°15' E), with an area of 5.3 km², max depth 15 m and mean depth 3.6 m, and Tjærebukta (69°13' N 29°11' E) with an area of 5.1 km², max depth 26 m and mean depth 6 m (Liso et al., 2013). The second lake, Skrukkebukta (69° 33' N 30° 7' E), is located 16 km downstream of the Nickel smelters (Terentjev et al., 2015) and has an area of 6.9 km², max depth of 38 m and mean depth of 14 m (Liso et al., 2013).



Figure 1: Map of the Pasvik watercourse (69° N, 30° E), indicating the sampled lakes Vaggatem (Tjærebukta and Ruskebukta) and Skrukkebukta and their geographic position at the border regions between Norway, Finland and Russia.

2.2 Fish community and food web structure

Altogether 15 different fish species have been recorded in the Pasvik watercourse. Whitefish (*Coregonus lavaretus*), vendace (*Coregonus albula*), perch (*Perca fluviatilis*), pike (*Esox lucius*), burbot (*Lota lota*), nine-spined stickleback (*Pungitius pungitius*), brown trout (*Salmo trutta*) and grayling (*Tymallus thymallus*) are considered the most important fish species in the study systems (Amundsen, 2015; Terentjev et al., 2015)

The dominant fish species in the Pasvik watercourse is whitefish, which consists of three trophically and genetically separated morphotypes (Præbel et al., 2013; Kelly et al., 2015). They are differentiated, in particular, by their morphology and number of gill rakers, and are referred to as small sparsely-rakered (SSR), large sparsely-rakered (LSR) and densely-rakered (DR) whitefish (Siwertson et al., 2010). The DR whitefish typically occupies the pelagic habitat feeding on zooplankton, whereas the LSR whitefish prefers benthic prey in the littoral habitat (Amundsen et al., 2004). The SSR morph typically feeds on benthic invertebrates in the profundal zone (Kahilainen et al., 2011; Amundsen, 2015).

Vendace is an invasive species in the Pasvik watercourse that has migrated downstream following its introduction to Lake Inari. The first specimens were observed in the upper part of the Pasvik watercourse in 1989 (Amundsen et al., 1999). DR whitefish dominated the pelagic habitat before the invasion of vendace, but have been displaced from that habitat by the more efficient zooplankton feeding vendace throughout much of the watercourse (Amundsen et al., 1999; Bøhn et al., 2008; Sandlund et al., 2013; Amundsen, 2015; Terentjev et al., 2015).

Perch is also numerous in the watercourse and linked to the benthic trophic compartment via its preference for littoral zone feeding (Amundsen, 2015). The diet of perch is life stage-dependent, given the ontogenetic niche shifts that occur as fish grow larger (Amundsen et al., 2003). Adult perch are piscivorous, feeding on nine-spined stickleback and whitefish (Amundsen et al., 2003).

Pike is the top predator in the Pasvik watercourse and is typically a shallow littoral feeder. Like perch, pike undergoes ontogenetic niche shifts (Amundsen et al., 2003). Preferred prey for adult pike mainly consists of whitefish but also nine-spined stickleback. Burbot is another apex predator present in low numbers that feeds in benthic habitats on whitefish and nine-

spine stickleback. In recent years, both pike and burbot have also been found to feed on pelagic residing vendace. Consequently, the separation of the pelagic and benthic food web compartments has become less pronounced since the invasion of vendace (Amundsen, 2015). Nine-spined stickleback plays an important role in the food web and is a dominant prey for the small to intermediate sized predatory fishes, particularly perch, pike and burbot (Amundsen et al., 2003).

The brown trout is the key top predator in the pelagic zone (Jensen et al., 2004; Amundsen, 2015). The species is mostly piscivorous and its main prey consists of coregonids (vendace and DR whitefish). After the watercourse became regulated, the reproduction and recruitment of brown trout was reduced and a compensatory annual stocking of 5000 brown trout > 25 cm has been carried out the last decades (Jensen et al., 2004). Grayling similarly suffered from hydropower reservoir impoundment due to the loss of available running water habitats (Jensen et al., 2004).

2.3 Fieldwork

2.3.1 Water sampling

Water samples were collected at the deeper area of the lakes. In Vaggatem, where the water column was well mixed, only surface water was collected. In Skrukkebukta, the water column was stratified (based on CTD profiles carried out in conjunction with sampling) and water was collected from the surface and at 22 m depth in the hypolimnion. For analysis of total organic carbon (TOC), 100 mL of water was transferred to an acid-washed amber glass bottle, while for total nitrogen (TN) and total phosphorus (TP) analysis, 100 mL of water was transferred to an acid-washed HDPE bottle. Water samples for TOC and TN/TP analyses were preserved with 1 mL concentrated H₂SO₄ and were stored in the dark and refrigerated until analysed.

For MeHg analyses, water was collected in 250 mL trace-metal clean, certified FLPE plastic bottles and stored in double plastic bags. The bottles were pre-loaded with 1 mL of concentrated trace-metal clean HCl. Samples were stored in the dark and at 4°C until analysed.

TOC, TN and TP concentrations were determined using standard and accredited methods at the Norwegian Institute for Water Research (NIVA; Kaste et al., 2017). MeHg analyses were also carried out at NIVA, as described in Braaten et al. (2014a, b).

2.3.2 Fish sampling

Fish sampling was carried out in September 2018 in Skrukkebukta and at two different locations in Vaggatem (Ruskebukta and Tjærebukta), hereafter referred to as Vaggatem unless otherwise stated. Gillnets were set during the evening and removed in the morning in Vaggatem on September 7-9 and in Skrukkebukta on September 10-11. Nets were set in all lake habitats: littoral, profundal and pelagic, with the aim of catching as many fish species and size ranges as possible. In the littoral zone of each lake, two different gill nets were used: bottom multi-mesh gill nets (nine mesh sizes from 10-55 mm) measuring 1,5 m high by 45 m long, and standard gill nets (various coarse mesh sizes), measuring 1.5-2 m high and 30 m long. Bottom multi-mesh gill nets were also used in the profundal zone in both Vaggatem and Skrukkebukta. In the pelagic zone of each lake, floating multi-mesh gill nets (45 m long and 6 m deep) were set above the deepest part of the lake in the upper 6 m, either as a single net or two tied together. Each gillnet was separated into nine panels of 5 m each, with mesh sizes ranging from 6-35 mm.

A total of 1811 and 516 fish were caught in Vaggatem and Skrukkebukta, respectively. The fish were removed from the gill nets and assigned an individual sample number. Whitefish were field-identified and grouped by morphotype by examining gill raker morphology following Kahilainen & Østbye (2006).

The fork length (mm) was measured and fish were weighed (g). For age determination, otoliths from whitefish, vendace, brown trout, burbot and grayling were removed and stored in 96 % ethanol, and cleithrum (pike) and operculum (perch) were sampled and stored in a paper envelope for later analysis in the lab. Stomachs were dissected out and stored in 96 % ethanol until analyzed.

For mercury and stable isotope analyses, subsamples (>5 g) of dorso-lateral muscle tissue were taken from each fish (n=573). For small fish where it was not possible to obtain a filet, the whole fish was sampled. Samples were put in zip-lock plastic bags and frozen at -20°C and stored until further processing.

The fish were divided into different length groups for each lake and species, and a subset of fish was selected for analysis, covering (to the degree that was possible) the following size ranges: < 10 cm, 10-15 cm, 15-20 cm, 25-30 cm, 30-35 cm, 35-40 cm and >40 cm. For the whitefish morphs, perch and vendace that were sampled in high numbers, a subsampling with a maximum of 10 specimens from each size group were randomly selected for the stable isotope and mercury analyses. For pike, burbot, brown trout and grayling, where fewer individuals were sampled, all specimens were used in the analyses. Of the 573 fish sampled for stable isotope and mercury analyses, 387 were selected, including 190 from Vaggatem and 197 from Skrukkebukta (Table 1). Two additional pike sampled in Vaggatem in 2017 are included in the analyses to increase the pike sample size. Thus, 389 fish are used for the analyses.

The length and age distributions of the different fish species differed to some extent between the two lakes (Table 1). There was a higher mean length and age for pike, perch and vendace in Skrukkebukta and the biggest specimens of perch and vendace were also caught there. The biggest pike and the oldest perch were on the other hand caught in Vaggatem. The three whitefish morphs had the highest mean length and age in Vaggatem.

Table 1: Mean length (mm) ± SD and min/max length of all examined individuals for Hg and stable isotope analyses (total n=389), calculated for all individuals (n) of each species, followed by mean age ±SD for all individuals (n) of each species where age data was available (total n=363), separated by lake. Numbers in bold are the highest mean when comparing Vaggatem and Skrukkebukta.

Fish species	Vaggatem								Skrukkebukta							
	n	Mean Length (mm)	±SD	min/max	n	Mean age	min/max	±SD	n	Mean Length (mm)	±SD	min/max	n	Mean Age	±SD	min/max
Pike	21	596.2	163.7	210/950	19	8.3	1/18	4.1	9	664.4	50.2	578/743	9	8.9	2.6	6/15
Perch	45	205.1	66.2	92/315	45	8.0	1/19	4.5	51	225.4	72.2	104/348	51	8.8	4.3	2/15
Burbot	1	440.0	-	-	1	6.0	-	-	5	320.8	76.7	235/440	4	5.0	1.9	3/8
Brown trout	3	475.7	72.6	411/577	-	-	-	-	5	372.2	46.2	296/436	5	4	0.6	3/5
Grayling	1	345.0	-	-	1	6.0	-	-	6	321.5	35.8	262/358	4	4.5	0.5	4/5
LSR whitefish	48	310.8	97.9	131/473	46	6.6	1/12	3	51	186.8	74.9	90/369	50	4.1	3.1	0/13
SSR whitefish	6	181.0	16.7	146/199	6	4.2	3/6	0.9	18	150.2	21.3	124/189	18	6.1	2.9	3/13
DR whitefish	47	203.5	75.9	78/335	39	4.2	0/10	2.9	30	129.1	54.8	61/245	29	2.4	2.2	0/7
Vendace	20	98.4	20.0	64/126	15	1.0	0/3	1.0	22	108.0	31.9	64/164	21	1.4	1.3	0/4
Total:	192				172				197				191			

2.3.3 Invertebrate sampling

Zooplankton was sampled with a 125 µm plankton net. For both pelagic and littoral zooplankton sampling horizontal hauls at a depth of 1-3 m were conducted in both Vaggatem (including Tjærebukta and Ruskebukta) and Skrukkebukta until approximately 3-5 g wet-weight of zooplankton material was collected (hauling for approximately 3-5 minutes). This resulted in a pooled sample of zooplankton material from both the littoral and pelagic zone in each lake.

To collect profundal benthos samples, an Eckman grab was used at a depth of 17 m in Tjærebukta, 14 m in Ruskebukta and 29 m in Skrukkebukta. Littoral benthic invertebrates were collected with kick nets in Vaggatem (Tjærebukta) and Skrukkebukta from soft-bottom sediments in the littoral zone. Additionally, pond snails (*Lymnaea* sp.) were manually picked from littoral rocks. Benthos samples were rinsed with water and passed through a 1 mm sieve. All individuals were grouped by taxonomic family, class or functional group and pooled as separate samples to obtain sufficient sample material (weight) for stable isotope analyses. Collected taxa included: zooplankton (all specimens from the hauls with the plankton net), *Pisidium* sp., gastropods (including *Lymnaea* sp., *Planorbis* sp., in both lakes, additionally *Valvata* sp. in Vaggatem), other insects (including alderflies *Sialis* sp. and caddisflies *Trichoptera* sp.) and profundal chironomids. All samples were stored in polyethylene vials and frozen at -20°C until analyzed.

2.4 Laboratory work and data analyses

2.4.1 Stomach, age and condition factor

The stomachs were opened and the degree of filling (0-100%) of total stomach volume was visually determined. Contents were examined under a stereo microscope, and the prey items were determined to the lowest practical taxonomic level: species, genus or family level. Prey abundance, i.e. the contribution of each prey type to the total stomach fullness was estimated on a percentage scale following Amundsen & Sánchez-Hernández (2019). The different prey types were divided into eight main prey groups; *Acanthocyclops* sp., benthic crustaceans, chironomids (larvae), fish, gastropods, other insects, *Pisidium* sp., surface insects + chironomid pupae and zooplankton.

The otoliths, opercula and cleithra used to determine the age of the fish were submerged in glycerol to clarify structure zonation before being read under a stereo-microscope. The opaque zones were counted from the center and outwards following Holden & Raitt (1974).

The condition factor (Fulton's K) was calculated for each fish based on the length-weight data using the equation:

$$K = \frac{100*V}{L^3} \quad (1)$$

where K is the condition factor of a fish individual, V is the weight (g) and L is the length (cm) of the fish (Nash et al., 2006). The condition factor is believed to be a good indicator of the general fitness of fish, assuming that heavier fish of a given length are in better condition (Booth & Keast, 1986; Bolger & Connolly, 1989). Additionally, the condition factor may be used to assess the effects of pollution on fish populations if other environmental factors affecting the fish are limited (Bervoets & Blust, 2003).

2.4.2 Stable isotopes

Tissue sampling and analysis of stable isotopes

Fish samples used for stable isotope analyses (SIA) were weighed before and after they were freeze-dried under pressures of 10-500 μ bar with a condenser temperature of $\sim -50^\circ\text{C}$ for 50-80 hours depending on species and sample type (whole fish or dorsal chunk). Any skin and bones were removed from the samples prior to freeze-drying. For small fish that were sampled as whole, the dorso-lateral muscle tissue from both sides was picked with a tweezer. For very small fish, all muscle tissue was used from both the dorsal and ventral side.

Once dried, the samples were ground to a fine homogenous powder by hand with an agate mortar and pestle. Between each sample, the mortar and pestle were thoroughly rinsed with distilled water and wiped with lint-free tissues. The powder from each sample was then separated into two different vials, one 2 ml Eppendorf vial (for SIA analyses) and one 14 ml falcon tube (for Hg-analyses).

From the dried homogenized muscle tissue, ~ 0.3 mg was used in the simultaneous analysis of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) stable isotopes and N and C content. All analyses were performed at the Environmental Isotope Laboratory, University of Waterloo, Ontario, Canada,

using a 4010 Elemental Analyzer (Costech instruments, Italy) coupled to a Delta plus XL (Thermo-Finnigan, Germany) continuous flow isotope ratio mass spectrometer (CFIRMS). Results from the stable isotope analyses are given in standard delta notation as:

$$\delta X = \left[\left(\frac{R_{sample}}{R_{standard}} - 1 \right) \right] * 1000 \quad (2)$$

where δX is the delta value of the sample for element X expressed in parts per thousand (permil) (‰), R is the molar ratio of the heavy to light isotope in the sample (numerator) or in an international reference standard (denominator), respectively. The standard for carbon is Vienna Pee Dee Belemnite and for nitrogen it is atmospheric nitrogen (Fry, 2006).

A mix of international and EIL in-house standards were analyzed in each run to determine the accuracy of $\delta^{13}\text{C}$ (IAEA CH3+ CH6 and USGS 40+41) and $\delta^{15}\text{N}$ (IAEA N1+ N2) values, with in-house standards (EIL-72, EGC-3, JSEC-01) cross-calibrated against the relevant international standard. In-house standards were run before, during, and after each batch of analyzed tissue samples as a means of detecting and controlling for analytical drift. Analytical precision was assessed by mean differences of one in ten duplicate samples, where the mean \pm standard deviation was 0.14 ± 0.2 ‰ for $\delta^{13}\text{C}$ and 0.18 ± 0.2 ‰ for $\delta^{15}\text{N}$.

The pooled invertebrate samples were freeze-dried with the same condenser temperature and pressure as the fish samples, but only dried for approximately 30 hours and in the same vials used for storage with the lid left open. After freeze-drying, shells from the mollusks were removed with tweezers. For stable isotope analyses, the same procedure as described above for the fish was used after drying. A sub-set of samples with suspected high CaCO_3 content or where preliminary data indicated higher than expected $\delta^{13}\text{C}$ values were acidified (e.g., Jacob et al., 2005) and repeat analyzed. Acidification was completed by adding 10% HCl to each sample under a fume hood. Samples were then dried, rinsed with distilled water and re-dried immediately in a lab furnace for 24 hours. Where significant differences for a sample group occurred, the acidified $\delta^{13}\text{C}$ values were retained for statistical analyses and paired with the non-acidified $\delta^{15}\text{N}$ data.

Stable isotopes as time-integrated measures of dietary sources and trophic position

$\delta^{15}\text{N}$ offers a time-integrated measure of an organism's trophic position and accounts for temporal and spatial variation in feeding at multiple levels of the food web (Vander Zanden et al., 1997). It has been estimated that the $\delta^{15}\text{N}$ values from plant to herbivore or from herbivore to carnivore increase approximately 2.2-3.4 ‰ in the consumer relative to its diet

(Fry, 2006). $\delta^{13}\text{C}$ can be used to determine primary sources of dietary carbon in organisms (Layman et al., 2012) and is often used to differentiate between consumers that rely on pelagic or benthic resources (Hecky & Hesslein, 1995), since pelagic and profundal primary carbon sources tend to have lower $\delta^{13}\text{C}$ values and littoral primary sources tend to have higher $\delta^{13}\text{C}$ values (France, 1995; Vander Zanden & Rasmussen, 1999). Combined $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ can then be used to relate fish tissue Hg concentrations to position in the foodweb as means of studying bioaccumulation, biomagnification and feeding habitats (Power et al., 2002; van der Velden et al., 2013).

$\delta^{15}\text{N}$ - values can be used to infer a time-integrated estimate of the trophic level (TL) of consumers in a food web by comparing the $\delta^{15}\text{N}$ of consumers relative to the $\delta^{15}\text{N}$ of a baseline defined by primary consumers (Vander Zanden & Rasmussen, 1999). The trophic level can be correlated to Hg concentrations in fish, which makes it a useful tool to track contaminant flows through ecosystems (Cabana & Rasmussen, 1994). Primary consumers have a trophic level of 2.0 and organisms that exclusively feed on primary consumers would have a trophic level of 3.0. In freshwater ecosystems piscivores can reach a trophic level of 5.0 (Vander Zanden & Rasmussen, 1999)

To estimate the $\delta^{15}\text{N}_{\text{baseline}}$, linear regression was used to test for any underlying relationships between the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of primary consumers in each lake. Insects (including *Trichoptera* sp. and *Sialis* sp.) were excluded from baseline estimates since *Sialis* larvae are predatory, while *Trichoptera* include several known predatory taxa. These insects also had higher $\delta^{15}\text{N}$ values than primary consumers in both lakes, further indicating that they occupy a higher trophic level, and supporting their exclusion from baseline estimates. Chironomids were also excluded from the baseline analyses due to the tendency of profundal primary consumers to have high $\delta^{15}\text{N}$ that does not necessarily reflect an elevated trophic position (Vander Zanden & Rasmussen, 1999).

If no underlying relationship was detected, $\delta^{15}\text{N}_{\text{baseline}}$ was set to the mean $\delta^{15}\text{N}$ value for primary consumers from the lake, and was used to calculate TL for each fish from that lake using the following equation:

$$\text{TL}_{\text{fish}} = 2 + (\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{baseline}}) / 3.4 \quad (3)$$

where TL is the trophic level for each fish, 2 is the TL of primary consumers (used as the baseline), $\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{baseline}}$ is the trophic level estimate of the specific fish and 3.4 is the

assumed parts per mil isotopic enrichment for each trophic step (e.g., Vander Zanden et al., 1997; Vander Zanden & Rasmussen, 1999).

If there was a linear relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for the primary consumers in a lake ($p < 0.05$), the mean $\delta^{15}\text{N}$ of primary consumers was not used as a baseline value. Instead, the underlying regression equation for the primary consumers for the lake was used to calculate a representative baseline $\delta^{15}\text{N}$ - value for each fish based on their $\delta^{13}\text{C}$ values as follows:

$$^{15}\text{N}_{\text{baseline}} = a + b (\delta^{13}\text{C}_{\text{fish}}) \quad (4)$$

where $\delta^{15}\text{N}_{\text{baseline}}$ is a calculated for each individual fish based on their $\delta^{13}\text{C}$ values using the regression equation for $\delta^{15}\text{N}$ vs. $\delta^{13}\text{C}$ for primary consumers from the lake (where a is the intercept, b is the slope and $\delta^{13}\text{C}_{\text{fish}}$ is the measured $\delta^{13}\text{C}$ for each fish). The calculated $\delta^{15}\text{N}_{\text{baseline}}$ was used with equation 3 to calculate the TL of each individual fish from that specific lake.

2.4.3 Mercury

Total mercury (THg) analyses were completed with a Milestone DMA 80 (Direct mercury analyzer, DMA-80, Milestone Inc., Shelton, USA) for the same individuals used for stable isotope analyses ($n=389$). Analyses were completed using thermal decomposition followed by atomic absorption spectroscopy following US Environmental Protection Agency (2007) with results expressed as $\mu\text{g g}^{-1}$ dry weight (dw). Certified reference materials (CRMs) were run at the beginning and end of every batch of 30 samples, with no less than 5 blanks run in each sample batch. The method detection limit was determined as $3 \times$ the standard deviation of the machine blanks (0.67 ng Hg). The used CRMs were obtained from the National Research Council of Canada, Canada (Lobster Hepatopancreas; TORT-3 and fish protein; DORM-4). The batch validation criterion was $\pm 10\%$ of the certified value for the reference materials (TORT-3; $0.292 \pm 0.029 \mu\text{g g}^{-1}$, DORM-4; $0.412 \pm 0.041 \mu\text{g g}^{-1}$). The batch was invalidated if the criterion was not met. The percent recoveries of the CRMs (mean percentage of certified value \pm standard deviation) were: TORT-3 (97.9 ± 5.6) and DORM-4 (98.0 ± 5.3). A machine blank was run in duplicate before each batch, as singles between each sample (to remove any possible sample to sample carry-over), between different tissues and taxa and as duplicates at the end of each batch. In addition, a blank nickel boat was run before each batch, between different tissues and taxa and as a duplicate at the end of each batch. DMA results were

acceptable when machine blanks and boat blanks were below 0.1 ng. If the criteria were not met, more blanks were run to clean the machine between each sample.

Approximately 40-50 mg of fine powder from each tissue sample (10-30 mg when sample mass was limited) was placed in nickel boats and combusted in the DMA. Sample duplicates were run every 10th sample, and for each batch, one sample triplicate was run. The mean relative standard deviation was 0.78% for the duplicates (n=42) and for the triplicates 0.92% (n=19).

The criterion for all duplicates and triplicates was a relative standard deviation <10% from the sample mean and were met for all duplicates and triplicates, $\leq 4.7\%$ and $\leq 2.8\%$, respectively. Total Hg concentrations ($\mu\text{g g}^{-1}$ dry-weight) were directly measured in all samples (n=389) with the DMA.

2.5 Statistical analyses

All statistical analyses were conducted with the open-source software Rstudio (version 1.2.5033, Rstudio Inc.) based on R, version 3.6.3 (2020 The R Foundation for Statistical computing).

Hg concentrations were log-transformed to reduce the variance of the data and are hereafter only referred to as Hg. Prior to testing any within and between lake differences in Hg concentrations among the fish species, a Shapiro-Wilk test was run to check if the data were normally distributed.

The data were not normally distributed, and the non-parametric Kruskal Wallis test was used for both lakes separately to determine if Hg concentrations varied significantly among fish species. As the Hg concentrations varied among fish species in both Skrukkebutka and Vaggatem, a non-parametric pairwise Wilcoxon rank-sum test was used to test which species that differed the most from each other within the lakes. Additionally, general linear models (GLM) were used to test the effects of different predictors (length, age, condition factor, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and lakes) on Hg concentrations for each fish species within and between lakes. ANCOVA type III was subsequently adopted to test the main effects. As length had a significant effect on Hg concentrations in all piscivorous fish and vendace (ANCOVA, $p < 0.05$, Table 2), Hg was length adjusted as follow:

$$\text{Hgs} = (\text{Hgi} / s) * L \quad (5)$$

where Hgs is the individual length adjusted Hg concentration, Hgi is the observed Hg concentration for the fish, s is the fish length (mm), and L is the mean fish length (mm) for the fish species within a lake. Length adjustment normalizes data that suffer from strong co-variation between Hg concentrations and fish size (Sonesten, 2003).

A non-parametric Wilcoxon rank-sum test was subsequently used to test between-lake differences in Hg concentrations of conspecific fish (length-adjusted Hg concentrations for the piscivores and vendace).

Biomagnification rates were estimated for both lakes based on the regression of Hg against $\delta^{15}\text{N}$ (giving an estimate of the average change in tissue Hg concentrations with increasing trophic position). The slope of the regression, also referred to as the trophic magnification

slope (TMS), indicates Hg biomagnification in a food web if the slope is >0 (Lavoie et al., 2013). TMS values for each lake were assessed for heterogeneity of variance with Levene's Test. Then ANCOVA was employed to determine if TMS values differ significantly between lakes using Hg as the dependent variable and lake as the independent variable in interaction with the covariate $\delta^{15}\text{N}$.

3 Results

The Secchi depths were 2 - 2.9 m in Vaggatem (Tjærebukta and Ruskebukta, respectively) and 3.5 m in Skrukkebukta. The surface temperature was ~ 13.5 °C in all lakes, with full circulation in Vaggatem and some stratification in Skrukkebukta with a hypolimnion temperature of 8.6 °C (22 m depth).

The water quality were similar in the two lakes but showed slightly higher concentrations of TOC, TP and MeHg in Vaggatem compared to both surface and deep water in Skrukkebukta. Details on physical and chemical variables measured for the water samples are included in Appendix Table 1.

3.1 Food web structure

3.1.1 Habitat use

The habitat distribution of fish was similar between the two lakes with perch and LSR whitefish being most common in the littoral zone and vendace dominating in the pelagic zone with few other species present. In contrast, the profundal zone had several species with fairly high abundances present (Figure 2). The abundance of vendace in the pelagic zone of Vaggatem was much higher (approx. >7x) than in Skrukkebukta. The habitat distribution of DR whitefish differed to some extent between the two lakes with the highest proportion

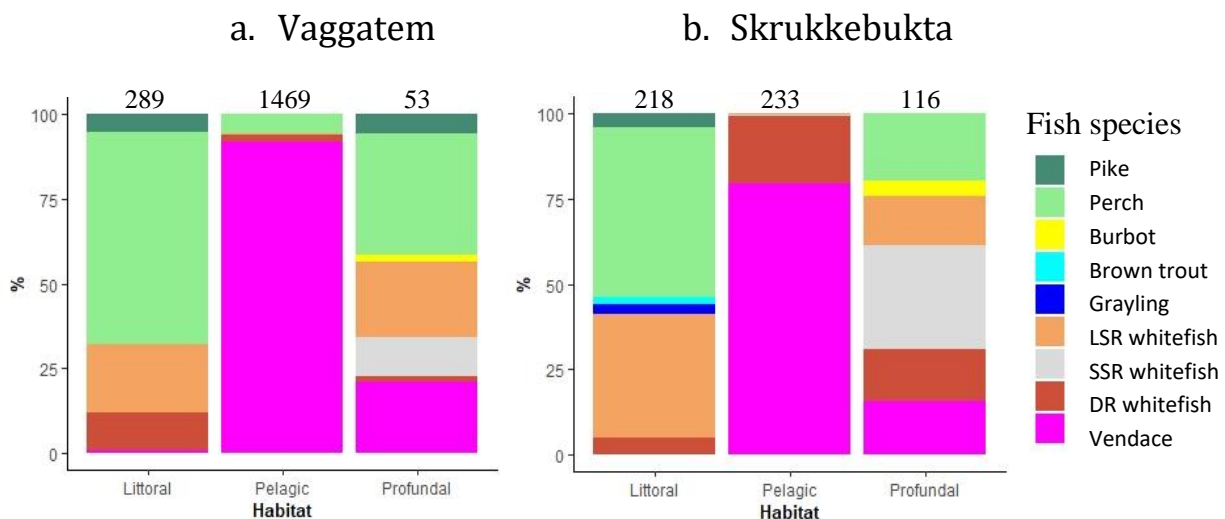


Figure 2: Relative composition of fish (%) of total catch from each habitat from a. Vaggatem b. Skrukkebukta. Numbers of fish caught in each habitat are indicated above the columns.

caught in the littoral zone in Vaggatem and in the pelagic zone in Skrukkebukta. Pike was caught both in the littoral and the profundal zones in Vaggatem, whereas in Skrukkebukta, the species was only caught in the littoral zone (Figure 2).

3.1.2 Diet

Based on gut contents, the fish diet was quite similar between the two lakes for conspecific fish (Figure 3). Pike fed exclusively on fish, while perch mainly had a fish diet but also included the benthic crustaceans *Eurycercus lamellatus* (19%) and *Asellus aquaticus* (14%) in Vaggatem, which differed from Skrukkebukta where benthic crustaceans were nearly absent in their diet (1%) (Appendix Table 2, 3). The diet of LSR whitefish comprised many different prey types in both lakes with other insects being the dominant prey category, mainly including cased *Trichoptera* larvae in both lakes. For SSR whitefish, the dominant prey was *Pisidium* sp. in Vaggatem, whereas *Acanthocyclops* sp., chironomids (larvae) and surface insects + chironomid pupae were the main prey in Skrukkebukta (Figure 3). The diet of DR whitefish differed strongly between the two lakes with zooplankton being the dominant prey in Skrukkebukta, contributing 74 % of the stomach contents compared to only 6 % in Vaggatem. The diet of DR whitefish was generally more variable in Vaggatem than in Skrukkebukta. Zooplankton dominated the diet of vendace in both lakes, although in Vaggatem, vendace also included some benthic prey. There were some size-related

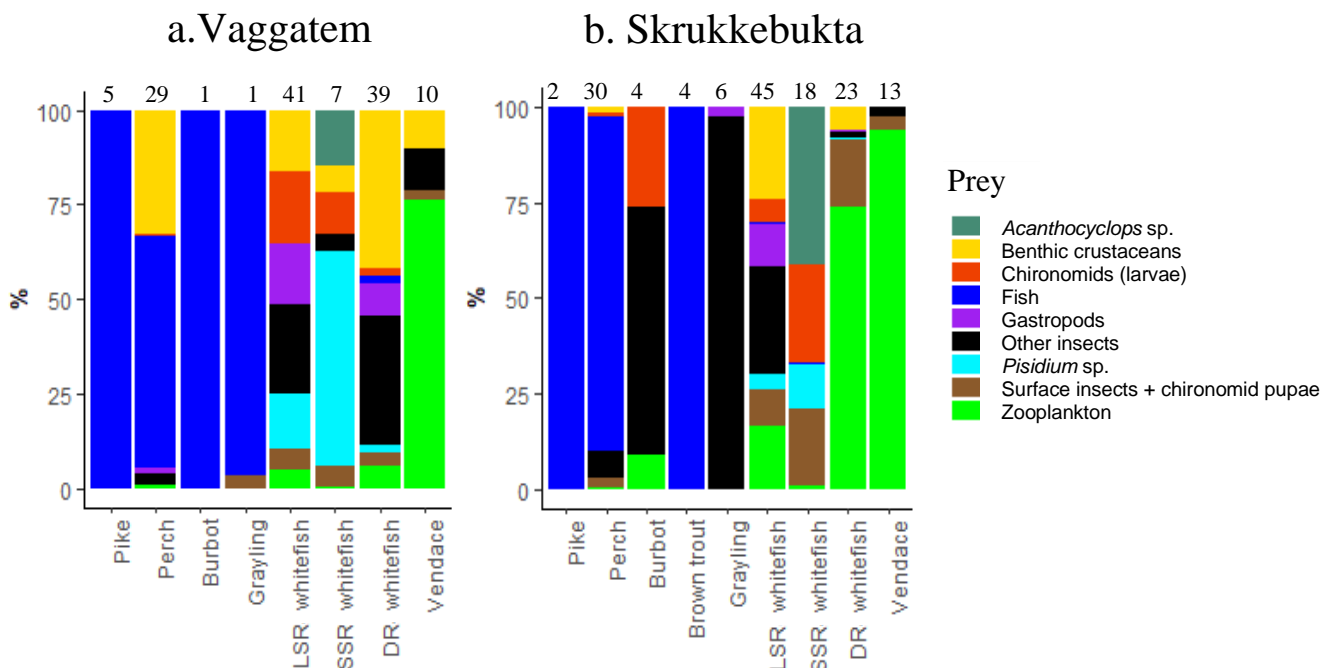


Figure 3: Mean percent abundance of the main prey groups from stomachs of different fish species from a. Vaggatem, b. Skrukkebukta. Numbers of fish with stomach content for each species are indicated above the columns. Stomach contents were scaled up to 100%.

differences in the utilization of prey types in both lakes. Smaller individuals of vendace typically feeding on cladoceran zooplankton while bigger individuals included insects, copepods and chironomid larvae in their diets (Appendix Table 4).

3.1.3 Stable isotopes and food web structure

Based on stable isotope biplots, the food web structure was similar for the two lakes (Figure 4). The fish species with the highest $\delta^{15}\text{N}$ were pike and brown trout (11.0 ± 1 and 10.7 ± 0.7) in Vaggatem and burbot and pike (11.7 ± 0.7 and 11.3 ± 0.5) in Skrukkebukta (Figure 4, Appendix Table 5, Appendix Figure 1). LSR whitefish was the fish species with the lowest $\delta^{15}\text{N}$ in Vaggatem, while DR whitefish had the lowest values in Skrukkebukta. In both lakes, grayling had the highest $\delta^{13}\text{C}$ values, while SSR whitefish had the lowest. Among invertebrates, $\delta^{13}\text{C}$ values were highest in gastropods and lowest in profundal chironomids. The latter also had high $\delta^{15}\text{N}$ -values in both lakes, although other insects had slightly higher values in Vaggatem. Gastropods had the lowest $\delta^{15}\text{N}$ in Vaggatem while *Pisidium* sp. had the lowest values in Skrukkebukta (Figure 4, Appendix Table 6).

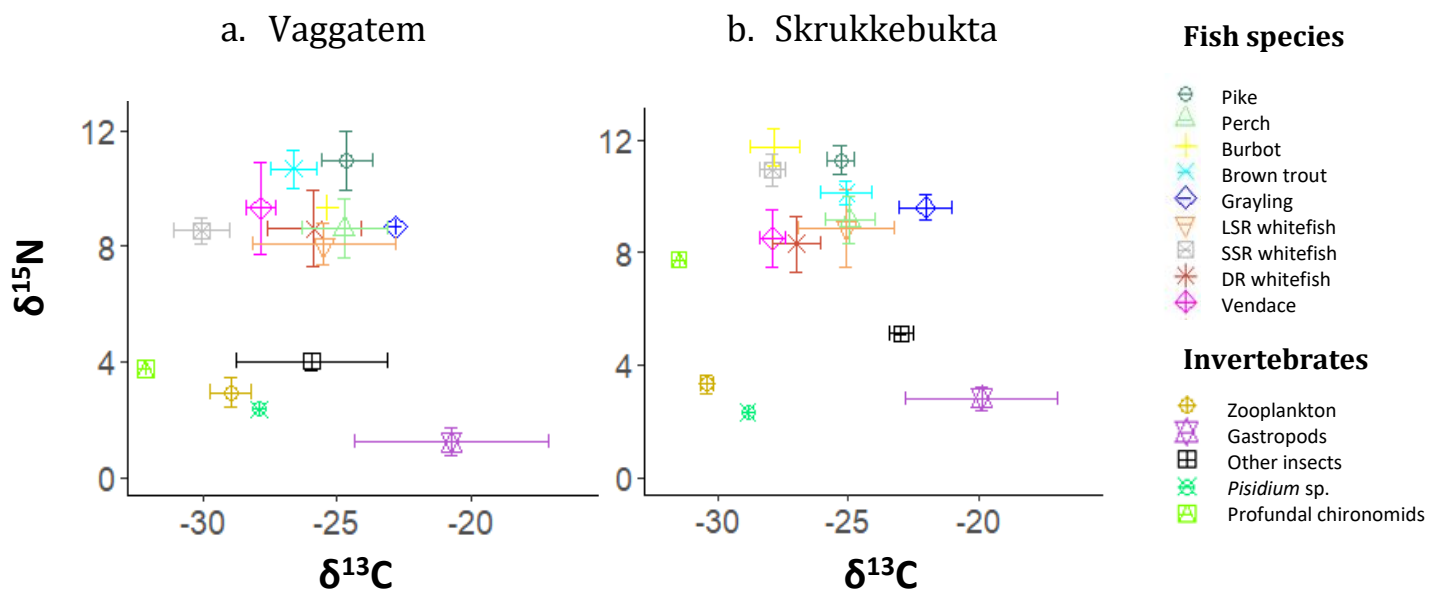


Figure 4: Stable isotope biplots showing the mean values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ($\pm\text{SD}$) of fish- and invertebrate samples from a. Vaggatem and b. Skrukkebukta.

There was a significant linear relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for primary consumers in Vaggatem ($p=0.02$, slope: -0.155 ± 0.05) but not in Skrukkebukta ($p=0.92$, slope: -0.006 ± 0.06) (Appendix Figure 2). The trophic level (TL) estimates for fish are therefore based on the baseline regression equation for Vaggatem and the mean baseline $\delta^{15}\text{N}$ value for Skrukkebukta (Appendix Figure 2).

The piscivores; pike, burbot and brown trout (as well as SSR whitefish in Skrukkebukta) had the highest estimated TL, with pike and burbot having the highest values in Vaggatem and Skrukkebukta, respectively. Perch had similar values to most of the coregonids which were the fishes with lowest TL. In both lakes, there was large individual variation in the trophic level range among the specimens of DR whitefish and vendace (Figure 5) and $\delta^{15}\text{N}$ increased with increasing length of vendace (Appendix Figure 3). Estimated trophic levels tended to be slightly higher for the same species in Vaggatem than in Skrukkebukta. Estimated trophic levels for SSR whitefish were on average one full trophic level higher in Skrukkebukta than in Vaggatem.

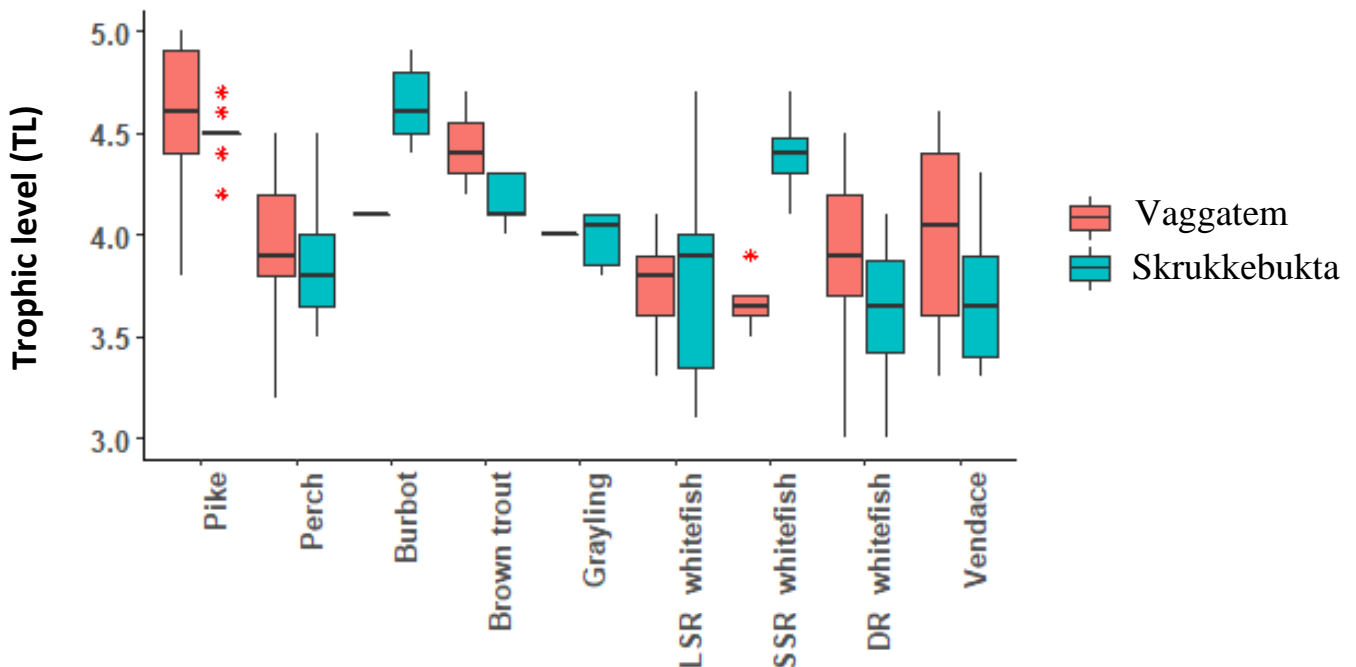


Figure 5: Boxplot of calculated trophic levels for each species, separated by lake: Vaggatem (red) and Skrukkebukta (blue). Outliers are marked with *.

3.2 Mercury

3.2.1 Differences in mercury within the lakes

The highest Hg concentrations were generally found in the piscivores in both lakes, especially in pike and perch. Among the coregonids, SSR whitefish tended to have the highest Hg concentrations, whereas vendace and LSR whitefish had the lowest concentrations in Vaggatem and Skrukkebukta, respectively. Two individuals caught in Skrukkebukta had particularly high Hg concentrations, one perch ($11.8 \mu\text{g g}^{-1}$) and one pike ($6.2 \mu\text{g g}^{-1}$; Appendix Figure 4, Appendix Table 7). Pike, perch, LSR whitefish and DR whitefish tended to have a larger range of Hg concentrations between specimens in contrast to the other species in both lakes (Appendix Figure 4). For most species, the Hg concentrations increased with fish size, except for brown trout in Vaggatem and LSR and SSR whitefish in Skrukkebukta (Appendix Figure 5).

Differences in Hg concentrations between fish species were significant both in Vaggatem and Skrukkebukta (Kruskal-Wallis: $\chi^2 = 71.62$, $df = 8$, $p < 0.001$ and $\chi^2 = 74.99$, $df = 8$, $p < 0.001$ respectively). Out of 36 pairwise comparisons for Hg concentrations between all fish species within a lake 11 were significant in Vaggatem and 20 in Skrukkebukta (Wilcoxon rank-sum test, all $p < 0.05$, Appendix Table 8,9). Pike had significantly higher Hg concentrations than all other species except for burbot, brown trout, and grayling in Vaggatem and perch in Skrukkebukta.

3.2.2 Predictors of Hg concentrations in fish

Generally, fish length significantly influenced Hg concentrations in piscivorous fish and vendace (Table 2). Age and $\delta^{15}\text{N}$ were also important predictors for Hg concentrations in most species, whereas the condition factor was an important predictor only for SSR whitefish (Table 2). Overall, $\delta^{15}\text{N}$ was a better predictor of Hg concentration than $\delta^{13}\text{C}$ (Table 2) but a weak positive relationship could be seen between $\delta^{13}\text{C}$ and Hg in Vaggatem ($p < 0.001$, slope: 0.05 ± 0.01) but not in Skrukkebukta ($p = 0.942$, slope: -0.001 ± 0.02) (Appendix Figure 6).

Table 2: The four different GLM:s (marked with different colors) used to test the effects of different predictors (factors) on Hg- concentrations for each fish species and each lake separately or both lakes simultaneously when adding lake as an additional factor, to see if lake had an effect on Hg- concentrations. Significant codes are used in the table: $p < 0.001 = ***$, $p < 0.01 = **$, $p < 0.05 = *$ (ANCOVA type III sum-of-squares). PI=pike, PE=perch, LSR=LSR whitefish, SSR=SSR whitefish, DR=DR whitefish, VE= Vendace. The white boxes with a diagonal line is not tested (both lakes are instead only tested simultaneously or separately for each lake)

GLM		Vaggatem and Skrukkebukta						Vaggatem						Skrukkebukta					
Response variable	Factor	PI	PE	LSR	SSR	DR	VE	PI	PE	LSR	SSR	DR	VE	PI	PE	LSR	SSR	DR	VE
Hg	Length	*	***				**		*				***	*	***				
	Age		*	***		***		*		***		***							
	K-factor		*	**						**	***						*		
	$\delta^{15}N$		*				***			***		**	***		***	*			
	$\delta^{13}C$		*								**								
	Lake	**			*														
Hg	Length		***	**		*	**		**	**			***	**	***	*			
	Age	**		***		***		*		***		***							
	$\delta^{15}N$			**			***					**	***		***	**			
	$\delta^{13}C$		*						*										
	Lake	**																	
Hg	Length	**	***			**	***												
	Lake	**	*		***	**													
Hg	$\delta^{15}N$							***	**						***	**		**	***
	$\delta^{13}C$							*				*	*			**			

3.2.3 Differences in mercury concentrations between Vaggatem and Skrukkebukta

Pike, perch, SSR whitefish, DR whitefish, and vendace had significantly higher mercury concentrations in Skrukkebukta than in Vaggatem (Wilcoxon rank-sum test, all $p < 0.05$, Figure 6, Appendix Table 10). Pike, perch, burbot, and SSR whitefish from Skrukkebukta had the individuals with the highest maximum Hg concentrations compared to the same species in Vaggatem. Brown trout, grayling, and LSR and DR whitefish had, on the other hand, higher maximum values in Vaggatem than in Skrukkebukta (Appendix Table 11).

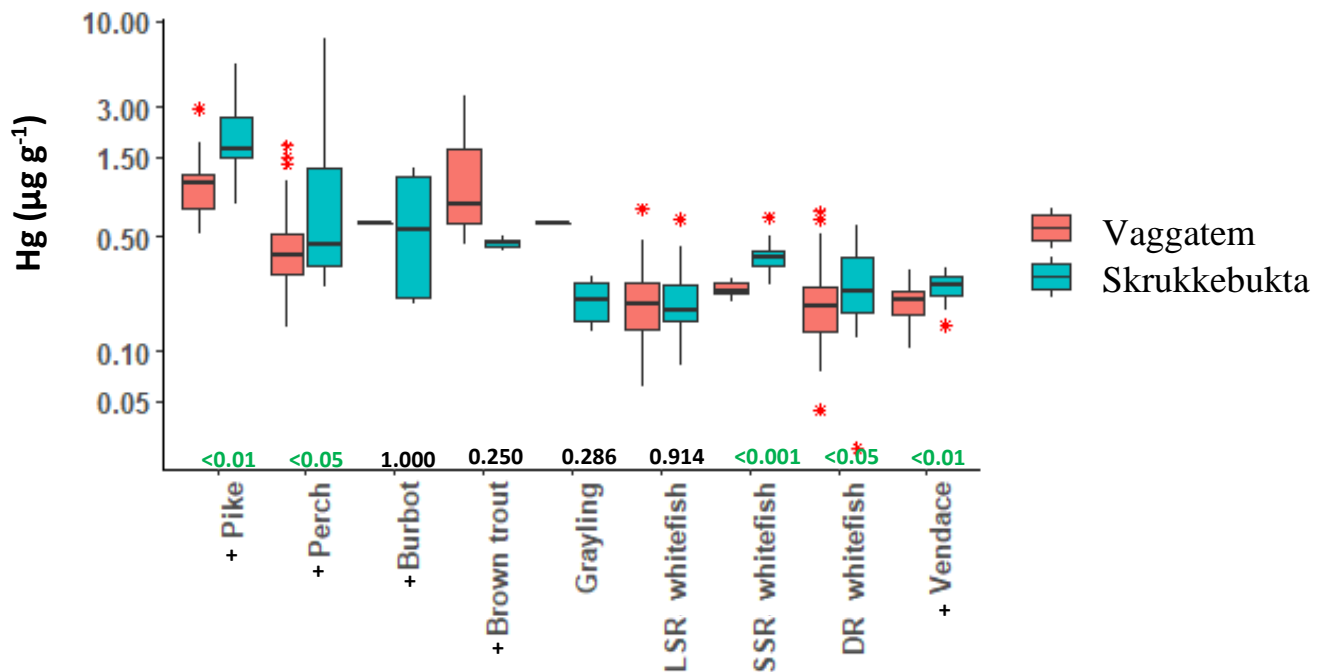


Figure 6: Boxplot of Hg concentrations ($\mu\text{g g}^{-1}$) in dry weight (dw) for each fish species separated by lake, Vaggatem (red) and Skrukkebukta (blue). The y-axis is showing the true Hg concentrations plotted on a logscale. Outliers are marked with *. Species that are marked with + have length adjusted Hg-values. P-values from Wilcoxon Rank Sum test are shown above each species name.

3.2.4 Biomagnification of mercury

There was no significant difference in the variance of Hg concentrations between the two lakes (Levene's Test, $F_{1,387}=0.184$, $p=0.669$). Hg concentrations in fish increased with increasing $\delta^{15}\text{N}$ -values in both lakes ($p<0.001$; Figure 7), indicating biomagnification of Hg in the food webs of the lakes. The regression slope was higher in Skrukkebukta (0.17 ± 0.02) than in Vaggatem (0.11 ± 0.02) and the slopes were significantly different (ANCOVA, $F_{1,385}=6,194$, $p=0.014$).

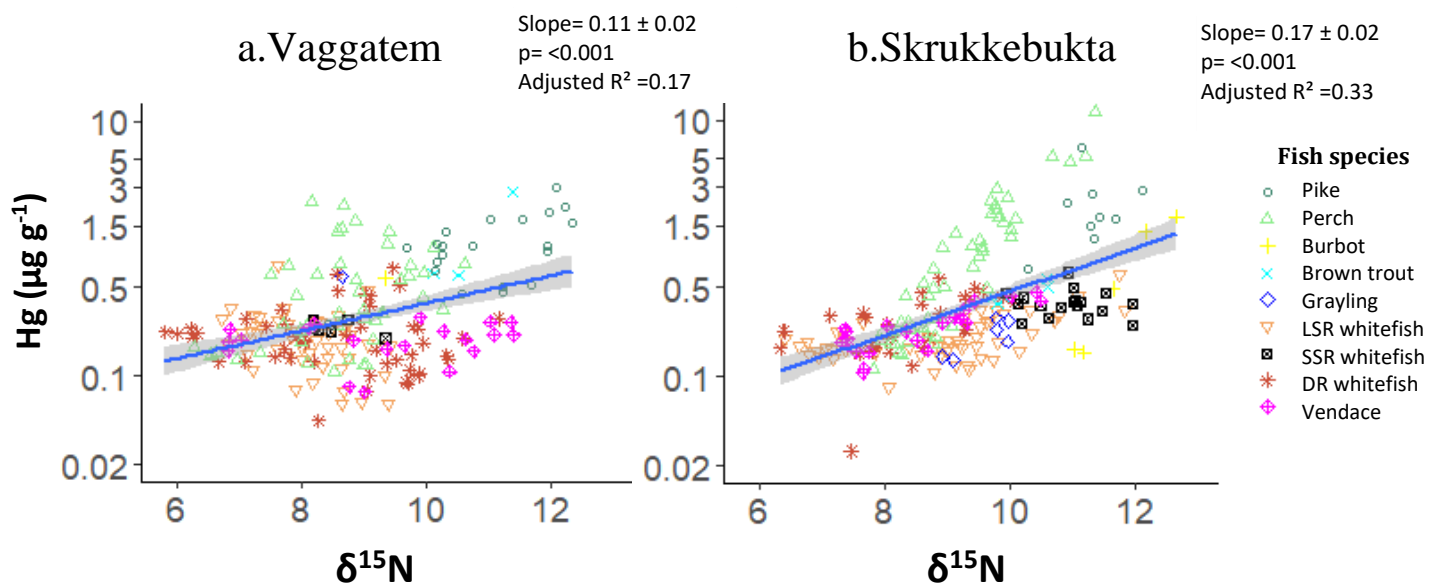


Figure 7. Relationship between Hg in dry weight (dw) and trophic position ($\delta^{15}\text{N}$). The slope shows the biomagnification rate, with 95% confidence intervals marked in grey. The y-axis shows the true Hg-values while the plot and regression line are on log scale.

4 Discussion

The present study showed that the food web structure of the fish community as represented by the habitat use, diet and isotopic signatures of the various fish species was similar between the two study lakes, although with some evident differences related to the trophic ecology of the coregonids. As expected, there were indications that benthivorous fish had lower Hg concentrations than fish feeding on pelagic food sources. As predicted, the Hg concentrations in piscivorous fish increased with size. In contrast to the expectations from previous findings, the current study revealed significant differences in Hg concentrations between the two lakes for most of the studied fish species, with the highest concentrations being found in Skrukkebukta downstream the Nickel smelters. Likewise, the biomagnification rate also differed, the overall pattern being a higher Hg accumulation and biomagnification rate in Skrukkebukta.

Food web structure

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the primary consumers observed in the present study have many similarities with previous studies from oligotrophic lakes (Vander Zanden & Rasmussen, 1999). Primary consumers consistently had lower $\delta^{15}\text{N}$ values than the vertebrates which reflected their low position in the trophic network (Amundsen, 2015). Their $\delta^{13}\text{C}$ values showed large variation with low values (e.g. in zooplankton) reflecting pelagic primary carbon sources such as phytoplankton (Post, 2002). High taxon values (e.g. in gastropods) reflected reliance on littoral primary carbon sources (e.g. benthic algae), and a combination of low $\delta^{13}\text{C}$ and elevated $\delta^{15}\text{N}$ values (e.g. in chironomids) reflected profundal sources (France, 1995; Vander Zanden & Rasmussen, 1999). Among the fishes, pike, perch and burbot were mainly distributed in the littoral zone, although they were also found in the profundal habitats of both lakes. Amundsen et al. (2003) found the same distribution pattern and suggested that these three species constitute a piscivorous guild in the benthic habitats and are important top predators in the Pasvik lakes. The stomach contents data confirmed that fish were an important prey for these species, and this was also supported by their high trophic level positions as estimated from the $\delta^{15}\text{N}$, especially for pike and burbot. Perch had lower $\delta^{15}\text{N}$ and trophic level than all other piscivores and similar isotopic signatures as LSR whitefish. This may reflect the mixed diet of perch and their transitioning in prey choices through their different life stages (Amundsen et al., 2003). Nine-spined stickleback were present in the stomachs of these fish which is a typical prey for perch in the transition stage from invertebrate feeding to a more piscivorous diet (Amundsen et al., 2003). The lower $\delta^{15}\text{N}$ of

perch compared to the other piscivores may therefore also partly be explained by the feeding on nine-spined sticklebacks and its lower position in the food web as shown by Amundsen (2015).

Pike and brown trout which were the top predators in Vaggatem differed in their $\delta^{13}\text{C}$ values, with lower values in brown trout indicating pelagic feeding (primarily on fish) and higher values in pike indicating a preference for littoral feeding. In Skrukkebukta where burbot and pike were the species with highest $\delta^{15}\text{N}$, burbot had lower $\delta^{13}\text{C}$, reflecting a profundal diet in contrast to more littoral feeding pike.

The pelagic zone was to a great extent dominated by vendace in both lakes, but DR whitefish were also quite commonly present in the pelagic zone of Skrukkebukta, which is in line with previous findings (Amundsen et al., 1999; Gjelland et al., 2007; Liso et al., 2013; Kelly et al., 2015). Lower $\delta^{13}\text{C}$ of DR whitefish in Skrukkebukta confirmed greater use of the pelagic zone by these whitefish compared to the DR whitefish in Vaggatem. The higher abundance of DR whitefish in the pelagic zone in Skrukkebukta may be the consequence of a later and less extensive establishment of vendace and thus a less pronounced habitat segregation of DR whitefish compared to Vaggatem (Amundsen et al., 1999; Bøhn & Amundsen, 2001) where DR whitefish were relegated from the pelagic to the profundal and littoral zones after the vendace invasion (Amundsen et al., 1999; Bøhn et al., 2008). Accordingly, most DR whitefish caught in Vaggatem were feeding on benthic prey, in contrast to zooplankton that were their main prey in Skrukkebukta. Gjelland et al. (2007) suggested that Skrukkebukta, which is deeper than Vaggatem, provides a larger and deeper pelagic habitat that can be utilized by DR whitefish to feed on zooplankton without strong competitive interactions with vendace. Gjelland et al. (2009) noted that both DR whitefish and vendace displayed diel vertical migration behaviors, inhabiting cooler, deeper water during the day, which may explain why both species were also found in the profundal zone.

Vendace are specialized zooplankton feeders (e.g., Bøhn et al., 2008), as also indicated from their low $\delta^{13}\text{C}$. Their stomach contents indicated on the other hand that they fed somewhat more on zoobenthos like benthic crustaceans, chironomid larvae and other insects in Vaggatem than in Skrukkebukta, as has been noted in a previous study (Liso et al., 2011). The higher range of $\delta^{15}\text{N}$ and trophic level estimations in Vaggatem for DR whitefish and vendace point to a greater degree of trophic diversity in the diet (Layman & Post, 2008) and reflected in diets consisting of zooplankton and prey from the littoral zone, which is the part

of a lake with the highest abundances, biomass and diversity of benthic macroinvertebrates (Kahilainen et al., 2003).

The observed habitat distributions of SSR whitefish and LSR whitefish are in line with the findings of other studies: the former morph typically residing in the profundal zone and the latter utilizing both littoral and profundal habitats (Bøhn et al., 2008; Kahilainen et al., 2011). Most of the food items in the stomachs of SSR whitefish were invertebrates that are common in profundal habitats, including chironomid larvae, *Pisidium* sp. and *Acanthocyclops* sp. (Amundsen et al., 2008; Kahilainen et al., 2017). Typical littoral invertebrates and insects were present to a certain degree, indicating that SSR whitefish mainly feed in the profundal zone but not exclusively. The low $\delta^{13}\text{C}$ of SSR whitefish confirms a diet mainly consisting of profundal invertebrates but the fact that chironomids have even lower $\delta^{13}\text{C}$ values, also points towards some inclusion of other prey types. Based on $\delta^{15}\text{N}$, SSR whitefish fed almost one trophic level higher in Skrukkebukta than in Vaggatem, which likely reflects the fact that in the deeper Skrukkebukta they may have relied more heavily on profundal invertebrates with high $\delta^{15}\text{N}$ rather than there being an actual difference in trophic level (Kahilainen et al., 2017). Præbel et al. (2013) similarly found particularly high $\delta^{15}\text{N}$ levels in both chironomids and SSR whitefish in Skrukkebukta. The dominant prey for SSR whitefish in Vaggatem was *Pisidium* sp., which had relatively low $\delta^{15}\text{N}$ values compared to chironomids. This seems to confirm that the higher $\delta^{15}\text{N}$ values in SSR whitefish from Skrukkebukta are caused by elevated levels in chironomids and are not a reflection of an elevated trophic position. A similar pattern is typical of profundal invertebrates relying on detritus and dead phytoplankton (Vander Zanden & Rasmussen, 1999), which is why the chironomids were excluded from estimates of baseline $\delta^{15}\text{N}$ in both lakes. The diet of LSR whitefish in both lakes was dominated by typical littoral prey, as has been reported from previous studies (e.g., Amundsen et al., 2004; Kahilainen et al., 2011; van Dorst, 2015). This is also supported by the higher $\delta^{13}\text{C}$ levels seen for the LSR whitefish, which is typical for littoral feeders (Post, 2002). A high $\delta^{13}\text{C}$ level was also evident for the gastropods, which are prey used often to reflect the littoral feeding in a lake (e.g., Post, 2002).

Mercury

Out of the 389 fish that were analyzed for Hg concentrations in muscle tissue, 17 fish exceeded the critical limit for human consumption (0.5 mg/kg wet weight equivalent to approx. 2-2.5 mg/kg dry weight (Kahilainen et al., 2017; Keva et al., 2017). All these fishes were piscivores and mostly included perch >25 cm, some big pike >60 cm, and one brown trout >40 cm. 71% of the fish that exceeded the limits were caught in Skrukkebukta, which is in line with observations from other studies in the watercourse (Christensen et al., 2015; 2020).

In both lakes, the piscivore fish species had higher Hg concentrations than the coregonids. This was expected as Hg biomagnifies in food webs (Morel et al., 1998). Piscivores that consume prey that are positioned at higher trophic levels compared to invertebrate feeders (Morel et al., 1998), will thus typically have the highest Hg concentrations (Amundsen et al., 1997; Amundsen, 2015). This was particularly evident for pike, but could also be seen in perch, burbot and brown trout. Perch that were positioned at a similar trophic level as LSR whitefish, as estimated from their stable isotope signatures, had significantly higher Hg concentrations, suggesting they predominantly preyed on lower trophic level forage fishes such as nine-spine stickleback. Species undergoing ontogenetic dietary shifts often exhibit a sharp increase in mercury concentration when they shift from invertebrates to fish (Lescord et al., 2018), which may explain the differences in Hg concentrations between the piscivorous species. Fish relying on invertebrates for a longer period of time during ontogeny will limit their bioaccumulation for longer, which may explain the significantly higher Hg concentrations seen in pike compared to perch (Neumann & Ward, 1999; Lescord et al., 2018), given that the former switch to piscivory sooner than the latter.

The coregonids, including the three whitefish morphs and vendace, differed to a large extent in their feeding ecology and consequently, in their Hg concentrations, as has been seen for polymorphic European whitefish in other subarctic lakes (Kahilainen et al., 2017). The reliance on zooplankton for vendace in both lakes and for DR whitefish in Skrukkebukta and the contrasting benthic diets of SSR and LSR whitefish likely contributes to these differences. Karimi et al. (2016) found that fish with a cladoceran-dominated pelagic diet had greater Hg concentrations than typical benthic feeding fish. These differences were caused by an overall higher Hg concentration in the prey but were also due to lower growth rates in pelagic. As pointed out in the introduction, benthic prey have higher caloric content and energy per gram consumed than zooplankton, which increases the growth rate for benthic feeding fish (Karimi

et al., 2016). Higher caloric content per gram increases the net biomass gain relative to the amount of ingested Hg (Power et al., 2002; Karimi et al., 2016) and may explain the differences in Hg concentrations seen between DR and LSR whitefish in Skrukkebukta. It would be reasonable to expect that vendace with a similar diet, habitat distribution and stable isotope signatures as DR whitefish in Skrukkebukta would also have significantly different Hg concentrations than LSR whitefish. However, no significant differences were detected. One possible explanation could be that the time of exposure to Hg is more limited in vendace due to their short lifespan (Amundsen et al., 2012), which may decrease the accumulation of Hg (Has-Schön et al., 2015) compared to the more long-lived LSR and DR whitefish (Østbye et al., 2006).

The significantly higher Hg concentrations for SSR whitefish than all other coregonids in Skrukkebukta can be explained by their utilization of the profundal habitat where they typically feed on invertebrates within and on the fine sediments (Keva et al., 2017) that in general have high Hg concentrations compared to pelagic and littoral taxa (Thomas et al., 2016; Kahilainen et al., 2017). Total Hg and MeHg concentrations are higher near the sediments, which is where mercury methylation often occurs (Korthals & Winfrey, 1987), consequently making bottom-feeding fish more prone to exposure from these sediments (Olk et al., 2016). The significantly higher Hg concentrations in SSR whitefish from Skrukkebukta compared to Vaggatem may also be connected to the sediments, with elevated Hg concentrations in the former lake being incorporated in the diet of the fish due to their feeding on substrate surfaces. Christensen et al. (2020) found significantly higher Hg concentrations in sediments from Skrukkebukta than in Vaggatem, which is also evident for Cu and Ni, the heavy metals that are emitted from the smelters in the largest amounts (Sandanger et al., 2013). Chironomids, which are an important mercury source for fish (Chételat et al., 2008), and other profundal invertebrates were the dominant prey for SSR whitefish in Skrukkebukta. Another explanation for the differences in Hg concentrations for SSR whitefish may be that Skrukkebukta is deeper (Gjelland et al., 2007, 2009; Kelly et al., 2015) and thus has a bigger profundal zone more heavily used for foraging by profundal fish, with higher use increasing Hg concentrations. This may occur regardless of any elevated levels in sediments since the profundal zone is where Hg methylation is greatest (Korthals & Winfrey, 1987).

Variation with ontogeny (i.e., size) was the most important explanatory variable for the observed Hg concentrations, with the Hg concentrations significantly increasing with increasing length for most fish species, in particular the piscivores and vendace. A similar

pattern was found in a study carried out in the same localities in 2014 (Amundsen et al., 2015) and has been seen in several other similar studies (Amundsen, 2015; Thomas et al., 2016; Ahonen et al., 2018; Lescord et al., 2018). For vendace, the importance of long-term bioaccumulation would likely be minor due to its short lifespan. The observed increase in Hg levels with length in vendace may instead be related to specific changes in diet as they become bigger (Amundsen, 2015) since smaller vendace typically feed on cladoceran zooplankton and bigger individuals include insects, copepods and chironomids in their diets. This is also supported by the fact that there was a distinct increase in $\delta^{15}\text{N}$ with increasing length of Vendace, indicating an ontogenetic dietary change resulting in a higher trophic level that may be important for the observed size-related increase in Hg concentrations. The importance of elevated $\delta^{15}\text{N}$ values and higher trophic level leading to increased Hg concentrations was particularly evident in the piscivorous fish, as has been shown in numerous other studies (e.g., Power et al., 2002; Eagles-Smith et al., 2008).

The significantly higher Hg concentrations of conspecific fish in Skrukkebukta compared to Vaggatem was not expected as most other studies investigating Hg concentrations in fish in the Pasvik watercourse have not detected any significant differences between the two lakes (Amundsen et al., 1997; Amundsen, 2015; Christensen et al., 2020). However, the current study used larger sample sizes than most of the previous studies, which may facilitated better statistical characterization of the variance and improved the statistical power of difference testing.

MeHg concentrations in water did not differ between the two lakes (Appendix Table 1), however, this is based on only one sampling date. Given that MeHg concentrations can have high spatial and seasonal variability and can respond strongly to changes in water level (Rudd, 1995; Liu et al., 2011), which might be expected in the regulated Pasvik river system, it is not possible to assess whether there are differences in aqueous concentrations of MeHg and food web exposure between these lakes.

The elevated Hg concentrations in perch and pike from Skrukkebukta may be the consequence of a generally higher concentration in the coregonids, which is an important prey for these piscivorous species. As previous mentioned, some perch were caught in the profundal zone, which is a habitat that often has elevated Hg concentrations due to its proximity to the sediments (Korthals et al., 1987; Rudd, 1995; Eagles-Smith et al., 2008). This is the prime habitat for SSR whitefish, which in Skrukkebukta had particularly high Hg

concentrations. This may also have increased the body burdens of Hg for perch that feed in the profundal zone with SSR whitefish as their most likely profundal fish prey. On the other hand, most perch were caught in the littoral zone and the stomach data suggests that they are mostly feeding on littoral fish (9-spined stickleback and whitefish), as has been noted in previous studies (Amundsen et al., 2003). The Hg concentrations clearly increased after perch reached 20 cm, probably caused by a switch to a fish diet (Amundsen et al., 2003). There were generally higher $\delta^{15}\text{N}$ values for the perch in Skrukkebukta compared to Vaggatem, possibly indicating a higher number of piscivorous perch in the former lake (also supported by the stomach content data).

Unlike perch, the biggest and oldest pike were actually found in Vaggatem and had lower Hg concentrations than smaller individuals in Skrukkebukta. While the length distribution of pike in Skrukkebukta was fairly clustered, with all specimens in the range 58-74 cm in contrast to 21-95 cm range seen in Vaggatem, comparisons between the two lakes were made using length-adjusted Hg concentrations. This points to actual differences in Hg concentrations in pike between the two lakes, possibly caused by elevated Hg concentrations in their prey related to the Nikel smelter.

The foraging of vendace and DR whitefish seemed to differ to a certain degree between the lakes, which may have affected the observed differences in Hg concentrations. More specifically, the inclusion of more benthic prey may have caused an Hg dilution in Vaggatem for both vendace and DR whitefish (Karimi et al., 2016). Another explanation could be that vendace and DR whitefish in Skrukkebukta may be affected by the higher Hg concentrations in the sediments as noted by Christensen et al. (2020), due to diel vertical migration behaviours facilitating use of the profundal zone (Gjelland et al., 2009). Additionally, zooplankton are also performing diel vertical migrations, which can further influence the mercury flux from the profundal to the pelagic zone (Kahilainen et al., 2017), thereby increasing Hg concentrations in fish feeding on zooplankton in Skrukkebukta. Thus, it is plausible that the smelter may have an impact on the higher Hg concentration in these fishes in Skrukkebukta.

Biomagnification of mercury

The observed differences in biomagnification rate between Vaggatem (0.11) and Skrukkebukta (0.17) were unexpected as the food web structures of the two lakes were hypothesized to be similar. It should, however be mentioned that the higher rate in

Skrukkebukta is strongly driven by the pike with high Hg concentrations and fairly low $\delta^{15}\text{N}$, thus steepening the regression line. Both biomagnification rates were in line with previous studies from freshwater systems (Clayden et al., 2013; Lescord et al., 2015), although the rate in Vaggatem was lower than most of the observed slopes in other studies of oligotrophic lakes (Clayden et al., 2013). Lescord et al. (2015) suggested that Hg biomagnification can differ between freshwater systems because of their physical and chemical characteristics. The size of the lake can affect the Hg concentrations in biota, which are often positively correlated with increasing surface area and depth as well as with greater catchment area (Evans et al., 2005; Clayden et al., 2013). Hence, the fact that Skrukkebukta is deeper than Vaggatem could possibly be an important contributor to the differences. Vaggatem and Skrukkebukta are surrounded by wetlands which have the potential to affect the Hg input into the lakes. Particulate and dissolved Hg can be transported through organic matter into downstream waters and MeHg is also produced within the wetlands (Driscoll et al., 1995; Rudd, 1995; Grigal, 2002;). The water data showed slightly higher concentrations of TOC, TN and TP in Vaggatem than in Skrukkebukta, which has been observed in earlier studies (Kashulin et al., 2003). Lakes with higher nutrient levels tend to have biota with lower Hg concentrations while higher biomagnification slopes have been detected in lakes with lower nutrients (Clayden et al., 2013). There are some farms and sewages which drain into the watercourse from the surrounding area that may contribute to additional inputs of nutrients (Dauvalter et al., 2011), possibly affecting the lakes differently. However, Sandlund et al. (2013) argued that the agricultural and human activity effects were negligible and did not change the water productivity noticeably within Pasvik watershed.

A likely explanation for the differences in biomagnification may be related to the vendace invasion and the differences in habitat use and diet of the coregonids that the invasion has caused. The dominance of vendace in the pelagic zone may lower ecosystem-wide biomagnification and consequently reduce the mercury transport to the top of the food web in Vaggatem because of the shorter life span and smaller size of vendace than the previous dominant DR whitefish, a pattern that is in line with a previous study from Lake Inari (Thomas et al., 2016). The more mixed diet in Vaggatem than in Skrukkebukta for most coregonids could cause a biodilution of Hg, consequently lowering the overall Hg concentrations in the food web and the slope of the relationship with increasing $\delta^{15}\text{N}$. High prey diversity in the diet, as seen in Vaggatem, may reduce the efficiency of Hg trophic transfer (Lavoie et al., 2013). Lastly, it should be mentioned that the smelters may impact the biomagnification in

some way. Higher Hg concentration in the prey of predatory species could increase the efficiency of the trophic transfer of Hg and the resulting biomagnification. On the other hand, biomagnification of Hg in freshwater systems is complex and increased Hg loading in a system may show the opposite pattern due to cellular competitive mechanisms with other elements (Lavoie et al., 2013). This can result in lower biomagnification in systems with higher Hg concentration in the lower part of the food web. It is therefore difficult to draw any firm conclusions about the smelters effect on the differences in biomagnification between the lakes. Hg concentrations in baseline organisms could be relevant to investigate in further studies.

Conclusions

The current study showed that the food web structure of the fish communities is similar in Vaggatem and Skrukkebukta, especially in respect to the piscivores at the top of the trophic network. Some differences were, however, evident for the coregonids and were probably caused by the more pronounced invasion and establishment of vendace in Vaggatem where it has affected the diet and habitat partitioning of vendace, DR whitefish and LSR whitefish. As hypothesized, the piscivores showed higher Hg concentrations than invertebrate feeders and Hg concentrations increased with size for the piscivores as well as the vendace. The littoral foraging LSR whitefish had significantly lower Hg concentrations than the pelagic foraging DR whitefish in Skrukkebukta. The same pattern was not evident in Vaggatem, probably because of the large dominance of vendace in the pelagic zone in this lake excluded whitefish and lead to a more varied diet in DR whitefish. All fish species that could be analyzed in sufficient sample sizes, had significantly higher Hg concentrations in downstream Lake Skrukkebukta. In this lake, some perch and pike even had Hg concentrations that exceeded the dietary limits for human consumption. An impact of the Nickel smelters on the Hg concentrations in fish from Skrukkebukta is plausible, but the feeding ecology also seems to contribute to the differences between the two lakes. This may mainly be due to impacts of the vendace invasion, which are more pronounced in Vaggatem. Differences between the two lakes in feeding ecology of the coregonids, lake size and depths, nutrients and other chemical parameters may also be affecting the biomagnification rate. Thus further studies are needed to draw any firm conclusions about the relative significance of the various factors contributing to the observed differences in Hg concentration in fish between the two lakes.

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Appendix

Appendix Table 1: Water samples collected in Vaggatem (Tjærebukta: September 8/9 -2018) and Skrukkebukta: September 10/9- 2018) showing total- organic carbon, nitrogen and phosphorous and MeHg.

	Skrukkebukta surface	Skrukkebukta deep (22m)	Vaggatem surface	Unit
Total organic carbon (TOC)	3,8	4,3	5,2	C/l
Total Nitrogen (TN)	94	200	140	µg/l
Total Phosphorous (TP)	5	7	9	µg P/l
MeHg	0.04	0.05	0.06	ng/l

Appendix Table 2: Stomach contents in percentage (%) abundance per prey type for each fish species in Vaggatem and other stomach content information.

Vaggatem								
Prey type	Pike	Perch	Burbot	Grayling	LSR whitefish	SSR whitefish	DR whitefish	Vendace
Acanthocyclops sp.	-	-	-	-	-	14.5	-	-
Benthic crustaceans	-	32.7	-	-	16.4	7.3	41.6	10.4
- <i>Eurycercus lamellatus</i>	-	18.5	-	-	12.8	6.8	40.2	7.5
- <i>Ostracoda</i>	-	-	-	-	0.1	0	0.6	2.9
- <i>Asellus Aquaticus</i>	-	14.2	-	-	3.2	0	0.5	-
- <i>Sida crystallina</i>	-	-	-	-	0.3	0.5	0.3	-
Chironomids (larvae)	-	0.4	-	-	18.8	10.8	2.0	9.3
Fish	100	61.4	100	96.6	-	-	2.4	-
- <i>Burbot</i>	73.3	-	-	-	-	-	-	-
- <i>Ninespined stickleback</i>	2.4	23.8	-	-	-	-	-	-
- <i>Pike</i>	24.3	8.8	-	-	-	-	-	-
- <i>Whitefish</i>	-	-	-	-	-	-	-	-
- <i>Unidentified fish</i>	-	28.8	100	96.6	-	-	2.4	-
Gastropods	-	1.8	-	-	16.0	-	8.3	-
- <i>Lymnaea sp.</i>	-	1.8	-	-	10.5	-	7.5	-
- <i>Planorbis sp.</i>	-	-	-	-	4.5	-	0.5	-
- <i>Valvata sp.</i>	-	-	-	-	1	-	0.3	-
Other insects	-	2.6	-	-	23.6	4.6	34.3	1.8
- <i>Trichoptera pupae</i>	-	-	-	-	-	-	20.8	-
- <i>Trichoptera with house larvae</i>	-	1.2	-	-	22.1	2.8	10.1	-
- <i>Trichoptea without house larvae</i>	-	1.3	-	-	0.6	-	0.3	-
- <i>Ephemeroptera larvae</i>	-	-	-	-	-	-	-	-
- <i>Plecoptera larvae</i>	-	0.1	-	-	-	-	-	-
- <i>Megaloptera larvae</i>	-	-	-	-	-	-	-	-
- <i>Tipulidae larvae</i>	-	-	-	-	-	-	-	-
- <i>Waterbugs</i>	-	-	-	-	0.7	0.2	0.2	-
- <i>Watermites</i>	-	-	-	-	0.1	-	1.5	1.8
- <i>Unidentified insect larvae</i>	-	-	-	-	0.1	1.6	1.4	-
Pisidium sp.	-	-	-	-	15.0	56.9	2.1	-
Surface insects + chironomid pupae	-	0.2	-	3.4	5.6	5.7	3.2	2.5
- <i>Surface insects</i>	-	-	-	3.4	5.3	-	1.9	-
- <i>Chironomid pupae</i>	-	0.2	-	-	0.3	5.7	1.3	2.5
Zooplankton	-	0.9	-	-	4.6	0.2	6.1	76
- <i>Bosmina sp.</i>	-	-	-	-	-	-	0.5	38.4
- <i>Daphnia sp.</i>	-	0.9	-	-	-	-	0.4	30
- <i>Holopedium sp.</i>	-	-	-	-	-	-	-	-
- <i>Bythotrephes sp.</i>	-	-	-	-	1.4	-	-	-
- <i>Polyphemus sp.</i>	-	-	-	-	0.8	0.2	3.5	-
- <i>Cyclopoid copepod</i>	-	-	-	-	2.4	-	1.2	2.9
- <i>Calanoid copepod</i>	-	-	-	-	-	-	0.1	1.1
- <i>Unidentified plankton</i>	-	-	-	-	0.1	-	0.4	3.6
Number of stomachs with content	5	29	1	1	41	7	39	10
Empty stomachs	14	15	0	0	8	3	0	10
Number of stomachs	19	44	1	1	49	10	39	20
Empty stomachs (%)	74	34	0	0	16	30	0	50

Appendix Table 3: Stomach contents in percentage (%) abundance per prey type for each fish species in Vaggatem and other stomach content information.

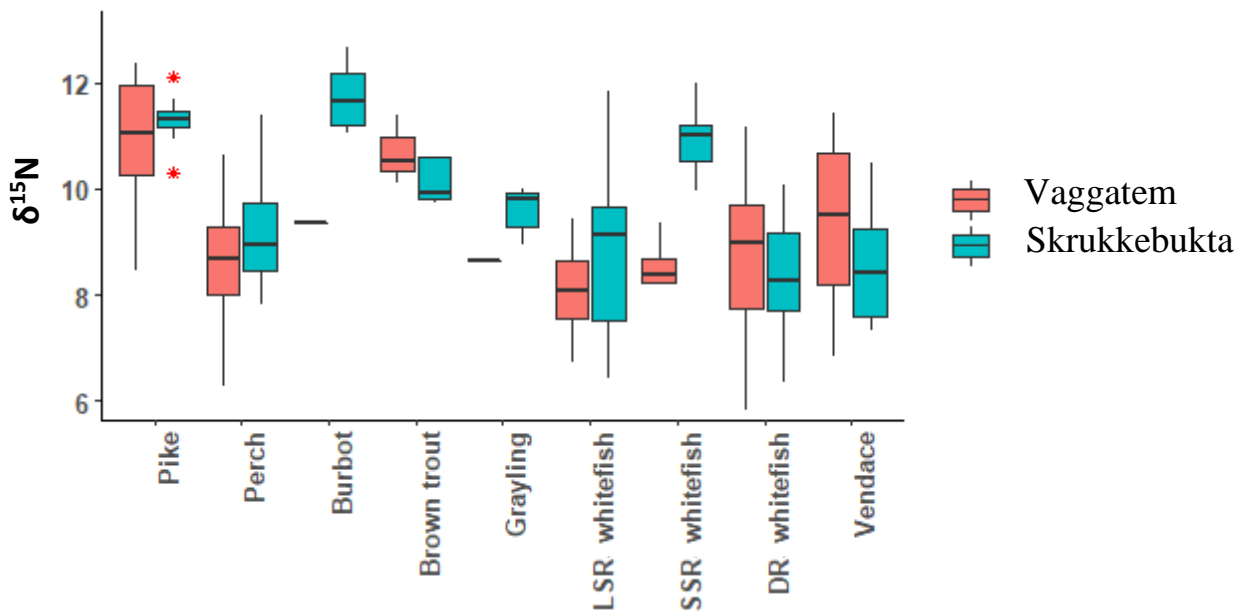
Skrukkebukta									
Prey type	Pike	Perch	Burbot	Brown trout	Grayling	LSR whitefish	SSR whitefish	DR whitefish	Vendace
Acanthocyclops sp.	-	-	-	-	-	-	41.4	-	-
Benthic crustaceans	-	1.2	-	-	-	23.9	-	5.8	-
- <i>Eurycercus lamellatus</i>	-	1.2	-	-	-	23.6	-	5.4	-
- <i>Ostracoda</i>	-	-	-	-	-	-	-	0.4	-
- <i>Asellus Aquaticus</i>	-	-	-	-	-	-	-	-	-
- <i>Sida crystallina</i>	-	-	-	-	-	0.3	-	-	-
Chironomids (larvae)	-	1.2	26.3	-	-	6.0	25.4	0.4	-
Fish	100	87.7	-	100	-	0.8	0.6	-	-
- <i>Burbot</i>	-	-	-	-	-	-	-	-	-
- <i>Ninespined stickleback</i>	-	13.9	-	-	-	-	-	-	-
- <i>Pike</i>	-	-	-	-	-	-	-	-	-
- <i>Whitefish</i>	100	13.1	-	27	-	-	-	-	-
- <i>Unidentified fish</i>	-	60.7	-	73	-	-	-	-	-
Gastropods	-	-	-	-	2.3	11.1	-	0.4	-
- <i>Lymnaea sp.</i>	-	-	-	-	2.3	4.6	-	-	-
- <i>Planorbis sp.</i>	-	-	-	-	-	5.9	-	0.4	-
- <i>Valvata sp.</i>	-	-	-	-	-	0.6	-	-	-
Other insects	-	7.1	64.9	-	97.7	28.0	0.1	1.3	2.5
- <i>Trichoptera pupae</i>	-	-	-	-	-	-	-	-	2.5
- <i>Trichoptera with house larvae</i>	-	3.9	12.3	-	96.0	17	0.1	0.3	-
- <i>Trichoptera without house larvae</i>	-	3	52.6	-	0.5	6.5	-	0.4	-
- <i>Ephemeroptera larvae</i>	-	-	-	-	-	-	-	-	-
- <i>Plecoptera larvae</i>	-	-	-	-	-	2.1	-	-	-
- <i>Megaloptera larvae</i>	-	-	-	-	-	-	-	-	-
- <i>Tipulidae larvae</i>	-	-	-	-	-	-	-	-	-
- <i>Waterbugs</i>	-	-	-	-	1.2	0.4	-	-	-
- <i>Watermites</i>	-	-	-	-	-	-	-	0.5	-
- <i>Unidentified insect larvae</i>	-	0.2	-	-	-	2.0	-	0.1	-
Pisidium sp.	-	-	-	-	-	4.4	11.5	0.8	-
Surface insects + chironomid pupae	-	2.6	-	-	-	9.4	20.1	17.2	3.8
- <i>Surface insects</i>	-	2.6	-	-	-	9.1	17	16.4	3.8
- <i>Chironomid pupae</i>	-	-	-	-	-	0.3	3.1	0.8	0
Zooplankton	-	0.2	8.8	-	-	16.4	0.9	74.1	93.7
- <i>Bosmina sp.</i>	-	0.1	-	-	-	0.2	0.9	57.9	57.5
- <i>Daphnia sp.</i>	-	-	-	-	-	0.1	-	2.8	0.5
- <i>Holopedium sp.</i>	-	-	-	-	-	-	-	-	-
- <i>Bythotrephes sp.</i>	-	-	-	-	-	-	-	-	-
- <i>Polyphemus sp.</i>	-	-	-	-	-	-	-	-	-
- <i>Cyclopoid copepod</i>	-	-	8.8	-	-	14.5	-	9.2	15.3
- <i>Calanoid copepod</i>	-	-	-	-	-	0.3	-	0.3	16.6
- <i>Unidentified plankton</i>	-	0.1	-	-	-	1.3	-	3.7	3.8
Number of stomachs with content	2	30	4	4	6	45	18	23	13
Empty stomachs	7	19	1	1	0	7	6	0	6
Total number of stomachs	9	49	5	5	6	52	24	23	19
Empty stomachs (%)	78	39	20	20	0	14	25	0	32

Appendix Table 4: Stomach content in percentage (%) abundance per prey type for all vendace with stomach contents, separated by length groups, < 100 mm and 100-150 mm for Vaggatem and Skrukkebukta.

Prey type	Vaggatem		Skrukkebukta	
	<100 mm	100 - 150 mm	<100 mm	100 - 150 mm
Benthic crustaceans	2.2	26.3	-	-
- <i>Eurycercus lamellatus</i>	2.2	17.9	-	-
- <i>Ostracoda</i>	-	8.4	-	-
Chironomids (larvae)	8.6	10.5	-	-
Other insects	-	5.3	4.5	-
- <i>Trichoptera pupae</i>	-	-	4.5	-
- <i>Watermites</i>	-	5.3	-	-
Surface insects + chironomid pupae	-	7.4	-	8.5
- <i>Surface insects</i>	-	-	-	8.5
- <i>Chironomid pupae</i>	-	7.4	-	-
Zooplankton	89.2	50.5	95.5	91.5
- <i>Bosmina</i> sp.	50.8	14.7	85.7	22.0
- <i>Daphnia</i> sp.	32.4	25.3	0.7	0.3
- <i>Cyclopoid copepod</i>	4.4	-	1.1	33.2
- <i>Calanoid copepod</i>	1.6	-	1.2	36.0
- <i>Unidentified plankton</i>	-	10.5	6.8	-

Appendix Table 5: Number of specimens within each fish species with mean values of $\delta^{15}\text{N} \pm \text{SD}$ and $\delta^{13}\text{C} \pm \text{SD}$ separated by lake, the same values are presented in Figure 4.

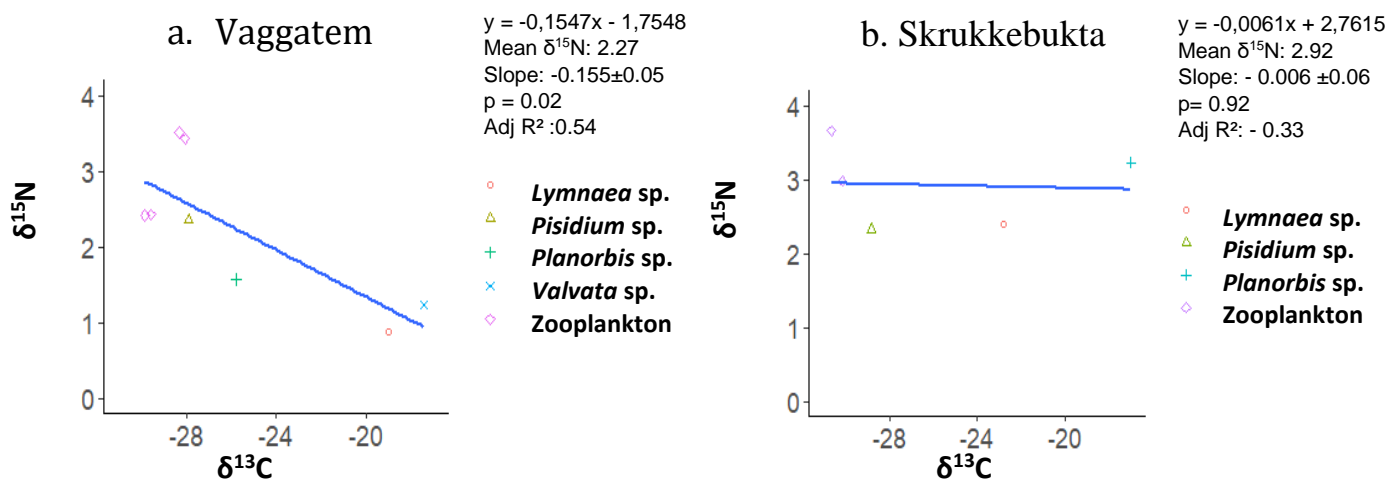
Fish	Vaggatem					Skrukkebukta				
	N	Mean $\delta^{15}\text{N}$	$\pm\text{SD}$	Mean $\delta^{13}\text{C}$	$\pm\text{SD}$	N	Mean $\delta^{15}\text{N}$	$\pm\text{SD}$	Mean $\delta^{13}\text{C}$	$\pm\text{SD}$
Pike	21	11.0	1.0	-24.6	1.0	9	11.3	0.5	-25.3	0.5
Perch	45	8.6	1.0	-24.7	1.6	51	9.2	0.9	-24.9	0.9
Burbot	1	9.3	0.0	-25.4	0.0	5	11.7	0.7	-27.8	1.0
Brown trout	3	10.7	0.7	-26.6	0.9	5	10.1	0.4	-25.1	1.0
Grayling	1	8.7	0.0	-22.8	0.0	6	9.6	0.5	-22.0	1.0
LSR whitefish	48	8.1	0.7	-25.5	2.6	51	8.9	1.4	-25.1	1.8
SSR whitefish	6	8.5	0.5	-30.1	1.0	18	10.9	0.6	-27.9	0.5
DR whitefish	47	8.6	1.3	-25.9	1.7	30	8.3	1.0	-27.0	0.9
Vendace	20	9.3	1.6	-27.8	0.5	22	8.5	1.0	-27.9	0.5



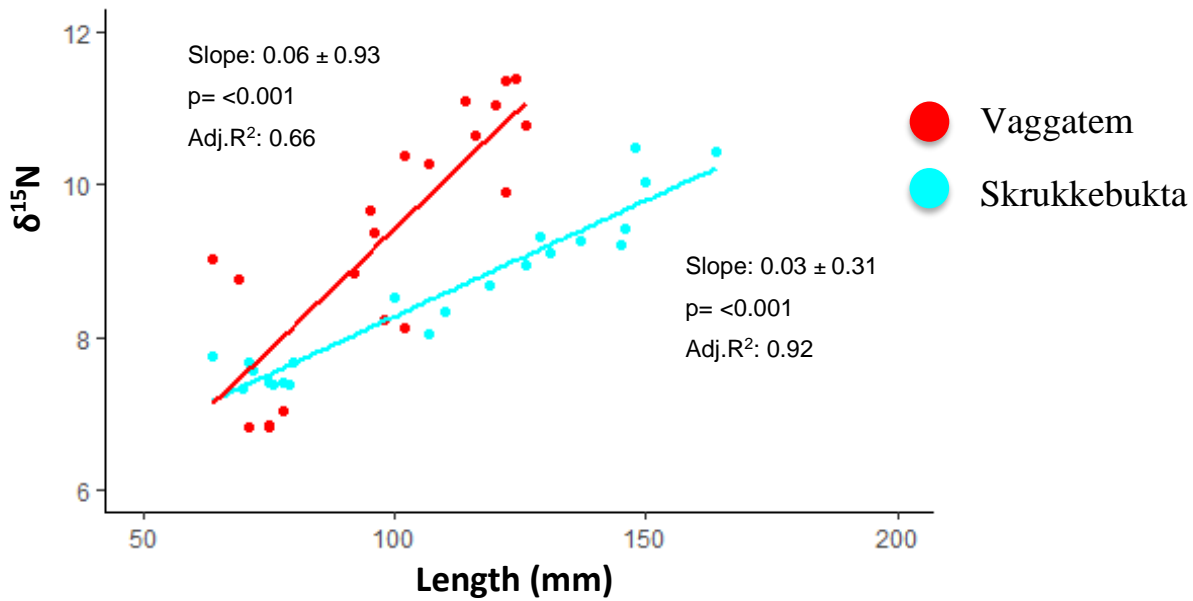
Appendix Figure 1: Boxplot of $\delta^{15}\text{N}$ -values of each species, separated by lake. Outliers are marked with*.

Appendix Table 6: Mean values of $\delta^{15}\text{N} \pm \text{SD}$ and $\delta^{13}\text{C} \pm \text{SD}$ for each invertebrate group that are used in Figure 4.

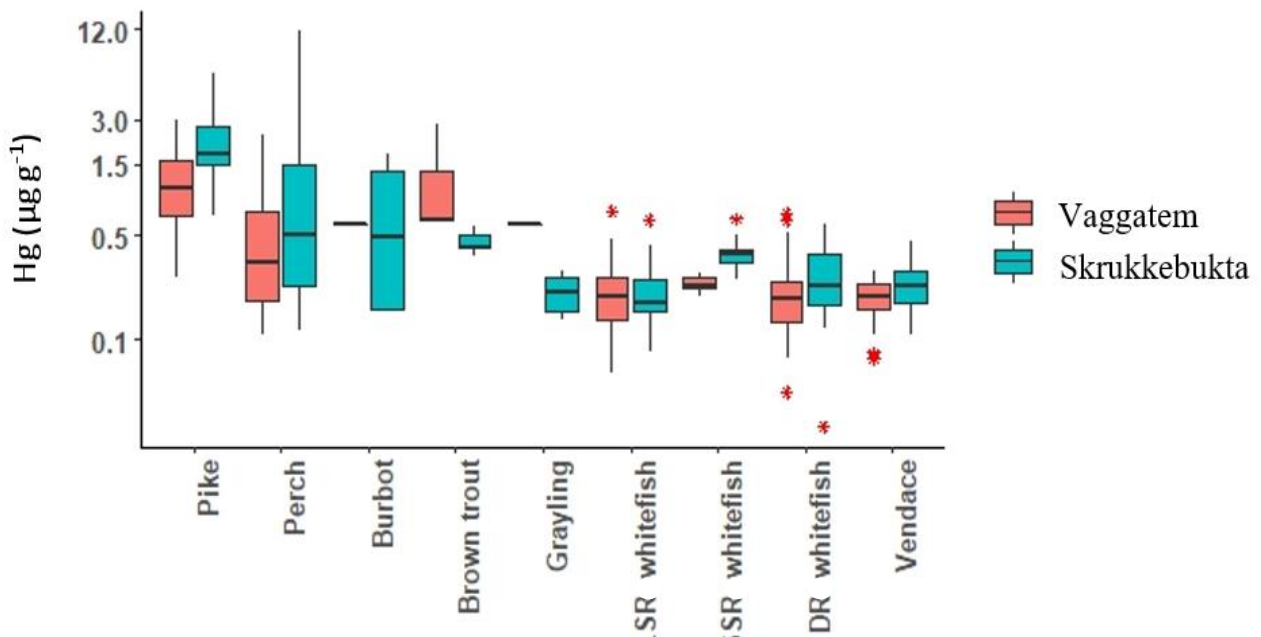
Vaggatem					Skrukkebukta				
Invertebrates	Mean $\delta^{15}\text{N}$	$\pm\text{SD}$	Mean $\delta^{13}\text{C}$	$\pm\text{SD}$	Invertebrates	Mean $\delta^{15}\text{N}$	$\pm\text{SD}$	Mean $\delta^{13}\text{C}$	$\pm\text{SD}$
Zooplankton	2.9	0.5	-29.0	0.8	Zooplankton	3.3	0.3	-30.4	0.3
Gastropoda <i>Lymnaea sp.</i> <i>Planorbis sp.</i> <i>Valvata sp.</i>	1.2	0.5	-20.7	3.6	Gastropoda <i>Lymnaea sp.</i> <i>Planorbis sp.</i>	2.8	0.4	-19.9	2.9
Insecta <i>Sialis sp.</i> <i>Trichoptera sp.</i>	4.0	0.3	-25.9	2.8	Insecta <i>Sialis sp.</i> <i>Trichoptera sp.</i>	5.1	0.0	-23.0	0.5
<i>Pisidium sp.</i>	2.4	0.0	-27.9	0.0	<i>Pisidium sp.</i>	2.3	0.0	-28.8	0.0
Profundal chironomids	3.8	0.0	-32.1	0.0	Profundal chironomids	7.8	0.0	-31.5	0.0



Appendix Figure 2. Estimated linear relationship $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for baseline invertebrates (primary consumers) in **a. Vaggatem** and **b. Skrukkebukta**. The regression equation, slope \pm SE, Adjusted R^2 , mean $\delta^{15}\text{N}$ and p -value are also presented.



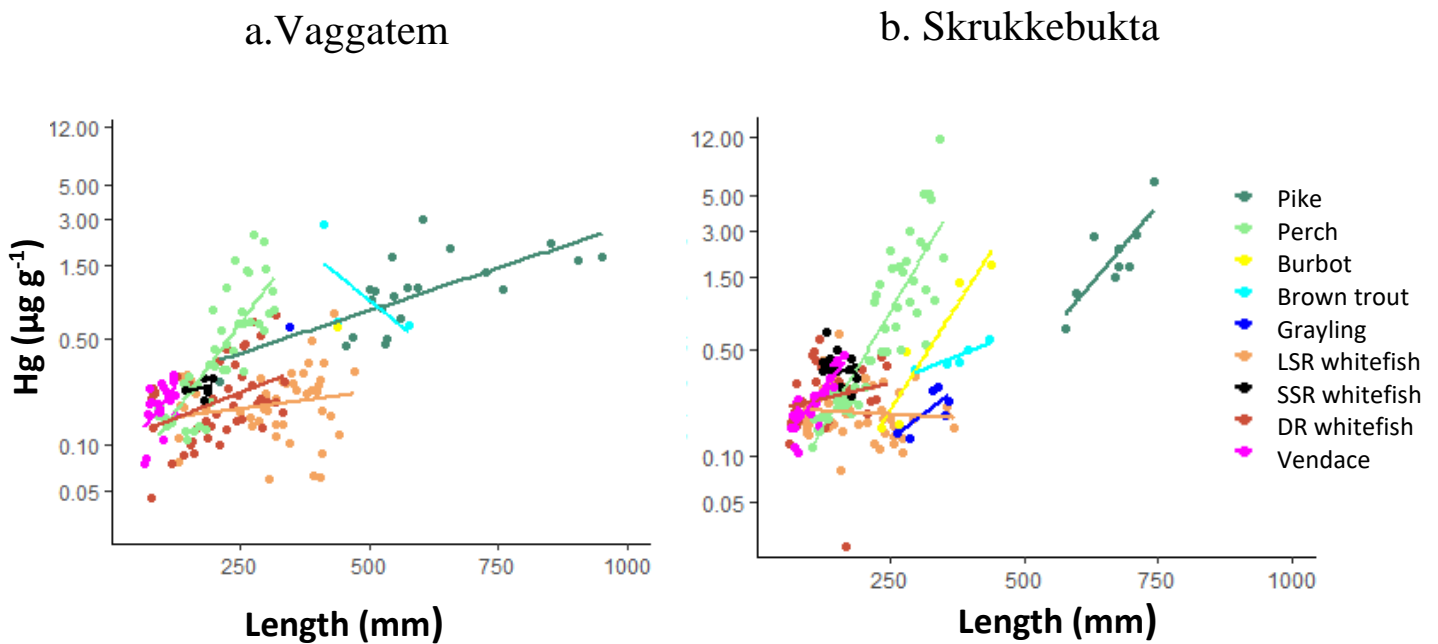
Appendix Figure 3: Relationship between $\delta^{15}\text{N}$ and length (mm) for vendace in Vaggatem (red) and Skrukkebukta (blue). Slope \pm SE, p-value and adj R^2 are indicated above the line for Vaggatem and beneath the line in Skrukkebukta.



Appendix Figure 4: Rawdata of Hg concentrations in dry weight (dw) for each fish species separated by lake, Vaggatem (red) and Skrukkebukta (blue). The y-axis shows the true Hg concentrations ($\mu\text{g g}^{-1}$) while the scale are log-transformed. Outliers are marked with *. Values are also presented in Appendix Table 7.

Appendix Table 7: Raw data for Hg- concentrations presented in boxplot (Appendix Figure 4). N= number of fish, mean Hg +/- standard deviation, median Hg and minimum and maximum Hg-concentrations for a fish species, separated by lake.

	VAGGATEM					SKRUKKEBUKTA				
	N	Mean Hg	+/- SD	Median Hg	Min/Max Hg	N	Mean Hg	+/- SD	Median Hg	Min/Max Hg
PIKE	21	1.15	0.67	1.04	0.23/3.0	9	2.3	1.62	1.73	0.69/6.89
PERCH	45	0.56	0.54	0.33	0.11/2.37	51	1.27	1.95	0.5	0.12/11.8
BURBOT	1	0.59	-	0.59	0.59	5	0.79	0.74	0.49	0.16/1.78
BROWN TROUT	3	1.36	1.26	0.64	0.62/2.81	5	0.45	0.08	0.42	0.37/0.58
GRAYLING	1	0.60	-	0.6	0.6	6	0.21	0.07	0.21	0.13/0.29
LSR WHITEFISH	48	0.21	0.12	0.20	0.06/0.73	51	0.21	0.09	0.18	0.08/0.63
SSR WHITEFISH	6	0.24	0.03	0.23	0.20/0.28	18	0.38	0.09	0.37	0.25/0.65
DR WHITEFISH	47	0.23	0.14	0.19	0.05/0.7	30	0.28	0.13	0.23	0.03/0.59
VENDACE	20	0.19	0.06	0.19	0.08/0.29	22	0.25	0.10	0.23	0.11/0.46



Appendix Figure 5: Relationship between Hg concentrations in μg^{-1} (dw) and length (mm) for each species for a. Vaggatem b. Skrukkebukta. The y-axis shows the true Hg-concentrations while the plot and regression line are on a logscale.

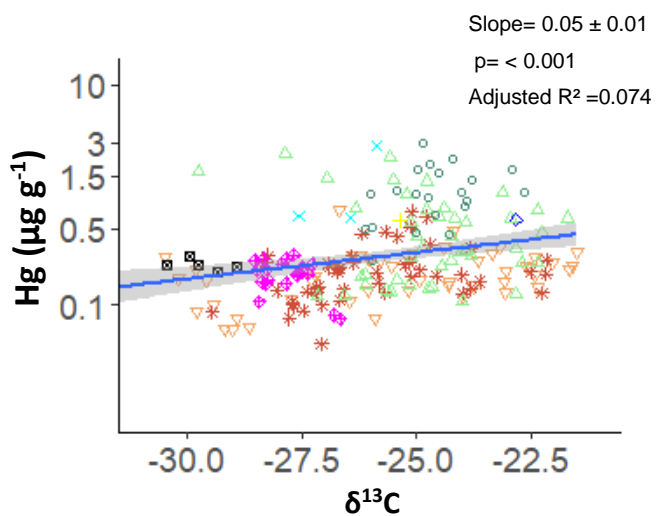
Appendix Table 8: p-values from Pairwise comparison Wilcoxon rank sum test on Hg concentrations between each species within Vaggatem. Bold numbers are statistically significant ($p < 0.05$). 11 out of 36 comparisons in total are significantly different.

Vaggatem								
	Pike	Perch	Burbot	Brown trout	Grayling	LSR whitefish	SSR whitefish	DR whitefish
Pike								
Perch	<0.001							
Burbot	0.677	0.858						
Brown trout	0.962	0.220	0.667					
Grayling	0.677	0.858	1.000	0.667				
LSR whitefish	<0.001	<0.001	0.196	0.002	0.196			
SSR whitefish	<0.001	0.311	0.411	0.071	0.411	0.291		
DR whitefish	<0.001	<0.001	0.225	0.003	0.225	0.962	0.275	
Vendace	<0.001	0.005	0.202	0.004	0.202	0.962	0.172	0.962

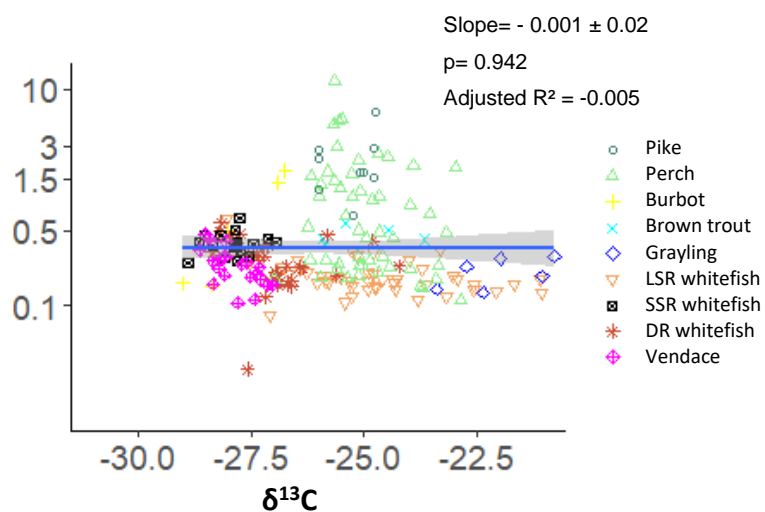
Appendix Table 9: P-values from Pairwise comparison Wilcoxon rank sum test on Hg concentrations between each species within Skrukkebukta. Bold numbers are statistically significant ($p < 0.05$). 20 out of 36 comparisons in total are significantly different

Skrukkebukta								
	Pike	Perch	Burbot	Brown trout	Grayling	LSR whitefish	SSR whitefish	DR whitefish
Pike								
Perch	0.010							
Burbot	0.072	0.681						
Brown trout	0.003	0.796	1.000					
Grayling	0.001	0.031	0.355	0.010				
LSR whitefish	<0.001	<0.001	0.192	0.002	0.847			
SSR whitefish	<0.001	0.380	0.697	0.125	0.001	<0.001		
DR whitefish	<0.001	0.001	0.399	0.020	0.358	0.020	0.011	
Vendace	<0.001	0.002	0.356	0.004	0.593	0.115	0.001	0.654

a. Vaggatem



b. Skrukkebukta



Appendix Figure 6: Relationship between Hg in $\mu\text{g g}^{-1}$ dry weight (dw) and $\delta^{13}\text{C}$ for all species for **a.** Vaggatem **b.** Skrukkebukta. 95% confidence intervals are marked in grey. The y-axis shows the true Hg-values while the plot and regression line are on a log scale.

Appendix Table 10. Wilcoxon rank sum test for comparisons of Hg-values of different fish species between Vaggatem and Skrukkebukta, presented in boxplot (Figure 6) (species that are length adjusted are marked with+)

Species	W	P-value
Pike+	31	0.003
Perch+	800	0.011
Burbot+	3	1.000
Brown trout+	12	0.250
Grayling	6	0.286
LSR whitefish	1208	0.914
SSR whitefish	4	<0.001
DR whitefish	494	0.027
Vendace+	100	0.002

Appendix Table 11: Overview of Hg-individuals that are presented in boxplot (Figure 6), separated by lake. N= number of fish, Mean Hg +/- standard deviation, median Hg-levels and minimum and maximum Hg-levels in individuals within a species. Species that are length adjusted are marked with +.

	VAGGATEM					SKRUKKEBUKTA				
	N	Mean Hg	+/- SD	Median Hg	Min/Max Hg	N	Mean Hg	+/- SD	Median Hg	Min/Max Hg
PIKE +	21	1.11	0.55	1.06	0.51/2.95	9	2.24	1.40	1.69	0.79/5.56
PERCH +	45	0.50	0.37	0.38	0.14/1.76	51	1.03	1.28	0.45	0.24/7.72
BURBOT +	1	0.59	0	0.59	0.59	5	0.68	0.52	0.55	0.19/1.29
BROWN TROUT +	3	1.58	1.68	0.79	0.44/3.51	5	0.45	0.03	0.46	0.41/0.49
GRAYLING	1	0.60	0	0.60	0.60	6	0.21	0.07	0.21	0.13/0.29
LSR WHITEFISH	48	0.21	0.12	0.20	0.06/0.73	51	0.21	0.09	0.18	0.08/0.65
SSR WHITEFISH	6	0.24	0.03	0.23	0.20/0.28	18	0.38	0.09	0.38	0.25/0.65
DR WHITEFISH	47	0.22	0.14	0.19	0.05/0.70	30	0.28	0.13	0.23	0.03/0.59
VENDACE +	20	0.19	0.05	0.20	0.10/0.31	22	0.25	0.05	0.25	0.14/0.33

