Environmental Toxicology

Ecological Drivers of Mercury Bioaccumulation in Fish of a Subarctic Watercourse

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Abstract: Mercury (Hg) is a serious concern for aquatic ecosystems because it may biomagnify to harmful concentrations within food webs and consequently end up in humans that eat fish. However, the trophic transfer of mercury through the aquatic food web may be impacted by several factors related to network complexity and the ecology of the species present. The present study addresses the interplay between trophic ecology and mercury contamination in the fish communities of two lakes in a pollution-impacted subarctic watercourse, exploring the role of both horizontal (feeding habitat) and vertical (trophic position) food web characteristics as drivers for the Hg contamination in fish. The lakes are located in the upper and lower parts of the watercourse, with the lower site located closer to, and downstream from, the main pollution source. The lakes have complex fish communities dominated by coregonids (polymorphic whitefish and invasive vendace) and several piscivorous species. Analyses of habitat use, stomach contents, and stable isotope signatures (δ^{15}N, δ^{13}C) revealed similar food web structures in the two lakes except for a few differences chiefly related to ecological effects of the invasive vendace. The piscivores had higher Hg concentrations than invertebrate-feeding fish. Concentrations increased with size and age for the piscivores and vendace, whereas habitat differences were of minor importance. Most fish species showed significant differences in Hg concentrations between the lakes, the highest values typically found in the downstream site where the biomagnification rate also was higher. Mercury levels in piscivorous fish included concentrations that exceed health authorization limits, with possible negative implications for fishing and human consumption. Our findings accentuate the importance of acquiring detailed knowledge of the drivers that can magnify Hg concentrations in fish and how these may vary within and among aquatic systems, to provide a scientific basis for adequate management strategies. *Environ Toxicol Chem* 2023;42:873–887. © 2023 The Authors. *Environmental Toxicology and Chemistry* published by Wiley Periodicals LLC on behalf of SETAC.

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INTRODUCTION

Mercury (Hg) is a potent neurotoxin that can bioaccumulate and biomagnify in food webs, making it an ecological and public health concern (Arctic Monitoring and Assessment Programme, 2011; Cosio, 2020; Driscoll et al., 2007). Large emissions from anthropogenic activities over the post-industrialization period are the primary sources of Hg pollution (Streets et al., 2011). Local pollution sources constitute a severe

hazard in populated and industrial areas, but long-range atmospheric transport may pose an additional threat to the environment and biota (Pacyna & Keeler, 1995; Pacyna et al., 2010; Sundseth et al., 2017). Freshwater systems are particularly sensitive to depositions of persistent pollutants because they may act as drainage sinks for the surrounding landscape (Wrona et al., 2013). High contamination levels may accordingly build up in lake ecosystems, where the Hg concentrations due to biomagnification may be especially high in predatory fish species at the top of aquatic food webs (Clayden et al., 2013; Kidd et al., 2012), thus representing a serious concern for human consumption of freshwater fish (Chan et al., 2003).

Methylmercury (MeHg), the predominant form of Hg in fish tissues (Bloom, 1992), biomagnifies through food webs because it is accumulated more rapidly than it is excreted by

organisms (Trudel & Rasmussen, 2006). The trophic transfer of Hg through the aquatic food web may be impacted by a number of factors, with the complexity of the fish community and trophic network, and most notably the number of trophic levels, being particularly important in the biomagnification process toward the top fish predators (Clayden et al., 2013; Kidd et al., 2012; Kozak et al., 2021). In addition, at the species and population level, the size and age of the fish may be important factors because larger and older individuals often show elevated Hg concentrations due to bioaccumulation (Backstrom et al., 2020; Burger & Gochfeld, 2011). Size-related patterns in Hg contamination may also be associated with ontogenetic niche shifts because larger piscivorous fish often feed at higher trophic levels, switching diets from invertebrate to fish prey as they grow (Boening, 2000; Eagles-Smith et al., 2008; Sánchez-Hernández et al., 2019).

Habitat use is another important factor that may impact Hg contamination in lacustrine fish (see Eagles-Smith et al., 2008; Karimi et al., 2016). 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 pattern that has also been shown in many other studies (see Chételat et al., 2013; Power et al., 2002; Kahilainen et al., 2017). Benthic invertebrates often have higher caloric content than zooplankton, which may result in somatic growth dilution of Hg in benthic-feeding fish (Karimi et al., 2016). Accordingly, both the horizontal (feeding habitat and food-web compartments) and vertical (trophic level) food web structure may influence Hg concentrations in fish tissue. Consequently, both habitat and diet utilization should be considered in attempting to characterize Hg contamination in fish communities and the potential drivers involved. A useful approach for addressing such trophic relationships is complementing habitat and diet studies with stable isotope analyses (Boecklen et al., 2011; Post, 2002; Vander Zanden & Rasmussen, 1999). The analysis of carbon and nitrogen stable isotopes can provide time-integrated information about diet and trophic position (Fry, 2006), with the carbon isotopes primarily reflecting habitat differences (Hecky & Hesslein, 1995) and the nitrogen isotopes quantifying the trophic level (Layman et al., 2012; Vander Zanden & Rasmussen, 1999).

Long-range atmospheric transported contaminants are widespread in Arctic and subarctic regions (Pacyna & Keeler, 1995; Sonne et al., 2021), whereas local emission sources are particularly important in areas with large industrial activities (Bradley & Morris, 1986; Dauvalter et al., 2011). The border area between Norway and Russia is heavily affected by such anthropogenic disturbances as a result of the metallurgical industry on the Russian side of the border (Amundsen et al., 1997, 2011; Zubova et al., 2020). The Nikel smelter, which over several decades has emitted large amounts of heavy metals (Sandanger et al., 2013; Zubova et al., 2020), is located in the vicinity of and drains wastewaters into the lower part of the Pasvik watercourse (Murmansk Region, Russia), the principal freshwater body in the region. The watershed has a diverse fish fauna for a subarctic region, including eight species commonly occurring in the lacustrine ecosystems that dominate the watercourse. European whitefish (*Coregonus lavaretus*) inhabit the littoral, pelagic, and profundal habitats of the lakes, existing in three distinct morphotypes typically allocated to each of the respective habitat types, with the densely rakered whitefish in the pelagic, the large sparsely rakered whitefish in the littoral, and the small sparsely rakered whitefish in the profundal (Præbel et al., 2013). Perch (*Perca fluviatilis*) is abundant in the littoral zone. Other native lacustrine fish include pike (*Esox lucius*), burbot (*Lota lota*), brown trout (*Salmo trutta*), and grayling (*Thymallus thymallus*). Nonnative vendace (*Coregonus albula*) has over recent decades become the dominant fish species in the pelagic habitat following its invasion in approximately 1990 (Amundsen et al., 1999, 2019; Bøhn et al., 2008). Together, these fish species and morphotypes comprise a complex trophic network in the lakes covering all major feeding habitats and several trophic levels, with pike, burbot, and brown trout as the top predators (Amundsen et al., 2003; Jensen et al., 2004).

The present study addresses how a multiple array of potential ecological drivers, including habitat utilization and feeding ecology of fish, their position in the trophic network, and their proximity to the pollution source, may impact Hg concentrations in the fish community of a pollution-impacted subarctic watercourse. Two lake localities were studied, located, respectively, in the lower and upper parts of the watercourse, the former being situated closer to, and downstream from, the metallurgic smelter. First we explored the horizontal and vertical food web structure of the fish communities using analyses of habitat occupancy, diet, and stable isotope signatures ($\delta^{15}N$ and $\delta^{13}C$) to determine whether any differences existed within and between the two lakes. Second, we studied how Hg concentrations varied with habitat use and diet, trophic level, and body size and age of the fish. We hypothesized that the Hg concentrations would increase with trophic level and size and age of the fish, and with the use of the pelagic habitat and food resources. Finally, we addressed possible differences in the Hg contaminations in fish between the two lakes, hypothesizing that the Hg concentrations would be higher in fish from the downstream lake, situated closer to the potential pollution source. Similarly, we also contrasted the Hg biomagnification rates between the two lakes, hypothesizing that the rate would be higher in the lake closest to the smelter.

MATERIALS AND METHODS

Study area

The Pasvik watercourse (69°N, 30°E; Supporting Information, Figure S1) 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. The Norwegian–Russian part of the watercourse has a total surface area of 142 km². The catchment area of the watercourse is large, with an area of 21 000 km², mostly located in Finland. The regional geology is bedrock, mainly gneiss, and the landscape is covered largely by birch (*Betula* sp.) and pinewood (*Pinus sylvestris*) forests and areas of *Sphagnum* bogs. 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). Mean annual precipitation in the area is 358 mm. There are seven water impoundments (hydropower reservoirs) in the watercourse between Lake Inari and the ocean. 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⁻¹ at the outlet. The lakes and reservoirs are ice-free from May/beginning of June to the end of October/early November, and are dimictic and oligotrophic with some humic impact. The fish communities are an attractive asset of the watercourse, providing for recreational and subsistence fishing and also supporting a small commercial fishery.

The metallurgic industry is located on the Russian side of the Pasvik watercourse in the Russian town of Nikel. The main facility consists of a large smelter located approximately 5 km from the main watercourse, which for several decades has emitted large amounts of sulfur dioxide (SO_2) and heavy metals, in particular nickel and copper, but also Hg (Sandanger et al., 2013; Zubova et al., 2020). Large quantities of metals are also discharged into the local water bodies through wastewater and runoff from the smelter site and associated slag piles (Amundsen et al., 1997, 2011; Dauvalter et al., 2011; Zubova et al., 2020). In December 2020, two years after the current study was carried out, the Nikel smelter was closed.

We took samples from two of the lakes in the Pasvik watercourse, Skrukkebukta and Vaggatem (Supporting Information, Figure S1). Skrukkebukta (69°33′N, 30°7′E) is located 16 km downstream from the Nikel smelter and has an area of 6.9 km², a maximum depth of 38 m, and a mean depth of 14 m. Vaggatem is located 40 km upstream from the Nikel smelter and consists of two openly connected lake areas: Tjærebukta (69°13′N, 29°11′E) with an area of 5.1 km², maximum depth 26 m and mean depth 6 m, and Ruskebukta (69°12′N, 29°15′E) with an area of 5.3 km², maximum depth 15 m, and mean depth 3.6 m.

Sample collections and analyses

Sampling was carried out in the two localities from September 6 to 11, 2018. Fish were sampled using multimesh gillnets with mesh sizes ranging from 6 to 55 mm (knot to knot). The gillnets were set in all the main lake habitats, using 1.5-m-high bottom nets in the littoral and profundal, and 6-m-high floating nets in the pelagic. For the sampling of fish, we obtained permission for gill net fishing from the County Governor of Finnmark with legal authority through LOV 1992-05-15 no. 47 §13. No ethical permission is required from the Norwegian Animal Research Authority for collection with gill nets and the associated euthanization of fish (FOR 1996-01-15 no. 23, the Norwegian Ministry of Agriculture and Food).

A total of 516 and 1811 fish were caught in Skrukkebukta and Vaggatem, respectively. The sampled fish were processed fresh in the field, and samples for the analysis of age, diet, Hg, and stable isotopes were adequately conserved and stored until further processing in the laboratory. Whitefish were identified and grouped by morphotype by examining gill raker morphology following Kahilainen and Østbye (2006). For all

fish, the sampling habitat (i.e., littoral, profundal, or pelagic), weight (g), and fork length (mm) were recorded. For age determination, otoliths were sampled from whitefish, vendace, brown trout, burbot, and grayling, cleithrum from pike, and operculum from perch. The otoliths, opercula, and cleithra were submerged in glycerol to clarify structural zonation before being read under a stereomicroscope. Stomachs were sampled and conserved in 70% ethanol for later dietary analysis, which was implemented using the relative fullness method (Amundsen & Sánchez-Hernández, 2019). The total fullness of all stomach contents was first visually assessed and expressed on a scale from empty (0%) to full (100%). The prey items were determined to the lowest practical taxonomic level, and then the fullness contribution of each prey category was assigned, summing up to the total stomach fullness. Prey abundance, that is, the contribution of each prey type to the total stomach fullness, was estimated on a percentage scale following Amundsen and Sánchez-Hernández (2019). The different prey types were divided into nine main prey categories: zooplankton, *Acanthocyclops* sp., benthic crustaceans, surface insects and chironomid pupae, chironomid larvae, other insects, gastropods, *Pisidium* sp., and fish.

A sample of >5 g of dorsolateral muscle tissue was collected for Hg and stable isotope analyses, frozen at −20 °C, and stored until further processing. For the three whitefish morphs, perch, and vendace that were sampled in high numbers, a subset of fish was selected for analyses, aiming to cover the size ranges of fish present. The remaining fish species were used without subsetting. In total, 389 fish were used for the stable isotope and Hg analyses, including 197 fish from Skrukkebukta and 192 fish from Vaggatem. The length and age distributions of the various 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 largest specimens of perch and vendace were also caught there. On the other hand, the largest pike and the oldest perch were caught in Vaggatem. The three whitefish morphs had the highest mean length and age in Vaggatem.

Samples of zooplankton and littoral and profundal zoobenthos were also collected for stable isotope analysis. Zooplankton was sampled with a 125-μm plankton net using horizontal hauls at a depth of 1–3 m in both localities until approximately 3–5 g of zooplankton material was collected (hauling for approximately 3–5 min). An Eckman grab was used to collect profundal benthos, whereas littoral benthic invertebrates were collected using kick nets with an additional sampling of snails (*Lymnaea* sp.) manually picked from littoral rocks. The grab and kick net samples were passed through a 1-mm sieve, and all retrieved individuals were grouped by taxonomic family, class, or functional group and pooled as required to obtain sufficient sample material for analyses. The collected taxa included: zooplankton (all specimens from the plankton net hauls), *Pisidium* sp., gastropods (including *Lymnaea* sp. and *Planorbis* sp. in both lakes, and in addition *Valvata* sp. in Vaggatem), other insects (littoral chironomids, alderflies *Sialis* sp. and caddisflies *Trichoptera* sp.), and profundal chironomids. All samples were stored in polyethylene vials and frozen at −20 °C until analysis.

TABLE 1: Number of observations (no.), mean length (mm), and age (years) ± SD, and range of all fish examined for the THg and stable isotope analyses in Skrukkebukta and Vaggatem

Fish species	Skrukkebukta								Vaggatem							
	No.	Mean length (mm)	±SD	Range	No.	Mean age (yr)	±SD	Range	No.	Mean length (mm)	±SD	Range	No.	Mean age (yr)	±SD	Range
Pike	9	664.4	50.2	578–743	9	8.9	2.6	6–15	21	596.2	163.7	210–950	19	8.3	4.1	1–18
Perch	51	225.4	72.2	104–348	51	8.8	4.3	2–15	45	205.1	66.2	92–315	45	8.0	4.5	1–19
Burbot	5	320.8	76.7	235–440	4	5.0	1.9	3–8	1	440.0	—	—	1	6.0	—	—
Brown trout	5	372.2	46.2	296–436	5	4	0.6	3–5	3	475.7	72.6	411–577	1	—	—	—
Grayling	6	321.5	35.8	262–358	4	4.5	0.5	4–5	1	345.0	—	—	1	6.0	—	—
LSR whitefish	51	186.8	74.9	90–369	50	4.1	3.1	0–13	48	310.8	97.9	131–473	46	6.6	3	1–12
SSR whitefish	18	150.2	21.3	124–189	18	6.1	2.9	3–13	6	181.0	16.7	146–199	6	4.2	0.9	3–6
DR whitefish	30	129.1	54.8	61–245	29	2.4	2.2	0–7	47	203.5	75.9	78–335	39	4.2	2.9	0–10
Vendace	22	108.0	31.9	64–164	21	1.4	1.3	0–4	20	98.4	20.0	64–126	15	1.0	1.0	0–3
Total:	**197**				**191**				**192**				**172**			

DR = densely rakered; LSR = large sparsely rakered; SSR = small sparsely rakered; THg = total mercury.

Stable isotopes

Stable carbon and nitrogen isotope analyses of fish muscle and invertebrate samples were performed at the Environmental Isotope Laboratory (EIL), University of Waterloo, Ontario, Canada, using a 4010 Elemental Analyzer (Costech Instruments) coupled to a Delta Plus XL (Thermo-Finnigan) continuous flow isotope ratio mass spectrometer. From each sample, approximately 0.3 mg of freeze-dried, homogenized powder was weighed into tin capsules prior to analysis. Stable carbon and nitrogen isotope ratios are expressed in standard delta notation ($\delta^{13}C$ and $\delta^{15}N$, respectively) relative to the international standards for carbon (Vienna PeeDee Belemnite; Craig, 1957) and nitrogen (atmospheric nitrogen; Mariotti, 1983). A mix of international and Environmental Isotope Laboratory in-house standards was analyzed in each run to determine the accuracy of $\delta^{13}C$ (IAEA CH3+CH6 and USGS 40+41) and $\delta^{15}N$ (IAEA N1+N2) values, with the in-house standards (EIL-72, EGC-3, JSEC-01) being 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 1 in 10 duplicate samples, with the mean ± standard deviation being $0.14 \pm 0.2‰$ for $\delta^{13}C$ and $0.18 \pm 0.2‰$ for $\delta^{15}N$. For the fish data, the C:N ratios in general did not exceed 3.5 (98%), with the remaining 2% falling in the 3.5–3.7 range. As a result of the uniformly low C:N values, lipid extraction or correction using mathematical models was not completed (Jardine et al., 2013). For invertebrates, a subset of samples with suspected high $CaCO_3$ content or when preliminary data indicated higher than expected $\delta^{13}C$ values, was acidified (see Jacob et al., 2005) and re-analyzed. When significant differences for a sample group occurred, the acidified $\delta^{13}C$ values were retained for statistical analyses and paired with the nonacidified $\delta^{15}N$ data. Differences in trophic structure between lakes were assessed using the community-wide comparative metrics proposed by Layman et al. (2007). To avoid biases caused by small sample sizes in the estimation of trophic niche space (Jackson et al., 2011), the Bayesian standard ellipse area corrected (SEAc) for sample size was used in place of the convex hull area estimate proposed by Layman et al. (2007), and estimated using Stable Isotope Bayesian Ellipses in R (SIBER; Jackson et al., 2011).

Mercury

We used total mercury (THg) analyses given the focus of fish, the generally high proportion of MeHg in THg (typically >90%) measured in fish (see Bloom, 1992; Madenjian et al., 2016; Riget et al., 2000), and the strong positive correlation observed between the two when assessed simultaneously in northern fish (Jewett et al., 2003). All THg analyses were completed with a Milestone Direct Mercury Analyzer (model DMA 80) for the same individuals used for the stable isotope analyses ($n = 389$). Analyses were completed using thermal decomposition followed by atomic absorption spectroscopy following US Environmental

Protection Agency (2007) method 7473, with results expressed as $\mu g\,g^{-1}$ dry weight. Certified reference materials (CRMs) were run at the beginning and end of every batch of 30 samples, with no fewer than five blanks run in each sample batch. The method detection limit was determined as 3× the standard deviation of the machine blanks (0.67 ng Hg). The CRMs used were obtained from the National Research Council of Canada (DORM-4; TORT-3, and fish protein; Lobster Hepatopancreas). The batch validation criterion was ±10% of the certified value for the reference materials (TORT-3: $n = 28$, $0.292 \pm 0.029\,\mu g\,g^{-1}$; DORM-4: $n = 28$, $0.412 \pm 0.041\,\mu g\,g^{-1}$). The percentage recoveries of the CRMs (mean percentage of certified value ± standard deviation) were: TORT-3 ($n = 28$, 97.9 ± 5.6) and DORM-4 ($n = 28$, 98.0 ± 5.3). Machine blanks were run in duplicate before each batch and between different tissues and taxa to remove any possible carry-over effects. All results were considered acceptable when machine blanks and boat blanks were below 0.1 ng.

Statistical analyses

Statistical analyses were conducted with the open-source software RStudio (Ver 2022.02.1) based on R (Ver 4.2.0; R Core Team). Between-lake dietary differences were analyzed for each fish species separately using contingency tables and Fisher's exact test. Total Hg concentrations were log10-transformed to reduce skewness and normalize data; however, the assumption of normal distribution was not met for all fish species. Hence, within-lake and between-species differences in THg concentrations were assessed with a Kruskal–Wallis rank sum test followed by a pairwise Wilcox rank-sum test using the Benjamini–Hochberg correction (Benjamini & Hochberg, 1995). To assess between-lake differences in THg concentrations among fish species, a pairwise Wilcox rank-sum test with the Benjamini–Hochberg correction was used on length-adjusted THg concentrations. Length-adjusted THg concentrations improve comparability among fish of different sizes and species and normalize data that suffer from strong covariation between THg concentrations and fish size (Sonesten, 2003). Total Hg was length adjusted for each fish species as follows:

$$THg_{adj} = THg_{obs} \times (L_{mean}/L)^{b} \qquad (1)$$

where THg_{adj} is the individual length-adjusted THg concentration, THg_{obs} is the observed THg concentration for the fish, L is the fish length (mm), L_{mean} is the mean fish length (mm) for the actual fish species, and b is the slope of a linear regression between log THg and log L.

Before conducting any further statistical analyses, $\delta^{15}N$ values were baseline-corrected to improve comparability between lakes and are referred to as $\delta^{15}N_{corr}$. Trophic metrics (e.g., $\delta^{15}N$ and $\delta^{13}C$ ranges, mean distance to centroid) were computed following methods described in Layman et al., 2007) and tested for between-lake differences using analysis of variance (ANOVA; see Zar, 2018) or Levene's homogeneity of variance test (Zar, 2018).

Fish generally grow larger with age. Thus the two variables are not independent and might present multicollinearity issues when dealing with THg concentrations in subsequent analyses. Hence THg concentrations were first correlated with fish age and length using Spearman's rank correlation coefficient. Although their correlation coefficients varied, these were somewhat similar for most species, indicating possible multicollinearity issues between length and age. Thus we used a consensus between two approaches to select the best predictor among fish age and length for THg concentrations without incurring multicollinearity issues. The first approach relied on a global model including THg concentrations as the dependent variable and length, age, $\delta^{15}N_{corr}$, $\delta^{13}C$, and lakes as independent variables on which stepwise regression was conducted. Multicollinearity between fish age and length was confirmed by variance inflation factor values over 5. The second approach relied on a robust correlation comparison proposed by Wilcox and Rousselet (2018) to understand the relative importance of age or length in terms of their association with THg concentrations. This method differs from Spearman correlations by explicitly comparing the association strength of THg concentrations with age and length, with and without accounting for the reciprocal influence of age and length. Once determined for each fish species separately, if either age or length was a better predictor for THg concentrations, analyses of covariance (ANCOVAs) were used to test for the effects of different independent variables (either length or age, $\delta^{15}N_{corr}$, $\delta^{13}C$, and lakes) on THg concentrations for each fish species in both lakes. Possible interactions between independent variables were assessed for each species separately and included in the model. Interactions, when present, were followed by the main effect analysis post hoc test with Bonferroni correction. The effect size was calculated with ε^2 because it is less biased than the more commonly used ω^2 (Okada, 2013). Subsequently, separate ANCOVAs were used for each lake and fish species to test the effects of different independent variables (either length or age, $\delta^{15}N_{corr}$, and $\delta^{13}C$) on THg concentrations.

Biomagnification rates were estimated for both lakes based on the regression of $\log_{10}$ THg against $\delta^{15}N_{corr}$ (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, indicates Hg biomagnification in a food web when it is above 0 (Lavoie et al., 2013). To determine whether biomagnification rates differed between lakes, ANCOVA was employed using $\log_{10}$ THg concentrations as the dependent variable and lake as the independent variable in interaction with the covariate $\delta^{15}N_{corr}$.

RESULTS

Habitat use

The habitat distribution of fish was similar between the two lakes. Perch and large sparsely rakered whitefish were most common in littoral habitats, and vendace dominated pelagic habitats, whereas the profundal habitat had a more balanced fish community (Figure 1). Vendace was particularly abundant
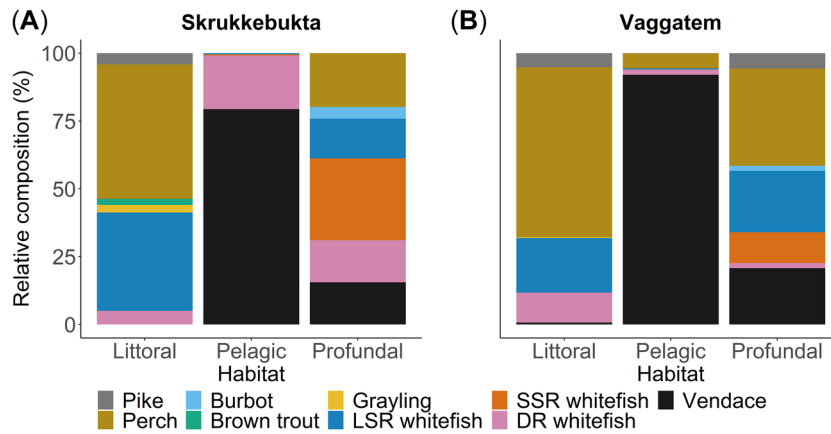
FIGURE 1: Relative composition of fish (%) of the total catch from each habitat type in (**A**) Skrukkebukta and (**B**) Vaggatem. For abbreviations, see Table 1 footnote.

in Vaggatem. The habitat distribution of densely rakered whitefish differed to some extent between the two lakes, with the largest proportions caught in the littoral in Vaggatem and in the pelagic in Skrukkebukta. Pike was present in the littoral and profundal zones in Vaggatem, whereas in Skrukkebukta, the species was only caught in the littoral. The small sparsely rakered whitefish and burbot were only caught in the profundal, and grayling was present only in littoral catches (Figure 1).

Diet

Except for pike, for which the dietary intake was identical in both lakes, the proportion of prey consumed by all other fish species varied significantly between lakes, especially for coregonids (Fisher's exact test, all $p < 0.001$; Figure 2). The diet of

large sparsely rakered whitefish was comprised of a large diversity of predominantly benthic invertebrate prey, including seven out of the nine main prey categories in both lakes. For the profundal dwelling small sparsely rakered whitefish, the dominant prey was *Pisidium* sp. in Vaggatem, whereas *Acanthocyclops* sp. and chironomid larvae dominated in Skrukkebukta (Figure 2). The diet of densely rakered whitefish differed strongly between the two lakes, with zooplankton being the dominant prey in Skrukkebukta, where it contributed 74% of the stomach contents compared with only 6% in Vaggatem. Typical littoral prey like benthic crustaceans (mainly *Eurycercus lamellatus*), trichopteran pupae and larvae, and snails dominated a highly diverse densely rakered whitefish diet in Vaggatem. In contrast, zooplankton dominated the diet of vendace in both lakes, although in Vaggatem, vendace also included benthic prey, mainly *E. lamellatus* and chironomid larvae. The noncoregonid fishes were mainly piscivorous. Pike fed
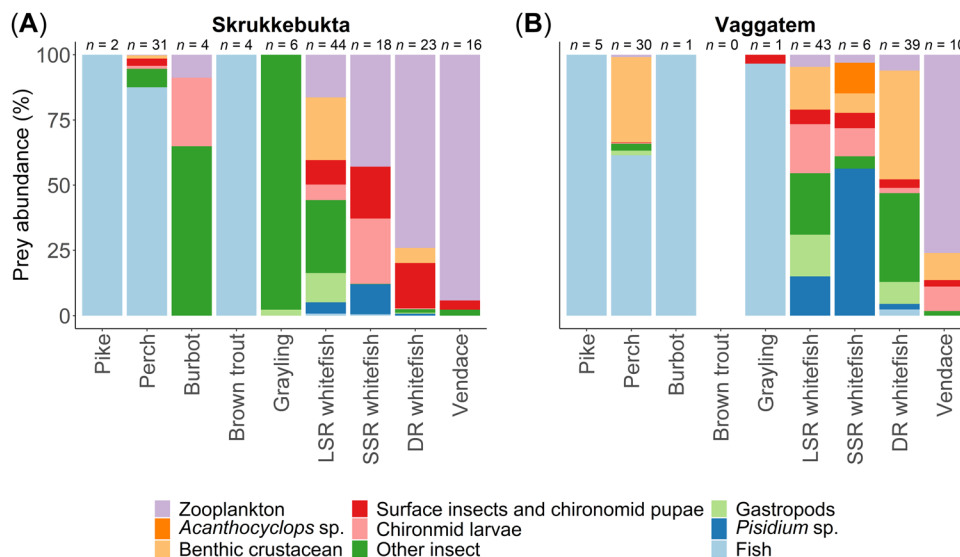

FIGURE 2: Dietary composition (prey abundance, %) of the main prey groups from the stomach contents of the different fish species from (**A**) Skrukkebukta and (**B**) Vaggatem. Numbers of fish with stomach contents for each species are indicated above the columns. For abbreviations, see Table 1 footnote.

exclusively on fish in both lakes, whereas perch partly supplemented a piscivorous diet with the benthic crustaceans *E. lamellatus* and *Asellus aquaticus* in Vaggatem. Burbot and grayling fed primarily on insects in Skrukkebukta, whereas the diet of a single individual of each species caught in Vaggagtem suggested a more piscivorous diet. For brown trout, stomach samples were only available from a few specimens in Skrukkebukta, which exclusively had fed on fish.

Stable isotopes and food web structure

Based on stable isotope biplots, the food web structure was similar in the two lakes, although some differences were also evident (Figure 3). The fish species with the highest $\delta^{15}N$ values were burbot, pike, and the profundal-dwelling small sparsely rakered whitefish in Skrukkebukta, and pike and brown trout in Vaggatem. The lowest $\delta^{15}N$ values in fish were for densely rakered whitefish in Skrukkebukta and large sparsely rakered whitefish in Vaggatem. The small sparsely rakered whitefish had the lowest $\delta^{13}C$ values in both lakes, whereas grayling had the highest. Moderately low $\delta^{13}C$ values were found for vendace in both lakes as well as for densely rakered whitefish and burbot in Skrukkebukta. Neither trophic diversity nor niche diversification within the fish community as measured by the among-species $\delta^{15}N$ and $\delta^{13}C$ ranges, respectively, differed significantly between lakes ($\delta^{15}N$ ANOVA $p = 0.326$; $\delta^{13}C$ ANOVA $p = 0.962$). As result, the total niche space (SEAc) defined by fish species' means did not differ appreciably (8.64‰^{2} in Skrukkebukta and 7.56‰^{2} in Vaggatem). Similarly, there were no significant differences in the average degree of trophic diversity (mean distance to centroid ANOVA $p = 0.785$), the density of fish species packing (mean nearest neighbor distance ANOVA $p = 0.326$), or the evenness of packing (standard deviation of nearest neighbor distance, Levene's homogeneity of variance $p = 0.546$) between the lakes. Among the invertebrates, the $\delta^{13}C$ values were lowest in profundal chironomids and highest in snails. The profundal chironomids had high $\delta^{15}N$ values in both lakes, with a particularly high level in Skrukkebukta. *Pisidium* sp. had the lowest values in Skrukkebukta, whereas snails had the lowest $\delta^{15}N$ in Vaggatem (Figure 3).

Mercury

The THg concentrations differed significantly among the fish species in both Skrukkebukta and Vaggatem (Kruskal–Wallis: $\chi^2 = 131.02$, $df = 8$, $p < 0.001$ and $\chi^2 = 111.32$, $df = 8$, $p < 0.001$, respectively). In both lakes, the highest THg concentrations were found in the piscivores, particularly in pike (Figure 4). Among the coregonids, small sparsely rakered whitefish had the highest THg concentrations, whereas the levels were more similar for vendace and densely rakered and large sparsely rakered whitefish. All but large sparsely rakered whitefish, brown trout, and grayling (small sample sizes for the latter two) had higher Hg concentrations in Skrukkebukta than in Vaggatem (Figure 4). Similarly, the individuals with the highest THg concentrations were found in Skrukkebukta.

The THg concentrations in large sparsely rakered whitefish from both lakes did not correlate with either length or age (Spearman's rank correlation, $R = -0.09-0.51$, all $p > 0.121$), whereas those of small sparsely rakered whitefish correlated significantly with age in Vaggatem (Spearman's rank correlation, $R = 0.48$, $p = 0.002$). For all other species that had sufficient data for statistical testing, THg concentrations were in both lakes significantly correlated with either age or length, or both (Spearman's rank correlation, $R = 0.37-1$, $p < 0.036$; Figure 5). Fish length or age, lake, $\delta^{15}N_{corr}$, and $\delta^{13}C$ were significant predictors of the THg concentration in several species (Table 2). Using the Bonferroni-adjusted α level of 0.025 for determining significance, there was a significant interaction between lakes and $\delta^{15}N_{corr}$ on THg concentrations in perch and densely rakered whitefish (ANCOVA, $F(1, 90) = 40.45$, $p < 0.001$ and $F(1, 62) = 6.09$, $p < 0.01$, respectively), indicating that the effect of $\delta15N_{corr}$ on THg concentrations depends on the lake, and vice versa. In perch, the simple main effect of lakes in perch was significant for Skrukkebukta ($p = <0.001$) but not for Vaggatem ($p = 0.034$), whereas in densely rakered whitefish, this was not significant for any of the lakes
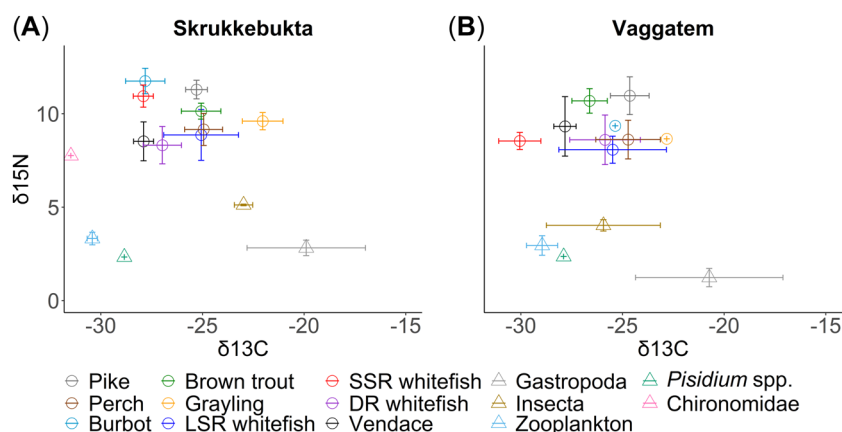

FIGURE 3: Stable isotope biplots showing the mean values of $\delta^{15}N$ and $\delta^{13}C$ (±SD) of fish and invertebrates from (**A**) Skrukkebukta and (**B**) Vaggatem. For abbreviations, see Table 1 footnote.
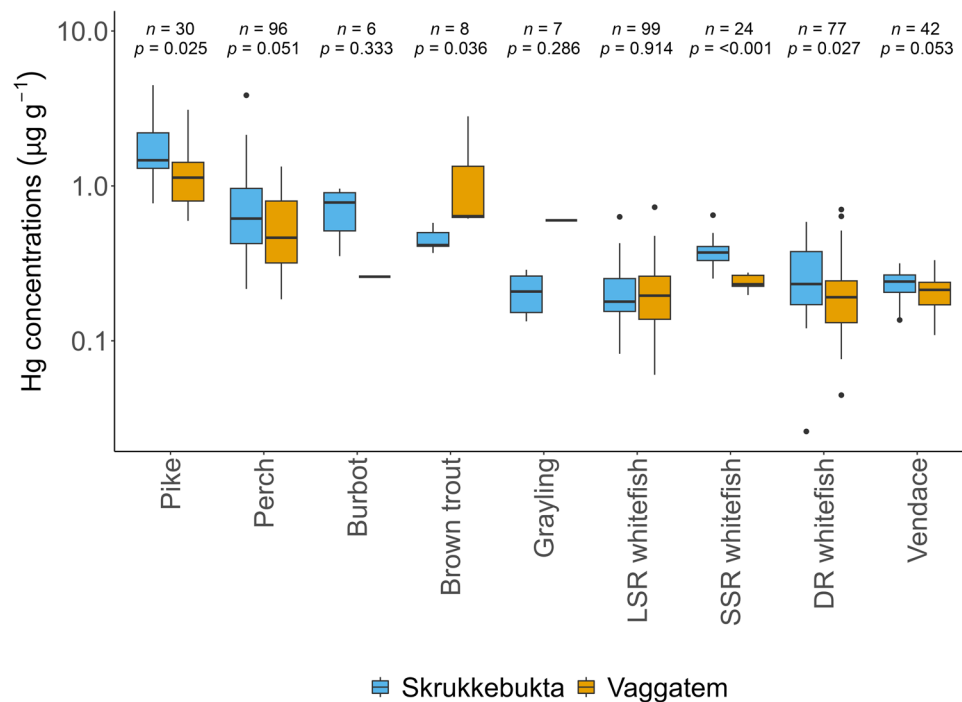
FIGURE 4: Boxplot of total mercury (THg) concentrations (μg g^{-1}) in dry weight for each fish species separated by lake, Skrukkebukta (blue) and Vaggatem (orange). Pike, perch, burbot, brown trout, and vendace have length-adjusted THg values. The p values derived from the Wilcoxon rank-sum test are shown in the upper part of the plot for each species. For abbreviations, see Table 1 footnote.

(Skrukkebukta, $p = 0.031$, and Vaggatem, $p = 0.121$). In large sparsely rakered whitefish, there were significant $\delta^{15}N_{corr}$ and $\delta^{13}C$ interactions with lakes and THg concentrations (ANCOVA, $F(1, 89) = 8.66$, $p = 0.004$ and $F(1, 89) = 19.01$, $p = <0.001$, respectively). The simple main effect of lakes was significant for $\delta^{15}N_{corr}$ in Skrukkebukta ($p = <0.001$) but not for Vaggatem ($p = 0.081$), and for $\delta^{13}C$ values this was not significant for either Skrukkebukta ($p = 0.360$) or Vaggatem ($p = 0.037$). Overall, when looking at each lake separately, $\delta^{15}N_{corr}$ was a better predictor of THg concentrations than $\delta^{13}C$. Accordingly, in both lakes, the THg concentration in fish increased with increasing $\delta^{15}N_{corr}$ values (Figure 6; all $p < 0.001$), confirming a biomagnification of THg in the lake food webs. The regression slope was steeper in Skrukkebukta (0.17 ± 0.02) than in Vaggatem (0.127 ± 0.02), and the slopes were significantly different (ANCOVA, $F_{1,385} = 7.690$, $p = 0.006$).

DISCUSSION

Our study demonstrates a complex interplay between trophic ecology and Hg contamination in the lacustrine fish communities of a subarctic watercourse. The food web structure of the fish communities as represented by habitat use, diet, and isotopic signatures of the various species and their relationship to each other was similar between contrasted study sites, although there were some evident differences, mostly related to the trophic ecology of the coregonids. There was a distinct increase in THg concentration with increasing $\delta^{15}N$ values and trophic level of the fish, whereas the expectation that pelagic fish would have higher concentrations than benthivorous fish was not supported. The THg concentrations increased significantly with both size and age for most species. In several fish species, THg concentrations were higher in Skrukkebukta than in Vaggatem. This difference could be due to Skrukkebukta's closer proximity to the Nikel smelting operation, which has been linked to higher concentrations of other metals (Amundsen et al., 1997, 2011; Zubova et al., 2020), but could also be influenced by ecological differences between the lakes. The biomagnification rate also differed between the two study sites, the overall pattern being more rapid THg accumulation and a greater biomagnification rate in Skrukkebukta.

The stable isotope signatures generally corroborated the observed habitat and diet use of the various fish species and morphs. Pike and perch were mainly distributed in the littoral but also occurred in the profundal, whereas burbot was found chiefly in the profundal. All three species fed predominantly or exclusively on fish. Amundsen et al. (2003) found a similar habitat distribution and diet pattern for these species and suggested that they constitute a benthic piscivorous guild of key top predators. This was supported by the present habitat and diet observations, with high $\delta^{15}N$ values confirming their high trophic positions, especially for pike and burbot. Perch had lower $\delta^{15}N$ values than the other piscivores, likely reflecting a more mixed diet related to their prolonged onto-genetic dietary transitioning from invertebrates to fish (Amundsen et al., 2003). High $\delta^{15}N$ values were seen in brown trout too, confirming their role as a piscivore top predator, which has also been documented from earlier studies in the
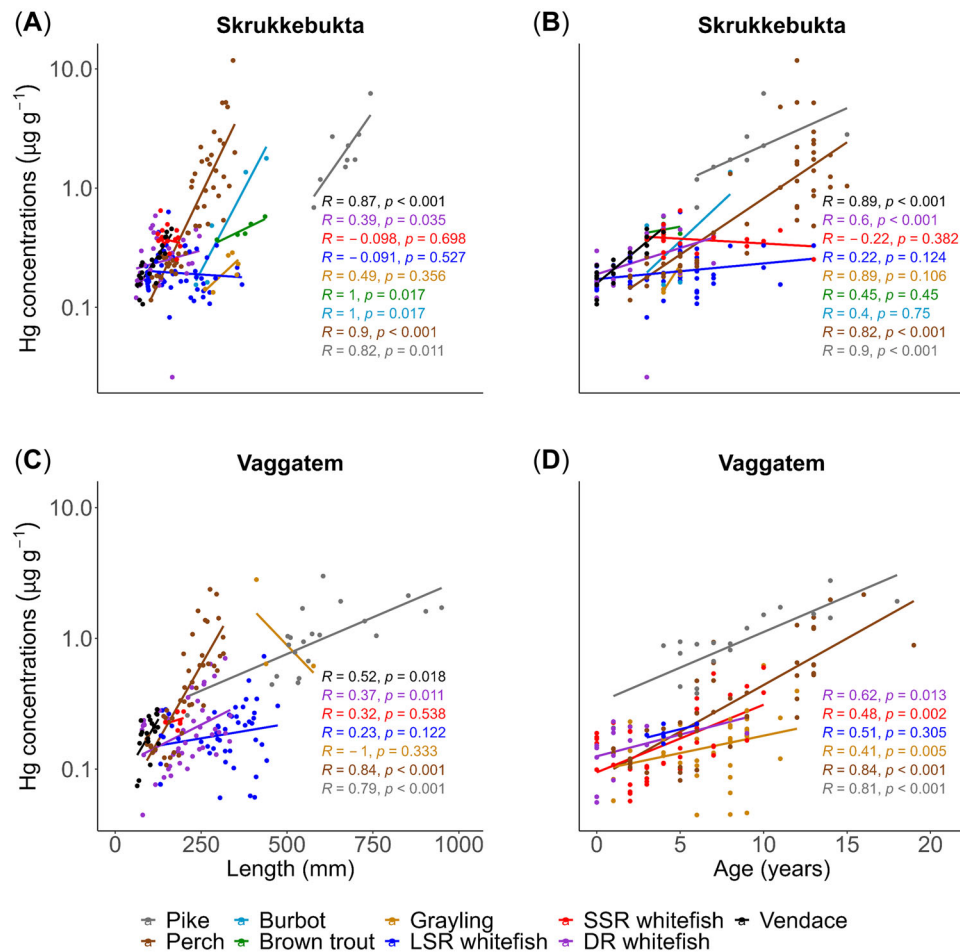
FIGURE 5: Relationships among total mercury (THg; µg g^{-1}) in dry weight length (mm; **A** and **C**), and age (years; **B** and **D**) for each fish species from (**A** and **B**) Skrukkebukta and (**C** and **D**) Vaggatem. The *p* and *R* values derived from the Spearman correlation coefficients are shown for each species. For abbreviations, see Table 1 footnote.

watercourse (Jensen et al., 2004). In Vaggatem, brown trout had lower δ^{13}C values than pike and the other piscivores, reflecting their predominant predation on small-sized, zooplanktivorous pelagic fish dominated by the abundant invasive vendace (Jensen et al., 2015). The higher δ^{13}C of brown trout in Skrukkebukta may be due to a higher proportion of the catch consisting of stocked brown trout (Jensen et al., 2004; Klütsch et al., 2021), which would include individuals having an isotopic signature influenced by fish-feed pellets (typically in the −22 to −19 range for farmed salmonids; Dempson & Power, 2004) during the first 2–3 years of their life. Burbot had the lowest δ^{13}C values among the piscivores in Skrukkebukta, reflecting a more profundal-oriented diet in contrast to, for example, the littoral-feeding pike, suggesting that burbot predominantly feed on the profundal-dwelling small sparsely rakered whitefish.

Vendace was the dominant fish species in the pelagic habitat of both lakes. However, densely rakered whitefish was also quite commonly present in the pelagic in Skrukkebukta, as has been noted in earlier studies (Gjelland et al., 2007; Kelly, 2015), and was further supported by their lower δ^{13}C values in Skrukkebukta than in Vaggatem. This may be a

consequence of the later and less extensive establishment of the invasive vendace in Skrukkebukta relative to Vaggatem (Amundsen et al., 1999; Bøhn & Amundsen, 2001; Kelly et al., 2022), with densely rakered whitefish being relegated from the pelagic to the benthic habitats within a few years after the vendace invasion (Amundsen et al., 1999, 2019; Bøhn & Amundsen, 2001; Bøhn et al., 2008). Accordingly, most densely rakered whitefish caught in Vaggatem during the present study were feeding on benthic prey, whereas zooplankton was still their main prey in Skrukkebukta. Gjelland et al. (2007) suggested that Skrukkebukta, being deeper than Vaggatem, provides a more extensive pelagic habitat that can be utilized by densely rakered whitefish to feed on zooplankton without competitive exclusion by vendace. Gjelland et al. (2009) found that both densely rakered whitefish and vendace displayed diel vertical migration behaviors, a factor that may facilitate their coexistence in the pelagic habitat in Skrukkebukta. Diel vertical migration has also been supported by an analysis of their oxygen and carbon stable isotopes (Kelly et al., 2015).

The observed habitat distributions of small sparsely rakered whitefish and large sparsely rakered whitefish are in line with the findings of other studies, with the former residing almost

TABLE 2: Ananlysis of covariance results of different predictors (either age or length, lake, $\delta^{13}C$, $\delta^{15}N_{corr}$) on THg concentrations for each fish species in both lakes and for each lake separately, including interactions, when these were present

Dependent variable	Independent variable	Pike p/ε^2	Perch p/ε^2	LSR whitefish p/ε^2	SSR whitefish p/ε^2	DR whitefish p/ε^2	Vendace p/ε^2
Both lakes							
THg	Age	**0.003**/0.259	—	**0.024**/0.033	—	**<0.001**/0.211	—
	Length	—	**<0.001**/0.352	—	0.901/0.001	—	**<0.001**/0.452
	Lake	**0.011**/0.182	**<0.001**/0.109	**<0.001**/0.167	0.080/0.149	0.051/0.042	0.096/0.033
	$\delta^{13}C$	0.568/0.008	**0.041**/0.014	**0.002**/0.064	0.873/0.001	0.141/0.024	0.355/0.010
	$\delta^{15}N_{corr}$	0.956/0	**<0.001**/0.108	0.519/0.003	0.475/0.023	0.751/0.001	**0.001**/0.161
	Locality: $\delta^{13}C$	—	—	**<0.001**/0.119	—	—	—
	Locality: $\delta^{15}N_{corr}$	—	**<0.001**/0.129	**0.004**/0.054	—	**0.016**/0.065	—
Skrukkebukta							
THg	Age	0.222/0.279	—	0.705/0.002	—	0.527/0.015	—
	Length	—	**<0.001**/0.202	—	0.653/0.014	—	**0.016**/0.255
	$\delta^{13}C$	0.947/0.001	0.410/0.005	**0.010**/0.123	0.561/0.024	0.447/0.022	0.138/0.087
	$\delta^{15}N_{corr}$	0.982/0	**<0.001**/0.474	**0.018**/0.101	0.813/0.004	0.247/0.051	0.731/0.004
Vaggatem							
THg	Age	**0.012**/0.345	—	**0.013**/0.121	—	**<0.001**/0.383	—
	Length	—	**<0.001**/0.646	—	0.667/0.087	—	**<0.001**/0.436
	$\delta^{13}C$	0.487/0.021	0.170/0.014	0.993/0	0.604/0.130	0.082/0.037	0.537/0.006
	$\delta^{15}N_{corr}$	0.944/0	**0.034**/0.036	**0.013**/0.122	0.671/0.085	**<0.001**/0.173	**<0.001**/0.321

Both p value (p: significant differences in bold) and effect size (ε^2) are shown.
DR = densely rakered; LSR = large sparsely rakered; SSR = small sparsely rakered; THg = total mercury.

exclusively in the profundal zone and the latter utilizing predominantly the littoral zone, but also profundal habitats (Bøhn et al., 2008; Kahilainen et al., 2011; Præbel et al., 2013). The diet of small sparsely rakered whitefish was accordingly dominated by typical profundal prey, including chironomid larvae, *Megacyclops* sp., and *Pisidium* sp. (Kahilainen et al., 2017), which was confirmed by the observed low $\delta^{13}C$ and high $\delta^{15}N$ values. The diet of large sparsely rakered whitefish in both lakes was dominated by typical littoral prey, as has been noted in previous studies (see Kahilainen et al., 2011; Kelly et al., 2022). Similarly, typical of littoral feeders (Post, 2002), the large sparsely rakered whitefish had higher $\delta^{13}C$ levels relative to vendace and the other two whitefish morphs.

In both study lakes, the piscivorous fish species had, as expected, significantly higher THg concentrations than the coregonids and grayling. The concentrations were particularly high in pike, which has also been reported from studies elsewhere (Kozak et al., 2021; Lockhart et al., 2005; Sharma et al., 2008). These high THg levels reflect their status as the most specialized piscivore in the Pasvik lakes, where they utilize all fish species as prey, including cannibalism (Amundsen et al., 2003; present study). Perch had high THg concentrations too, which was somewhat surprising considering that their $\delta^{15}N$ isotope signatures positioned them at a trophic level that was lower than the other piscivores and similar to large sparsely rakered whitefish. A plausible reason for this comparative difference is the slow somatic growth rate and high longevity of perch in the Pasvik watercourse, which may have resulted in inverse growth dilution of Hg, as has been reported for other European perch populations (Rask et al., 2021).

Another significant contributor to the high THg concentrations in perch may relate to their multistep ontogenetic dietary shifts. Small-sized nine-spine stickleback (*Pungitus pungitus*) are used as a "stepping stone" from benthivory to piscivory, making it possible for perch to start on a piscivorous diet at relatively small sizes (Amundsen et al., 2003). Species undergoing ontogenetic dietary shifts often exhibit a sharp increase in their Hg concentration when they shift from invertebrates to fish (Lescord et al., 2018), which may explain the high THg concentrations seen in both perch and the other piscivores. On the other hand, fish relying on invertebrates for a prolonged time during ontogeny will limit their Hg bioaccumulation for an extended period (Lescord et al., 2018; Neumann & Ward, 1999). This may explain the significantly higher Hg concentrations seen in pike compared with perch, burbot, and brown trout, becausethe former switch to an exclusive piscivorous diet sooner than the latter three species (Amundsen et al., 2003).

Next to trophic position, change-over ontogeny, represented by size and age of fish, was the most important explanatory variable for the observed THg concentrations. The concentrations significantly increased with increasing size and age for most fish species, particularly for the piscivores and vendace. A similar pattern has been found in earlier studies in the watercourse (Amundsen et al., 1997) and in several other studies of the same or similar fish species (Ahonen et al., 2018; Lescord et al., 2018; Thomas et al., 2016). The size- and age-related changes in THg concentrations were mainly driven
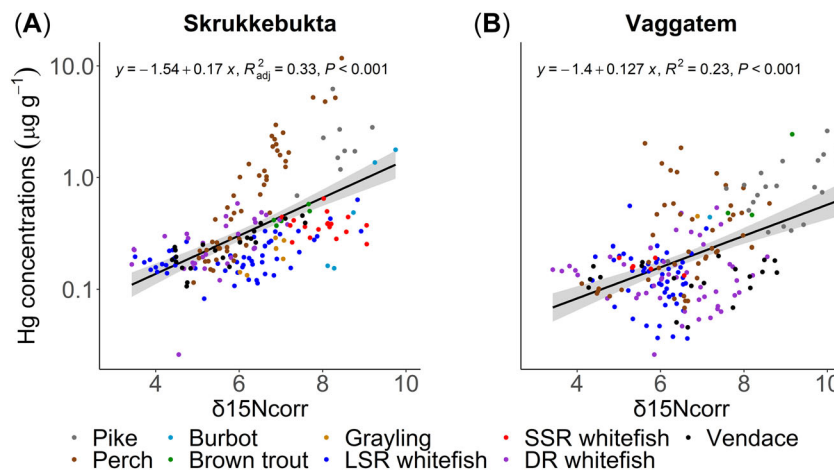
(A) **Skrukkebukta**   **(B)** **Vaggatem**

$y = -1.54 + 0.17\,x$, $R^2_{adj} = 0.33$, $P < 0.001$ $y = -1.4 + 0.127\,x$, $R^2 = 0.23$, $P < 0.001$

Hg concentrations (μg g^{-1})

$\delta 15N_{corr}$

Pike Burbot Grayling SSR whitefish · Vendace
Perch Brown trout LSR whitefish DR whitefish

FIGURE 6: Relationship between total mercury (THg) in dry weight and trophic position ($\delta^{15}N_{corr}$) in (**A**) Skrukkebukta and (**B**) Vaggatem. The regression line shows the biomagnification rate, with 95% confidence intervals marked in gray. The regression equation, adjusted R^2, and *p* value are indicated in the upper part of the plot. For abbreviations, see Table 1 footnote.

by ontogenetic dietary shifts, in particular the transition from invertebrates to fish prey in the piscivores as they grow older and larger. This was supported by the observed increases in $\delta^{15}N$ values with increasing body size, as well as by the positive correlations seen between the THg and $\delta^{15}N$ levels. Furthermore, intraspecific variations in THg concentrations are strongly related to trophic position, because most ontogenetic dietary shifts result in an increase in trophic level and thereby enhanced Hg intake.

The coregonids, including the three whitefish morphs and vendace, differed to a large extent in their feeding ecology and to some extent in their THg concentrations, as has also been seen for polymorphic European whitefish in other subarctic lakes (Kahilainen et al., 2017). The contrasting benthic diets of small sparsely rakered and large sparsely rakered whitefish combined with the reliance on zooplankton for vendace in both lakes, and for densely rakered whitefish in Skrukkebukta, likely contribute to these differences. However, in contrast to our hypothesis, the highest Hg concentrations were not observed in the pelagic-feeding coregonids but rather in the profundal-dwelling small sparsely rakered whitefish. This contrasts with the findings of Kahilainen et al. (2017), who concluded that pelagic whitefish morphs had the highest THg concentrations relative to profundal and littoral morphs. Karimi et al. (2016) similarly found that fish with a cladoceran-dominated pelagic diet had greater Hg concentrations than typical benthic feeding fish, primarily because of the overall higher THg concentrations in pelagic prey. Hence it was reasonable to expect that particularly vendace with their predominant pelagic habitat use, diet, and stable isotope signatures would have higher THg concentrations than the benthic whitefish morphs, but this was not the case. A likely explanation for this outcome is the combined effect of growth dilution and limited THg exposure time (Thomas et al., 2016; Ward et al., 2010), resulting from the fast growth and short lifespan of vendace in the study lakes (Amundsen et al., 2012). This might restrain overall THg accumulation in vendace relative to the longer lived whitefish morphs (see Table 1 and Sandlund et al., 2013). For the densely rakered whitefish morph, the

presence of the invasive vendace has resulted in a competitive relegation away from the use of pelagic resources, especially in Vaggatem (Bøhn et al., 2008; Kelly et al., 2022), which may explain the relatively low THg concentrations in densely rakered whitefish there. As for the small sparsely rakered whitefish, the higher THg concentrations compared with the other coregonids are associated with their specialized utilization of the profundal habitat, where they typically feed on chironomid larvae and other invertebrates within and on the sediments, prey types that in general have high THg concentrations compared with pelagic and littoral taxa (Chételat et al., 2008; Kahilainen et al., 2017; Thomas et al., 2016). Total Hg and MeHg concentrations are typically higher near the sediments, where Hg methylation often occurs (Korthals & Winfrey, 1987), consequently making bottom-feeding fish more prone to exposure from these sediments (Olk et al., 2016).

For most fish species, the recorded THg concentrations were higher in downstream Skrukkebukta than in upstream Vaggatem. These site differences may be related to the proximity of Skrukkebukta to the metallurgic smelter, suggesting that the smelter may constitute a significant Hg pollution source in addition to other heavy metal contaminants like nickel and copper that occur in elevated concentrations in sediments and fish in the Pasvik watercourse (Amundsen et al., 1997, 2011; Dauvalter et al., 2011). However, previous studies have not found any significant differences in the Hg concentrations of fish between these two sites (Amundsen et al., 1997, 2011), possibly as a result of lower statistical power relative to the larger sample sizes that were retrieved for the present study. This reflects that the differences between the two localities are fairly modest, and that other factors than the impact of the local pollution source should also be considered. For example, differences in trophic network conditions that influence habitat-specific foraging may drive between-lake differences (see Karimi et al., 2016). The larger profundal and pelagic areas in Skrukkebukta may enhance Hg contamination for small sparsely rakered whitefish feeding on sediment-residing invertebrates that typically have high Hg levels (Chételat et al., 2008; Kahilainen et al., 2017; Thomas

et al., 2016). Vertical diel migratory behavior in vendace and densely rakered whitefish, resulting in the inclusion of profundal prey (Gjelland et al., 2009; Kelly et al., 2015), would similarly favor higher THg concentrations in Skrukkebukta, with possible knock-on effects for the piscivorous species utilizing these coregonids as prey. In contrast, the less voluminous pelagic habitat in Vaggatem may have restricted pelagic foraging and reduced THg bioaccumulation in vendace and densely rakered whitefish as a result of greater littoral feeding. Both species have been shown to include more littoral prey in their diet there (Bøhn et al., 2008), which thus may reduce their Hg accumulation rates (Karimi et al., 2016).

The fish community in Pasvik provides for recreational, subsistence, and commercial fishing, making elevated THg concentrations a concern for the utilization of fish as food. Of the 389 fish that were analyzed for THg concentrations in the present study, 17 fish exceeded the Norwegian national health authorization limits for human consumption (0.5 µg g^{-1} wet wt, or approximately 2 µg g^{-1} dry wt). Seventy-one percent of these fish were caught in Skrukkebukta, and all of them were piscivores, making up >20% of the samples of large-sized perch (>25 cm), pike (>40 cm), and brown trout (>30 cm), which are the sizes typically targeted by the local fishery. In contrast, all examined whitefish, which used to be the prime target species for the traditional subsistence fishing, were well below the authorization limits. Fishing in the watercourse has changed over the last decades toward enhanced recreational fishing for brown trout and pike, and a higher utilization of perch in the commercial and subsistence fishing. In this respect, it should be noted that the abundance and relative importance of perch in the lacustrine fish communities have increased over the last decades due to climate warming effects (Smalås, 2021). Combined with the elevated THg concentrations in perch, this may imply that local fishing will come to rely on more highly contaminated fish. Climate change may affect the Hg levels of Arctic biota in many ways, but there is limited knowledge about northern freshwater systems, and further studies of key drivers and impacts have been called for (McKinney et al., 2022).

CONCLUSIONS

Our findings accentuate the complex interplay between trophic ecology and Hg contamination as demonstrated in the lacustrine fish communities of a pollution-impacted subarctic watercourse. Our study reveals that in addition to the vertical food web structure and trophic position of the fish, several other factors may affect the biomagnification processes and contamination levels in aquatic food webs. These are the complexity of the trophic network, the size, age, and ontogenetic niche shifts of the size-structured fish populations, and the impact of a local pollution point-source. The polymorphic whitefish populations and their sibling invasive species, vendace, clearly add to this complexity. Polymorphism is a recurrent phenomenon among salmonid fish species in postglacial lakes (Bernatchez, 2004; Klemetsen, 2010; Skúlason & Smith, 1995).

Accordingly, the observed complexity may represent a common feature in respect to trophic transfer and biomagnification of Hg through the food web of northern freshwater systems. In concert with plausible knock-on effects for the piscivore top predators, these factors emerge as important drivers of enhanced biomagnification rates and elevated Hg levels, particularly in closer proximity to the pollution source. The use of pelagic habitat and food resources did not result in the expected increase in THg concentrations in fish, a result suggestive of a growth-dilution effect on the short-lived, rapidly growing invasive vendace. Profundal-dwelling fish were apparently prone to a higher Hg exposure from feeding near the sediments, especially in the more pollution-impacted locality. The high Hg concentrations revealed in the piscivorous fish species, including concentrations that exceed the health authorization limits, emphasize the societal importance of our findings because this may have negative implications for local fishing and resource utilization. To develop management strategies that adequately address these issues, it is essential to understand the drivers that can magnify the THg concentrations and how they may vary within and among systems, as exemplified by the present study.

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