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Fish muscle mercury concentration and bioaccumulation fluctuate year-round - Insights from cyprinid and percid fishes in a humic boreal lake

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ABSTRACT

Boreal lakes demonstrate pronounced seasonality, where the warm open-water season and subsequent cold and ice-covered season dominate natural cycles. While fish muscle total mercury concentration (mg/kg) [THg] is well documented in open-water summer months, there is limited knowledge on the ice-covered winter and spring mercury dynamics in fish from various foraging and thermal guilds. This year-round study tested how seasonality influences [THg] and its bioaccumulation in three percids, perch (*Perca fluviatilis*), pikeperch (*Sander lucioperca*), ruffe (*Gymnocephalus cernua*), and three cyprinids, roach (*Rutilus rutilus*), bleak (*Alburnus alburnus*), and bream (*Abramis brama*) in deep boreal mesotrophic Lake Pääjärvi, southern Finland. Fish were sampled and [THg] was quantified in the dorsal muscle during four seasons in this humic lake. Bioaccumulation regression slopes (mean \pm STD, 0.039 ± 0.030 , range 0.013–0.114) between [THg] and fish length were steepest during and after spawning and shallowest during autumn and winter for all species. Fish [THg] was significantly higher in the winter-spring than summer-autumn in all percids, however, not in cyprinids. The lowest [THg] was observed in summer and autumn, likely due to recovery from spring spawning, somatic growth and lipid accumulation. Fish [THg] was best described by multiple regression models (R_{adj}^2 : 52–76%) which included total length and varying combinations of seasonally changing environmental (water temperature, total carbon, total nitrogen, and oxygen saturation) and biotic factors (gonadosomatic index, and sex) in all species. The seasonal variation in [THg] and bioaccumulation slopes across multiple species suggests a need for standardized sampling seasons in long-term monitoring to avoid any seasonality bias. From the fisheries and fish consumption perspective in seasonally ice-covered lakes, monitoring of both winter-spring and summer-autumn would improve knowledge of [THg] variation in fish muscle.

1. Introduction

Northern ecosystems experience long-range atmospheric mercury (Hg) deposition, especially from lower latitudes, originating from both natural and anthropogenic sources (AMAP, 2021). Globally, current levels of Hg are many times higher than in a natural state, and some aquatic systems across the planet have now reached levels elevated enough to pose a risk to consumers (UNEP, 2019; AMAP, 2021). Despite decreasing levels of atmospheric Hg in many regions, ongoing climate change may mobilize Hg stored in soil and further elevate Hg levels in the environment and in biota (Wang et al., 2019; Chételat et al., 2022; McKinney et al., 2022). Notably, snow and ice melt are significant sources of Hg transport into aquatic systems during the spring, and alterations to biogeochemical and ecological processes also influence the

Hg cycle (Chen et al., 2018; Chételat et al., 2022). Increased Hg transport into aquatic systems poses a risk to local and remote communities as well as to predators in the natural environment (Renzoni et al., 1998; Cristol et al., 2008; Kidd et al., 2012; AMAP, 2021). The more toxic form of Hg, monomethylmercury (MeHg⁺), poses a health risk to humans primarily through fish consumption (WHO, 2008; Houston, 2011; Yaginuma-Sakurai et al., 2012), as total Hg concentration (mg/kg) [THg] in adult fish muscle is mainly composed of (>90%) MeHg⁺ (Bloom, 1992; Lescord et al., 2018). Although winter gillnet fishing is important for subsistence fishing in northern communities, nutritional quality regarding year-round fluctuations in [THg] is poorly understood. Elevated [THg] has been observed in boreal regions (Munthe et al., 2007; Gandhi et al., 2014; Thomas et al., 2018), and the neurotoxicity of MeHg⁺ (Mergler et al., 2007) gives precedence for ongoing monitoring

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of Hg contamination in aquatic systems.

A holistic understanding of Hg bioaccumulation processes requires studies which include multiple species in the same systems to understand how species of differing physiology, habitat, and dietary specialization may diverge within the same ecosystem and wider region (Thomas et al., 2016, 2018; Ahonen et al., 2018). Trophic position and foraging guild are strong indicators of Hg concentration in aquatic species, as those feeding at higher trophic levels typically contain higher levels of Hg (Buck et al., 2019; Zhang et al., 2021; McKinney et al., 2022; Johnston et al., 2022). Some fish species, such as European perch (*Perca fluviatilis*) and pikeperch (*Sander lucioperca*), exhibit ontogenetic diet shifts from invertebrates to fish, which subsequently increase [THg] in muscle tissue (e.g., Hayden et al., 2014; Thomas et al., 2016). Other species, notably omnivores, such as some cyprinids, typically contain lower amounts of mercury in muscle than carnivorous fish, such as percids (e.g., Luczynska et al., 2018). Habitat-specific foraging must also be considered due to generally higher [THg] in pelagic species compared to littoral ones (Karimi et al., 2016; Thomas et al., 2016; Kahilainen et al., 2017). Hg bioaccumulates in fish with size and age, however, extended summer seasons and warmer average temperatures may promote bioaccumulation in fish, e.g., via increased preference towards pelagic prey and increased food chain length (Swanson et al., 2011; Ahonen et al., 2018; Kozak et al., 2021; McKinney et al., 2022). From a seasonal perspective, increased Hg concentration in salmonid fish during the winter is due to starvation and use of energy stores (Keva et al., 2017; Martyniuk et al., 2020), though it is not known how relevant this process is in a wider range of species. Additionally, gonad development and spawning are energetically demanding processes influencing Hg dynamics in fish, as elevated [THg] and bioaccumulation have been observed during the spawning season (Keva et al., 2017; Nowosad et al., 2019). The condition of fish improves during the subsequent somatic growth season, in the warmer and prey abundant summer, when fish recover energy stores and increase in mass.

Winter has long been considered as the season of dormancy and death for fish (Hurst, 2007), and scientific fieldwork takes place less frequently during this season due to harsh environmental conditions and logistical challenges (Studd et al., 2021; Sutton et al., 2021). Contrasted against environmental conditions during the summer, the presence of ice and snow, and drastically lower light, temperature, and oxygen concentration in aquatic systems and perturbations to nitrogen and carbon cycles are defining and influential attributes of the winter season in the northern hemisphere (Studd et al., 2021; Sutton et al., 2021). These attributes reduce productivity in aquatic systems and pressure aquatic communities in the colder months (Studd et al., 2021). Winter months prove to be deterministic for availability of food and overall connectivity between seasons (Hampton et al., 2017). In lakes, ice cover is a primary driver in maintaining diverse communities due to different thermal guilds, where cold conditions under the ice benefit cold-water species and hinder warm-water species (Shuter et al., 2012; McMeans et al., 2020). While harsh winter conditions can be costly to some pelagic species relying on limited zooplankton prey resources under lake ice (Hayden et al., 2022), some cold-water species may gain wider habitat and prey resource availability (Guzzo et al., 2017; McMeans et al., 2020). European whitefish (*Coregonus lavaretus*) and Arctic charr (*Salvelinus alpinus*) have been observed utilizing lipid reserves for energy when resources are scarce in winter, followed by a period of lipid accumulation in the warmer months (Luzzana et al., 1996; Jørgensen et al., 1997). Seasonally changing light and temperature conditions also induce gonad development and spawning activities (Wanzenböck et al., 2012), and combined with seasonal productivity fluctuations, also regulate growth and lipid dynamics in fish (Griffiths and Kirkwood, 1995; Braaten et al., 2014; Hayden et al., 2014; Kahilainen et al., 2016). For example, essential fatty acid concentrations of DHA and EPA in muscle decrease during spawning, suggesting selective mobilization of lipids towards gonadal development and spawning activities (Mairese et al., 2006; Strandberg et al., 2017; Keva et al., 2019).

Potential consequences to human health due to seasonal variation in fish [THg] may disproportionately affect northern communities relying on local resources during the harshest conditions of the year (Wheatley and Wheatley, 2000; Seabert et al., 2014; Sheehan et al., 2014), and limited knowledge of such consequences may benefit from multiple sampling periods throughout the year. The maximum dietary limits for human consumption set by the EU Commission Regulation (1881/2006) are 0.5 mg kg⁻¹ wet weight for non-predatory fish and 1.0 mg kg⁻¹ w.w. for some predatory fish, which were not exceeded here. This study focuses on six common spring spawning fish species from different foraging and thermal guilds in boreal lakes. Three percids: the cool-water adapted generalist European perch (*Perca fluviatilis*), benthivorous ruffe (*Gymnocephalus cernua*) and warm-water adapted piscivorous pikeperch (*Sander lucioperca*), and three warm-water adapted cyprinids: planktivorous bleak (*Alburnus alburnus*), benthivorous bream (*Abramis brama*) and omnivorous roach (*Rutilus rutilus*), were sampled in a humic boreal lake with the aim to test how year-round seasonal environmental variability influences [THg] and THg bioaccumulation in these species. Though all six of these species are spring spawners, they are different regarding physiology and foraging guild. The larger pikeperch and bream, medium-sized roach and perch, and smaller ruffe and bleak utilize different habitats, resources and foraging strategies. Perch and pikeperch shift ontogenetically from invertebrates to fish prey using all habitats in different life phases (Ginter et al., 2011), while ruffe typically utilize littoral and profundal habitats (Hayden et al., 2015). Of the three cyprinids, the bleak is the smallest and generally feeds in the littoral and pelagic, while the larger roach and bream tend to primarily rely on littoral resources (Vinni et al., 2000). Ruffe, bleak and roach tend to reach sexual maturity at a small size, perch and bream at a middle size and pikeperch at a large size (Heibo et al., 2005; Blanck and Lamouroux, 2007; Lappalainen et al., 2008; Vainikka et al., 2017).

The current study focuses on six spring spawning fish species collected from a deep boreal humic lake in southern Finland to understand potential year-round variability of [THg] and THg bioaccumulation in a diverse fish community. The following predictions were set:

1. The bioaccumulation of THg over the course of a year has been shown to notably increase during and after spawning in autumn spawning European whitefish (Keva et al., 2017). Based on this previous study, it was expected that higher bioaccumulation of THg indeed occurs during and after spawning when the bioaccumulation slopes of all species in the same lake will be significantly steeper near their spring spawning period compared to the rest of the year.
2. Environmental limitations during colder conditions have been shown to cause THg to concentrate in muscle tissue during winter in European whitefish (Keva et al., 2017). Therefore, it is expected that if this THg concentration phenomenon also occurs in other fish species, then it is detectable through higher measured [THg] in muscle tissue during winter and spring, and lower in summer and autumn due to the growth dilution in all species in the same lake.
3. If season plays a deterministic role in Hg dynamics in fish, then it is expected that fish biotic variables, such as sex, in conjunction with seasonally changing environmental variables, such as water temperature, will be selected in species-specific multiple linear regression models to explain [THg] in fish muscle.

2. Methods

2.1. Study site and fish community

Lake Pääjärvi (hereafter L. Pääjärvi - 61°04'N, 25°08'E, 103 m a.s.l., water level regulation amplitude 0.6 m) is a boreal lake located in southern Finland (Supplementary Fig. S1). L. Pääjärvi is a humic mesotrophic lake (DOC 11 mg L⁻¹, Tot-P 10 µg L⁻¹, Tot-N 1300 µg L⁻¹)

with a surface area of 13.5 km², mean depth of 14.4 m, maximum depth of 85.0 m and a Secchi depth of 2.0 m (Huotari et al., 2013; Supplementary Table S1). The ice-covered period typically lasts from December to April, though yearly variation is high. In 2020, ice cover on the lake began in February and lasted until April (40 days), and in 2021 from mid-January to mid-April (99 days). L. Pääjärvi has a catchment area of 210.1 km², primarily composed of forest, peatland, and agricultural land (Huotari et al., 2013). Visible light (400–700 nm) was measured using a LI-COR light meter (LI-COR Biosciences, Lincoln, U.S.A.) to define compensation depth (i.e., depth where 1% of surface light remains), and Secchi depth was measured. Water temperature (accuracy ± 0.1 °C), oxygen concentration (mg L⁻¹) and oxygen saturation (%) were measured using a YSI-meter (YSI Inc., Yellow Springs, U.S.A.) (Supplementary Table S1). During winter months, mean ice and snow depths were measured from three nearby stations (accuracy ±1 cm). Water chemistry samples were taken from the deepest area of L. Pääjärvi and transported for further analyses at the Lammi Biological Station laboratory (Supplementary Fig. S1). Measurements for total nitrogen (µg L⁻¹), total phosphorus (µg L⁻¹), dissolved organic carbon (mg L⁻¹), alkalinity (mmol L⁻¹), pH, chlorophyll *a* (µg L⁻¹) and water colour (Pt L⁻¹) were conducted either during sampling or on the following day (details in Huotari et al., 2013).

L. Pääjärvi contains 14 fish species, of which the six most abundant include bleak, bream, roach, European perch, pikeperch and ruffe were selected due to their high availability in all seasons. Other less abundant species include rudd (*Scardinius erythrophthalmus*), northern pike (*Esox lucius*), burbot (*Lota lota*), smelt (*Osmerus eperlanus*), vendace (*Coregonus albula*), whitefish, stone loach (*Barbatula barbatula*) and common bullhead (*Cottus gobio*). Summer-old pikeperch and whitefish are stocked in L. Pääjärvi. Whitefish is stocked annually, and pikeperch more occasionally, though pikeperch also reproduce naturally in L. Pääjärvi.

2.2. Sampling method and processing

Monthly fish sampling was conducted from March 2020 to March 2021 and sporadically until the end of October 2021. Year-round data was available from six abundant fish species (bleak, bream, roach, perch, pikeperch and ruffe) to study seasonal [THg] variation in white dorsal muscle (Table 1). Fish were sampled from littoral, pelagic and profundal habitats using a gillnet series of eight 30 × 1.8 m nets with randomly ordered mesh sizes (knot to knot: 12, 15, 20, 25, 30, 35, 45, and 60 mm) and one 30 × 1.5 m Nordic multimesh gillnet (12 × 2.5 m wide nets, mesh sizes: 5–55 mm) set overnight. Fish were removed from the gill nets and euthanized by cerebral concussion, resulting in immediate death, and put on ice for transport to the laboratory. Fish were

stored and frozen for subsequent analyses (−20 °C). Fishing licenses were obtained from the Pääjärvi Fishing Association and the Centre for Economic Development, Transport and the Environment.

Fish were identified to species, counted, and measured for total length (±1 mm) and weight (±0.1 g), from which Fulton's *k* condition factor was calculated (Nash et al., 2006):

$$k = \frac{M}{TL^3} \times 100$$

where *M* is fish body mass (g) and *TL* is total length (cm).

Sex was visually determined, gonads were weighed (accuracy 0.01 g) and gonadosomatic index (*GSI*) was calculated (Bagenal, 1978):

$$GSI = \frac{GM}{SM} \times 100$$

where *GM* is gonadal mass (g) and *SM* is somatic mass (body mass without gonad mass) (g).

One sample of white dorsal muscle below the dorsal fin and above the lateral line was taken from each individual and stored in 2 ml plastic vials, frozen, and freeze-dried at −54 °C for 48 h using a Christ Freeze Dryer (Alpha 1–2 LDplus) (Martin Christ Gefriertrocknungsanlagen GmbH, Osterode am Harz, Germany).

2.3. [THg] measurement and species considerations

All freeze-dried samples were pulverized and weighed (20–30 mg dry weight) for [THg] analyses using a Direct Mercury Analyzer (DMA-80) (Milestone S.r.l., Sorisole, Italy). Blank samples (mean ± SD, 0.00005 ± 0.0005 mg kg⁻¹ d.w., n = 261) and a certified reference material (DORM-4, National Research Council Canada) with known [THg] (0.410 ± 0.055 mg kg⁻¹ d.w.) were used in the beginning and end of each run (0.408 ± 0.0216 mg kg⁻¹ d.w., mean recovery = 99.4%, n = 261). Every fifth sample was duplicated. An acceptable difference between the [THg] of duplicates was set to <10% for samples to be used for further analyses.

A total of 3368 fish were collected and a sample of dorsal muscle from each individual was tested for [THg]. No bleak were captured during winter months. The length distribution was skewed in all species, therefore, a representative random sample from each species was selected before subsequent statistical analyses. Individuals were randomly selected in each season in roughly equal numbers of individuals per size category, resulting in a subsample of 2332 fish selected for the subsequent analyses (69.2% of sampled fish).

Sampling months were grouped into seasons (Winter: January, February, March; Spring: April, May, June; Summer: July, August,

Table 1
Attributes and [THg] information of Lake Pääjärvi fish population.

Attribute	Variable	Bleak	Bream	Roach	Perch	Pikeperch	Ruffe
Fish metric	Total length _{avg} (cm)	14.2	27.1	18.5	16.3	29.2	9.1
	n	150	74	706	689	421	292
[THg]	Spawning	Late June	June	Early June	Late May	June	June
	Annual [THg] _{avg}	0.51 ± 0.22	0.28 ± 0.17	0.29 ± 0.15	0.49 ± 0.29	0.67 ± 0.46	0.75 ± 0.42
	Range	0.20–1.87	0.09–0.81	0.07–1.25	0.11–2.09	0.11–3.24	0.10–2.41
	Winter [THg] _{avg}	–	0.37 ± 0.18	0.31 ± 0.17	0.52 ± 0.28	0.86 ± 0.50	0.64 ± 0.25
	Spring [THg] _{avg}	0.57 ± 0.19	0.29 ± 0.18	0.32 ± 0.15	0.60 ± 0.32	0.78 ± 0.50	0.92 ± 0.40
	Summer [THg] _{avg}	0.50 ± 0.23	0.26 ± 0.17	0.29 ± 0.15	0.46 ± 0.27	0.56 ± 0.39	0.74 ± 0.51
	Autumn [THg] _{avg}	0.41 ± 0.22	0.19 ± 0.07	0.26 ± 0.13	0.42 ± 0.22	0.70 ± 0.52	0.63 ± 0.30
[THg] % difference	Autumn - Spring	32.2	40.3	19.7	36.8	11.5	37.9
	Autumn - Summer	18.3	30.4	9.1	9.5	21.5	16.1
	Autumn - Winter	–	61.7	15.2	23.2	20.8	1.1
	Spring - Summer	14.1	10.2	10.6	27.6	32.8	22.1
	Spring - Winter	–	22.8	4.6	13.9	9.3	36.8
Summer - Winter	–	32.8	6.1	13.8	41.8	15.0	

*Variables are average total length, sample size (n), percentage of the total species catch randomly selected for use in study, spawning period, average original [THg] ([THg]_{avg}, mean ± SD, mg kg⁻¹ d.w.) annually with range and seasonal [THg]_{avg} with the highest seasonal [THg]_{avg} bolded, and the percentage difference in [THg] between seasons.

September; Autumn: October, November, December). Winter has several defining attributes, such as the shortest days and coldest temperatures of the year (Studd et al., 2021). Here, the winter season was interpreted to include only those months in which lake ice is typically consistent throughout the entire month (Shuter et al., 2012). Spring includes the spawning period of all spring spawning species (April–June), and summer is defined as when L. Pääjärvi typically achieves summer stratification (July–September) (Ruuhijärvi, 1974).

2.4. Statistical analyses

[THg] was \log_{10} transformed (\log_{10} [THg]) to meet assumptions of normality before subsequent testing. Bioaccumulation rate is inferred from the slope of the regression between \log_{10} [THg] and total length. To test whether the bioaccumulation rates in spring spawning species are highest near species' spawning season and lowest in autumn, the bioaccumulation rate in each season for each species was assessed. An ANCOVA was performed between \log_{10} [THg] and total length with season as a covariate to identify whether a significant difference between bioaccumulation slopes exists among seasons. Pairwise t-tests of regression slopes were conducted where a significant difference among seasonal slopes was detected.

\log_{10} [THg] was adjusted for total length in each season (Sonesten,

2003; Braaten et al., 2019; Knott et al., 2022) by adding the residuals of the calculated season-specific linear regressions of \log_{10} [THg] and total length to the original \log_{10} [THg] values. To test whether fish muscle [THg] is highest in winter and spring, and lowest in summer and autumn, the relationship between length adjusted \log_{10} [THg] values and season was tested with ANOVA to determine if a significant difference exists between seasons for each species and a Tukey's HSD test was used to assess pairwise differences between seasons. If the assumption of homogeneity of variance was violated, Welch's ANOVA was performed with a Games-Howell post hoc test.

To assess whether \log_{10} [THg] is best described by a combination of seasonally changing environmental and biotic variables, collinearity among 21 biological and environmental variables was assessed with a Pearson correlation, and variables with a coefficient under 0.6 were selected for further analyses. Forward stepwise multiple linear regression models were used to explain \log_{10} [THg]. Variables were added to the model and the best model was selected based on minimum AIC value for each species.

The statistical significance limit to reject null hypotheses (alpha) was set to 0.05. All statistical analyses were conducted using R version 3.5.3 (R Core Team, 2019).

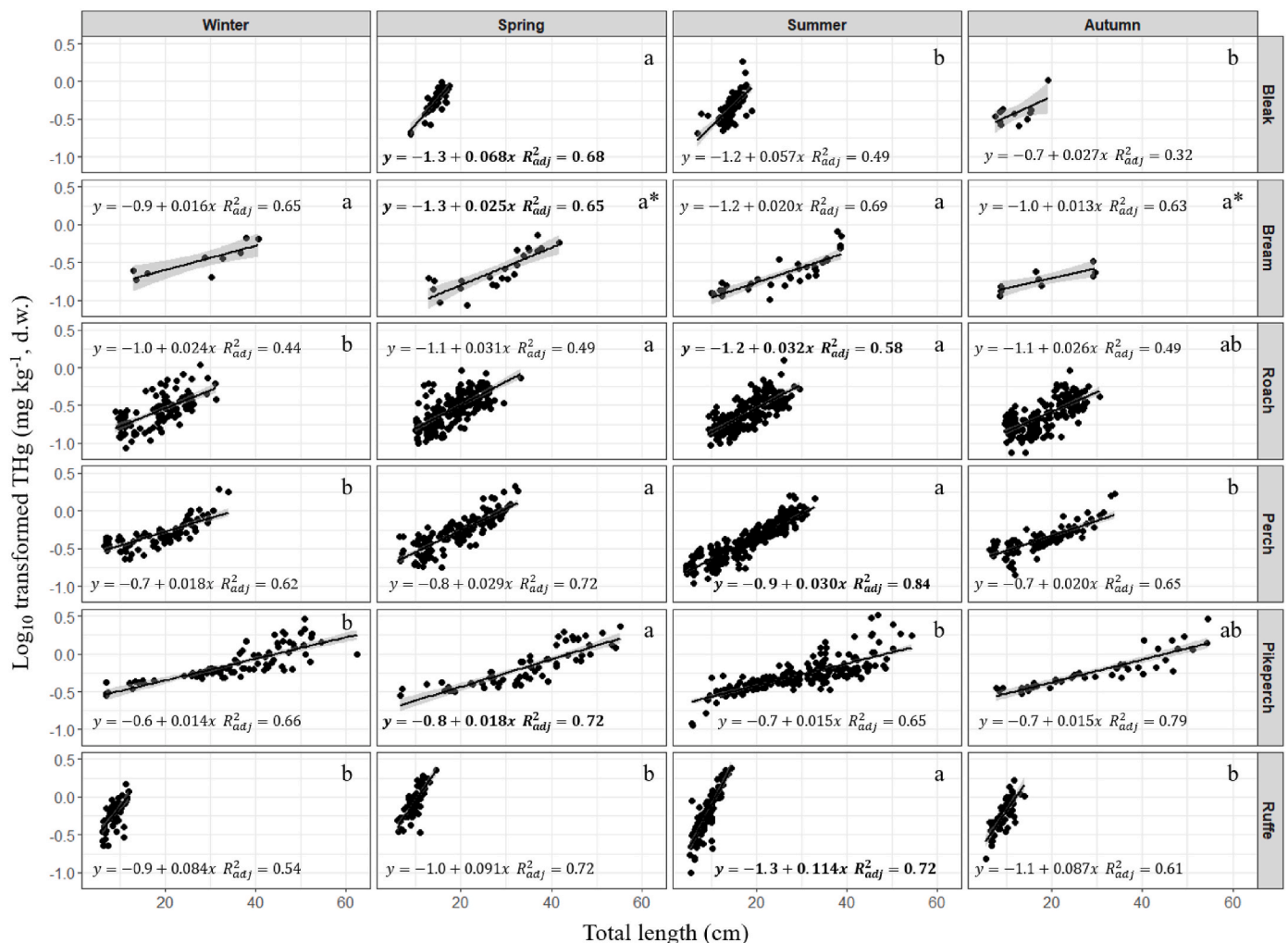


Fig. 1. Seasonal bioaccumulation of \log_{10} [THg] described with linear regression (all regressions $p < 0.05$) for species in L. Pääjärvi. The regression line with 95% confidence interval, equation and adjusted R^2 value are shown for statistical significance. Steepest slope representing bioaccumulation of mercury is bolded for each species. No winter data was available for bleak. Pairwise t-tests of slopes between seasons, identified with letters, demonstrate which seasons are significantly different. Asterisks identify seasons of near significance in bream ($p = 0.069$). Groups represented by different letters are significantly different (for details, see Supplementary Table S2).

3. Results

3.1. Bioaccumulation of THg

Season-specific linear regressions between $\log_{10}[\text{THg}]$ and total length were significant in all seasons ($p < 0.05$) and in all species. ANCOVA analyses found that seasonal bioaccumulation slopes were significantly different in all species (Fig. 1, Supplementary Table S2), though an interaction between season and length was found in bleak, roach, perch, and ruffe. In all species, the steepest slopes of bioaccumulation were in the spring or summer and the shallowest slopes were in winter or autumn (Fig. 1). At least one significant ($p < 0.05$) or near-significant (Pairwise t -test, Bream: Spring – Autumn, $p = 0.07$) pairwise difference between bioaccumulation slopes was exhibited in all species, and most significantly between the seasons of steepest and shallowest bioaccumulation slopes (pairwise t -test, season comparison, p ; bleak: autumn-summer, $p = 0.007$, bream: autumn-spring, $p = 0.069$, roach: summer-winter, $p = 0.014$, perch: summer-winter, $p < 0.001$, pikeperch, spring-winter, $p = 0.022$, ruffe: summer-winter, $p = 0.013$).

3.2. Length adjusted $\log_{10}[\text{THg}]$ in dorsal muscle

Seasonal differences in length adjusted $\log_{10}[\text{THg}]$ were found in all percid species ($p < 0.05$), however, none were identified in any cyprinids (Fig. 2, Supplementary Table S3). Where ANOVA analyses detected seasonal differences in length adjusted $\log_{10}[\text{THg}]$, pairwise comparisons detected significant differences between the seasons of highest and

lowest mean length adjusted $\log_{10}[\text{THg}]$ ($p < 0.05$), as well as between other seasons (Fig. 2). The highest mean length adjusted $\log_{10}[\text{THg}]$ in pikeperch was during winter and the lowest in summer. The mean length adjusted $\log_{10}[\text{THg}]$ was highest in the spring and lowest in the autumn in the other percid species. Significant differences in mean length adjusted $\log_{10}[\text{THg}]$ were not detected between summer and autumn in any species, and the only significant difference between winter and spring was found in ruffe. Whilst no significant seasonal differences were identified in cyprinids, the highest mean length adjusted $\log_{10}[\text{THg}]$ and original $[\text{THg}]$ values were observed in winter or spring, and the lowest were in autumn (Fig. 2, Table 1).

3.3. Biotic and environmental variables explaining $\log_{10}[\text{THg}]$

Stepwise multiple regression was used to analyse the most significant biotic and environmental factors influencing $\log_{10}[\text{THg}]$. Following collinearity analyses, a set of seven biotic and environmental factors were included in the full model for each species: $\log_{10}[\text{THg}] \sim \text{total length (TL)} + \text{gonadosomatic index (GSI)} + \text{sex} + \text{water temperature at 0–3 m (Temp}_{0-3}) + \text{oxygen saturation at 3–20 m (OS}_{3-20}) + \text{total nitrogen (Tot-N)} + \text{total organic carbon (TOC)}$ (Fig. 2, Supplementary Table S4, Supplementary Table S5). The final models for all species indicated that the total length is the primary determining factor of $\log_{10}[\text{THg}]$, however, biotic (GSI and sex) and seasonally changing environmental factors (water temperature, oxygen and nutrients) bore strong relevance to explaining the remaining variance. The final models for all species explained 66–77% of variation $\log_{10}[\text{THg}]$ with exception

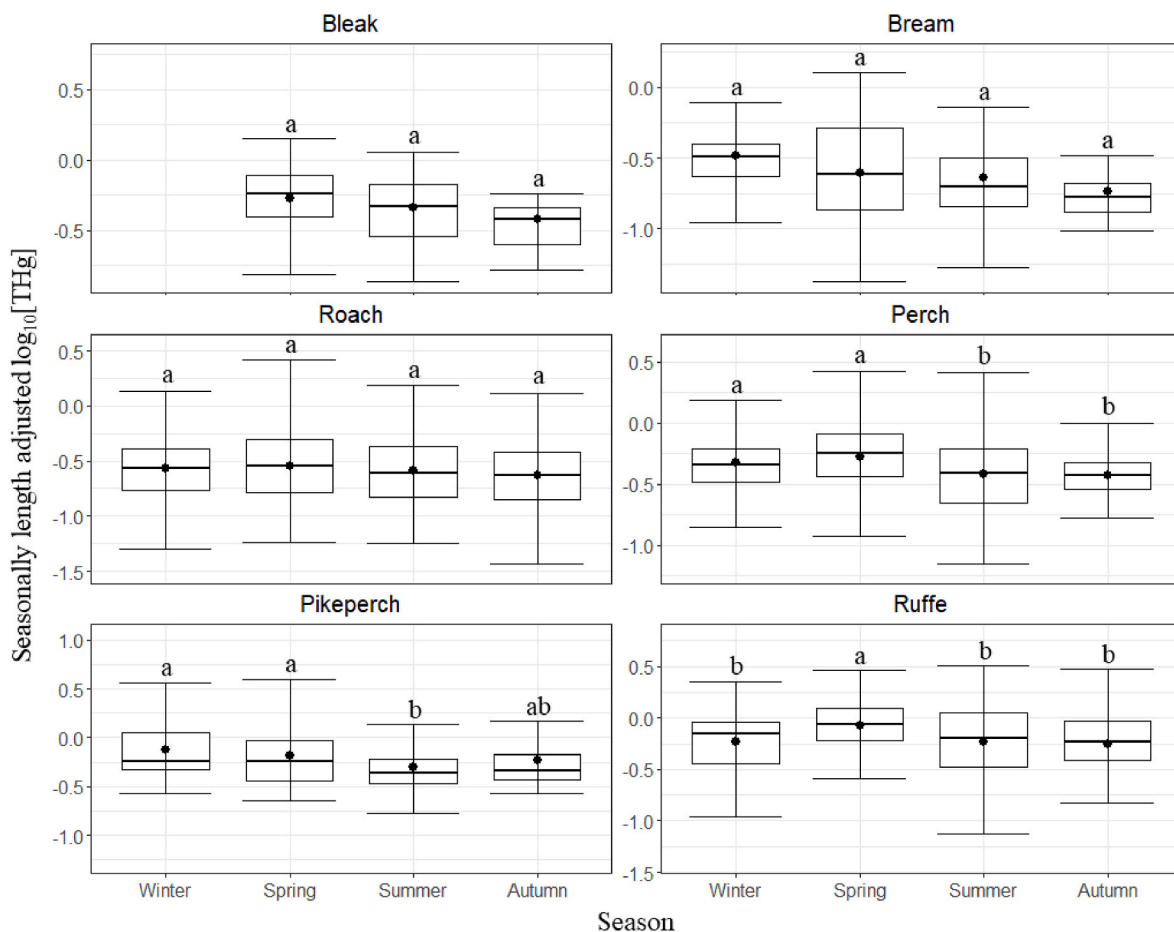


Fig. 2. Seasonal comparison of length adjusted $\log_{10}[\text{THg}]$ for species in L. Pääjärvi. Black dots near the center of box plots represent the mean value and the horizontal line represents the median value. Length adjusted $\log_{10}[\text{THg}]$ was analysed with either an ANOVA or a Welch's ANOVA test followed by either Tukey's HSD or Games-Howell post-hoc test in each species. The post-hoc test visibly demonstrates which seasons are significantly different by using different letters. Groups represented by different letters are significantly different ($a > b$, $p < 0.05$) (for details, see Supplementary Table S3). Note that scales are species-specific.

to bleak and roach, for which the final models respectively explained 58 and 52% of the variation (Table 2).

4. Discussion

4.1. Seasonality of THg bioaccumulation

Bioaccumulation regression slopes demonstrated fluctuations throughout the year, which were primarily tied to the seasonal cycle of reproduction, winter recovery and somatic growth. The maximum difference in slope between seasons was noted in bleak (autumn-spring), followed by bream (autumn-spring), perch (summer-winter), ruffe (summer-winter) and pikeperch (spring-winter). In general, the steepest regression slopes were observed during or after the spawning season in spring and summer, contrasted by significantly shallower slopes in autumn and winter. Previous studies show that fish gonad development requires significant energy expenditures from lipid stores (Jørgensen et al., 1997; Finstad et al., 2003; Braaten et al., 2014; Keva et al., 2017), which are fully accumulated in autumn, even for spring spawning fish, and likely explain the observed shallower bioaccumulation rates. Mature fish likely mobilize lipids to meet energy requirements required for gonadal development and spawning activities, as observed in percids and salmonids (Luzzana et al., 1996; Mairesse et al., 2006). Keva et al. (2017) found that whitefish bioaccumulate THg at the highest rate during and after the spawning period in December and February, as observed in this study, though during a different spawning period in spring. Özyurt et al. (2012) suggested that increased feeding activity observed in pikeperch during spring was tied to gonad development, thus paralleling the variability of bioaccumulation tied to reproduction highlighted in this study. Similar to whitefish, all studied species show highest bioaccumulation during (spring) or shortly after (summer) spawning. The annual peak abundance of prey in summer (Kahilainen et al., 2005; Hayden et al., 2014) serves as the primary timeframe for recovery, somatic growth, and bioaccumulation of Hg. The lower rates of THg bioaccumulation in the autumn for the studied species suggests that species have replenished lipid reserves, thus lower rates of feeding may occur once recovered (Borcherding et al., 2007). Most species exhibited decreasing bioaccumulation to some extent in autumn following the growing season and recovery of energy reserves. Additionally, lower levels of activity during winter compared to other seasons is typical, especially in warm-water species (Wang and Eckmann, 1994; Jurajda et al., 2018; McMeans et al., 2020), thus providing reasoning for the observed lowered rate of THg bioaccumulation in the winter due to lower levels of activity and feeding. Fish may also pursue prey items which contain less THg in winter months, as observed in perch shifting to invertebrate prey from fish (Jacobsen et al., 2002). Winter is of exceptional importance for young-of-year fish, as this season serves as a survival bottleneck for smaller size cohorts, e.g., perch, pikeperch, and roach (Jepsen and Berg, 2002; Kirjasniemi and Valtonen, 2006; Hurst, 2007; Borcherding et al., 2007; Heermann et al., 2009).

4.2. Seasonality of length adjusted \log_{10} THg

This study found significant seasonal differences in length adjusted \log_{10} [THg] in percids. Length adjusted \log_{10} [THg] generally peaked in winter-spring and decreased in summer-autumn. Fish undergo somatic growth and lipid storing during the warm months, which is contrasted to some extent by the winter reduction of activity and starvation while metabolizing stored lipids for survival (Griffiths and Kirkwood, 1995). The seasonal mean length adjusted \log_{10} [THg] in L. Pääjärvi percid fish generally followed the summer Hg growth dilution and winter Hg concentrating trend previously observed in whitefish (Keva et al., 2017), and though the same trend is visible in the cyprinid species, no significant seasonal differences were detected. Higher observed mean length adjusted \log_{10} [THg] tied to Hg concentrating in the fish muscle during the cold winter and spring is caused by winter starvation via lower

Table 2

Multiple stepwise linear regression analyses with forward selection to explain \log_{10} total Hg concentration [THg] for species in L. Pääjärvi.

Species	Model	AIC	R ² adj	RSME	F (d.f.)	p
Bleak	TL	-197.10	0.46	0.119	F _{1,140} = 120.8	<0.001
	TL + OS ₃₋₂₀	-222.19	0.55	0.109	F _{2,139} = 87.2	<0.001
	TL + OS ₃₋₂₀ + Temp ₀₋₃	-227.98	0.57	0.106	F _{3,138} = 63.5	<0.001
	TL + OS₃₋₂₀ + Temp₀₋₃ + TotN	-229.56	0.58	0.105	F_{4,137} = 49.4	<0.001
Bream	TL	-65.70	0.65	0.135	F _{1,58} = 110.6	<0.001
	TL + GSI	-73.42	0.70	0.126	F _{2,57} = 68.9	<0.001
	TL + GSI - TotN	-76.59	0.72	0.122	F_{3,56} = 50.9	<0.001
Roach	TL	-637.48	0.49	0.152	F _{1,689} = 657.9	<0.001
	TL + Sex	-660.07	0.50	0.150	F _{2,688} = 352.8	<0.001
	TL + Sex + OS ₃₋₂₀	-672.19	0.51	0.148	F _{3,687} = 244.4	<0.001
	TL + Sex + OS₃₋₂₀ + TOC	-674.81	0.52	0.148	F_{4,686} = 185.4	<0.001
Perch	TL	-947.63	0.73	0.118	F _{1,659} = 1805.0	<0.001
	TL - Temp ₀₋₃	-995.33	0.75	0.114	F _{2,658} = 997.1	<0.001
	TL - Temp ₀₋₃ + OS ₃₋₂₀	-1004.37	0.75	0.113	F _{3,657} = 678.6	<0.001
	TL - Temp ₀₋₃ + OS ₃₋₂₀ + TOC	-1005.25	0.76	0.113	F _{4,656} = 511.1	<0.001
	TL - Temp₀₋₃ + OS₃₋₂₀ + TOC + Sex	-1005.54	0.76	0.112	F_{5,655} = 410.1	<0.001
	Pikeperch	TL	-471.88	0.69	0.129	F _{1,376} = 822.8
Ruffe	TL - Temp ₀₋₃	-480.30	0.69	0.127	F _{2,374} = 427.0	<0.001
	TL - Temp₀₋₃ + TotN	-481.06	0.69	0.129	F_{1,376} = 822.8	<0.001
	TL	-292.01	0.63	0.143	F _{1,281} = 484.8	<0.001
	TL + OS ₃₋₂₀	-300.65	0.64	0.141	F _{2,280} = 256.2	<0.001
	TL + OS ₃₋₂₀ + TotN	-302.54	0.65	0.140	F _{3,279} = 173.8	<0.001
	TL + OS ₃₋₂₀ + TotN + TOC	-307.56	0.65	0.139	F _{4,278} = 134.2	<0.001
Pikeperch	TL + OS ₃₋₂₀ + TotN + TOC + Sex	-307.56	0.66	0.139	F _{5,277} = 108.7	<0.001
	TL + OS ₃₋₂₀ + TotN + TOC + Sex + Temp ₀₋₃	-307.56	0.66	0.138	F _{6,276} = 91.6	<0.001
	TL + OS₃₋₂₀ + TotN + TOC + Sex + Temp₀₋₃ + GSI	-308.37	0.66	0.137	F_{7,275} = 80.6	<0.001

*Variables are total length (TL), gonadosomatic index (GSI), sex, water temperature at 0–3 m (Temp₀₋₃), oxygen saturation 3–20 m (OS₃₋₂₀), total nitrogen (TotN), total organic carbon (TOC). Final models for each species are bolded.

activity and prey availability (Hurst, 2007; Shuter et al., 2012; Hayden et al., 2015), and increased gonadal development energy requirements (Jørgensen et al., 1997; Finstad et al., 2003; Braaten et al., 2014; Keva et al., 2017). High reproductive effort has been connected to high winter mortality in several fish species, e.g., brook trout, *Salvelinus fontinalis* (Hutchings et al., 1999), bleak (Almeida et al., 2014) and whitefish (Hayden et al., 2022). However, large mature individuals with higher lipid reserves remained more active in winter, especially percids, which suggests that effective energy storage is a successful strategy for surviving the harsh winter months (Thompson et al., 1991; Huss et al., 2008; Heermann et al., 2009).

Lowered somatic growth rate in mature individuals due to investment in gonadosomatic growth elevates muscle Hg concentration during and after spawning, thus resulting in higher concentrations in larger and mature fish. Although winter is considered to be the season of highest Hg concentration, the average values of length adjusted \log_{10} [THg] in bleak, roach, perch, and ruffe peaked in the spring, whereas the lowest averages were in the autumn, suggesting that these species may require a higher energy investment towards gonadal development followed by a longer period of spawning recovery (Rinchard and Kestemont, 1996; Lappalainen et al., 2008). The magnitude of [THg] fluctuations throughout the year were distinctly different between percids and cyprinids in L. Pääjärvi. This can be explained by the differing activity levels and diets of these two groups. Whilst cyprinids feed at a relatively low intensity during winter and spring (Griffiths and Kirkwood, 1995; Nunn et al., 2008; Jurajda et al., 2018), perch, pikeperch, and ruffe remain active carnivores throughout the year, even during these colder months (Eckmann and Imbrock, 1996; Kováč, 1998; Kangur et al., 1999; Lappalainen and Vinni, 2005; Kirjasniemi and Valtonen, 2006; Hayden et al., 2015). Perch and pikeperch shift ontogenetically from invertebrates to fish (Mehner et al., 1996; Sutela and Hyvärinen, 2002), and pursue active prey items, which requires energy-intensive hunting and habitat shifts throughout the year (Eckmann and Imbrock, 1996; Jepsen et al., 1999; Lappalainen and Vinni, 2005; Huuskonen et al., 2019). Despite the necessary energetic effort, these percids feeding on fish benefit from consuming prey with a higher lipid content, thus facilitating increased accumulation of lipid reserves for winter survival and gonad development (Sulistyo et al., 1998; Blanchard et al., 2005). Ruffe, though not piscivorous, actively pursue a diverse carnivorous diet year-round and could, therefore, have high lipid reserves (Jamet, 1994; Kangur et al., 1999; Eckmann, 2004; Hayden et al., 2015). *Mysis relicta* is present in L. Pääjärvi and are available prey in winter, thus potentially providing a valuable food source at a higher trophic level for ruffe and smaller size categories of perch and pikeperch (Ikonen et al., 2005; Borchherding et al., 2007).

By contrast to percids, much lower levels of activity during the colder months have been observed in roach and bream. Although still lower than in summer, Jurajda et al. (2018) observed higher bream activity levels in winter than previously thought. The omnivorous roach and benthivorous bream tend to feed on benthic macroinvertebrates, zooplankton, macrophytes, periphyton and phytoplankton (Jamet, 1994; Persson and Brönmark, 2002), however, reduced feeding activity has been observed in cyprinids over the winter (Jepsen and Berg, 2002). Bleak differ from the other studied cyprinids in an observed preference towards cladocerans and surface captured insects in pelagic and littoral habitats (Vinni et al., 2000; Almeida et al., 2017). These prey resources are absent during the ice-covered winter months and no bleak were captured during this season, thus highlighting very low activity levels. Bleak may be an example of a species of high or complete reliance on summer-accumulated lipid reserves over winter, and the short life cycle length of this species suggests that winter mortality is high. Feeding at lower trophic levels and maintaining a low activity level during the colder months aligns with the insignificant [THg] fluctuations throughout the year observed in the L. Pääjärvi cyprinids. The findings of this study suggest that cyprinids reduce activity to conserve energy and rely on energy stores over the winter, as previously observed in

roach (Griffiths and Kirkwood, 1995). While this study demonstrates that dorsal muscle [THg] in the studied species are seasonally dynamic, seasonal patterns in lipid dynamics (Blanchard et al., 2005; Kahilainen et al., 2016; Keva et al., 2019) should be further explored.

4.3. Environmental seasonality and biotic variables relationship with [THg] in fish muscle

Environmental variables with strong seasonal signals explained \log_{10} [THg] in the multiple regression models, including total nitrogen, total carbon, oxygen saturation and water temperature. Previous studies have identified the sampling season as important for modelling [THg] in several species (Braaten et al., 2014; Kahilainen et al., 2016; Keva et al., 2017; Knott et al., 2022), thus lending to the importance of the seasonal variation identified in this study. Productivity, defined by the nutrient content in subarctic lakes, has also been identified as one of the key variables to understanding [THg] in numerous species (Ahonen et al., 2018). The seasonality of variables describing productivity in L. Pääjärvi are shown to play a predictive role in understanding the [THg] found in fish.

The seasonality observed in these environmental variables is deterministic in physiological responses in fish, which has been previously characterized by the condition factor and used as a predictor of Hg concentration in whitefish (Keva et al., 2017) and Arctic charr (Martyniuk et al., 2020). Spawning related variables (GSI or sex) were selected to explain \log_{10} [THg] in bream, roach, perch, and ruffe, which supports previous work demonstrating that sex-specific biological variables and maturity influence Hg concentration in fish muscle (Braaten et al., 2014; Estlander et al., 2017; Keva et al., 2017). Female-biased sexual dimorphism is typical in many fish species, and reaching maturity quicker will consequently decrease somatic growth and increase gonad growth, thereby influencing Hg dynamics along the variable of sex (Kahilainen et al., 2017). In some species, male fish ingest more food and, therefore, more Hg, typically due to higher energy expenditure from higher metabolic rate and swimming activity (Madenjian et al., 2016), as observed in this study. However, decreased feeding activity, metabolic costs and food conversion efficiencies following the onset of maturity have also been found in percid males compared to females utilizing the same habitats, perhaps to reduce predation risk (Rennie et al., 2008; Prchalová et al., 2022). In the case of roach, perch and ruffe, the regressions modelled \log_{10} [THg] as positively related to male individuals, which typically grow slower than females (Estlander et al., 2017; Žák et al., 2020; Prchalová et al., 2022). Mature adult perch (GSI avg, male: 3.31%, females: 3.97%), roach (GSI avg, male: 3.67%, females: 7.34%) and ruffe (GSI avg, male: 2.79%, females: 5.13%) from L. Pääjärvi exhibited smaller GSI in males than females for both species, which may suggest that males in these species eliminate less THg than females. Another sex-related variable, GSI, was selected to explain \log_{10} [THg] in bream and ruffe, supporting the previously discussed energetic cost of gonad development and concentrating of Hg in muscle. The relationship between GSI and [THg] corresponds to the highest \log_{10} [THg] in the winter for bream, and in the spring for ruffe, just prior to or during spawning, thus highlighting the species-specific spawning and gonad development periods of fish (Keva et al., 2017).

4.4. Relevance for human health and monitoring of wild fish

Results show that [THg] found in some commonly consumed fish, such as perch, is significantly higher during the winter and spring compared to the rest of the year. [THg] in all fish tested were below the maximum European limit set by the EU Commission Regulation (1881/2006) (0.5 mg kg⁻¹ wet weight for non-predatory fish, and 1.0 mg kg⁻¹ w.w. for pike and many other predatory fish). The highest [THg] (0.7 mg kg⁻¹ w.w.) (dry: wet conversion factor of 5 (Magalhães et al., 2007; Cresson et al., 2014; Cresson et al., 2015)) was measured in a spring-caught 46.9 cm male pikeperch specimen. Average [THg]

measured in the L. Pääjärvi species (Table 1) are similar to those previously observed in Fennoscandia (Ahonen et al., 2018; Braaten et al., 2019), though ruffe, while within health limits, was comparatively high (mean annual $0.2 \text{ mg kg}^{-1} \text{ w.w.}$), potentially due to consumption of crustaceans (*M. relicta*) positioned relatively high in the food chain (e.g., Cabana et al., 1994). This, however, does not diminish the increased [THg] observed in the winter and spring and increased rates of THg bioaccumulation near the spawning season and subsequent recovery. As the percid fish in this study demonstrated significant seasonal differences in [THg] and THg bioaccumulation, and considering that perch and pikeperch are commonly fished for human consumption, more frequent boreal [THg] monitoring in wild fish during the winter should be considered. The results of this study suggest that standardized sampling times throughout the year to measure seasonal changes in different species should be developed with respect to [THg] maximums during winter-spring (e.g., March) and minimums in summer-autumn (e.g., August) to understand overall [THg] variation in freshwater fish (Table 1). Such a sampling scheme should also prioritize achieving a large sample size (e.g., 20–30 individuals) and broad range of size categories for each species to calculate the implied bioaccumulation regression slope, as current monitoring practices present limitations. In Finland, monitoring generally targets a small sample size (10 individuals) of medium-sized fish. For example, perch is limited to a monitoring size of 15–20 cm (Kangas, 2018), lower than the typically selected size of >25 cm for human consumption. To achieve a deeper understanding of Hg accumulation in lake food webs, enhanced monitoring of top predator species (pikeperch, pike and burbot) is of key importance. As ice fishing is a common pastime in Finland, local cooperation can be sourced for winter samples.

5. Conclusions

This study contributes to the limited scientific knowledge on seasonal Hg dynamics in boreal fish communities. Clear seasonal trends of [THg] in fish muscle and bioaccumulation of THg were noted in all studied L. Pääjärvi fish species. These species demonstrated elevated bioaccumulation of THg in the spring and summer seasons during and after spring spawning in all studied species, contrasted by lower rates in the autumn and winter. In percid species, [THg] was highest during the winter and spring due to Hg concentrating and lowest in the summer and autumn seasons due to somatic growth dilution. Cyprinids, while generally following this trend, did not show significantly different seasonal [THg] values. Additionally, this study confirmed that both biotic and environmental factors explain [THg] in fish muscle: the total length of fish was identified as the primary factor for determining [THg], in combination with seasonal environmental (water temperature at 0–3 m, total carbon, total nitrogen and oxygen saturation) and biotic variables (gonadosomatic index and sex). Further studies should consider assessing whether the same seasonal trends are significant in other contaminants commonly found in fish, such as per- and polyfluorinated substances (PFAS) and polychlorinated biphenyls (PCBs). Development of a standardized sampling scheme to effectively identify and measure seasonal changes in different species by sampling key freshwater species in winter-spring and summer-autumn should be considered in northern countries. This year-round scheme should include a representative sample size composed of a broad size and age range for each species to achieve a better understanding of both [THg] and THg bioaccumulation in key fish species in lake food webs.

Author contributions

AJP: Conceptualization, Methodology, Software, Validation, Formal Analysis, Investigation, Data Curation, Writing – Original Draft, Writing – Review & Editing, Visualization, Funding acquisition. SJT: Conceptualization, Supervision, Writing – Review & Editing. HML: Investigation, Data curation, Writing – Review & Editing. ESE: Investigation, Data

curation, Writing – Review & Editing. KKK: Conceptualization, Supervision, Methodology, Resources, Formal Analysis, Investigation, Data curation, Writing – Review & Editing, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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