



Investigating the diet source influence on freshwater fish mercury bioaccumulation and fatty acids—Experiences from Swedish lakes and Chinese reservoirs

Pianpian Wu¹ · Haiyu Yan² · Martin J. Kainz^{3,4} · Brian Branfireun⁵ · Ann-Kristin Bergström⁶ · Min Jing^{2,7} · Kevin Bishop¹

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Abstract

Dietary uptake is key for transferring potentially toxic contaminants, such as mercury (Hg) and essential dietary nutrients, such as polyunsaturated fatty acids (PUFA), to consumers at higher trophic levels of aquatic food webs. We evaluated the role of diet sources for Hg bioaccumulation and PUFA retention in fish across lake food webs in seven Swedish lakes and two Chinese reservoirs. Fish total Hg (THg) and methyl-Hg (MeHg) differed greatly between the two countries: the Chinese fish contained less than 300 ng g⁻¹ dry weight (d.w.) THg with less than 50% as MeHg, versus the Swedish fishes which contained approximately 2000 ng g⁻¹ d.w. THg and nearly 100% as MeHg. Fatty acids enrichment of linoleic acids (LIN) were more prevalent in the Chinese fishes regardless of size ($p < 0.05$). Here we examined food web length, fish growth rates, and fatty acids patterns in relation to the quality of fish as a food source for both Hg and FA. Contrary to the expectation that biodilution of Hg throughout the food chain would explain these differences, a more complex picture emerged with high levels of Hg at the base of the food web in the Chinese reservoirs, a decoupling of fatty acid and Hg bioaccumulation, and a major role for both fish stocking and fish feed. It is hoped that this work will provide a nuanced picture of fish quality as a food source in different ecosystems.

Introduction

Mercury (Hg) bioaccumulation patterns in freshwater food webs have been widely reported (Fitzgerald et al. 2007;

Booth and Zeller 2005; Wang and Wang 2010). For the highly bioavailable methylmercury (MeHg), high aqueous concentrations promote higher MeHg levels in marine plankton (Hammerschmidt et al. 2013). Nevertheless, the relationship between aqueous MeHg concentrations and fish MeHg contents that also considers the situation at the base of the food web is not well defined globally (Wu et al. 2019a). High degrees of Hg bioaccumulation in aquatic ecosystems, especially in boreal freshwaters, have commonly been attributed to ecosystem characteristics of dissolved organic matter (DOM), pH, and nutrient status, as well as the length and complexity of the food chain (French et al. 2014; Edmonds et al. 2012; Gorski et al. 2008; Le Faucheur et al. 2014; Lindqvist et al. 1991). For many Chinese lakes/reservoirs, Hg bioaccumulates to lower concentrations, despite generally higher Hg levels in surface waters and sediments. This has often been attributed to biodilution associated with relatively high levels of nutrients (Liu et al. 2012). The role of diet sources (i.e., dietary fatty acids and potentially toxic Hg) on the food quality of the fish, however, has rarely been accounted for in much detail. Limited research has covered the topic of diet contribution to mercury bioaccumulation in freshwater food webs (Kainz et al.

✉ Haiyu Yan
yanhaiyu@mail.gyig.ac.cn

- ¹ Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden
- ² State Key Laboratory of Environmental Geochemistry, Institute of Geochemistry, Chinese Academy of Sciences, Guiyang, China
- ³ WasserCluster - Biologische Station Lunz, Inter-University Center for Aquatic Ecosystem Research, Lunz am See, Austria
- ⁴ Research Lab for Aquatic Ecosystems and -Health, Danube University Krems, Krems, Austria
- ⁵ Department of Biology, Western University, London, ON, Canada
- ⁶ Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden
- ⁷ School of Public Health, the Key Laboratory of Environmental Pollution Monitoring and Disease Control, Ministry of Education, Guizhou Medical University, Guiyang 550025, China

2017; de Wit et al. 2012; Kainz et al. 2006), and this is even rarer in Chinese freshwaters (Razavi et al. 2014). This highlights that investigations with a holistic approach that includes the base of the food web are needed in Chinese freshwaters as well as in oligotrophic freshwaters to assess the major local influences on each system and the differences between systems. Comparative studies between the two systems may provide even more insight.

We conducted field studies in both China and Sweden to explore the transfer of potentially toxic contaminant MeHg and fatty acids (FA) as highly required dietary nutrients across different trophic levels in selected freshwater ecosystems. Seven Swedish lakes and two Chinese reservoirs (both are common types of lentic water ecosystems in the corresponding country (Sobek et al. 2007); Yang and Lu 2014; Gao and Zhang 2010) with different trophic status were investigated in the late summer to autumn period in 2015. Samples included water, plankton (in different size-fractions: seston (<25 µm in Sweden), microplankton (64–112 µm in China; 25–100 µm in Sweden), mesozooplankton (112–500 µm in China; 100–500 µm in Sweden) and macrozooplankton (>500 µm in Sweden), macro-invertebrates (mainly insects), and fishes (perches as dominant Swedish fish samples, and carps for China). We identified the total Hg and MeHg content of each sample type, stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$), as well as fatty acids portfolio. While some components of this investigation have been reported separately for each country, (Jing et al. 2021; Wu et al. 2019b; Jing et al. 2020) no comparison has been made of food web mercury accumulation and fatty acids in the Swedish and Chinese waters. Here, we present comparison of food chain lengths, Hg bioconcentration factors, and various food sources represented by fatty acids profiles, overlaying on already contrasting Hg bioaccumulation across these freshwater ecosystems. Furthermore, we expected that despite differences in how fatty acids and Hg bioaccumulate, there would be a correlation between these two aspects of fish food quality, since more Hg would increase the need for the protective features of FA. The goal of this paper is to gain a more detailed understanding of trophic web differences in bioaccumulation patterns of potentially toxic MeHg and physiologically required dietary FAs of oligotrophic Swedish and eutrophic Chinese lakes.

Materials and methods

Sampling

Our sampling campaigns covered seven lakes in Sweden and two reservoirs in China (Table 1). Sampling and Hg analysis in Chinese reservoirs and Swedish lakes were

Table 1 Sampled lakes/reservoirs in Sweden and China

Lake name (abbreviation), Country	Lake treatment	Trophic status
Erken (ER), Sweden	Reference	Mesotrophic
Nedre Björntjärn (NBT), Sweden	N addition & Clearcut	Oligotrophic
Övre Björntjärn (OBT), Sweden	Clearcut	Oligotrophic
Stortjärn (STOT), Sweden	Clearcut Reference	Oligotrophic
Mångstretjärn (MST), Sweden	N addition Reference	Oligotrophic
Lillsjöleden (LSL), Sweden	Clearcut	Oligotrophic*
Struptjärn (STRT), Sweden	Clearcut	Oligotrophic
Hongfeng reservoir (HF), China	Restored from aquaculture	Eutrophic
Wujiangdu reservoir (WJD), China	Aquaculture	Eutrophic

*Invasive green algae present during sampling

conducted by the Institute of Geochemistry, Chinese Academy of Sciences and the Swedish University of Agricultural Sciences, respectively.

The Swedish lakes (except for Lake Erken) were located close to each other in the Västerbotten region of northern Sweden where Umeå University assisted in the sampling. The catchment areas, particularly those situated in the Västerbotten region, consist mainly of coniferous forest (*Picea abies*, *Pinus sylvestris*) and open Sphagnum dominated mires. Sampling at Lake Erken, located in the Stockholm region of eastern Sweden, was assisted by Uppsala University. Whole lake fertilization experiments with nitrogen (N) addition were implemented in Nedre Björntjärn in 2012 and 2013 (Deininger et al. 2017), while forest clearcutting activity took place in the beginning of 2013 in Lillsjöleden and Struptjärn. Lake Övre Björntjärn and Nedre Björntjärn were clearcut in the beginning of June 2014. And in late 2014, Lake Lillsjöleden and Struptjärn underwent additional further forest harvesting (see (Deininger et al. 2019)).

For the Swedish side of the Sino-Swedish synthesis, sampling was carried out using nets in the summer 2015. Attributes sampled were lake water, plankton, macro-invertebrates, and fish for Hg (including MeHg), fatty acid profiles, and stable isotope analysis.

Collection of biological samples in China was carried out in two artificial karst reservoirs of the Wujiang River in Guizhou, Southwest China during summer 2015. The Wujiang River is one of the largest tributaries of the Yangtze River. It has a subtropical climate and is located in a Hg mineralisation zone with high natural Hg release due to the high Hg concentration in the bedrock. Two eutrophic reservoirs with a long history of aquaculture were selected for this study:

- a. a reservoir with ongoing aquaculture that began in 1999, Wujiangdu (WJD) Reservoir (106°8'26" E, 26°35'20" N), located in the main stream of Wujiang River. It is characterised by a high density of net-caged fish production for aquaculture; and
- b. the Hongfeng (HF) Reservoir (106°26'16" E, 26°29'30" N), located in the tributary of Wujiang River. This is the drinking-water source for the city of Guiyang. After a 12-year history of aquaculture activities (1995–2007), HF was restored from aquaculture in 2007 to promote water quality and nature preservation.

Fish samples across these sites in Sweden and China were obtained by net fishing. After recording the length and mass of freshly sampled fish, about 10–20 g of fish dorsal muscle from each sample was collected under clean conditions, freeze dried and then homogenized with a ball mill grinder and stored at -80°C until analysis for mercury species and fatty acids. Sample weight before and after freeze drying were also recorded for dorsal muscle moisture level calculations. The fish dorsal muscle samples had moisture contents around $78.7 \pm 3\%$.

Plankton and macroinvertebrate taxonomy

Phytoplankton samples (plankton size fraction of 25–100 μm and $<25 \mu\text{m}$) were fixed with Lugol, and variable volume (5 to 50 μL) was settled following the Utermöhl method (Utermöhl 1958). Samples were counted on an inverted microscope (Leica DMI 3000 B) and at least 400 cells were identified to the genus level. Phytoplankton biovolumes were assigned using reference data (Kremer et al. 2014). The identification of zooplankton and macroinvertebrates was carried out by the SWEDAC accredited Biodiversity Lab at the Department of Aquatic Sciences and Assessment (Swedish University of Agricultural Sciences, Uppsala). The zooplankton samples (plankton size fraction of 100–500 μm and $>500 \mu\text{m}$) taken from both surface and hypolimnion lake water were taxonomically identified using a stereo microscope (Nikon Eclipse Ti-U) at 75x for counting zooplankton numbers and 150x for species identification, respectively. The identification of the taxonomic composition of macroinvertebrates was done using a stereo microscope (Nikon SMZ1000) at a magnification range from x6 to x100, by sorting individuals of abundant taxa to the lowest possible taxonomic unit (i.e., species, genus, or, in some cases, family or order level) upon collection on ice. Then the sorted samples were stored at -20°C before freeze-drying and homogenization using an agate mortar and pestle for further analysis of Hg and fatty acids.

Total mercury and methylmercury analysis

Total Hg and MeHg concentrations of water were analysed by the Swedish Environmental Institute (IVL). The MeHg concentration of water was determined by gas chromatography (GC)/cold vapour atomic fluorescence spectrometer (CVAFS), following US EPA 1630 method (USEPA 1998), with a detection limit of 0.02 ng L^{-1} and a quantitation limit of 0.06 ng L^{-1} . The total Hg concentration in water was also identified by CVAFS following US EPA 1631 method (USEPA 2002) and performed by IVL. The method has a detection limit of 0.05 ng L^{-1} and a quantitation limit of 0.1 ng L^{-1} .

Total Hg and MeHg contents in plankton and macroinvertebrates were measured by Analytical Services at the Biotron Centre for Experimental Climate Change Research at Western University in London, Canada. Total Hg contents ([THg]) in plankton and macroinvertebrate samples were analysed with a DMA-80 Total Mercury Analyser (Milestone Srl) employing US EPA method 7473 (USEPA 2007), or solid-sampling thermal decomposition amalgamation atomic absorption spectrometry (TDA AAS). The equipment's method detection limit was documented as 0.1 ng. The precision of measurement from replicate analyses was greater than 80%. Samples, blanks, CRMs (DORM-2 with [THg] of $4.64 \pm 0.26 \mu\text{g g}^{-1}$ d.w., TORT-2 with [THg] of $0.27 \pm 0.06 \mu\text{g g}^{-1}$ d.w., MESS-3 with [THg] of $0.091 \pm 0.009 \mu\text{g g}^{-1}$ d.w.) were run at least once per every 10 samples to assess analysis accuracy. Recoveries for CRMs were within $100 \pm 20\%$, while blanks were $<10\%$ of the lowest sample [THg].

MeHg contents ([MeHg]) in plankton and macroinvertebrate samples were analysed with a Tekran® 2700 Methyl Mercury Auto-Analysis System (Model 2700; Tekran Instrument Corporation.). The equipment is equipped with an atomic fluorescence detection (following EPA Method 1630 (USEPA 1998)) that has a method detection limit of $0.002 \text{ ng Hg L}^{-1}$. Method blanks were $0.045 \pm 0.01 \text{ ng Hg L}^{-1}$. Sample replicates and CRMs (IAEA-086 with [MeHg] of $0.258 \pm 0.022 \mu\text{g g}^{-1}$ d.w., DORM-3 with [MeHg] of $0.355 \pm 0.056 \mu\text{g g}^{-1}$ d.w., and TORT-3 with [MeHg] of $0.137 \pm 0.012 \mu\text{g g}^{-1}$ d.w.) were run at least once per every 15 samples to assess analysis accuracy (method relative percent difference $<35\%$).

For each investigated freshwater, the bioconcentration factor (BCF) for aqueous MeHg to zooplankton was calculated as the log-transformed ratio between [MeHg] in zooplankton ($[\text{MeHg}]_{\text{zooplankton}}$, i.e., ng MeHg g^{-1} dry weight (d.w.)) and [MeHg] in water ($[\text{MeHg}]_{\text{water}}$, i.e., ng MeHg mL^{-1}) (Gómez-Regalado et al. 2023):

$$BCF = \log\left(\frac{[\text{MeHg}]_{\text{zooplankton}}}{[\text{MeHg}]_{\text{water}}}\right) \quad (1)$$

For THg analysis of biota samples from the Chinese reservoirs, 0.1–0.2 g of freeze-dried samples were digested in HNO₃:H₂SO₄ (7:3 v/v) at 95 °C for 3 h before being measured using CVAFS (Brooks Rand Model III, Seattle, USA). For MeHg analysis of biota samples from Chinese reservoirs, 0.1–0.2 g freeze-dried samples were digested in 5 mL of 25% KOH solution and heated for three hours at 75–80 °C. The digestion was diluted with Milli-Q water (18.2 MΩ/cm resistivity; Millipore) to a certain volume prior to analysis (Yan et al. 2006). MeHg was separated by GC and then quantified by CVAFS. The quality control consisted of using duplicates, method blanks and certified reference materials (CRMs). Blank spikes and duplicates were taken regularly (>10% of samples) throughout each sampling process. TORT-2 from the National Research Council of Canada was used as the CRM. Recovery of THg and MeHg in the CRM was 106 ± 1.9 and 101 ± 2.0%, respectively. The concentrations of THg and MeHg are reported as ng per g dry weight (d.w.).

Fatty acids analysis

Fatty acids analysis was performed at WasserCluster Biologische Station in Lunz am See, Austria. Lipids were extracted and analysed from freeze-dried, homogenized samples (ca. 3–10 mg d.w.) using chloroform:methanol (2:1 v/v) as described in detail by Heissenberger et al. (2010). Total lipids were quantified as mass fractions (mg lipids g⁻¹ d.w.) gravimetrically using duplicate measurements. Known volumes of total lipid extracts were derivatized to fatty acid methyl esters (FAME) using H₂SO₄-methanol (incubated at 50 °C for 16 h). FAME were dried under N₂ before being re-dissolved in hexane and run on a gas chromatograph (Thermo Scientific™ TRACE™ Gas Chromatograph coupled to flame ionization detection) with a Supelco™ SP-2560 column used for separation of FAME. FAME were identified by comparison of their retention times with known standards (37-component FAME mix, Supelco™ 47885-U; bacterial fatty acids, Supelco™ 47080-U; and the following individual FAME standards: stearidonic acid, O5130 SIGMA™; and n-3 docosapentaenoic acid, Supelco™ 47563-U) and quantified with reference to seven-point calibration curves derived from 2.5, 50, 100, 250, 500, 1000, 2000 ng μL⁻¹ solutions of the FAME standard for each identified FA. FAME were expressed as mass fractions (mg FA g dry wt⁻¹) and as individual FA relative values (% of total identified FA).

A group of 6 fatty acids were investigated as algal-derived FA compounds: linoleic acid (LIN; 18:2*n*-6), α-linoleic acid (ALA; 18:3*n*-3), arachidonic acid (ARA; 20:4*n*-6), eicosapentaenoic acid (EPA; 20:5*n*-3), stearidonic acid (SDA; 18:4*n*-3), and docosahexaenoic acid (DHA; 22:6*n*-3). These fatty acids are considered essential to the

somatic growth of various consumers, as they are integral parts of cell membranes (Kainz and Mazumder 2005; Tallima and El Ridi 2018), therefore essential fatty acids (EFA) because consumers cannot produce or only partly convert these FA. The odd-saturated and branched-chained FA (e.g., the sum of C15:0 and C17:0 and their iso- and anteiso-homologues, also known as mono-unsaturated FA) were analysed as bacterial-derived FA (BFA), while long-chain saturated FAs were considered as terrestrial plant derived FA (terr. FA) (Sun et al. 2000). A BFA/PUFA ratio was also calculated based on FA mass fractions, and the ratio was used to indicate zooplankton grazing on bacteria versus phytoplankton (Kainz and Mazumder 2005; Brett et al. 2009).

Stable isotopes analysis

Subsets of plankton and macroinvertebrate samples were selected for stable isotope analysis to identify the natural abundance of ¹³C and ¹⁵N. The amount of biological tissue used for stable isotope analysis was approximately 1 mg per sample. Stable carbon and nitrogen (δ¹³C and δ¹⁵N) isotopes were determined using a MAT-252 mass spectrometer and expressed as ‰ using δ¹³C and δ¹⁵N notations relative to the International Standard PVDB and the atmospheric nitrogen isotopic ratio. The analysis was carried out by the Stable Isotope Facility at UC Davis, United States. Stable isotope values were expressed in δ notation as parts per mill deviation from a standard reference. The δ¹³C or δ¹⁵N of fish samples were calculated to compare isotope ratios in organism samples using the following formula:

$$\delta^{13}\text{C or } \delta^{15}\text{N} = \left[\left(R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right] \times 1000 \quad (2)$$

where R is ¹³C:¹²C, or ¹⁵N:¹⁴N.

Stable carbon isotope values (δ¹³C) were used to assess the consumption of aquatic vs. terrestrial organisms in consumers. The δ¹³C values become generally isotopically lighter with increasing terrestrial proportions of the diet (McCutchan et al. 2005). The δ¹⁵N values increases in organisms with increasing trophic level, thus the food chain length of the investigated freshwaters was assessed. Because δ¹⁵N values are a measure of trophic position and food chain length, we used the regression slope of the regression of log-transformed [Hg] vs. δ¹⁵N values to assess Hg biomagnification across systems (Lavoie et al. 2013).

For estimating trophic positions of aquatic organisms, we used reported mean trophic fractionations values for δ¹⁵N of 3.4‰ (1 SD = 1.3‰) (Post 2002; Borga et al. 2013). Therefore, we used the δ¹⁵N value to calculate the food chain length and TLs in the investigated freshwaters. The following calculation is the most frequently used formula

for estimating TL of a freshwater consumer:

$$TL_{consumer} = (\delta^{15}N_{consumer} - \delta^{15}N_{base})/3.4\text{‰} + \lambda \quad (3)$$

where $TL_{consumer}$ is the trophic level of the consumer, $\delta^{15}N_{consumer}$ is the $\delta^{15}N$ value of the consumer, $\delta^{15}N_{base}$ is the $\delta^{15}N$ value of the baseline, and λ is the trophic position of the organism used to estimate $\delta^{15}N_{base}$ (e.g., $\lambda = 1$ for a primary producer).

To calculate food chain length of investigated freshwaters, we used the formula below:

$$Food\ chain\ length = TL_{piscivorous/omnivorous} - 1 \quad (4)$$

Statistical analysis

The statistical data analysis of the data was performed using the software JMP 10 (© SAS Institute Inc.) and R. Log transformations were carried out to achieve normality and resolve heteroscedasticity prior to statistical testing with regression analysis. The level of significance for all tests was set at 3 levels (weak: $0.1 > p > 0.05$, moderate: $0.05 > p > 0.01$, and strong: $p < 0.01$).

Results and discussion

A summary of the number of Hg, stable isotope, and fatty acid analyses in the biological samples collected from the reservoirs in China and lakes in Sweden are found in Table 2 and results from the Hg and stable isotope analyses are reported in Table 3. The latter are grouped by treatment or history of the waterbody. Total Hg (THg) content in both phytoplankton (China: 22.8 ± 20.9 ng g⁻¹ d.w., Sweden 9.8 ± 2.7 ng g⁻¹ d.w.) and zooplankton (China: 20.2 ± 9.3 ng g⁻¹ d.w., Sweden: 13.8 ± 4.5 ng g⁻¹ d.w.) across the Chinese reservoirs and Lake Erken (ER) were within the same order of magnitude with no significant difference ($p > 0.05$). Macroinvertebrates [THg] in the Chinese reservoirs (141.9 ± 44 ng g⁻¹ d.w.) even surpassed ER (55.6 ± 42.6 ng g⁻¹ d.w.) at statistical significance

($F(1,18) = 12.7$, $p < 0.05$). Further on at higher trophic level, fish [THg] and [MeHg] differed greatly in samples from the two countries. In the Chinese reservoirs, fish contained <300 ng g⁻¹ d.w. THg and only $<50\%$ MeHg/THg, whereas fish from Swedish freshwater lakes contained $\sim 6\text{--}7$ times higher [THg] (i.e., ~ 2000 ng g⁻¹ d.w.), of which almost all was methylated Hg ($\sim 100\%$ MeHg). Similar observations of fish Hg bioaccumulation patterns have been reported in earlier Swedish and Chinese regional studies (Liu et al. 2012; Nguetseng et al. 2015). Yet the present study is the first to report a comparison of Hg and FA in Swedish and Chinese aquatic food webs where the sampling campaigns have been coordinated to facilitate comparison. It was estimated that algal biomass dilution in eutrophic water greatly contributed to low fish Hg in Chinese reservoirs (Liu et al. 2012). However, this alone does not explain similar or even higher primary consumer Hg concentrations in plankton and macroinvertebrates from Chinese reservoirs compared to samples from Swedish lakes.

We divided fish into two size groups, based on the fish length (cm): Big fish (>15 cm) and small fish (<15 cm for fish collected from China, ~ 10 cm for fish collected from Sweden). The fish size categorization is important due to changing feeding behaviour of fish during their life span, while in Chinese Reservoirs the big fish mostly referred to cultured fish, and small fishes are wild fish (Thorpe 1977; Leclerc et al. 2011). A summary of fish size and Hg concentrations (total Hg and MeHg) is summarized in Table 4. Big omnivorous fish had significantly higher [Hg] than those in small fishes from Swedish lakes. The opposite pattern was found in the Chinese reservoirs where small fish had significantly higher [Hg] than bigger fish.

The HF reservoir food chain length was highest among all investigated water bodies (Table 5). There were also more fish species with different feeding behaviour sampled from the HF and WJD reservoirs (*Megalobrama amblycephala*, *Aristichthys nobilis*, *Ctenopharynx odon idellus*, *Silurus asotus*, *Hemiculter leucisculus*, etc.). Thus the Chinese reservoirs had a higher fish biodiversity than the Swedish lakes which were dominated by perch (*Perca fluviatilis*). This is contrary to the expectation that low fish Hg

Table 2 Summary of biological samples grouped by treatment/impoundment history and number of biological samples analyzed for Hg

Treatment	Phytoplankton	Zooplankton	Macroinvertebrates	Fish
Aquaculture, China	2	2	/	27
Restored from aquaculture, China	2	2	7	18
Clearcut, Sweden	6	6	17	20
N addition & Clearcut, Sweden	2	2	2	10
Reference, Sweden*	6	6	30	43

*Including lake Erken (ER), Stortjärn (STOT), and Mångstretjärn (MST)

Table 3 Summary of total Hg and MeHg, and stable isotopes in biological samples grouped by treatment/impoundment history

Treatment	THg(ng g^{-1} d.w.)	MeHg(ng g^{-1} d.w.)	MeHg/THg %	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Phytoplankton					
Aquaculture, China	8	1.59	19.9	-33.41	2.91
Restored from aquaculture, China	37.6	1.88	5.0	-35.75	19.89
Clearcut, Sweden	233.01 \pm 199.41 (6)	8.93 \pm 9.73 (3)	6.2 \pm 0.09 (3)	-28.43 \pm 0.51 (6)	1.47 \pm 0.50 (6)
N addition & Clearcut, Sweden	588.59 \pm 1.39 (2)	3.67 \pm 0.59 (2)	0.6 \pm 0.01 (2)	-28.67 \pm 0.14 (2)	1.25 \pm 0.58 (2)
Reference, Sweden	141.73 \pm 147.47 (6)	3.06 \pm 2.07 (3)	2.8 \pm 0.03 (3)	-23.41 \pm 7.97 (6)	3.22 \pm 2.04 (5)
Zooplankton					
Aquaculture, China	13.64	0.48	3.50	-33.96	3.03
Restored from aquaculture, China	26.81	1.06	3.90	-34.75	21.05
Clearcut, Sweden	188.04 \pm 115.79 (6)	9.03 \pm 2.91 (2)	5.10 \pm 0.03 (2)	-28.51 \pm 0.39 (6)	1.52 \pm 0.66 (6)
N addition & Clearcut, Sweden	394.03 \pm 32.47 (2)	5.34 \pm 3.38 (2)	1.40 \pm 0.01 (2)	-29.15 \pm 0.16 (2)	1.20 \pm 0.14 (2)
Reference, Sweden	142.92 \pm 113.96 (6)	2.24 \pm 2.88 (2)	1.30 \pm 0.01 (2)	-24.40 \pm 6.56 (6)	3.07 \pm 1.02 (6)
Macroinvertebrates					
Aquaculture, China	/	/	/	/	/
Restored from aquaculture, China	141.93 \pm 43.96 (4)	69.12 \pm 55.80 (3)	44.20 \pm 0.30 (3)	-25.20 \pm 3.59 (4)	12.17 \pm 1.63 (4)
Clearcut, Sweden	241.38 \pm 117.51 (11)	222.52 \pm 63.94 (3)	74.80 \pm 0.07 (3)	-31.07 \pm 2.08 (15)	4.07 \pm 1.70 (15)
N addition & Clearcut, Sweden	144.24	/	/	-34.84	4.58
Reference, Sweden	106.88 \pm 124.93 (24)	27.56 \pm 46.10 (5)	36.00 \pm 0.35 (5)	-25.15 \pm 5.70 (29)	3.76 \pm 1.55 (29)
Fish					
Aquaculture, China	115.50 \pm 164.40 (17)	40.66 \pm 50.64 (14)	39.40 \pm 0.11 (14)	-25.87 \pm 2.80 (17)	10.12 \pm 2.20 (16)
Restored from aquaculture, China	394.31 \pm 299.86 (24)	152.72 \pm 158.01 (20)	40.50 \pm 0.11 (20)	-26.00 \pm 3.92 (20)	15.35 \pm 2.86 (20)
Clearcut, Sweden	1831.34 \pm 933.51 (20)	1545.47 \pm 1021.19 (20)	82.10 \pm 0.15 (20)	-32.02 \pm 0.93 (20)	7.75 \pm 1.06 (20)
N addition & Clearcut, Sweden	3672.22 \pm 3058.76 (10)	3226.59 \pm 3016.72 (10)	81.50 \pm 0.13 (10)	-30.66 \pm 0.59 (10)	9.94 \pm 0.40 (10)
Reference, Sweden	1648.03 \pm 2232.98 (43)	1455.89 \pm 2127.96 (41)	79.40 \pm 0.12 (41)	-29.64 \pm 2.02 (33)	8.85 \pm 1.84 (33)

Total Hg and MeHg concentrations in dry weight (d.w.) and stated as Mean \pm Standard deviation (Number of samples if more than 1)

levels in the Chinese reservoirs would be associated with simpler and shorter food chains relative to the Swedish lakes with high Hg levels in fish. The BCF was also significantly lower in the Chinese reservoirs and the mesotrophic freshwaters (WJD, HF, and ER) in comparison to the other Swedish lakes that were more oligotrophic. This is consistent with previous studies using BCF as an indicator of mercury bioaccumulation efficiency (Wu et al. 2019a).

Most of the fishes sampled from the Swedish lakes were perch (*Perca fluviatilis*), while we had some exceptions from lake Erken, where a few roach (*Rutilus rutilus*) and ruffe (*Gymnocephalus cernua*) were also collected. Unlike omnivorous feeding by perch, roach are typically planktivores, while ruffe are more benthivores (Savino and Kostich 2000). In perch and ruffe, fish length positively predicted both total and MeHg ($R^2 > 0.88$, $p < 0.05$). However, EFA contents were generally negatively related to fish length (i.e., $\log\text{LIN}$, $\log\text{ARA}$, $\log\text{EPA}$, or $\log\text{ALA} \sim \log\text{length}$: $R^2 > 0.55$, $p < 0.035$, except for DHA and SDA. The dietary

biomarkers for algal (PUFA), bacterial (BFA), and terrestrial diets (terr. FA) as well as individual EFA (LIN, ARA, EPA, DHA, SDA, and ALA) negatively predicted [THg] and [MeHg] in perch and ruffe. In roach, however, fish length negatively predicted [THg] ($R^2 = 0.77$, $p = 0.05$, close to statistical significance) and [MeHg] ($R^2 = 0.97$, $p = 0.002$) and growth dilution in roach may have caused lower Hg bioaccumulation in roach. PUFA, BFA, ARA, EPA, and DHA positively predicted roach [THg] from Lake Erken (PUFA: $R^2 = 0.82$, $p = 0.03$; BFA: $R^2 = 0.98$, $p = 0.001$; ARA: $R^2 = 0.92$, $p = 0.01$; EPA: $R^2 = 0.86$, $p = 0.02$; DHA: $R^2 = 0.85$, $p = 0.03$). This suggests that roach are exposed to plankton food sources enriched in both Hg and FA.

A total of 14 different fish species were sampled from Chinese lakes with most of them restricted to two different feeding behaviours: planktivorous and omnivorous. PUFA negatively predicted total Hg ($R^2 = 0.81$, $p = 0.006$) and MeHg ($R^2 = 0.95$, $p = 0.0002$) in planktivorous fishes. We

Table 4 Summary of fish size in length and weight, MeHg content (ng per g d.w.⁻¹), and the proportion of methylated Hg (% MeHg)

Fish	China					Sweden				
	Nr	Length (cm)	Weight (g)	MeHg (ng g ⁻¹ d.w.)	%MeHg	Nr	Length (cm)	Weight (g)	MeHg (ng g ⁻¹ d.w.)	%MeHg
Big	27	42.5 ± 11.3	1037.6 ± 616.4	43.5 ± 46.2	38.1 ± 9.9	36	22.4 ± 7.2	168.7 ± 180.7	2779.5 ± 2588.8	83.6 ± 11.3
	Planktivorous	16	43.1 ± 5.5	1012 ± 419	144.7 ± 253.2	3	20.7 ± 1.8	88.3 ± 18.9	233.1 ± 27.0	74.7 ± 7.0
	Omnivorous	7	29.9 ± 10.6	502.4 ± 570.2	19.1 ± 5.8	33	23.4 ± 7.4	189.8 ± 183.9	3159.9 ± 2636.0	84.2 ± 12.1
	Piscivorous	4	59.5 ± 4.8	1869.3 ± 438.1	26.9 ± 14.9	/	/	/	/	/
Small	Average	43.8	1105.3	58.6	38.9	148.9	22.9	148.9	2057.5	80.8
	Bottom dweller	20	10.4 ± 2.7	15.1 ± 9.3	199.8 ± 167.3	39	10.0 ± 2.2	11.3 ± 8.1	757.9 ± 458.6	78.2 ± 12.7
	Planktivorous	4	8.6 ± 0.5	10.1 ± 0.2	77.4 ± 4.4	5	8.7 ± 0.9	6.4 ± 2.2	283.4 ± 171.8	69.2 ± 5.5
	Omnivorous	2	9.1 ± 1.6	5.5 ± 6.4	/	2	13.7 ± 0.4	24.5 ± 4.9	337.8 ± 6.3	85
Average	14	11.1 ± 2.9	18.0 ± 9.6	257.2 ± 165.4	32	10.1 ± 2.2	11.6 ± 8.2	878.6 ± 447.6	78.5 ± 13.6	
		9.8	12.2	178.1	40.8	10.6	13.5	564.4	77.7	

Nr represent the number of samples collected for the analysis in this study. Fish size and MeHg concentrations marked in Mean ± Standard deviation

Table 5 Food chain length and bioconcentration factors (BCF, log transformed) of investigated lakes calculated from stable isotope analysis of ¹⁵N for piscivorous/omnivorous fish according to formula [4], and MeHg concentrations in primary consumer and water samples according to formula [1], respectively

	Food chain length	BCF
ER (Reference)	4.56	3.52
LSL(Clearcut)	3.19	4.32
OBT (Clearcut)	3.71	4.58
STRT (Clearcut)	3.30	4.65
STOT (Clearcut Reference)	3.04	4.43
MST (N addition reference)	3.78	/
NBT (N addition & Clearcut)	3.70	4.02
HF (Restored from aquaculture)	5.89	3.50
WJD (Aquaculture)	3.77	1.74

couldn't find any statistically significant correlation between any FA with Hg content in the Chinese omnivorous fishes. Length did however correlate negatively for both total Hg and MeHg. Total Hg: R² = 0.54, p = 0.0012; MeHg: R² = 0.53, p = 0.003). These last two sets of relationships from the Chinese reservoirs point to the role of fish stocking, where the larger fish are more likely to be stocked, and thus not bioaccumulating the FAs or elevated Hg from the base of the food web in the Chinese reservoirs Hg during much of their lives.

The only statistically significant correlation in Swedish lakes between mercury species and the FA was for the relationship between terr.FA and MeHg in small fish after forest clear-cutting. In other words, allochthonous FAs positively predicted MeHg concentrations in Swedish fishes less than 10 cm long from the forest clearcut catchment (R² = 0.54, p = 0.02). This is in line with earlier investigation of fatty acids and Hg bioaccumulation in macroinvertebrates from the same sampling campaign in Swedish lakes (Wu et al. 2019b).

We further investigated the distribution of FAs in fish muscles across the lakes and reservoirs in the different countries. The PUFA (Fig. 1a) and LIN contents (%; Fig. 1b) were significantly higher (p < 0.05) in small fish from Chinese reservoirs than their Swedish counterparts. Except for omega-3 (w-3), ALA, and EPA, small fishes from Swedish lakes had significantly higher (p < 0.05) BFA, terr.FA, SDA, ARA, and DHA. Like the small fishes, LIN was also significantly higher in big fishes from Chinese lakes (%; Fig. 1b). However, there was no significant difference in PUFA or ALA contents for big fish between the Chinese and Swedish freshwater ecosystems (%; Fig. 1). All the rest of the FA profiles were significantly higher in Swedish big fishes, which includes BFA, terr.FA, w-3, SDA, ARA, EPA, DHA.

We compared relative FA values (%) in fish across lakes and reservoirs. This revealed a generally higher omega-3

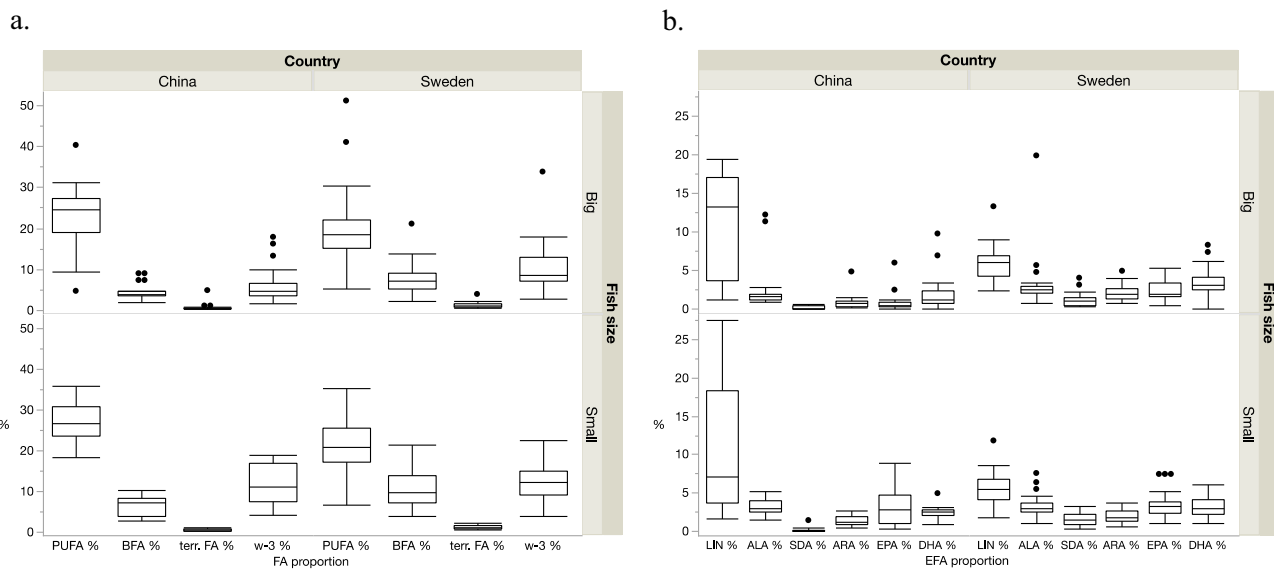


Fig. 1 Left **(a)** Boxplot of dietary biomarkers of FAs in percentage in big and small fishes from different countries. PUFA: polyunsaturated fatty acids, BFA: bacterial fatty acids, terr.FA:terrestrial fatty acids, w-3: omega 3 fatty acids. Right **(b)** Boxplot of EFAs, in percentage in big and small fishes from different countries. Algal-derived fatty acids—

LIN:linoleic acid (18:2*n*-6), ALA α -linoleic acid (18:3*n*-3), ARA arachidonic acid (20:4*n*-6), EPA eicosapentaenoic acid (20:5*n*-3), SDA stearidonic acid (18:4*n*-3), and DHA docosahexaenoic acid (22:6*n*-3)

PUFA content in fish from Swedish freshwater lakes (ANOVA statistics $F(1,119) = 8.52$, $p = 0.0042$), but LIN% was significantly higher in fish from Chinese reservoirs (ANOVA statistics $F(1,119) = 32.62$, $p < 0.0001$). It is assumed that fish from Chinese reservoirs feed significantly more on terrestrial food sources that are less enriched in omega-3 PUFA. This also reflects that fish muscle FA quality was higher in the Swedish fish. Interestingly, this pattern of FA percentage difference is not consistent with FA in zooplankton: Zooplankton omega-3 PUFA and LIN were both higher in Chinese reservoirs. This could reflect strong LIN-enriched food influence for fish in Chinese reservoirs, probably provided by external food supply. This means that the fish ingest relatively less food from the base of the food web where the phytoplankton and zooplankton are rich in omega-3 and PUFA.

Interestingly, PUFA in big fishes from Chinese lakes negatively predicted [THg] and [MeHg] ($R^2 > 0.29$, $p < 0.01$). LIN increased simultaneously with increasing fish length for small fish from Chinese lakes (positively correlation, $R^2 = 0.46$, $p = 0.0009$). However, we noticed different trends in big fishes from Chinese lakes where LIN negatively predicted total Hg and MeHg ($R^2 = 0.32$, $p = 0.004$). Changes in EFAs in big and small fishes across different lakes were consistent regardless of fish length variation. It is speculated that plant-derived fish food, made of cooked soybean and corn, is an important LIN enriched food source for fish in Chinese reservoirs. This is validated from our FA profile analysis of fish food

(Jing et al. 2020). This type of fish food exists commonly in Chinese reservoirs, either used as fish food in aquaculture, or as fish bait for anglers in local reservoirs. Fish intake of this type of plant-derived nutrient-rich food is likely to require less effort, compared to feeding on free floating phytoplankton and zooplankton or even macro-invertebrates. Therefore, this contributes to much higher LIN observed in fish from the Chinese reservoirs.

We calculated the fish growth rate as the ratio of length and weight (length/weight) (Rocha et al. 2015). This was used to test if there was growth dilution in fish belonging to different size groups. Neither [Hg] nor dietary biomarkers in big fishes sampled from Chinese lakes were sensitive ($p > 0.05$) towards change in fish size, in terms of length, weight, or growth rate. Hg contents ([THg] and [MeHg]) increased significantly ($p < 0.05$) with length and weight in small fishes from China, as well as both big and small fishes from Sweden. All three dietary biomarkers, particularly PUFA ($R^2 > 0.18$), decreased with increasing fish length or weight in big fishes from Sweden. However, dietary source FA biomarkers in small fishes from either China or Sweden were not sensitive towards the change in size. Fish [THg] and [MeHg] also decreased when growth rate increased in small fishes from China, as well as in both big and small fishes from Sweden. We thus argue that fast growth dilution in fish contributes to lower Hg bioaccumulation with increasing fish size consistent with Ward et al. (2010) with the exception of the large fish in China that were likely to have been stocked into the reservoirs (Hu et al. 2021; Guo et al. 2012).

Conclusion

Contrary to conventional expectations, our investigation revealed that in the Chinese reservoirs, where fish had low Hg concentrations, the food chain lengths were longer and more enriched in essential fatty acids than in the Swedish lakes. There were similarities of higher LIN enrichment in fish samples across all sites, yet the Chinese reservoir fish samples had strikingly higher LIN concentrations. This is likely a result of anthropogenic food sources. Fish Hg bioaccumulation in smaller fish spending their life in the nutrient-rich Chinese reservoirs appeared to be diluted by rapid fish growth driven by fish feed and therefore not limited by uptake of FA from plankton. Such discrepancies in independent Hg accumulation and FA enrichment contrasted with co-accumulation patterns of Hg and fatty acids observed in previous empirical studies outside of China.

This work provides a more holistic understanding of how different freshwater ecosystem features and fish feeding behaviour indicated by the profile of fatty acids and stable isotopes can influence differences in bioaccumulation of potentially toxic Hg. Further comparative work with contrasting landscapes such as done here between Sweden and China can further elucidate the contribution and influence of specific components of the food web on the resulting quality of fish as a food source for people.

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Author contributions PW, HY, MK, A-KB, BB and KB contributed to the study conception and design. PW, MJ and MK performed material preparation, data collection and analysis. PW prepared the manuscript with contributions from all co-authors.

Compliance with ethical standards

Conflict of interest The authors declare no competing interests.

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