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RESEARCH ARTICLE

Characteristics of plankton Hg bioaccumulations based on a global data set and the implications for aquatic systems with aggravating nutrient imbalance

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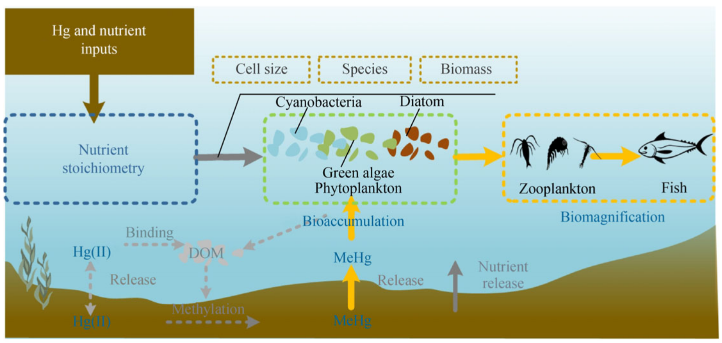
HIGHLIGHTS

• Hg bioaccumulation by phytoplankton varies among aquatic ecosystems.
• Active Hg uptake may exist for the phytoplankton in aquatic ecosystems.
• Impacts of nutrient imbalance on food chain Hg transfer should be addressed.

GRAPHIC ABSTRACT



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ABSTRACT

The bioaccumulation of mercury (Hg) in aquatic ecosystem poses a potential health risk to human being and aquatic organism. Bioaccumulations by plankton represent a crucial process of Hg transfer from water to aquatic food chain. However, the current understanding of major factors affecting Hg accumulation by plankton is inadequate. In this study, a data set of 89 aquatic ecosystems worldwide, including inland water, nearshore water and open sea, was established. Key factors influencing plankton Hg bioaccumulation (i.e., plankton species, cell sizes and biomasses) were discussed. The results indicated that total Hg (THg) and methylmercury (MeHg) concentrations in plankton in inland waters were significantly higher than those in nearshore waters and open seas. Bioaccumulation factors for the logarithm of THg and MeHg of phytoplankton were 2.4–6.0 and 2.6–6.7 L/kg, respectively, in all aquatic ecosystems. They could be further biomagnified by a factor of 2.1–15.1 and 5.3–28.2 from phytoplankton to zooplankton. Higher MeHg concentrations were observed with the increases of cell size for both phyto- and zooplankton. A contrasting trend was observed between the plankton biomasses and BAF_{MeHg}, with a positive relationship for zooplankton and a negative relationship for phytoplankton. Plankton physiologic traits impose constraints on the rates of nutrients and contaminants obtaining process from water. Nowadays, many aquatic ecosystems are facing rapid shifts in nutrient compositions. We suggested that these potential influences on the growth and composition of plankton should be incorporated in future aquatic Hg modeling and ecological risk assessments.

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1 Introduction

During the past decades, Hg discharges to aquatic environments have been largely intensified due to increasingly

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intensive human activities (Kocman et al., 2017; Obrist et al., 2018; Liu et al., 2019). The majority of Hg released into the surface water was in the form of inorganic Hg (IHg) (Guédron et al., 2017; Kim et al., 2017; Pirarath et al., 2021). While under the anaerobic or anoxic conditions such as bottom water (Ribeiro Guevara et al., 2008), sediment and water boundary (Lei et al., 2019) and wetlands (Liem-Nguyen et al., 2021), the IHg could be further converted into the more neurotoxic MeHg with the involvements of anaerobic microorganisms such as sulfate-reducing and iron-reducing bacteria (Wu et al., 2011; Si et al., 2015). The excessive intake of MeHg may induce neurological diseases for adults and neurocognitive dysfunctions for the fetus (Budnik and Casteleyn, 2019), which previously occurred in Japan in 1950s named Minamata Disease (Eriksen and Perrez, 2014). Previous studies have warned about the potential risks for sensitive populations even exposed to a low dose of MeHg (Dai et al., 2021). Strong Hg bioaccumulation and biomagnification along aquatic food chain could lead to the high Hg concentrations in high-trophic level predators, with a biomagnification factor (log-scale) up to 5.0–7.7 L/kg (Meili, 1991; Clayden et al., 2013). Although there are several entry routes for Hg being uptaken into the human beings (e.g., rice consumption, air inhalation, water intake) (Višnjevec et al., 2014; Zhao et al., 2019), consumption of Hg containing aquatic products is acknowledged to be the dominant path (Višnjevec et al., 2014; Wu et al., 2020). The accumulated Hg in carnivorous fish could reach a level that causes the concerns of researchers and government managers (Nguetseng et al., 2015). The US Food and Drug Administration sets the limit of daily oral MeHg intake below 0.1 μg/kg bodyweight; the fish with high Hg (e.g., King mackerel, Swordfish) are not recommended for daily consumptions (US FDA, 2017). The European Union Water Framework Directive set its environmental quality standard for THg in fish to 20 μg/kg (wet weight). However, Hg levels in the fish, for example breams, have regularly exceeded the limits (Nguetseng et al., 2015).

Hg transfer from water to high trophic level organism includes 3 steps listed below: 1) phytoplankton Hg bioaccumulation; 2) transfer to zooplankton and phytophagous fish; 3) ingestion of plankton and phytophagous fish by omnivorous and carnivorous fish (Lehnherr, 2014). Organisms at higher trophic levels have higher energy demands and tend to ingest more food, which facilitates the food chain transfer of Hg (Wu et al., 2020). By binding with proteins, MeHg is difficult to be excreted out of the organisms (Wu and Wang, 2011). Thus, a longer food web and more complicated food structures could lead to the higher Hg concentrations in high trophic level predators (Ouédraogo et al., 2015). Hg bioaccumulation by the plankton represents a fundamental step of Hg transfer from water to aquatic organism (Yoshino et al., 2020). Previous studies have revealed that the biomagnification along the whole food chain from water to plankton (Minamata Bay, Japan: $10^{7.0}$–$10^{7.3}$; Lake Balaton, Hungary: $10^{6.1}$–$10^{6.4}$; Apostle island, USA: $10^{4.4}$–$10^{5.3}$; Lake Taihu, China:$10^{4.2}$–$10^{4.4}$) is higher than that from the plankton to the fish (Minamata Bay, Japan: 4.6–6.2; Lake Balaton, Hungary:7.8–14.8; Apostle island, USA: 2.0–10.2; Lake Taihu, China: 3.9–6.5) (Hirota et al., 1974; Nguyen et al., 2005; Rolfhus et al., 2011; Liu et al., 2012). Therefore, even small differences in Hg bioaccumulation by plankton could have measurable consequences on the overall biomagnification of Hg in aquatic food chains (Pickhardt and Fisher, 2007). However, in aquatic Hg modeling, these parameters were usually simplified and assumed to be within a small range (Tong et al., 2012; Lehnherr, 2014). In natural waters, there are large variations of Hg in plankton across the regions, resulting in a bioaccumulation factor (BAF, log-scale) of Hg from the water to plankton at a range of 2.4–5.9 L/kg for THg and 2.6–6.7 L/kg for MeHg, respectively (Pickhardt et al., 2005; Schartup et al., 2015; Wu et al., 2019a). This indicates the importance of the plankton species compositions and regional environmental conditions in determining the Hg transfers along aquatic food chain.

In addition to Hg, another major issue in the aquatic ecosystems is the changing of nutrient concentrations and elemental stoichiometry, which are closely related to the plankton species composition, their biomass and cell size (Elser et al., 2000; Finkel et al., 2010; Huisman et al., 2018; Tong et al., 2020). For instance, in the Lake Zurich, Switzerland, the nitrogen (N) enrichment relative to the phosphorus (P) had favored dominance of *P. rubescens* at the losses of other phytoplankton (Posch et al., 2012). Lake Taihu, China, has shifted from the mesotrophic status in the 1960s to eutrophic status in the 2000s, with the dominant plankton shifting from diatom to cyanobacteria (Wang et al., 2019). Similar changes have also been reported in the nearshore waters (Burson et al., 2016; Zhang et al., 2020a). Nutrient stoichiometry, an indicator closely related to plankton cell size, is currently changing in aquatic ecosystems (Finkel et al., 2010). Increasing water N/P ratios are frequently reported worldwide (Penuelas et al., 2020). The negative correlation between N/P and diversity of zoo- and phytoplankton is associated with the shortened pathway and lower transfer rate of matter and energy along with trophic webs under the P limitation (Elser et al., 2000; Abonyi et al., 2020). It might provoke the rise and fall of plankton communities and progressions of their specy, which could influence the Hg accumulation and biomagnification in the aquatic food chains.

Plankton represents a critical path for Hg uptake to aquatic food chains from water. However, our understanding of the factors determining Hg accumulations in aquatic ecosystems across the regions was still limited. Regional differences in plankton Hg bioaccumulation were rarely identified from the global perspective. In this study, we set up a global data set for plankton Hg bioaccumulations in 89 aquatic ecosystems, dividing into inland waters, nearshore waters, and open seas. Quantitative correlations between Hg bioaccumulation in planktons and their physiologic characteristics (e.g., species, cell sizes and biomasses) were analyzed. The potential impacts of changing nutrient concentrations and stoichiometries to Hg bioaccumulation by planktons were discussed. The outcome can contribute to the improved aquatic Hg modeling in future. We suggest that the impact of changing nutrients to Hg transfers in aquatic food chain and health risk for the human beings should be addressed.

2 Materials and methods

2.1 Data collections

We identified and selected the relevant publications from the Web of Science™ that contained measured THg or MeHg concentrations in water and phyto-/zooplankton in the aquatic environment. Both field monitoring and laboratory studies were included. The keywords in the topic field included "mercury and phytoplankton" or "mercury and zooplankton" or "mercury and algae". The year of publications was not restricted. We further searched for the keywords "food chain", "accumulation" or "biodilution" from the results. The online searching was carried out on 22 March, 2019. Initially, a total of 589 publications were collected, and the majority of them were published after the 2005. The subsequent screening was performed according to the following rules: 1) publications that report Hg accumulations; 2) publications that report THg or MeHg concentrations and their bioaccumulations in the plankton. We finally set up a data set involving phyto- and zooplankton from 89 aquatic ecosystems with their details in the Tables S1 and S2. The study sites distribute in the six continents and three oceans. The majority of these sites were located in the east of Asia and north-east of North America. Based on the locations of these aquatic ecosystems, we divided them into three groups: the inland water (including lakes, rivers, reservoirs, and wetlands, 57 sites), nearshore water (22 sites) and open sea (10 sites). THg/MeHg concentrations in waters and planktons were collected and unified for the data analysis. It should be noted that the differences of sampling times in different studies were not strictly discriminated. The additional information, such as coordinate, plankton species, biomass and cell size, in original publication was carefully reviewed and collected for the subsequent analysis.

2.2 Original data handling and analysis

2.2.1 BAF values in the phytoplankton

Across all 89 aquatic ecosystems, the data about THg and MeHg concentrations in water samples, phytoplankton and zooplankton were collected. For some studies, THg and MeHg concentrations in planktons were reported on the dry weight basis. In these cases, a water content of 80% was assumed and applied to convert the concentrations into the wet weight basis (US EPA, 2012; Wickham et al., 2019; Wu et al., 2019b). Totally, we obtained THg or MeHg concentration in phytoplankton from 35 sites (127 samples) and that in zooplankton from 66 sites (581 samples). The paired water and plankton samples in aquatic ecosystems were used to estimate the BAF values for the phyto- and zooplankton. The BAF value (L/kg) was unified as the mass ratio of THg or MeHg in the planktons (ng/kg) and in waters (ng/L) (Long et al., 2018). The biomagnification factor (BMF, unitless) was defined as the mass ratio of the THg or MeHg in the zooplankton and phytoplankton (Rolfhus et al., 2011).

2.2.2 Data about plankton species, cell size and their biomass

To further explore relationships between physiologic characteristics of plankton and their Hg bioaccumulation, we also collected information about plankton species, cell sizes, and plankton density in previous studies. After examining the publications carefully, a total of 12 publications with information of specific species were collected, 7 phytoplankton species (*S. capricornutu*, *Cosmarium botrytis*, *Schizothrix calcicola*, *Thallasiosira* spp., *Chlamydomonas reinhardtii*, *Cryptomonas ozolini*, and *Synechocystis* sp.) and 6 zooplankton species (*Family Aeshnidae*, *Order Amphipoda*, *Heptageniidae*, *Littoral Chironomidae*, *Limnephilidae* and *Profundal Chironomidae*). A more detailed description for the cell size, volume and surface area for these plankton species was provided in Table S3.

Based on the reported sizes in the publications, we had classified the phytoplankton into three size categories: 0.2–5, 5–20 and >20 μm (Gosnell and Mason, 2015; Gosnell et al., 2017). The zooplankton was classified into four size categories: < 0.5, 0.1–1, 1–2 and >2 mm (Hammerschmidt et al., 2013; Schartup et al., 2015). The detailed information was provided in the Supplementary Data set S1. Since the separation of different plankton species was difficult in the field monitoring, the biomass for a certain size plankton may include different planktons. Few studies reported the plankton biomasses directly. We used an alternative indicator, chlorophyll a (Chl-a) concentration, to represent the phytoplankton abundances in waters (Schartup et al., 2018). The data was available in 53 aquatic ecosystems, with the Chl-a values ranging from ~0.08 to 28.8 μg/L (Table S4). The data of biomass for zooplankton was available for a total of 14 ecosystems, ranging from 4.6 to 142.5 μg/L (Table S5). A log-transformation of data was applied to check if the original data was normally distributed. One-way ANOVA analysis was applied to compare statistical differences in different categories. The linear regression analysis was applied to characterize the relationships between the Hg bioaccumulation, cell sizes and biomasses of the plankton. The statistical analysis was performed by the SPSS 23.0 statistical package. The level of significance criteria was set at 0.05 for all the statistical tests.

3 Results

3.1 Summary of Hg concentrations in aquatic ecosystems

Across all the investigated ecosystems, THg concentrations in waters ranged from 2 pg/L to 7.1 ng/L, with a median of 0.8 ng/L ($n = 98$); while the MeHg ranged from 0.3 pg/L to 1.9 ng/L, with a median of 25 pg/L ($n = 117$, Fig. 1(A)). A positive relationship was observed between THg and MeHg concentrations in waters ($p < 0.05$, $n = 42$, Fig. S1(A)). For plankton, the average THg concentration was 24.6 (0.2–1174.9) ng/g (median and range, $n = 293$); while the corresponding average MeHg value was 8.7 (0.06–540) ng/g ($n = 415$). THg concentrations in phytoplankton (0.3–66.8 ng/g) approached the values in zooplankton (0.4–84.6 ng/g, $p = 0.73$ by one-way ANOVA, Fig. 1). However, the average MeHg concentration was much higher in zooplankton (0.02–12.3 ng/g, $n = 351$) than that in phytoplankton (0.10–43.3 ng/g, $n = 64$, $p < 0.01$). The percentage of MeHg in the THg was higher in zooplankton (19.4(0.09–76.41) %, $n = 29$) than that in phytoplankton (11.7(0.0–69.0) %, $n = 15$, $p < 0.05$, Fig. S2). Positive relationships were observed between THg and MeHg concentrations in both of phytoplankton ($p < 0.01$, $n = 15$, Fig. S1(B)) and zooplankton ($p < 0.01$, $n = 29$, Fig. S1(C)).

BAF_{THg} and BAF_{MeHg} values in the phytoplankton were 2.4–6.0 and 2.6–6.7 ($n = 64$) L/kg (log-scale), respectively (Fig. 2(A)). BAF_{MeHg} values were higher than BAF_{THg} values, indicating that phytoplankton has much stronger bioaccumulation of MeHg than THg. Our data set further revealed BAF_{THg} and BAF_{MeHg} values for zooplankton were 2.1–7.3 ($n = 231$) and 2.9–8.2 ($n = 347$) L/kg, respectively (Fig. 2(B), in log-scale). BAF_{MeHg} for zooplankton was 5.0 times higher than BAF_{THg}, while for phytoplankton, the value was only 2.0 times. This indicated that the MeHg are subject to stronger bioaccumulation with the increase of the trophic levels. Some previous studies have reported that the MeHg can be bioaccumulated and biomagnified significantly along aquatic food chains, such as 4.1–5.2 L/kg (log-scale) in Baihua Lake, China (Liu et al., 2012), 4.6–4.9 L/kg in Chequamegon Bay, USA (Rolfhus et al., 2011), 5.6–6.4 L/kg in Babeni Reservoir, Romania (Bravo et al., 2014) and 7.0–7.8 L/kg in the Minamata Bay, Japan (Hirota et al., 1974). This indicates that the MeHg bioaccumulation by planktons (with the log[BAF_{MeHg}] of 2.6–6.7 L/kg) is crucial in the Hg transfers along the aquatic food chain (Fig. 2).

3.2 Comparison of plankton Hg bioaccumulation in different ecosystems

The results suggested that characteristics of Hg accumulation by the plankton could vary largely in different categories of ecosystems (i.e., inland water, nearshore water and open sea). A summary of THg and MeHg concentrations in waters and planktons from different types of aquatic ecosystems was provided in Table 1 and Figs. S3 and S4. In general, both of THg and MeHg concentrations in the inland water (THg: 2.2±1.8 ng/L, $n = 46$; MeHg: 0.20±0.32 ng/L, $n = 68$) were much higher than those in the nearshore waters (THg: 1.4±1.8 ng/L, $n = 21$; MeHg: 20.0±1.0 pg/L, $n = 18$, $p < 0.05$) and in the

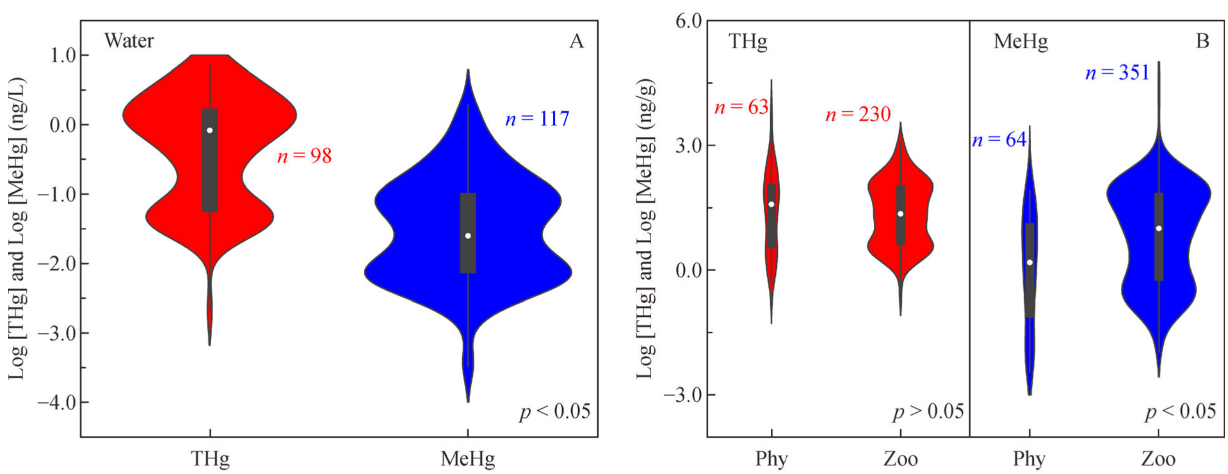

Fig. 1 THg and MeHg concentrations in waters (A), phytoplankton and zooplankton (B) in aquatic ecosystems ("Phy": phytoplankton, "Zoo": zooplankton).

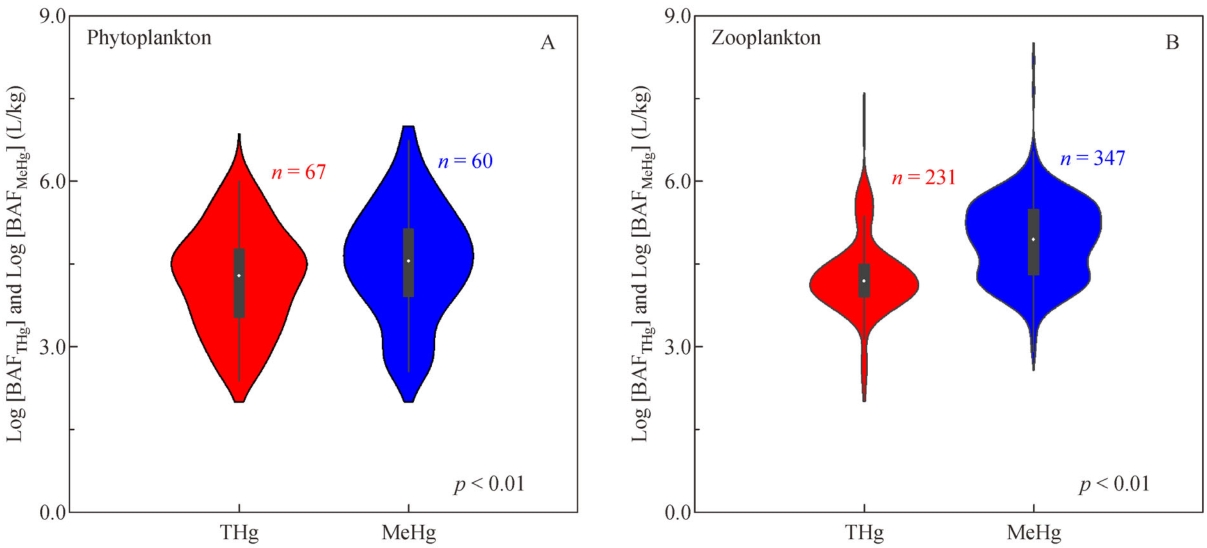

Fig. 2 BAF$_{THg}$ and BAF$_{MeHg}$ values (L/kg, log-scale) for phytoplankton (A) and zooplankton (B) in aquatic ecosystems.

open seas (THg: 46.0±2.0 pg/L, n = 31; MeHg: 7.0±2.0 pg/L, $n = 31$, $p < 0.05$) (Fig. S3). Higher Hg concentrations in the inland waters could be explained by larger aquatic Hg inputs and limited dilution capacities (Liu et al., 2016a; 2016b). Previous studies have estimated that about 800–2200 Mg/year of Hg entered into the freshwater ecosystems globally (Sunderland and Mason, 2007; Kocman et al., 2017). Consistent with the trends of Hg concentrations in waters, we found that THg and MeHg in both phyto- and zooplankton in the inland waters were higher than those in nearshore water ($p < 0.01$) and open sea ($p < 0.01$, Fig. S4). The measured MeHg concentration in the zooplankton in inland water was 92.3 (2.0–537.0) ng/g (n = 186), but 3.8 (0.02–93.3) ng/g (n = 110) in the open seas. Compared to the difference of Hg concentrations in the plankton, their BAF values had less fluctuations in different types of ecosystems. For example, the Log[BAF$_{MeHg}$] value of phytoplankton in inland water was 3.7–5.9 L/kg (n = 16), which were close to the values in the open seas (3.3–5.7 L/kg, n = 20, Fig. 3).

3.3 Impacts of physiologic characteristics on plankton Hg bioaccumulation

Prior studies have reported that the type of plankton species and their physiologic characteristics can strongly influence plankton Hg bioaccumulation (Poste et al., 2019; Tada and Marumoto, 2020; Zhang et al., 2020b). We found that the extents of MeHg accumulations by phytoplankton could vary largely among the different species (Fig. 4). Log[BAF$_{MeHg}$] value ranges from 5.3 to 6.6 L/kg among 7 phytoplankton species, with an average of 5.8 L/kg. The maximum BAF$_{MeHg}$ was observed in *Synechocystis* sp. and the minimum was observed in *Cosmarium botrytis* (Fig. 4(A)). Log[BAF$_{MeHg}$] value for zooplankton ranged from 5.9 to 6.7 L/kg among 6 zooplankton species, with an average of 6.2 L/kg. The maximum was observed in *Profundal Chironomidae*, and the minimum was observed in *Limnephilidae* (Fig. 4(B)). In general, BAF$_{MeHg}$ values for the phytoplankton (5.4–6.6 L/kg) had bigger variations than those for zooplankton (5.9–6.7 L/kg). Variations of BAF$_{MeHg}$ values in different plankton species indicate the importance of plankton species compositions in the Hg transfer along the aquatic food chains (Ouédraogo et al., 2015; Fox et al., 2017).

We further investigated the relationship between plankton cell sizes, biomasses and Hg bioaccumulation extents in the planktons. Cell size is believed to be an important factor in influencing the plankton Hg bioaccumulations in waters based on the passive diffusion hypothesis (Schartup et al., 2018; Tada and Marumoto, 2020). Our results indicated that THg concentration and its bioaccumulation in plankton had differential trends with increasing of cell size (Fig. 5). Both THg and MeHg in plankton increased with increasing cell sizes. THg and MeHg concentrations in phytoplankton with cell sizes higher than 20 μm were 51.3 and 2.2 ng/g, and they were 19 and 22 times higher than those in phytoplankton with the sizes smaller than 5 μm (Fig. 5(A)). Similarly, the BAF values were higher in the large-size phytoplankton than the small-size ones. For zooplankton, MeHg concentrations showed positive correlation with zooplankton size ($p < 0.01$), but no relationship was observed for THg. BAF$_{MeHg}$ value for zooplankton increased with the increasing cell sizes ($p < 0.01$); while the BAF$_{THg}$ values showed no trends in relation to cell sizes ($p > 0.1$, Fig. 5(B)).

Prior studies have indicated that growth dilution in a more productive ecosystem could lead to lower MeHg concentrations in the aquatic food chains (Poste et al., 2015; Brito et al., 2017). We analyzed the potential

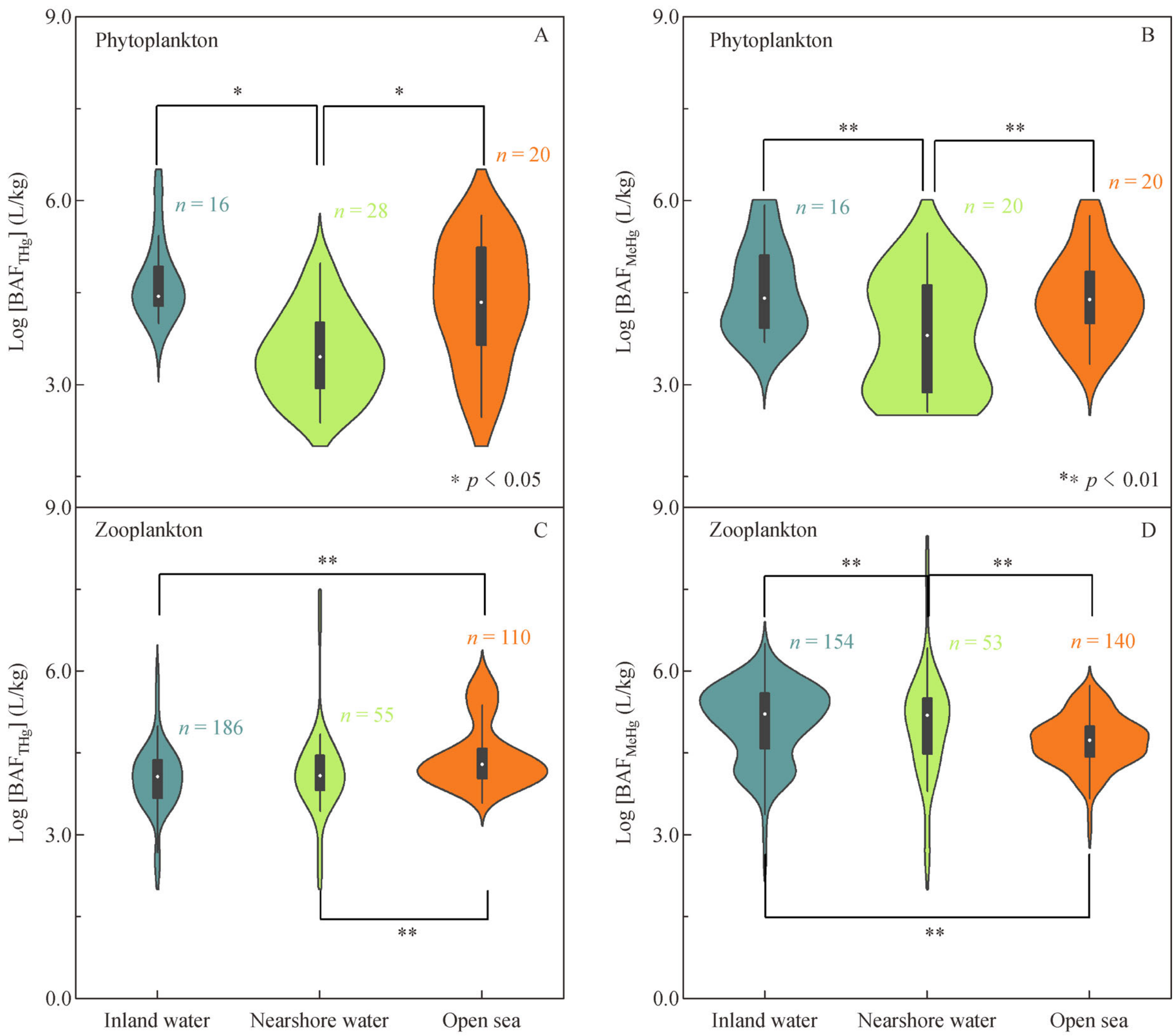

Fig. 3 Comparison of BAF_{THg} and BAF_{MeHg} value (L/kg, log-scale) in the phytoplankton (A and B) and zooplankton (C and D) in inland water, nearshore water and open sea.

relationship between plankton density and extent of Hg bioaccumulation in plankton. Similar to previous studies (Schartup et al., 2018), we used the Chl-a to characterize phytoplankton densities in the water. The regression analysis indicated a negative correlation between MeHg, $BAF_{MeHg,}$ and Chl-a (Fig. 6). A 10 μg/L increase in Chl-a could lead to a decrease of MeHg in the phytoplankton by 11.7 ([MeHg] = −1.17 × [Chl-a] + 34.6, $p < 0.05$, $n = 49$, Fig. 6(A)) and a decrease of $Log[BAF_{MeHg}]$ by 0.04 ($Log[BAF_{MeHg}]$ = −0.04 × [Chl-a] + 5.9, $p < 0.05$, $n = 38$, Fig. 6(B)). By contrast, the THg ($p > 0.05$, $n = 48$) and BAF_{THg} ($p > 0.05$, $n = 28$) in phytoplankton had not changed with the increases of Chl-a. For zooplankton, both of MeHg and BAF_{MeHg} had positive correlations with the zooplankton density in waters ([MeHg] = 0.31 × $[Zoo_{bio}]$ + 12.4 ($p < 0.05$, $n = 14$) and $Log[BAF_{MeHg}]$ = 0.0064 × $[Zoo_{bio}]$ + 5.5 ($p < 0.05$, $n = 14$, Fig. 6). Unlike the phytoplankton, zooplankton's growth dilutes MeHg body burden, but they may consume greater quantities of MeHg enriched preys of larger sizes (Schartup et al., 2018). This may lead to a positive correlation between the MeHg and zooplankton biomass (Gosnell et al., 2017). In contrast to MeHg, THg and BAF_{THg} values had an insignificant correlation with plankton density, suggesting that IHg and MeHg accumulations in plankton follow different mechanism.

4 Discussion

Hg accumulation by the plankton is a key process influencing concentrations of Hg in high trophic-level organisms, since phyto- and zooplankton are the material bases for entire food chain (Pickhardt and Fisher, 2007; Yoshino et al., 2020). Previous field monitoring and modeling results orginlally hypothesized that MeHg in

Table 1 Comparison of Hg concentrations in water and planktons in different types of aquatic ecosystems[a)]

Types of aquatic ecosystems	Hg concentrations or BAF value	All	Inland water	Nearshore water	Open sea
Water	THg (ng/L)	2.3±0.6 (n = 98)[b)]	2.2±1.2 (n = 46)	1.4±0.4 (n = 21)	(46±15) × 10^{-3} (n = 31)
	MeHg (ng/L)	(10.0±2.0) × 10^{-2} (n = 117)	0.2±0.2 (n = 68)	(20.0±8.0) × 10^{-3} (n = 18)	(7.0±0.4) × 10^{-3} (n = 31)
Phytoplankton	THg (ng/g)	72.2±17.4 (n = 63)	328.9±119.4 (n = 7)	11.0±5.1 (n = 33)	45.6±15.9 (n = 23)
	MeHg (ng/g)	1.0±2.2 (n = 64)	26.6±4.0 (n = 16)	0.6±0.2 (n = 28)	8.6±3.6 (n = 20)
	Log [BAF_{THg}] (L/kg)	4.9±0.2 (n = 67)	5.4±0.2 (n = 11)	4.2±0.1 (n = 27)	5.0±0.2 (n = 20)
	Log [BAF_{MeHg}] (L/kg)	5.2±0.1 (n = 60)	5.2±0.2 (n = 16)	4.5±0.2 (n = 24)	5.2±0.2 (n = 20)
Zooplankton	THg (ng/g)	21.9±1.2 (n = 230)	204.2±35.5 (n = 78)	33.1±3.2 (n = 60)	7.7±2.1 (n = 92)
	MeHg (ng/g)	6.61±3.5 (n = 351)	92.3±5.4 (n = 186)	6.3±1.0 (n = 55)	3.8±0.3 (n = 110)
	Log [BAF_{THg}] (L/kg)	5.0±1.04 (n = 231)	4.7±1.1 (n = 50)	4.8±0.7 (n = 50)	5.2±1.1 (n = 131)
	Log [BAF_{MeHg}] (L/kg)	5.6±1.0 (n = 347)	5.8±0.9 (n = 154)	5.7±1.1 (n = 53)	5.4±1.3 (n = 140)

Notes: a) Concentration of THg and MeHg in the plankton was based on the wet weight. b) Number in brackets represents the number of samples across all the aquatic systems

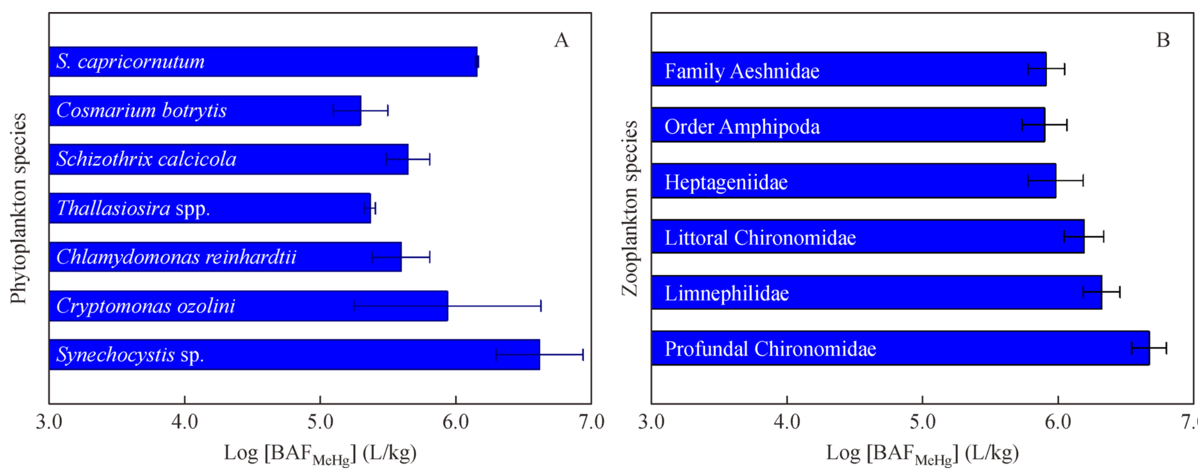

Fig. 4 A comparison about the bioaccumulations of MeHg by different phytoplankton (A) and zooplankton (B).

phytoplankton would change linearly with the water MeHg and then propagate to the higher trophic level pretators (Driscoll et al., 2012; Lavoie et al., 2013; Zhang et al., 2020b). However, the recent studies recognized that Hg bioaccumulation by plankton could be controlled by a combination of multiple factors, such as Hg availability, plankton growth, productivity and dissolved organic matter in waters. These factors can impose positive or negative impacts on plankton Hg bioaccumulations (Soerensen et al., 2016; Gosnell et al., 2017).

Based on the global and across-system data set, we found that Log[BAF_{MeHg}] values in phytoplankton ranged from 2.4 to 6.0 L/kg (n = 49). Although MeHg concentration was very low in water (0.3 pg/L–1.9 ng/L, n = 117, Fig. 1(A)), the accumulated MeHg in phytoplankton could be up to 0.3–66.8 ng/g (Fig. 1(B)). As summarized in Table 2, due to dietary uptake and assimilation, the subsequent MeHg biomagnification could be 3.3–69.2 with the increasing trophic level. With accumulations along the food chain, Hg concentrations in carnivorous fish could be significantly elevated, exceeding the thresholds for safe consumption (e.g. 20 μg/kg for

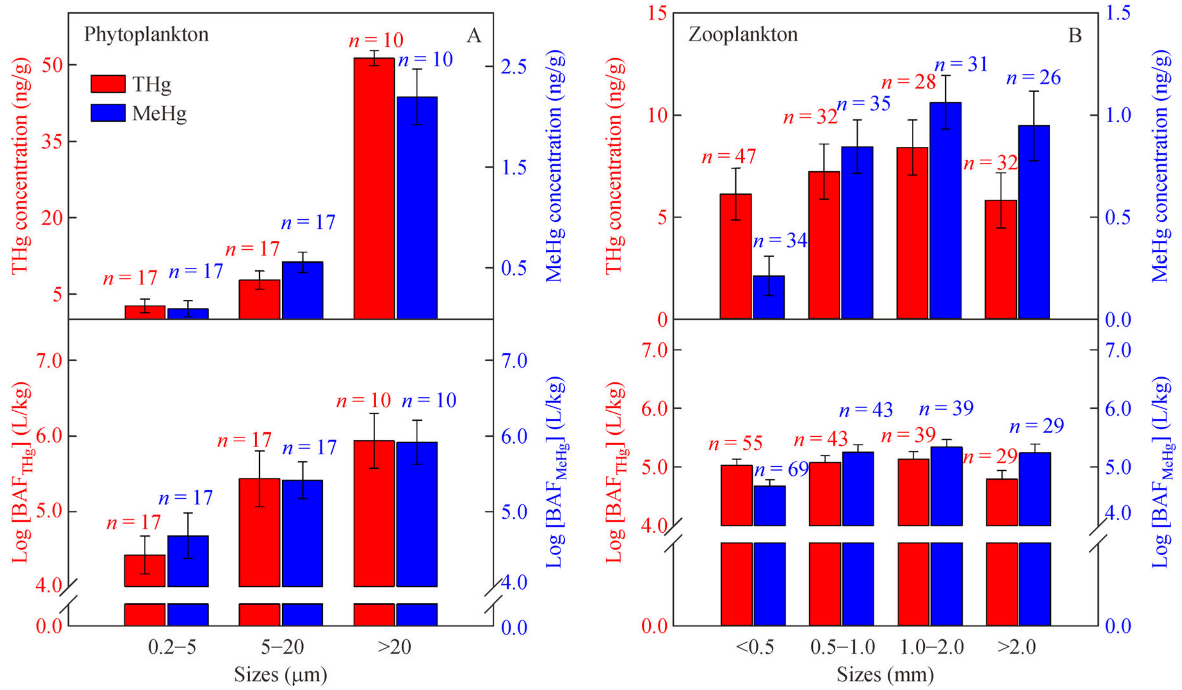

Fig. 5 Hg concentrations and BAF values (log-scale) for phyto- (A) and zooplankton (B) with different cell sizes.

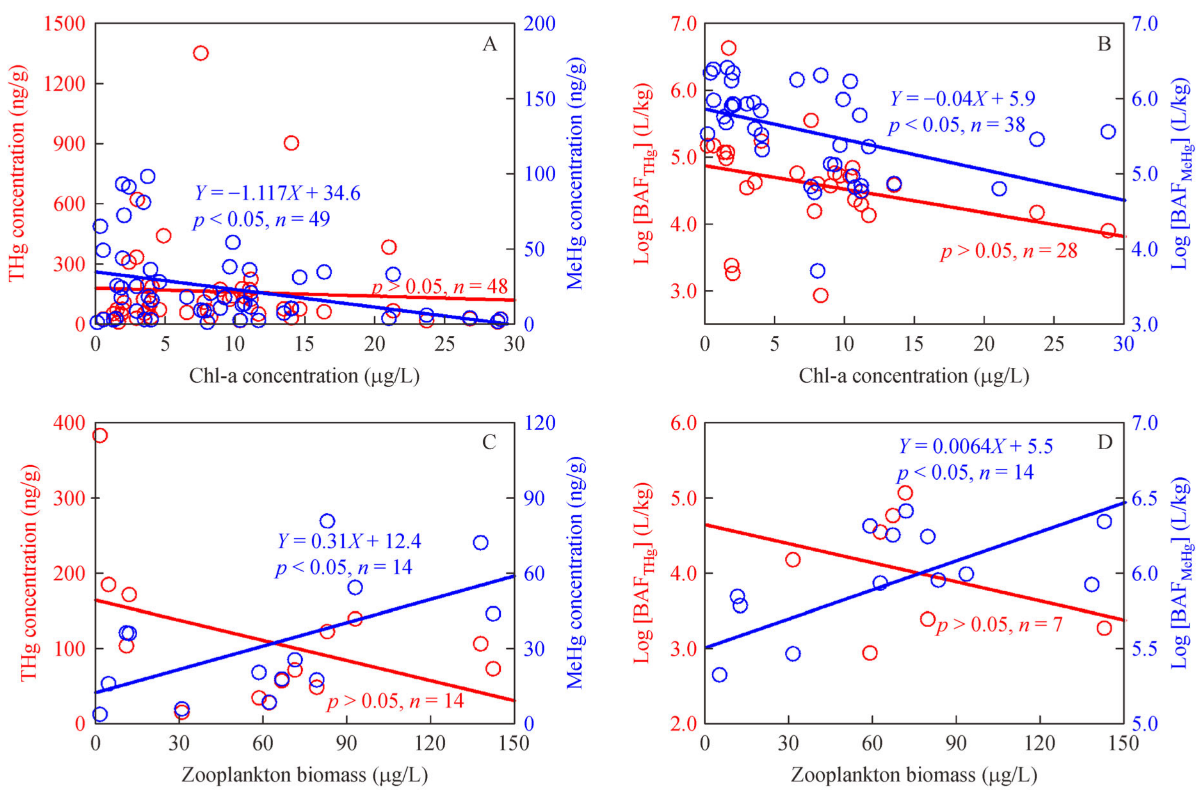

Fig. 6 Relationships between plankton biomass: Chl-a and concentration of THg and MeHg in phytoplankton (A); Chl-a and BAF values of THg and MeHg in phytoplankton (B); zooplankton biomass and concentration of THg and MeHg in zooplankton (C) and zooplankton biomass and BAF values of THg and MeHg in zooplankton (D).

Table 2 MeHg bioaccumulation and biomagnification in aquatic food webs

Aquatic ecosystems	Type	Log [BAF_{MeHg}] (L/kg)			BMF_{MeHg}			References
		Phy	Zoo	Prey-fish	Zoo/Phy	Prey-fish/Phy	Prey-fish/Zoo	
Minamata Bay, Japan	Nearshore water	7.0	7.3	7.7	2.0	4.6	6.2	Hirota et al., 1974
Long Island Sound, USA	Nearshore water	5.2	5.6	6.5	13.2	3.3	4.0	Gosnell et al., 2017
Chequamegon Bay, USA	Nearshore water	4.6	5.6	5.9	6.5	16.6	2.1	Rolfhus et al., 2011
Voyageurs, Canada	Inland water	4.6	5.8	6.5	15.1	52.5	4.9	Wiener et al., 2006
Isle Royale, USA	Inland water	5.6	5.9	6.1	3.9	7.8	2.0	Gorski et al., 2003
Apostle islands, USA	Inland water	4.4	5.3	5.4	8.1	10.2	2.0	Rolfhus et al., 2011
Southern Wisconsin, USA	Inland water	4.7	5.9	6.1	14.5	40.7	2.8	Herrin et al., 1998
Northern Wisconsin, USA	Inland water	5.3	5.4	6.2	1.6	14.5	8.5	Watras et al., 1998
Lake Balaton, Hungary	Inland water	6.1	6.4	7.3	2.0	14.8	7.8	Nguyen et al., 2005
ELA Uplands, Canada	Inland water	5.1	5.8	6.5	4.5	24.0	5.4	Hall et al., 2005
Baihua Reservoir, China	Inland water	4.1	4.0	5.1	1.5	8.9	13.2	Liu et al., 2012
Taihu Lake, China	Inland water	4.2	4.4	5.0	1.7	6.5	3.9	Wang et al., 2012
Babeni, Romania	Inland water	5.6	5.7	6.4	1.2	6.6	5.4	Bravo et al.,2014
Lagoon of Venice, Italy	Inland water	5.2	6.4	7.1	13.8	69.2	5.0	Dominik et al., 2014

Notes: a) "Zoo/phy": Zooplankton prey on phytoplankton; "Prey-fish/phy": Prey-fish prey on phytoplankton; "Prey-fish/zoo": Prey-fish prey on zooplankton; b) Average and range of Log[BAF_{MeHg}] are 5.1 (4.1–7.0) for phytoplankton, 5.7 (4.0–7.3) for zooplankton and 6.3 (5.0–7.7) for prey-fish, respectively. c) Average and range of BMF_{MeHg} are 6.4 (1.2–15) for the process that zooplankton prey on phytoplankton, 20.0 (3.3–69.2) for the process prey-fish prey on phytoplankton and 5.2 (1.9–13.2) for the process that prey-fish prey on zooplankton, respectively.

THg) (Nguetseng et al., 2015). The direct Hg uptake from water by high-trophic level organisms is usually small (Tong et al., 2017; Schartup et al., 2018). Thus, the Hg concentration in the high trophic level organisms is largely influenced by the degree of MeHg initially bioaccumulated in the phytoplankton. However, the plankton Hg bioaccumulation abilities could vary in different types of aquatic ecosystems, which might be attributed to the differences of plankton species, their biomass (Lee and Fisher, 2016) and availabilities of Hg in the aquatic ecosystems (Kainz and Mazumder, 2005; Ndu et al., 2018).

Hg bioaccumulation by planktons could be largely influenced by the physiologic characteristics of plankton, while many physiologic and ecological processes in the plankton can be related to cell size directly or indirectly (Finkel et al., 2007; Kim et al., 2014; Schulhof et al., 2019). The degree of MeHg enrichment in algal cells in the natural community could also depend on size of predominant cell in plankton assemblage (Le Faucheur et al., 2014). Passive diffusion of MeHg through cell membrane of phytoplankton was initially believed to be a dominant pathway for the MeHg accumulation. Mason et al., (1996) had first demonstrated this plankton Hg uptake pathway by using the marine diatom *Thalassiosira weissflogii*. In their investigations, the plankton MeHg uptake rate was linearly correlated with the K_{OW} of Hg in the exposure solutions. The passive diffusion through algal membrane was thus believed to be the main mechanism of Hg uptakes by plankton (Mason et al., 1996; Pickhardt and Fisher, 2007). This hypothesis is welcome by the modelers due to the simple numeric simulations and it has been widely applied in the aquatic Hg modeling (Schartup et al., 2018; Wu et al., 2020). Based on this hypothesis, small-size phytoplankton usually has significantly higher MeHg uptake rates than the large-size ones due to the great ratios of cell surfaces to cell volumes (Lee and Fisher, 2016; Zhang et al., 2020b). However, this hypothesis of passive diffusion cannot explain the results from some field monitoring (Gosnell and Mason, 2015). For instance, an investigation in the Long Island Sound indicated that phytoplankton with sizes >20 μm had much higher THg or MeHg concentration than those with sizes < 5 μm (Gosnell et al., 2017). Similar positive correlation was also observed in our global data set as shown in Fig. 5, which might be explained by another MeHg uptake mechanism through the facilitated transport. This mechanism was proved by the experiments with the algae exposed to MeHg in the dark, which would result in the decreases of MeHg uptakes (Lee and Fisher, 2016). In a study in river systems, the volume concentration factors of inorganic Hg were similar for the living and the heat-killed cells, but values of MeHg in living cells were 1.5–5.0 times greater than those in dead cells (Pickhardt and Fisher, 2007; Tada and Marumoto, 2020). The heat-killed diatoms were shown to contain less MeHg in the cytoplasm, where the total cellular Hg in dead diatoms was 4%–64% less compared with that in the living cells (Pickhardt and Fisher, 2007).

Hg biomagnification along the food chains largely depends on plankton species in water; while nutrient concentrations, stoichiometry and climate factors can impact the plankton species and abundance (Finkel et al., 2010; Razavi et al., 2015; Huisman et al., 2018; Paerl et al., 2020). Phytoplanktons range over nine orders of magnitude in cell volumes, which affected the physiologic factor and ecological function, such as metabolic rates, nutrient diffusions and uptakes, and grazing rates (Waite et al., 1997; Finkel et al., 2010). These changes may affect the functioning of entire ecosystem and nutrient cycle. Nutrient supply in water can lead to a large extent control cell sizes and taxonomic structures of phytoplankton community (Sterner and Elser, 2003; Borics et al., 2021). As shown in the Redfield ratio, the natural assembles of marine planktons tend to present the molar C:N:P ratios of 106:16:1 (Redfield, 1934). In the freshwater ecosystems, P limitation for algal growths could occur when the ratio of TN/TP mass is above 23; while N limitation occurs when this ratio is lower than 9 (Guildford and Hecky, 2000). The variability of nutrient inputs into the surface waters could act as a downward selective factor on phytoplankton cell size (Grizzetti et al., 2012; Burson et al., 2016; Penuelas et al., 2020). Over vast area of the oceans, N, P and Fe are limiting elements which form minimum nutrient requirements for some larger phytoplankton (Finkel et al., 2010). However in inland and nearshore waters, due to the enrichments of one single nutrient (Penuelas et al., 2020) and human mitigation measures (Tong et al., 2020; Wang et al., 2021), the increasing N/P ratio becomes widespread (Burson et al., 2016). In a total of 66 lakes with continuous temporal monitoring, 55 lakes had experienced rapid increases in the N/P (Penuelas et al., 2020). Similar conditions also occurred in China's coastal waters (Zhang et al., 2020a) and freshwater lakes (Tong et al., 2020). For zooplankton, high N/P stoichiometry and P limitation bring low-quality foods. High C/P ratios resulting in P limitations are connected with inferior food quality, leading to C excess for zooplankton (Alvarez-Fernandez et al., 2018; Bergström et al., 2018; Lorenz et al., 2019). This phenomena has different impacts on zooplankton with different sizes, since the low-quality food is less friendly to the larger zooplankton (Karpowicz et al., 2019). Although it has been acknowledged that the plankton species composition in water is changing rapidly, this information has been rarely used in existing aquatic Hg models, resulting in large inaccuracies in the modeling results and future predictions (Lee and Fisher, 2016; Schartup et al., 2019).

5 Conclusions

Impacts of plankton species composition on aquatic Hg cycling and subsequent Hg exposure risk for human beings are believed to be a missing part in the current aquatic Hg modeling. Our results suggested that Hg concentrations in plankton in inland waters were significantly higher than those in nearshore water and open seas. BAF (log-scale) for THg and MeHg in phytoplankton were 2.4–6.0 and 2.6–6.7 L/kg respectively. Higher MeHg were observed for both phyto- and zooplankton with bigger cells. It should be noted that some other factors (e.g., DOM in water, water temperature and climate) also affect the plankton Hg bioaccumulation. Results from this study could be useful for assessing Hg pollutions in the natural waters, but they should be interpreted with care. For the natural algal community, Hg is impossible to be measured correctly due to the difficulty in separating plankton. More information about the phytoplankton community structures is necessary before the results of this study can be impelemted in aquatic Hg modeling.

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