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RESEARCH

Mercury biomagnification in tropical western Pacific ecosystems: new insights from trophic structure and amino acid signatures of epi- and mesopelagic organisms

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Abstract Mercury (Hg) biomagnification in food webs is crucial for understanding ecological risks of Hg exposure and has become a pressing global concern. Recent research suggests that Hg biomagnification is a complex biological and ecological process. For instance, Hg readily binds to the amino acid cysteine, forming Hg-cysteine complexes that may play a key role in bioaccumulation. However, evidence of Hg transfer through oceanic food web remains limited, and the role of Hg-cysteine complexes has yet to be systematically explored or compared across oceanic species. Here, we employed an integrated approach utilizing total mercury (THg), methylmercury (MeHg), stable carbon and nitrogen isotopes, and amino acid concentrations to investigate Hg biomagnification mechanisms in 16 epipelagic and mesopelagic organisms (116 samples) from the tropical western Pacific, including crustacean zooplankton, cephalopods, teleost fish and sharks. The results of stable isotope analysis showed interspecific trophic positions ranging from 2.00 to 4.32. A significant positive linear relationship was found between the natural logarithm of THg or MeHg concentrations ($\mu g \cdot g^{-1}$ dw) and trophic positions. The trophic magnification factor values all exceeded 1, indicating clear biomagnification across successive trophic positions. In addition, a positive relationship between logarithm of cysteine and THg or MeHg (excluding shark species) suggests that Hg-cysteine complexes may play a key role in Hg bioaccumulation in teleost. However, this mechanism may not apply for elasmobranchs. Our findings demonstrate a high rate of Hg biomagnification in the tropical western Pacific and highlights the potential role of cysteine in modulating Hg transfer. These insights can improve ecological risk assessment of Hg in oceanic ecosystems and enhance our understanding of Hg trophic dynamics at the molecular level.

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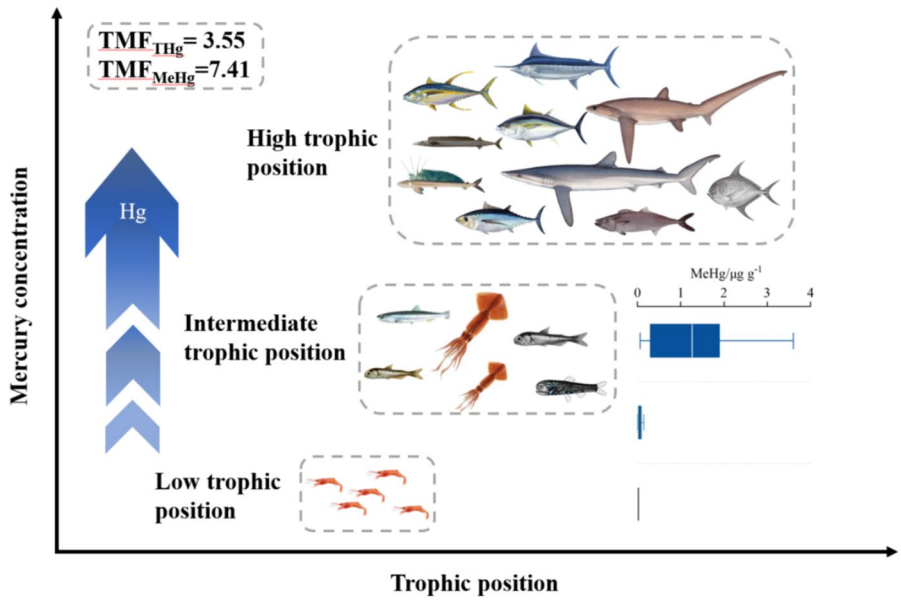
Graphical abstract



Keywords Total mercury · Methylmercury · Stable isotopes · Cysteine · Trophic magnification factor · Trophic dynamics

Introduction

Mercury (Hg) is recognized as a global environmental issue that can affect the health of biota and ecosystems. In marine ecosystems, inorganic oxidized Hg can transform into potent neurotoxin methylmercury (MeHg) via microbial methylation (Hsu-Kim et al. 2013). Microorganisms can transfer MeHg to the next trophic position or excrete it into the surrounding water, where it can be adsorbed by plankton and subsequently bioaccumulated through the food web (Rigét et al. 2007), ultimately leading to accumulating large concentrations of Hg in marine predators (Renzoni et al. 1998). This process of biomagnification into the food web presents critical implications for fisheries and environmental management. Hg exposure can produce a series of toxicological effects such as reducing growth rates, impairing reproduction, damaging the nervous system, and causing oxidative stress (Barrera-Garcia et al. 2012; Grieshaber et al. 2021; Pan et al. 2022; Sandheinrich and Drevnick 2016).

Stable isotope analysis (SIA) has been used in trophic ecology as a useful tracer of energy flow and is frequently used to clarify the relative trophic position of species in marine food webs (Deniro and Epstein 1981; Minagawa and Wada 1984). In general, $\delta^{15}N$ values can provide knowledge of trophic relationships since ^{15}N is relatively enriched in consumer tissues at a constant rate (2 ~ 4‰). In contrast, $\delta^{13}C$ values typically exhibit lower trophic fractionation (0.8 ~ 1‰) and are used to identify the consumer's original dietary carbon source (Peterson and Fry 1987; Post 2002). Therefore, SIA can provide valuable information about trophic structure and help reveal Hg transfer through food webs (Cabana and Rasmussen 1994; Dehn et al. 2006; Bisi et al. 2012). Studies on Hg biomagnification rates have primarily focused on coastal food webs (Corbisier et al. 2006; Lin et al. 2007; Kehrig et al. 2013), with fewer data available for oceanic food webs. It is worth nothing that oceanic ecosystems sustain many seafood, such as tuna and high-conservation priority species (e.g. marine mammals, seabirds and sharks). And the differences in Hg biomagnification among food webs may result in various pathways (Power et al. 2002;

Hilgendag et al. 2022). Therefore, understanding whether Hg biomagnification magnitude in oceanic ecosystems is critically important, which may pose a risk not only to higher-trophic-position species, but also to humans who regularly consume marine products (Sun et al. 2020).

Biomagnification is a complex biological and ecological process. It is reported that trophic transfer of Hg in aquatic food webs is closely coupled to the metabolism (e.g., subcellular distribution and assimilation efficiency) of Hg (Adediran et al. 2019; Wang 2012). Furthermore, Hg has been shown to conjugate with cysteine as the complex of Hg-cysteine, leading to the accumulation in fish muscle protein (Harris et al. 2003; Lemes and Wang 2009; Leaner and Mason 2002). Thus, the trophic transfer of Hg may relate to cystine content (Simmons-Willis et al. 2002; Thera et al. 2019). Zhang et al (2021) observed a positive regression between MeHg and cysteine in aquatic food webs of Poyang Lake. However, the effects of amino acid metabolism, especially cysteine, on the prey-predator relationships and the trophic transfer of Hg, have been rarely explored in oceanic ecosystem. This knowledge gap has hampered our insights to how marine predators balance their nutritional and/or energetic requirements with the adverse effects of contaminant trophic transfer (Raubenheimer et al. 2009; Raubenheimer et al. 2011). Therefore, establishing linkages between amino acids and Hg in oceanic food webs would enhance our ability to understand and predict how ongoing environmental changes and feeding shifts may affect Hg dynamics.

In this study, a total of 116 organisms were collected from the tropical western Pacific. Hg concentrations, cysteine content and the $\delta^{13}C$ and $\delta^{15}N$ values measured were used to establish regional baseline data to inform environmental monitoring and food safety concerns. The main objectives of this study were to 1) Quantify THg and MeHg concentrations in marine organisms from a tropical western Pacific food web, 2) Investigate trophic relationships using stable isotope analysis and assess biomagnification through the trophic magnification factors (TMF) calculations, and 3) Analyze the role of cysteine content in influencing Hg accumulation.

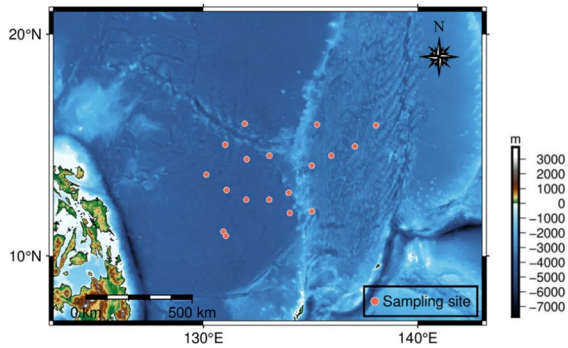


Fig. 1 Sampling sites in the tropical western Pacific

Material and methods

Sample and tissue collection

All samples were obtained by the scientific vessel "SONGHANG" of Shanghai Ocean University in the tropical western Pacific between 2021 and 2023 (10 °N ~ 16 °N, 130 °E ~ 138 °E) (Fig. 1). The shark specimens were found as bycatch in the tuna longline survey. The total length (TL) of each species was measured. A total of 116 muscle tissues were collected from 16 species, including crustacean zooplankton, cephalopods, teleost fish and sharks (Table 1). All muscle samples were stored frozen at −20 °C onboard.

Stable isotope analysis

Muscle tissues were directly utilized for the SIA, except for the shark species, which were rinsed repeatedly with deionized water to remove the potential impacts of urea (Li et al. 2016). All samples were freeze-dried at −55 °C for ≥ 24 h using a Christ Alpha 1–4 LD plus Freeze Dryer (Martin Christ; Osterode am Harz, GER) and then ground into a fine powder using a Mixer Mill MM 400 (Retsch). Approximately 1.5 mg of dried samples were weighed into 0.03 g tin capsules and analyzed using an IsoPrime 100 isotope ratio mass spectrometer (IsoPrime Corporation, Cheadle, UK) and a vario IsoPrime cube elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany). The isotope compositions of the samples were expressed as $\delta^{13}C$ and $\delta^{15}N$ notation in parts per thousand (‰). The standard reference materials for C and N were Pee Dee Belemnite carbonate and atmospheric N_2, respectively. Every tenth sample was run in triplicate of Organic Analytical Standard,

Table 1 Total mercury (THg) concentrations (dw), methylmercury (MeHg) concentrations (dw), $\delta^{13}C$, $\delta^{15}N$ values and cysteine concentrations (dw) of each species (mean ± standard deviation)

Species	Number	TL/cm	$\delta^{13}C$/‰	$\delta^{15}N$/‰	THg/μg g^{-1}	MeHg/μg g^{-1}	MeHg/THg/%	TP^{-1}	Cysteine / nmol g^{-1}
Crustacean zooplankton	10	/	−18.75	2.76	0.06	0.02	42.74	2	1.51
Encrasicholina punctifer	5	4.41(1.13)	−18.66(0.16)	3.23(0.53)	0.04(0.01)	0.01(0.01)	25.79	2.08(0.09)	3.29
Symplectoteuthis oualaniensis	6	10.52(5.18)	−18.24(0.56)	5.62(1.08)	0.06(0.02)	0.03(0.02)	44.17	2.50(0.21)	3.73
Symbolophorus evermanni	22	5.65(2.11)	−19.15(0.62)	6.27(0.81)	0.15(0.27)	0.09(0.04)	57.33	2.63(0.16)	3.26
Myctophum spinosum	6	6.13(3.54)	−19.08(0.39)	6.26(0.63)	0.07(0.05)	0.05(0.06)	72.06	2.63(0.12)	3.01
Myctophum asperum	5	9.84(2.37)	−19.90(1.52)	7.51(1.06)	0.09(0.05)	0.03(0.02)	35.29	2.88(0.22)	4.07
Makaira mazara	5	216.75(13.38)	−16.45(0.29)	11.14(1.15)	2.43(1.06)	2.02(0.41)	83.13	3.78(0.32)	4.96
Taractichthys steindachneri	7	67.67(8.50)	−16.94(0.29)	12.37(0.37)	1.17(0.61)	0.84(0.10)	71.79	4.16(0.12)	4.27
Lepidocybium flavobrunneum	2	112.56(6.71)	−19.23(0.58)	12.09(0.33)	3.42(1.11)	3.22(0.91)	94.24	4.07(0.02)	2.36
Gempylus serpens	2	110.12(5.68)	−16.96(0.23)	11.54(0.38)	1.44(0.25)	1.22(0.31)	84.72	3.90(0.08)	4.11
Alepisaurus ferox	12	106.93(30.81)	−18.06(0.31)	10.32(0.58)	0.13(0.06)	0.12(0.04)	90.23	3.56(0.15)	4.03(0.52)
Thunnus obesus	3	125.12(10.25)	−17.36(0.38)	11.81(0.58)	1.97(0.26)	1.80(0.38)	91.37	3.98(0.67)	4.33
Thunnus alalunga	6	114.67(26.39)	−18.27(0.75)	10.23(0.87)	1.13(0.31)	0.89(0.31)	78.76	3.53(0.23)	5.30
Thunnus albacares	6	142.50(17.68)	−16.87(0.30)	10.65(1.10)	0.76(0.56)	0.63(0.53)	82.90	3.56(0.28)	4.31
Prionace glauca	19	203.88(14.10)	−19.11(0.50)	12.85(0.86)	4.49(2.78)	3.62(2.16)	80.51	4.32(0.31)	2.85(1.01)
Alopias superciliosus	1	310	−17.75	12.55	4.07	3.60	88.45	4.21	2.31

*Protein content of Crustacean zooplankton was reported by Donnelly et al (1994)

Protein ($\delta^{13}C = --26.98‰$ and $\delta^{15}N = 5.96‰$), to assess the within-run precision, and a blank sample was run every ten samples to clear off residual gases. The analytical errors were approximately 0.20‰ for both $\delta^{13}C$ and $\delta^{15}N$ values.

Total mercury analysis

THg concentrations in muscle tissues were determined via thermal decomposition (combustion), amalgamation, and atomic absorption spectrometry using a calibrated DMA-80 Direct Mercury Analyzer (Milestone, Italy). Approximately 200 mg of dried and homogenized powders were loaded into the DMA-80, dried and burned at a temperature of 650 °C in an oxygen atmosphere (Maurice et al. 2021; Li et al. 2023). The measurements in tissues were conducted as follows: drying time 100 s, decomposition time 150 s, and waiting time 10 s. Quality control procedures included the analysis of laboratory method blanks, duplicate tissue samples, and certified reference materials (DORM-4) (O'Bryhim et al. 2017). The blanks values less than 0.015 $\mu g \cdot g^{-1}$, DW. The precision of duplicate samples ranged from 1.80% to 7.41%, and the percentage recovery for the certified reference materials ranged from 95 to 108%. Limits of detection (LOD) and quantification (LOQ) defined as the concentrations corresponding to three and ten times the standard deviation of the absorbance signal of ten reagent blanks divided by the calibration slope. The LOD value was 0.024 $\mu g \cdot g^{-1}$ and the LOQ value was 0.08 $\mu g \cdot g^{-1}$.

Methylmercury analysis

MeHg extraction was performed and modified according to established method (Maggi et al. 2009; Li et al. 2023). Approximately 0.5 g dried and ground muscle sample was weighed and transferred in 50 mL polypropylene tube with screw caps and hydrolyzed with 10 mL of HBr (47 ~ 49%, AR). After 10 min of shaking using a mechanical shaker, 20 mL toluene (99.7%, AR) was added following shake for 30 min. Sample was centrifuged (4000 rpm for 5 min) and the supernatant was separated to another 50 mL tube. The process was repeated once, and the combined organic extracts were subjected twice to back extraction with 6 mL of 1% (v/w) L-cysteine aqueous solution (dissolved 1% L-cysteinium chloride, 12.5% anhydrous sodium sulfate and 0.775% sodium acetate) to strip methylmercury from toluene. Then, the extract was immediately analyzed with DMA-80. The blanks values less than 0.015 $\mu g \cdot g^{-1}$, DW. The precision of duplicate samples ranged from 3.44% to 6.52%. The DORM-4 (n = 3) was analyzed and the percentage recovery for the certified reference materials ranged from 90 to 98%. The LOD value was 0.021 $\mu g \cdot g^{-1}$ and the LOQ value was 0.07 $\mu g \cdot g^{-1}$.

Amino acid concentrations of species

Amino acid content was determined using the method specified in China Food and Drug Administration (2016). Briefly, 0.5 g of muscle and 10 mL of 12 mol/L hydrochloric acid were placed in a 30 mL brown digestion tube and placed in an oven at 110 °C for 22 h. Following the filtration of the residue, 1.0 mL of the filtrate was transferred to a tube and dried in a vacuum oven at 45 °C. Next, the dried sample was drained three times with deionized water, 2 mL of citric acid solution was added, and the sample was stored for analysis.

The hydrolyzed samples were separated using an Inertsil ODS-3 C18 column (4.6 mm × 150 mm, 7°μm, GL Sciences Inc., Tokyo, Japan), and amino acid composition was determined using the liquid chromatography (L-8800, Hitachi Co., Ltd., Tokyo, Japan). The column was Inertsil ODS-3 C18 (4.6 mm × 150 mm, 7°μm, GL Sciences Inc., Tokyo, Japan). The mobile phase was a mixed buffer of sodium citrate and citric acid with pH 3.2, 3.3, 4.0, and 4.9, and a ninhydrin buffer with a mass fraction of 4%. The total flow rate of sodium citrate buffer was kept constant at 0.4 $mL \cdot min^{-1}$. Injection volume: 20 μL.

The LOD, and LOQ were detected by diluting the mixed 17 amino acids standard solutions (0.1 $\mu mol \cdot mL^{-1}$) with 0.02 $mol \cdot L^{-1}$ HCl to a concentration range of 1 ~ 250 $\mu g \cdot mL^{-1}$. The LOD value was 0.07 nmol g^{-1} and the LOQ value was 0.23 nmol g^{-1}. The precision ranged from 0.31 to 0.37%, which was obtained by adding the mixed standard stock solution to the sample and detecting five replicates. The spike recovery was calculated by detecting high, medium, and low concentrations of the mixed standard stock solution (1 ~ 50 $\mu mol \cdot mL^{-1}$) added to the samples and was between 86 and 102%.

Trophic position and trophic magnification factor

Trophic positions (TP) based on stable isotope data were estimated for each sampled species, using the following equation (Post 2002):

$$TP = \frac{\delta^{15}N_{consumer} - \delta^{15}N_{base}}{\Delta N} + TP_{base}$$

where $\delta^{15}N_{consumer}$ is the predator's $\delta^{15}N$ signature, $\delta^{15}N_{base}$ is the baseline $\delta^{15}N$ for the local food web, and TP_{base} is the trophic position of the baseline. In this research, the average primary consumer $\delta^{15}N$ of crustacean zooplankton was assumed as representative baseline, and thus $TP_{base} = 2$. The $\Delta N = 3.4‰$ represents the trophic fractionation factors of $\delta^{15}N$ Post (2002). Trophic fractionation is well known to vary based on a range of factors, including species, and diet content itself, but we have not been directly assessed for our study species and areas. The variation of the selected constants affects only the absolute values of the TP between species and not their relative relationships. Therefore, it does not influence our aim of identifying trophic structure and the transfer of Hg in food webs.

To assess the biomagnification of Hg in a food web (Fisk et al. 2001), the trophic magnification factor (TMF) was calculated using the following formulas:

$$Log_{10}C = a + b * TP$$

$$TMF = 10^{b}$$

where a represents intercept and b represents slope. The TMF > 1 indicates biomagnification of the Hg along the food web, while < 1 suggests decreasing concentration with increasing trophic positions.

Statistical analyses

The Kolmogorov–Smirnov test was used in order to test for normality of the data. ANOVA and post hoc Tukey tests were used for comparing differences in $\delta^{13}C$ and $\delta^{15}N$ values, and THg and MeHg concentrations among species. The nonparametric Kruskal–Wallis and post hoc multiple comparison tests were applied when the data distribution did not follow the rules of normal distribution. Descriptive statistics were used to calculate mean THg and MeHg concentrations, which were compared with values reported in previous studies of other marine food webs. Patterns of Hg accumulation were examined by simple linear regression and Pearson's correlation coefficient (r) to assess the relationship between log-transformed THg or MeHg concentrations and the TP of each species. In addition, linear regression analyses incorporating cysteine content was conducted to examine whether cysteine content explained additional variation in Log THg and Log MeHg concentrations. All statistical analyses were performed using Origin 2023 and SPSS 22.0.

Results

Stable isotope values and trophic position

A total of 16 species were examined in the present study. The stable isotopic ratios and trophic positions of each species are summarized in Table 1. Significant differences in $\delta^{13}C$ values were observed between species ($P < 0.05$) with the lowest $\delta^{13}C$ values observed for *Myctophum asperum* (ranging from −21.52 to −18.15‰). *Makaira mazara* showed the highest $\delta^{13}C$ values (ranging from −16.70 to −16.05‰). Contrastingly, $\delta^{15}N$ increased from Crustacean zooplankton (2.76‰) to sharks (11.58 to 11.86 ‰ in *Prionace glauca*), while most large teleost fish presented intermediate $\delta^{15}N$ values. Significant differences in $\delta^{15}N$ values were present among each species (Table 1, $P < 0.05$). An increase in $\delta^{15}N$ values corresponds to a rise in trophic position, with approximately two trophic position from primary consumers ($TP_{Crustacean\ zooplankton} = 2$) to top predators ($TP_{Prionace\ glauca} = 4.32 \pm 0.31$, Fig. 2).

Mercury biomagnification

THg and MeHg were detectable in all samples collected from the tropical western Pacific, which significantly increase from primary consumers to top predators (Fig. 3). THg ranges from 0.06 $\mu g \cdot g^{-1}$, DW (crustacean zooplankton) to 4.49 ± 2.78 $\mu g \cdot g^{-1}$, DW (*P. glauca*) while MeHg ranges from 0.02 $\mu g \cdot g^{-1}$, DW (crustacean zooplankton) to 3.62 ± 2.16 $\mu g \cdot g^{-1}$, DW (*P. glauca*). Large teleost samples showed significantly higher THg and MeHg concentrations than

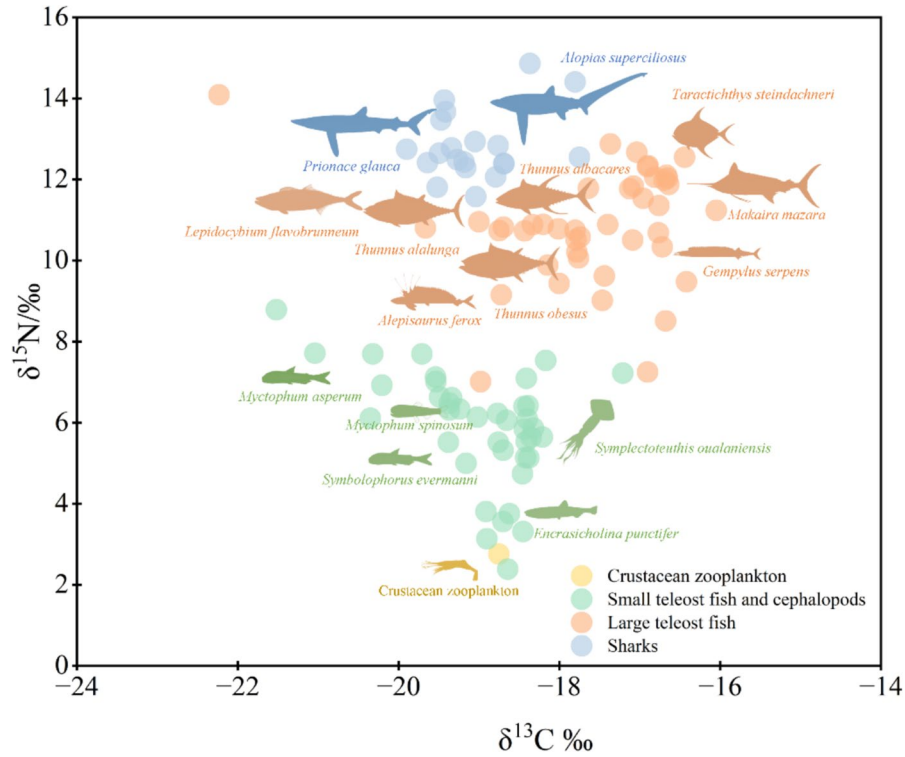


Fig. 2 $\delta^{13}C$ and $\delta^{15}N$ values of species in food web of the tropical western Pacific

cephalopods and small teleost species ($P<0.05$). Significant differences were also observed among large teleost species ($P<0.05$), while there was no significant difference between any of the four small teleost species and cephalopods ($P>0.05$). The highest proportion of MeHg (94.24% of THg) was found in *Lepidocybium flavobrunneum*, while *Encrasicholina punctifer* showed the lowest proportion of MeHg (25.79% of THg).

Trophic magnification of Hg was assessed by regressing contaminant concentrations against TP for all analyzed samples. A significant positive linear relationship was observed between log-transformed concentrations of THg and MeHg and TP (linear regression, $P<0.05$) with estimated slopes of 0.55 and 0.87 respectively (Fig. 4). TMF, derived from measured TP for THg and MeHg across crustacean zooplankton, cephalopods, small teleost fish, large teleost fish and sharks were 3.55 and 7.41. All TMFs exceeded 1, indicating consistent biomagnification of Hg and MeHg through the food web and suggest substantial Hg accumulation from the lower to higher trophic positions.

Effect of cysteine on the biomagnification of Hg

The sulfur-containing amino acid cysteine was present in low concentrations among all species (range from 1.51 to 5.30 nmol·g^{-1}, Table 1). No significant linear regressions were found between cysteine content and log-transformed concentrations of THg or MeHg when all species were included ($P>0.05$) (Fig. 5A, C). However, when shark species were excluded from the analysis, significant positive correlations emerged between cysteine content and log-transformed THg and MeHg concentrations ($P<0.05$) (Fig. 5B, D).

Discussion

Trophic structure

Understanding the structure of a food web is imperative for interpreting patterns of Hg biomagnification, as the interspecific relationships among organisms within a food web determine the efficiency with which energy and contaminants are transferred

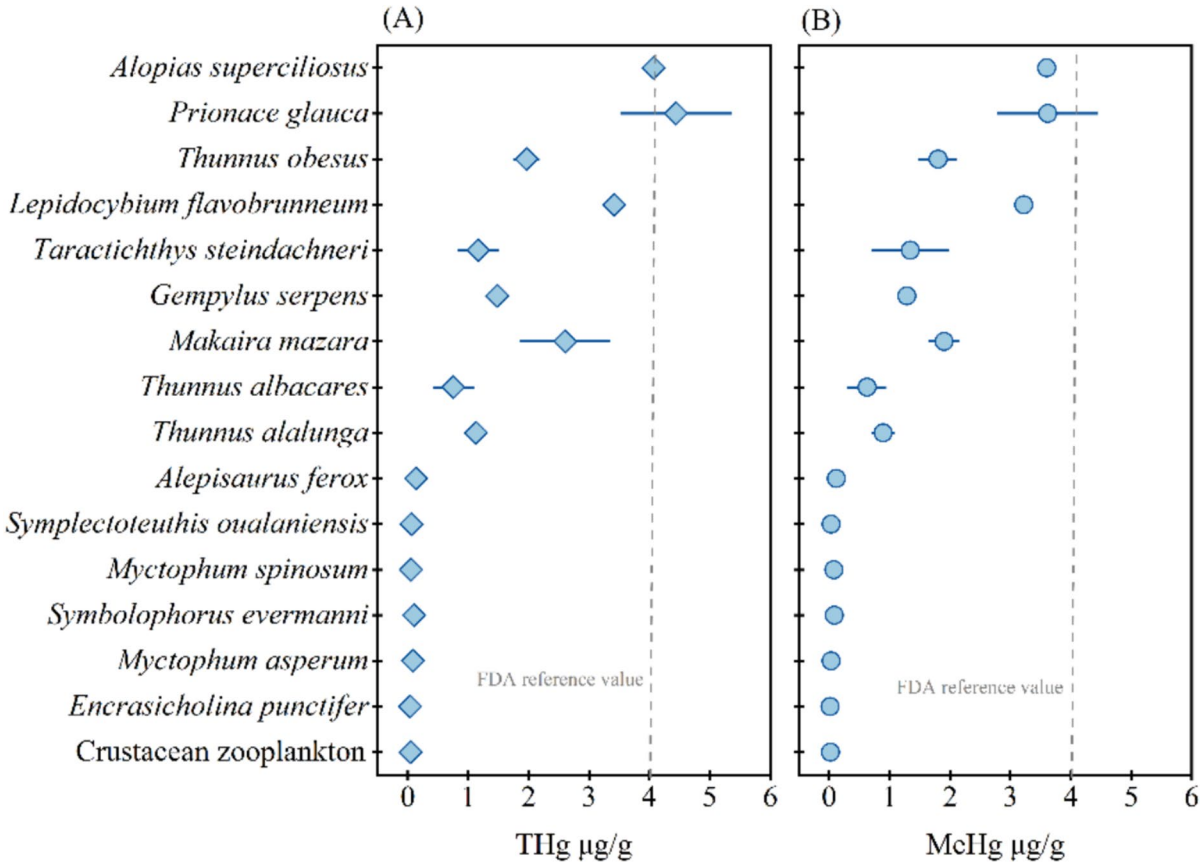


Fig. 3 **A** Total mercury (THg) concentrations and **B** methylmercury (MeHg) concentrations in muscle (μg g^{-1}, dry weight) for each species sampled in the tropical western Pacific

between trophic positions (Hobson et al. 2002). Pairing food web structural analyses with biomagnification calculations informed our understanding of dietary Hg pathways in an under-studied tropical ocean environment. In this study, the food web displayed considerable trophic diversity, consistent with the high structural complexity observed in marine ecosystems (Rigét et al. 2007; Bisi et al. 2012). Specifically, considerable variability in $\delta^{13}C$ values (−19.90‰ and −16.45‰) were observed among species, indicating multiple carbon sources entering the food web. In general, ecosystem $\delta^{13}C$ values are influenced by broad-scale patterns, and $\delta^{13}C$ can decrease with increasing depth to approximately -1.0% (Sheu et al. 1996; Graham et al. 2010). Mesopelagic organisms (e.g., Myctophiformes) spend extensive periods in deeper waters (200–1000 m, St John et al. 2016), contributing to their relatively lower $\delta^{13}C$ values. Meanwhile, top predator (e.g., sharks and tunas), typically exhibit broader horizontal movements or seasonal large-scale movement across oceanographic provinces (Stevens et al. 2010; Sibert et al. 2010), explaining their more enriched $\delta^{13}C$ values.

$\delta^{15}N$ values are extensively employed as indicators of trophic position due to relatively large and consistent enrichment with each trophic transfer (Post 2002; Hussey et al. 2014). In this study, $\delta^{15}N$ values varied by 12.47‰ across species, which is equivalent to an approximate difference of 2 trophic positions, assuming a trophic enrichment factor of 3.40‰ (Post et al. 2002). These isotopically derived TPs were consistent with previous estimates based on stomach content analysis. For example, sharks (e.g. blue shark) were found at high trophic position consistent with their known diets of large predatory

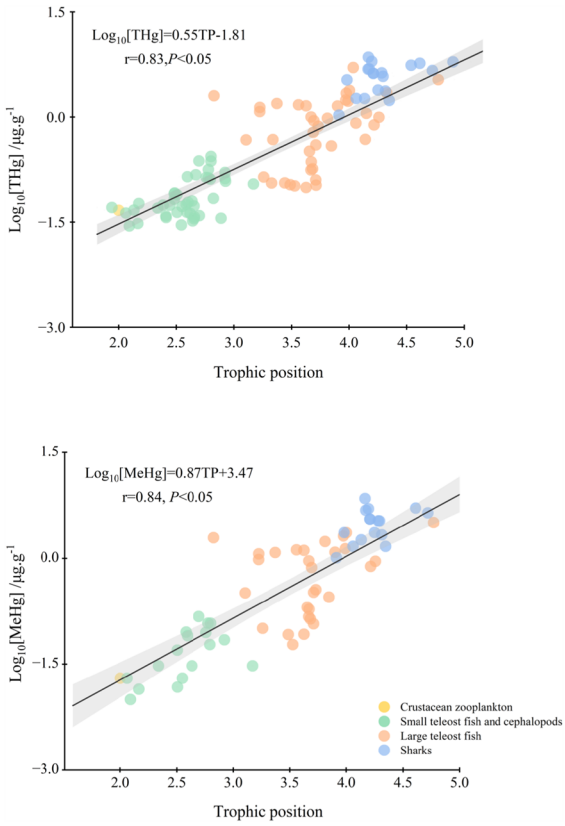


Fig. 4 Relationship between $\delta^{15}N$ values and log-transformed concentrations of total mercury (THg) or methylmercury (MeHg) in organisms from the tropical western Pacific food web. The linear relationships and Pearson's correlation coefficient (r) were shown in the figure. Shadow area: 95% confidence intervals

fish, squids and myctophids (Cortés 1999; Fujinami et al. 2018). Similarly, tunas are known to primarily feed on cephalopods (Bertrand et al. 2002; Romeo et al. 2012). Interestingly, we found that cephalopods had relatively low TP (2.63 ± 0.16) compared to other studies (Murphy et al. 2020), possibly due to their relatively small body size.

Biomagnification of Hg

Linear regression of log-transformed Hg concentrations against TP, along with calculations of TMF, offers a reliable quantitative framework for evaluating Hg biomagnification patterns across ecosystems (Rigét et al. 2007; Borgå et al. 2012). In this study, both THg and MeHg concentrations increased with trophic positions with regression slopes of 0.55 (THg) and 0.87 (MeHg). These values are comparable to those reported in other marine ecosystems, for example 0.54 (value converted, THg) in the North West Territories, Canada (Atwell et al. 1998), 0.48 (value converted, THg) and 0.88 (value converted, MeHg) in the West Greenland (Rigét et al. 2007), 0.53 (value converted, THg) and 0.59 (value converted, MeHg) in North water Polynya (Campbell et al. 2005), and 0.50 (winter, value converted, THg) to 0.55 (summer, value converted, THg) in off the Brazilian tropical coast (Bisi et al. 2012). This suggests consistency in Hg accumulation mechanisms across reasons which may reflect similar physiological traits among species, including membranes structures, lipid content, and thiol-containing biomolecules that facilitate Hg uptake and retention in muscle tissue (Gray 2002; Rigét et al. 2007; Bridges and Zalups 2005). However, the slopes observed here were higher than those reported in some systems, such as the Sepetiba Bay food web (Bisi et al. 2012) and the Arctic food web (Swanson and Kidd 2010). This inconsistency among studies may be linked to the distinct composition of the food webs and/or potential spatial heterogeneity of Hg which may affect Hg bioavailability. TMF values in this study also exceed those reported for the Indian Ocean (2.2, $R^2 = 0.4$, Boldrocchi et al. 2021) and the Baltic Sea (3.58 ~ 4.02, $R^2 = 0.7 \sim 0.82$, Vainio et al. 2022). But were lower than the extreme TMF of 25.12 (value converted, $R^2 = 0.53$) reported for the Alaskan Arctic region (Dehn et al. 2006). Despite regional variability, the consistent finding of TMF > 1 confirms that dietary uptake is the dominant Hg exposure pathway in high trophic organisms (Gray 2002; Bisi et al. 2012). Overall, the tropical western Pacific food web presented a relatively elevated rate of Hg biomagnification.

The highest mean THg and MeHg concentrations were found in *P. glauca* and *Alopias superciliosus* in this study, frequently exceeding the FDA reference value of 4 μg g^{-1} dw (exceeding number: *P. glauca*, $n_{THg} = 10$, $n_{MeHg} = 6$, *A.superciliosus*: $n_{THg} = 1$, FDA 2020). Such elevated levels may be attributed to long lifespan and high trophic status, as Hg bioaccumulation is influenced by both food web length (Lavoie et al. 2010). and biological half-life (Kunito et al. 2004). Considering that *P. glauca* and *A.superciliosus* are listed as 'Near Threatened' or "Vulnerable" by the International Union for Conservation of Nature (IUCN) (Huang et al. 2022) and pose potential health

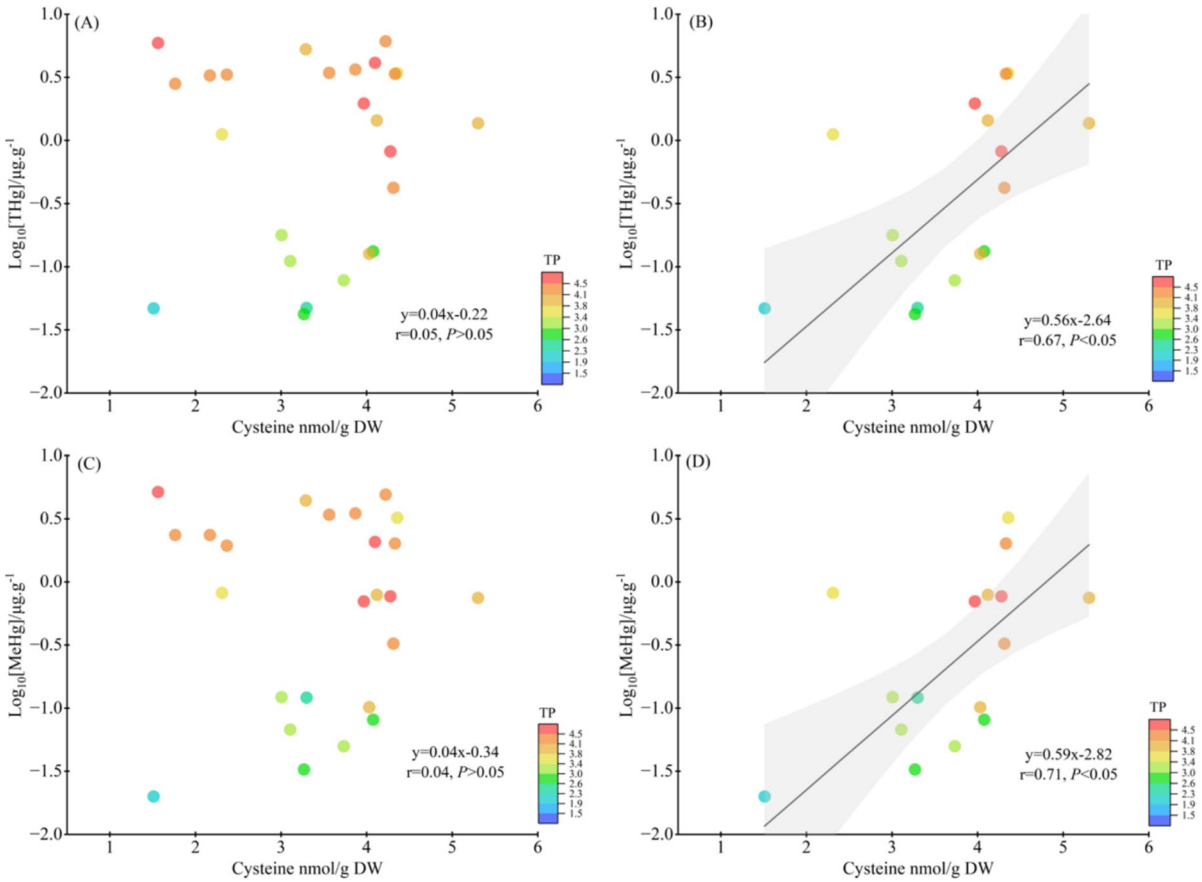


Fig. 5 Log-transformed THg or MeHg (ng g^{-1}, DW) versus TP and cysteine concentrations (nmol g^{-1}, DW) of the tropical western Pacific. The linear relationships and Pearson's correlation coefficient (r) were shown in the figure. Shadow area: 95% confidence intervals. **A** and **C** were all species. **B** and **D** do not include shark species

risks to consumers, harvesting this species for human consumption should be avoided.

Role of cysteine in Hg accumulation

Methylmercury (MeHg) in fish muscle is predominantly bound to cysteine, forming MeHg–cysteine complexes that play a central role in its storage, uptake, transport, and distribution (Harris et al. 2003). Our results showed a significant positive relationship between log-transformed THg/MeHg and cysteine content in all species except sharks. This suggests that cysteine availability influences Hg bioaccumulation, likely though the formation of MeHg-cysteine complexes within organism tissue. This pattern aligns with studies showing similar correlations between trace metal (including Hg) and protein-lipid composition in Atlantic bluefin tuna (*Thunnus thynnus*) (Milatou et al. 2023) and between MeHg and cysteine in freshwater food webs (Zhang et al. 2021). In support of this, predators have the capacity to assimilate certain metals present in the soluble protein components of their prey, with Hg uptake facilitated MeHg-cysteine complexes transported (Rainbow et al. 2011) through neutral amino-acid carriers (Leaner and Mason 2002). Sharks, however, may deviate from this pattern. Despite diets and habitats, they showed higher Hg concentrations than predatory teleost, likely due to unique physiological traits including slow growth, longevity, nitrogen metabolic cycling, and reduced elimination capacity that increases contaminant retentions (Storelli et al. 2001; Tiktak et al. 2020; Thera et al. 2022; Goyanna et al.

2023). Transgenerational exposure of Hg via yolk, uterine secretions, and/or placental transfer may also contribute to elevated Hg accumulation in viviparous elasmobranchs (Adams and McMichael 1999). In addition, factors such as temperature, digestive processes, and protein composition can also influence Hg uptake (Rainbow et al. 2011; Wood et al. 2012).

Although it is vital to understand the relationship between nutritional composition and Hg biomagnification, fluctuations of amino acid concentrations in species can be difficult to decipher through stable isotopes values (Doucett et al. 1999). Marine predators are frequently regarded as dietary generalists for consuming a wide range of prey and often rely on multiple preys to achieve their nutritional requirements in different life stages or areas (Machovsky-Capuska and Raubenheimer 2020). Incorporating stomach content analysis could improve understanding of dietary pathways. Additionally, due to interspecific differences in physiology (Wood et al. 2012), there is a need for further research into the mechanisms of Hg biotransformation, biomagnification, and elimination across marine taxa.

Conclusions

This study applied a multidisciplinary approach to better understand mercury (Hg) biomagnification processes in the tropical western Pacific ecosystem. Despite a unbalanced sample size, stable isotope analysis effectively revealed trophic structure of the studied species. The significant positive linear relationship between trophic position (TP) and both THg and MeHg concentrations, along with TMF values greater than 1, confirm clear evidence of Hg biomagnification throughout the oceanic food web. The elevated biomagnification rates observed for MeHg indicate potential health risks for top predators such as sharks, as well as for human consumers. Moreover, this study presents evidence that Hg biomagnification is associated with cysteine content in teleost, providing new insights into how nutrient composition may influence contaminant dynamics within marine food webs. Nevertheless, the understanding of biomagnification for Hg in the oceanic food webs is still limited. In the future, more studies are necessary to determine MeHg concentrations to ideal comparisons across oceanic food web. Research efforts also should focus on biomagnification mechanisms, to better assess the potential impact of oceanic food webs. In addition, further research is needed to elucidate the physiological mechanisms underlying Hg biomagnification, including tissue-specific accumulation and biotransformation pathways, to enhance ecological risk assessments and inform conservation strategies.

Author contributions YS, and YL conceived and designed the experiments. YS and JZ provided the tissue samples. YS performed the experiments and analyzed the data with the help of HP, KB, YG, and YL. All authors provided editorial advice and agreed that this version of the manuscript was accepted for submission.

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Data availability The raw data supporting the conclusions of this article will be made available by the authors without undue reservation.

Declarations

Conflict of interest The authors declare no competing interests.

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