Marine Pollution Bulletin 218 (2025) 118209

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Mercury bioaccumulation and biomagnification in mesopelagic biota

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ARTICLE INFO

Keywords:
Myctophids
Squid
Compound-specific isotope analysis of amino acids
Tasman Sea
Body burden

ABSTRACT

This study investigated the distribution and biomagnification pathways of total mercury (THg) concentrations in three mesopelagic species in the Tasman Sea: two fish (*Diaphus hudsoni*, *Metelectrona ventralis*) and one predatory squid (*Lycoteuthis lorigera*). THg concentrations in muscle tissue ranged from 0.06 to 0.26 μg g^{-1} dry weight (DW) and were consistently higher in liver tissue (0.15–0.96 μg g^{-1} DW) across all species. Species-specific variations in THg bioaccumulation and the liver-to-muscle THg ratio suggested differences in mercury metabolism. Stable isotope ratios of carbon ($\delta^{13}C$) varied across tissues and species, reflecting a diverse range of bathypelagic habitat utilisation (−19.46 to −16.72 ‰). Bulk and amino acid nitrogen ($\delta^{15}N$) isotopes provided robust estimates of mean trophic positions of fish (ranging 3.1 to 3.5) and squid (4.3). THg concentrations correlated with isotopic trophic indicators only in L. *lorigera*, and increased with body size in *M. ventralis* and L. *lorigera*, but not in *D. hudsoni*. THg biomagnification factors between fish and squid ranged between 0.54 and 1.45, indicating limited biomagnification, as confirmed with trophic magnification factors in the liver (1.89) and muscle (0.78). Spatial differences in THg concentrations were evident with higher levels in the eastern region for all species, likely driven by local ecological and environmental conditions. These results highlight the complexity of THg dynamics in mesopelagic food webs and provide important baseline data for future bioaccumulation studies in this and other oceanic regions.

1. Introduction

Mercury (Hg) is a highly toxic environmental pollutant, with its organic form (methylmercury; MeHg) posing significant risks to ecosystems and humans (Gworek et al., 2020; Rice et al., 2014). MeHg disrupts cellular processes by damaging microtubules, impairing mitochondrial function, promoting lipid peroxidation, and increasing neurotoxic compounds (Jaishankar et al., 2014). It can cross the placental barrier, causing chromosomal aberrations and is classified as mutagenic and teratogenic, adversely affecting the central nervous system, muscular function, and kidneys (Basu, 2023; Wu et al., 2025). Due to its strong affinity for protein binding, Hg bioaccumulates in organisms and biomagnifies through food webs (Bargagli et al., 1998; Bloom, 1992; Seco et al., 2021). Hg enters marine food webs primarily via phytoplankton and bacteria (Harding et al., 2018), which actively uptake Hg from seawater. Methylation of inorganic Hg MeHg, the highly toxic and bioavailable form, typically occurs within sediments (Hsu-Kim et al., 2013), facilitated by microbial activity, particularly by sulfate-reducing and iron-reducing bacteria (Tang et al., 2020). Phytoplankton can concentrate MeHg up to a million-fold relative to the surrounding water (Lehnherr, 2014). This leads to substantially higher concentrations in larger top predators such as swordfish, tuna, and marine mammals (Ackerman et al., 2007; Baishaw et al., 2007; Bargagli et al., 1998; Burger and Gochfeld, 2011).

Mid-trophic organisms play a critical role in mercury bioaccumulation and biomagnification, transferring contaminants from primary producers to apex predators and influencing mercury movement through ecosystems, including its impact on humans (Choy et al., 2009; Dunning and Brandt, 1985). In oceanic environments, mesopelagic fish (Goetsch et al., 2018; Iglesias et al., 2023) and squid (Amaratunga, 1983; Coll et al., 2013; Smale, 1996; Young and Olsen, 2007) make up a substantial portion of biomass and play essential intermediary roles in food webs. Despite existing studies on mercury concentrations in select species and regions, data remain sparse for most mesopelagic fish (Zhang et al., 2024) and squid (Seco et al., 2020). This knowledge gap is particularly evident in the Tasman Sea, a biologically diverse region between Australia and New Zealand that supports key fisheries (AFMA, 2024), including tuna, sharks, and demersal fishes

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https://doi.org/10.1016/j.marpolbul.2025.118209
Received 24 February 2025; Received in revised form 19 May 2025; Accepted 19 May 2025

(Buxton et al., 2006; Goldsworthy et al., 2003). Higher trophic predators such as sharks and tuna, which inhabit the upper and mid-slopes of southeastern Australia, have been shown to accumulate total mercury (THg), particularly MeHg, at levels exceeding recommended thresholds, primarily through their diet (Pethybridge et al., 2010a). However, the specific pathways of mercury biomagnification within these ecosystems remain poorly understood.

The extent of Hg biomagnification, measured as the concentration ratio between a consumer and its diet (Connell, 1989; Fisk et al., 2001), depends on food web structure, habitat characteristics, and environmental physicochemical properties (Lavoie et al., 2013; Yoshino et al., 2020). The biomagnification factor (BMF) quantifies contaminant transfer between trophic positions, while the trophic magnification factor (TMF), derived from the slope of the concentrations against trophic position, evaluates chemical transfer across food webs (Fisk et al., 2001). The bioconcentration factors for MeHg in fish are exceptionally high, typically ranging between 10^6 and 10^8, with MeHg comprising 99 % of THg in fish (Wiener and Spry, 1996). Stable isotope analyses of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), including compound-specific amino acid isotope analysis (AA-SIA) offers detailed insights into food web structures and Hg bioaccumulation patterns (Hebert and Popp, 2018; Layman et al., 2012; Wang et al., 2024). In marine food webs, nitrogen isotopes typically exhibit a predictable enrichment of +3.4 ‰ per trophic position, reflecting the stepwise assimilation of nitrogen in consumer tissues (Minagawa and Wada, 1984), while $\delta^{13}C$ tends to enrich by approximately +1 ‰ per trophic position, providing insights into feeding habitats (Boecklen et al., 2011). $\delta^{13}C$ is particularly useful for distinguishing feeding locations, such as shallow versus deep waters, or different water masses across latitudinal gradients, thus offering valuable information on habitat use and ecosystem connectivity (Michener and Kaufman, 2007; Whitfield et al., 2022). AA-SIA of $\delta^{15}N$ is thought to provide greater precision and accuracy in determining an organisms trophic positions, as it accounts for basal nitrogen isotopic variability in the food web and eliminates the need to compare consumer isotopic values to those of potential prey (Nielsen et al., 2015).

This study examined THg concentrations and bioaccumulation in dominant mesopelagic fish and squid species from the Tasman Sea, with a focus on their potential transfer to higher trophic predators. Using $\delta^{13}C$ and $\delta^{15}N$ isotope data and regression models, trophic positions, trophic magnification factors, and biomagnification factors, were estimated to examine THg transfer and bioavailability. The key objectives were to: (i) evaluate intra- and inter-specific differences in THg concentrations across tissues and species; (ii) compare bulk $\delta^{13}C$ and $\delta^{15}N$ values for three species and AA-SIA for two fish species to assess trophic influences; (iii) analyze the relationships between THg concentrations, body size, and trophic position to examine bioaccumulation at the species level; (iv) examine Hg biomagnification at the community level in both muscle and liver tissues; and (v) assess spatial variations in THg distribution.

2. Materials and methods

2.1. Study area and sample collection

Fish and squid samples were collected at two sites within the Tasman Sea (40°S-41°S, 153°E-163°E) from 14 to 16 June 2008 (Zhang et al., 2024). All samples were collected at night from 0 to 1000 m using a midwater open and closing (MIDOC) net system attached to the rear of a demersal trawl deployed from the fishing vessel *FV Rehua*. Upon collection, samples were identified to the species level onboard and promptly frozen at −18 °C. Each fish and squid species were segregated and preserved in plastic bags. Subsequently, individuals were transferred to laboratory facilities and stored at −20 °C for further analyses. Standard length (SL) for fish and mantle length (ML) for squid measurements were taken with precision to the nearest 0.01 mm, and weights were recorded to the nearest 0.0001 g wet weight (WW). The SL of *Diaphus hudsoni* ranged from 37.05 to 79.53 mm, with a mean (± SD) of 62.51 ± 11.14 mm, while *Metelectrona ventralis* measured between 63.25 and 94.04 mm, averaging 80.23 ± 5.97 mm. The ML of the mesopelagic squid *Lycoteuthis lorigera* varied from 57.41 to 144.52 mm, with a mean of 85.01 ± 30.66 mm. WW ranged from 0.83 to 7.78 g (3.97 ± 1.70 g) for *D. hudsoni*, 4.31 to 15.96 g (9.26 ± 2.30 g) for *M. ventralis*, and 14.95 to 196.30 g (53.67 ± 60.86 g) for *L. lorigera*.

2.2. Total mercury analysis

Prior to the analytical process, fish specimens were dissected into muscle (without skin), gills, heart, brain, liver, kidney, intestine, gonad and eye. Squid specimens were dissected into liver (digestive gland) and mantle. For muscle tissue in fish, each individual specimen was used to measure THg level. However, for all other tissues (gills, heart, brain, liver, kidney, intestine, gonads, and eyes), samples were pooled by species to ensure sufficient biomass for accurate measurement. In the case of squid, mantle tissue was analyzed individually for each specimen ($n = 45$), while liver samples were collected from only some individuals ($n = 14$) to quantify THg. After that, tissue samples were freeze-dried at −80 °C for 48 h and subsequently homogenized into a fine powder using the Mixer Mill MM 200 (Retsch). Approximately 0.05 g of each dry tissue sample was measured for THg concentration by a sequence of thermal decomposition, amalgamation, and atomic absorption spectrometry, using a pre-calibrated DMA-80 Direct Mercury Analyzer (Milestone, Italy) at Shanghai Ocean University. The sequential steps were constituted by 100 s of desiccation, 150 s of decomposition, and 10 s waiting period. For quality control procedures, the precision and reproducibility of the method were evaluated through: i) blank (empty quartz boats, three before each sample); ii) replicated fish sample analyses for all individuals, and iii) certified reference material: DORM-4 (0.412 ± 0.036 μg g^{-1}). The THg concentrations in the blank samples varied from 0.002 to 0.015 μg g^{-1} and the relative difference of replicated samples exhibited a range of 1 to 3 %. The THg concentrations in the certified reference material ranged from 0.401 to 0.421 μg g^{-1} and the percentage recovery for DORM-4 ranged from 97 % to 102 %. Method detection limits (MDLs) were determined as three standard deviations above the mean blank levels, which is 0.019 μg g^{-1}, and the blanks did not fall above the MDLs. Total mercury concentration was quantified by expressing it as the total amount of mercury per gram (μg g^{-1}) of dry weight (DW).

2.3. Bulk stable isotope analysis

Approximately 1.5 mg of freeze-dried tissue was vortexed in a 15 ml centrifuge tube with 10 ml deionized water for 1 min. After 20 h soaking at room temperature, samples were centrifuged for 3 min and the water removed. The water wash process was repeated a further two times, before then being freeze-dried. Samples were then soaked in a 15 ml centrifuge tube filled with a volume of 12 ml of 2:1 dichloromethane-methanol solution for 20 h, replaced with 8 ml of the solution and left to stand for 2 h followed by centrifugation at 6000 rpm for 3 min (Li et al., 2024). Treated liver samples were dried in an air-circulating oven at 40 °C.

Samples were weighed (~1.5 mg) into tin capsules and analyzed using an IsoPrime 100 isotope ratio mass spectrometer (IsoPrime Corporation; Cheadle, UK) and vario ISOTOPE cube elemental analyzer (Elementar Analysensysteme GmbH; Hanau, Germany) at Shanghai Ocean University. The $\delta^{13}C$ and $\delta^{15}N$ values of samples were calculated according to the following equation:

$$\delta X = \left(R_{sample}/R_{standard}\right) - 1 \quad (1)$$

where X is ^{13}C or ^{15}N, R_{sample} and $R_{standard}$ represent the ratios of $\delta^{13}C$ or $\delta^{15}N$ of the sample and the standard, respectively. The standard reference used was Pee Dee Belemnite (PDB) for carbon and atmospheric N_2 for nitrogen. A laboratory reference (protein, − 26.98 ‰ for carbon and

5.96 ‰ for nitrogen) was run every ten samples. The analytical errors of $\delta^{13}C$ and $\delta^{15}N$ values were ± 0.05 ‰ and ± 0.06 ‰, respectively.

Corrected $\delta^{13}C$ data were calculated for non-lipid remove fish muscle tissue:

$$\delta^{13}C^{'} = \delta^{13}C_{bulk} - 3.32 + 0.99^{*} C : N_{bulk} \quad (2)$$

And trophic position (TP) was estimated using isotopic data from muscle tissue:

$$TP_x = \left[\left(\delta^{15}N_x - \delta^{15}N_{ref}\right)/3.2\right] + TP_{ref} \quad (3)$$

where $\delta^{15}N_x$ is the $\delta^{15}N$ value (‰) for individual *x* muscle tissue; $\delta^{15}N_{ref}$ is the $\delta^{15}N$ value (‰) for the baseline organism; 3.2 is the average trophic enrichment factor between fish muscle and its food (Davenport and Bax, 2002) and TP_{ref} is the assumed trophic position of the baseline organism. Trophic positions were calculated using two estimates of $\delta^{15}N_{ref}$ (Flynn and Kloser, 2012). First, $\delta^{15}N$ values for *E. signifera/similis* recorded in the eastern, central and western sectors of the abyssal basin were applied to the calculations for those sectors. As described below, $\delta^{15}N$ for *E. signifera/similis* was high compared to other macrocrustacea in the region. TP for *E. signifera/similis* in the Tasman Sea was therefore assumed to be 3 for the purposes of the calculation (Davenport and Bax, 2002).

2.4. Compound specific stable isotope analysis of amino acid

Frozen (−20 °C) fish muscle tissues samples were analyzed for individual amino acid $\delta^{15}N$ values ($\delta^{15}N_{AA}$) using methods described in Friscourt et al. (2024) at the Commonwealth Scientific and Industrial Research Organisation (CSIRO) laboratories in Hobart, Australia. Briefly, samples underwent acid hydrolysis and were dried under a stream of N_2 at 60 °C. The samples were re-dissolved in hydrogen chloride (HCl) and purified using GracePure TM SPE Cation-X cartridges eluted with HCl. Samples were esterified using acetyl chloride in isopropanol (1:4) and heated at 110 °C for 1 h and dried under N_2 at 60 °C. They were trifluoroacetylated with $C_4F_6O_3$ and CH_2Cl_2 at 100 °C for 15 min, dried again, and redissolved in C_6H_{14}/ CH_2Cl_2 (4:1) and an aqueous phosphate buffer (pH 7.0). The amino acid layer was extracted via liquid-liquid extraction, dried under N_2, trifluoroacetylated again, redissolved in $CH_3CO_2CH_2CH_3$. The $\delta^{15}N_{AA}$ values were determined using a Trace 1310 GC- IsolinkII interfaced with a Delta V Plus isotope ratio mass spectrometer (IRMS). Samples were injected at 180 °C onto a forte BPX5 capillary column with controlled helium flow, following a temperature program from 50 °C to 300 °C. Measurements were conducted in duplicate, standardized with amino acids with known $\delta^{15}N$ values, and normalised using calibration curves. While the specific composition of our in-house reference standard is proprietary, it comprises seven free amino acids with predefined $\delta^{15}N$ values. Reproducibility for pure amino acids averaged 0.44 ‰ (σ), ranging from ±0.01 ‰ to ±0.88 ‰. For glutamic acid and phenylalanine, it averaged 0.35 ‰ (σ) with a ranged of ±0.01 ‰ to ±0.85 ‰. The standard deviation for multiple injections averaged 0.18 ‰ (± 0.13 ‰ to ±0.56 ‰) for $\delta^{15}N$ values.

2.5. Estimation of TMF and BMF

To investigate the biomagnification of mercury within the food web, we calculated biomagnification factor (BMF) between each of the two myctophid fish species and squid. The BMF is calculated as follows:

$$BMF = \left(\left[THg\right]_{predator} / \left[THg\right]_{prey}\right) / \left(TP_{predator} - TP_{prey}\right) \quad (4)$$

Trophic magnification factors (TMF) of THg across the broader food web were calculated for liver and muscle tissue with the method of Borga et al. (2012) according to the following equation:

$$TMF = 10^{b} \quad (5)$$

with b taken as the slope in the equation Log concentration of THg = a + b × TP; where a is the intercept and b is the slope. The regression of log-transformed THg concentrations against TP was included in Fig. S1.

TPs in both BMF and TMF equations are based on trophic position estimates quantified using bulk $\delta^{15}N$ values.

2.6. Statistical analysis

The results were expressed as range and mean ± standard deviation. The normality and homogeneity of the data were assessed using the Shapiro-Wilk test and Bartlett's test, respectively. Species differences in muscle tissue THg concentrations and bulk $\delta^{13}C$ and $\delta^{15}N$ values were assessed using the Kruskal-Wallis test. The same test was employed to evaluate differences in THg, $\delta^{13}C$, and $\delta^{15}N$ across body sections (muscle and liver) in two fish species and to examine regional differences for the squid species. Mann-Whitney *U* tests were performed to investigate body section differences in THg, $\delta^{13}C$, and $\delta^{15}N$ for the squid species and regional differences for myctophid fish species. Statistical significance was determined using a significance level of $p < 0.05$. To explore the relationships between log-transformed THg and $\delta^{13}C$, $\delta^{15}N$, length, and trophic position, linear regression models were applied to each of the three species, providing estimates for regression coefficients (b and a), R^2, and *p*-values. Additionally, linear regression was conducted at the community level to examine the relationships between THg concentrations and $\delta^{13}C$, $\delta^{15}N$, and size/length across muscle and liver tissues. For the two myctophid fish species, linear regression was used to assess the relationship between amino acid $\delta^{15}N$ values and THg concentrations, bulk $\delta^{13}C$ values, and bulk $\delta^{15}N$ values. Concentrations of THg in whole specimens of *D. hudsoni* and *M. ventralis*, as reported by Zhang et al. (2024) from the same sampling period and surveys, were used to compare with muscle and liver THg concentrations presented in this study. All statistical analyses were performed using R version 4.2.1 (Team, 2020).

3. Results and discussion

3.1. Differences in THg concentrations between tissues and species

Significant differences in THg concentrations across tissues were observed for all species ($p < 0.001$; Table S1). Liver tissue consistently showed highest THg concentrations, reflecting its key role in detoxification and short-term metal storage in fish (Liu et al., 2011) and squid (Ahmad et al., 2015; Lacoue-Labarthe et al., 2009; Minet et al., 2021; Penicaud et al., 2017; Rodrigo and Costa, 2017). In *D. hudsoni* (Table 1), mean THg concentrations were highest in the liver (mean: 0.96 μg g^{-1} DW), followed by the heart and muscle while the brain, eye, gill, intestine, kidney and gonad had the lowest concentrations. In *M. ventralis*, THg concentrations were consistently low across tissues, though highest concentrations in descending order were shown in the liver (0.15 μg g^{-1} DW), followed by the kidney, muscle, brain, eye, and gonad. Similarly, squid L. *lorigera* exhibited tissue-specific variation, with the liver containing the highest THg concentration (0.29 μg g^{-1} DW) compared to the muscle (0.11 μg g^{-1} DW). These results are consistent with previous studies with Pethybridge et al. (2010b) highlighting the liver as a primary site of THg accumulations for L. *lorigera* and *D. danae*. In other cephalopods, higher mantle THg concentrations than in the liver have been shown in the Southern Ocean species, such as *Moroteuthopsis longimana* (Seco et al., 2020; Xavier et al., 2016). In a diverse range of squid sampled in the north-easter Atlantic ocean, liver THg concentrations were reported to be similar to, lower than, or higher than those in other tissues, depending on the species (Bustamante et al., 2006).

Mean THg concentrations in both liver and muscle were significantly higher in the smaller myctophid fish *D. hudsoni*, than the squid L. *lorigera*

Table 1
Sample size (n), total mercury concentrations (THg μg g^{-1}; dry weight: DW), bulk $\delta^{13}C$ values, bulk $\delta^{15}N$ values, carbon-to-nitrogen ratio (C:N), estimated trophic position (TP) based on bulk $\delta^{15}N$ values in mean ± standard deviations for two myctophid species (DH: *Diaphus hudsoni and* MV: *Metelectrona ventralis*) and one squid species (LL: *Lycoteuthis lorigera*) across different body parts.

		n	THg DW	$\delta^{13}C'$ (‰)	$\delta^{15}N$ (‰)	C:N	TP
DH	Brain	3	0.16 ± 0.05	−18.50 ± 1.40	9.58 ± 2.45	3.17 ± 0.09	
	Eye	4	0.17 ± 0.05	−17.76 ± 0.35	13.05 ± 0.82	3.22 ± 0.10	
	Gill	4	0.16 ± 0.05	−18.01 ± 0.29	11.50 ± 0.10	3.18 ± 0.00	
	Gonad	1	0.13				
	Heart	2	0.38; 0.40	−17.73; −19.34	9.57; 12.11	3.14; 3.20	
	Intestine	2	0.28; 0.36	−19.42; −19.10	10.44; 11.10	3.16	
	Kidney	1	0.30	−18.06	14.08	3.15	
	Liver	4	0.96 ± 0.50	−17.62 ± 0.37	13.41 ± 0.38	3.17 ± 0.04	
	Muscle	34	0.26 ± 0.13	−18.99 ± 0.48	11.81 ± 0.72	4.48 ± 1.15	3.51 ± 0.21
MV	Brain	3	0.02 ± 0.00	−18.38 ± 0.47	9.68 ± 1.76	3.21 ± 0.08	
	Eye	6	0.03 ± 0.00	−17.95 ± 0.39	11.98 ± 0.78	3.22 ± 0.06	
	Gill	5	0.04 ± 0.01	−18.86 ± 1.02	9.76 ± 2.45	3.21 ± 0.08	
	Gonad	3	0.01 ± 0.00	−18.30 ± 0.27	11.67 ± 0.82	3.17 ± 0.01	
	Heart	3	0.07 ± 0.01	−17.55 ± 0.17	12.55 ± 0.41	3.20 ± 0.02	
	Intestine	2	0.06; 0.07	−17.87; −18.27	12.47; 13.61	3.10; 3.15	
	Kidney	1	0.10	−17.76	13.31	3.14	
	Liver	5	0.15 ± 0.04	−17.72 ± 0.37	12.71 ± 0.68	3.18 ± 0.03	
	Muscle	26	0.06 ± 0.02	−19.46 ± 0.69	10.12 ± 1.86	4.60 ± 0.87	3.11 ± 0.57
LL	Liver	14	0.29 ± 0.21	−18.55 ± 0.47	11.31 ± 0.93	3.33 ± 0.19	
	Muscle	45	0.11 ± 0.05	−16.72 ± 0.39	14.09 ± 0.55	2.99 ± 0.04	4.27 ± 0.25

and the myctophid *M. ventralis*. These differences likely reflect variation in diet, trophic position, and habitat use among species. Calculated liver-to-muscle THg ratio further emphasised species-specific differences in THg accumulation and metabolism (Goldstein et al., 1996). The higher ratio found in *D. hudsoni* (3.6) than *M. ventralis* (2.5) and L. *lorigera* (2.6), indicates higher THg sequestration in the liver of *D. hudsoni*, potentially due to more efficient detoxification or higher exposure to dietary mercury. Such species-specific differences in tissue-specific THg concentrations have been reported elsewhere for muscle tissue in fish (Chen et al., 2025; Romero-Romero et al., 2022) and mantle tissue in squid (Minet et al., 2021).

Comparison with whole-body THg concentrations further underscores the importance of organ-specific analysis. In a literature review, Zhang et al. (2024) reported whole body THg concentrations across 85 mesopelagic fish species globally, ranging from 0.02 to 11.74 μg g^{-1} DW. They also measured whole body THg concentrations in 16 mesopelagic fish species sampled in the Tasman Sea (ranging from 0.02 to 0.48 μg g^{-1} DW), with mean values of 0.2 μg g^{-1} DW for *D. hudsoni* and 0.06 μg g^{-1} DW for *M. ventralis*. These whole body concentrations are markedly lower than the liver, kidney and heart concentrations observed in our study and highlight the high capacity of these organs to accumulate THg in both fish species. Few studies have assessed whole body Hg concentrations in squid with reported ranges of between 0.04 and 3.56 μg g^{-1} DW and indications that digestive gland weakly contributes to total body burden of THg (Bustamante et al., 2006; Mok et al., 2014; Pethybridge et al., 2010b). These reports, together with our findings, highlight species-specific differences in Hg tissue distribution, detoxification and storage processes, particularly in squid, and emphasize the need for caution when interpreting ecological or toxicological burdens.

3.2. Trophic inferences from stable isotopes

Bulk stable $\delta^{13}C$ and $\delta^{15}N$ isotope values in muscle tissue significantly differed between species (Kruskal-Wallis H test: $\delta^{13}C$, $H = 89.32$, $p < 0.001$; $\delta^{15}N$, $H = 1036$, $p < 0.001$). $\delta^{13}C$ values were most depleted in *D. hudsoni* (−18.99 ± 0.48 ‰) and *M. ventralis* (−19.46 ± 0.69 ‰) compared to L. *lorigera* (−16.72 ± 0.39 ‰). Conversely, bulk $\delta^{15}N$ values were highest in L. *lorigera* (14.09 ± 0.55 ‰) relative to *D. hudsoni* (11.81 ± 0.72 ‰) and *M. ventralis* (10.12 ± 1.86 ‰). The lower $\delta^{15}N$ values and estimated trophic positions (*M. ventralis* - 3.11 and *D. hudsoni* - 3.51) observed in two myctophid species suggest their potential role as prey for the squid L. *lorigera* (TP: 4.27). These isotope values in *M. ventralis* and *D. hudsoni* also align with Flynn and Kloser (2012) in this region. The high $\delta^{13}C$ variability between the myctophid fishes and squid may reflect habitat and dietary differences (Ruiz-Cooley et al., 2006; Takai et al., 2000). Relative to other isotope-based food web studies, this study shows small trophic differences between mesopleagic fish and squid (Coll et al., 2013; Merten et al., 2017), which likely indicates opportunistic feeding behavior of L. *lorigera*.

Tissue-specific isotopic variations are likely driven by differences in metabolism and turnover rates (Hussey et al., 2012; Malpica-Cruz et al., 2012). Intraspecific isotopic variations across tissues (Table 1) were also significant ($p < 0.05$; Table S1) for each species. In *D. hudsoni*, $\delta^{13}C$ values ranged from −18.99 ‰ in muscle to −17.62 ‰ in liver, while $\delta^{15}N$ ranged from 9.58 ‰ in brain to 14.08 ‰ in kidney. *M. ventralis* exhibited $\delta^{13}C$ values from −19.46 ‰ in muscle to −17.55 ‰ in heart and $\delta^{15}N$ values from 9.68 ‰ in brain to 13.31 ‰ in kidney. The C:N ratio across tissues was consistent, ranging from 3.13 (intestine) to 4.60 (muscle). For the squid, *L. lorigera*, $\delta^{13}C$ values were higher in muscle (−16.72 ‰) compared to liver (−18.55 ‰), while $\delta^{15}N$ values were significantly elevated in muscle (14.09 ‰) compared with the liver (11.31 ‰). The C:N ratios in L. *lorigera* muscle (2.99) was lower than in liver (3.33). The higher $\delta^{15}N$ values in kidney and liver tissues of *D. hudsoni* and *M. ventralis* contrasts with findings where muscle often exhibits higher $\delta^{15}N$ values (Chen et al., 2012; Vander Zanden et al., 2015).

In this study, the $\delta^{15}N$ values of individual AAs in the muscle tissues of *D. hudsoni* and *M. ventralis* reveal distinct patterns across species (Table 2). Four groups of AAs were categorized based on their ecological functions: trophic, trophic or source, source, and metabolic (Gillies et al., 2012; Nielsen et al., 2015). Trophic AAs alanine, valine, and leucine exhibit higher $\delta^{15}N$ values in *D. hudsoni* compared to *M. ventralis*, while source AAs glycine and phenylalanine were more enriched in *D. hudsoni*. These values fall within ranges reported in prior AA-SIA studies on mesopelagic fish trophic ecology. Choy et al. (2012) reported $\delta^{15}NAA$ values for species from two dominant mesopleagic fish families (Myctophidae and Stomiidae) accross global regions thatranged from −2.4 to 4.7 for $\delta^{15}N_{Phe}$ and 14.7 to 21.9 for $\delta^{15}N_{Glu}$. In the Tasman Sea, they showed that myctophid, *Lampanyctus australis*, exhibited $\delta^{15}N_{Phe}$ values of 2.6 ± 0.9 and $\delta^{15}N_{Glu}$ values of 19.7 ± 0.9 which was lower than values reported in our two study myctophid species. Hetherington et al. (2017) reported AA-SIA values of lanternfish (*Myctophum nitidulum* and *Symbolophorus reversus*) from the eastern tropical Pacific, where $\delta^{15}N_{Phe}$ ranged from −1.5 to 6.1 and $\delta\ \delta^{15}N_{Glu}$ from 13.1 to 23.9. Compared to this study, $\delta^{15}N_{Phe}$ for both *D. hudsoni* and *M. ventralis* falls at the lower end of this range, while $\delta^{15}N_{Glu}$ values (13.51 to 21.72 on average) were similar.

3.3. Hg bioaccumulation and trophic influences

Bioaccumulation and biomagnification are key processes in

Table 2
Amino acid $\delta^{15}N$ (‰) isotopic data and correlation statistical results (*p*-value) with bulk $\delta^{13}C$, bulk $\delta^{15}N$ and log-transformed total mercury (logTHg) from two myctophid fish species (*Diaphus hudsoni* and *Metelectrona ventralis*) muscle tissue.

		D. hudsoni	*M. ventralis*	Bulk $\delta^{13}C$	Bulk $\delta^{15}N$	logTHg
		$n = 30$	n = 30	p-value	p-value	p-value
Trophic						
Ala	Alanine	23.14 ± 3.94	14.38 ± 5.35	0.36	0.12	0.00
Val	Valine	21.40 ± 4.30	12.78 ± 4.25	0.73	0.15	0.00
Asp	Aspartic acid	17.97 ± 3.91	10.70 ± 4.00	0.05	0.00	0.00
Leu	Leucine	21.28 ± 4.54	11.71 ± 4.78	0.03	0.00	0.00
Glu	Glutamate acid	21.72 ± 4.73	13.51 ± 5.27	0.08	0.00	0.00
Pro	Proline	18.83 ± 2.78	16.00 ± 4.49	0.93	0.04	0.06
Trophic/Source						
Ser	Serine	−1.82 ± 2.72	0.71 ± 3.92	0.32	0.19	0.02
Gly	Glycine	−4.79 ± 4.25	−5.03 ± 4.44	0.92	0.37	0.75
Source						
Phe	Phenylalanine	−0.71 ± 3.53	−4.25 ± 3.95	0.09	0.02	0.00
Lys	Lysine	3.24 ± 1.80	0.49 ± 2.70	0.58	0.03	0.04
Metabolic						
Thr	Threonine	−23.74 ± 2.11	−20.87 ± 2.96	0.12	0.06	0.00
Meth	Methionine	6.59 ± 3.95	−0.16 ± 4.34	0.16	0.02	0.00

understanding contaminant distribution within ecosystems. Bioaccumulation refers to the accumulation of substances within the tissues of individual organisms over time (Clayden et al., 2015; Lavoie et al., 2013). Body size has been shown to be a key driver of Hg bioaccumulation at the organism and population level (Wang, 2012) and also at the community and ecosystem scale (Kidd et al., 2012; Knightes et al., 2009). In our study positive size correlations with THg concentrations in muscle tissue were shown for *M. ventralis* ($R^2 = 0.19$, $p = 0.03$), and L. *lorigera* ($R^2 = 0.51$, $p < 0.01$), but not *D. hudsoni* despite it demonstrating a large size range (Table 3).

Table 3
Regression analysis of total mercury concentrations (logTHg) in the muscle tissue of *Diaphus hudsoni, Metelectrona ventralis*, and *Lycoteuthis lorigera* as a function of isotopic nitrogen ($\delta^{15}N$), carbon source ($\delta^{13}C$), standard length/mantle length (SL), and trophic position (TP).

	Factor	b (slope)	a (intercept)	R^2	p-value
D. hudsoni	$\delta^{13}C$	−0.07	−2.79	0.01	0.67
	$\delta^{15}N$	0.03	−1.74	0.00	0.83
	SL	0.00	−1.59	0.00	0.74
	TP	−0.66	0.88	0.10	0.07
M. ventralis	$\delta^{13}C$	0.08	−1.22	0.04	0.31
	$\delta^{15}N$	0.02	−3.04	0.03	0.40
	SL	0.02	−4.35	0.19	0.03
	TP	0.07	−3.01	0.02	0.45
L. lorigera	$\delta^{13}C$	−0.58	−11.97	0.29	0.00
	$\delta^{15}N$	−0.11	−0.81	0.02	0.28
	SL	0.01	−3.23	0.51	0.00
	TP	−0.79	1.03	0.23	0.00

Trophic position and habitat association have also been shown to be key factors that influence THg bioaccumulation in marine organisms including mesopelagic fish (Choy et al., 2009; Pethybridge et al., 2010b) and squid (Seco et al., 2021; Seco et al., 2020). In this study, we found species-specific patterns in the direction and strength of correlations with isotopic trophic indicators determined by bulk isotope analysis (Table 3). For both fish *D. hudsoni* and *M. ventralis* no trophic indicators ($\delta^{13}C$ and $\delta^{15}N$) significantly correlated with THg (all $p > 0.05$), although bulk TP estimates showed a weak trend for *D. hudsoni* ($R^2 = 0.10$, $p = 0.07$). In contrast, the squid L. *lorigera* exhibited a significant negative correlation between THg in muscle tissue and $\delta^{13}C$ ($R^2 = 0.29$, $p < 0.01$) and bulk TP ($R^2 = 0.23$, $p < 0.01$).

The trophic ecology and mercury bioaccumulation patterns of *D. hudsoni* and *M. ventralis* reveal notable complexities. Despite *D. hudsoni* exhibiting the highest THg concentrations and a broad size range, the absence of correlations between THg concentrations and body size or trophic indicators suggests minimal ontogenetic dietary shifts or potential growth dilution effects due to rapid turnover rates (Buck et al., 2019). However, the lack of association between THg and $\delta^{13}C$ values in *D. hudsoni* likely indicates stable vertical and horizontal habitat use throughout its life cycle. Amino acid $\delta^{15}N$ values (both trophic and source) highlight significant trophic differences between *D. hudsoni* and *M. ventralis*, reinforcing their distinct feeding ecologies. The $\delta^{15}N$ values correlate more strongly with trophic position (bulk $\delta^{15}N$) than with feeding habitat (bulk $\delta^{13}C$; Table 2). Furthermore, source AAs exhibit a stronger correlation with THg than trophic amino acids. Across both species, all $\delta^{15}N$ AA values, except for proline and glycine, show significant correlations ($p < 0.05$) with THg concentrations (Table 2). The stronger correlation between source AAs and THg suggests that baseline nitrogen sources play a crucial role in Hg accumulation (Martinez et al., 2020; Matthews et al., 2020).

3.4. Hg biomagnification

Hg biomagnification refers to the progressive increase in contaminant concentrations across trophic positions (Lavoie et al., 2013). Biomagnification factors (BMFs) are commonly used to quantify the extent to which contaminants increase between a likely predator and its prey. BMF > 1 is indicative of biomagnification within the food chain, where organisms at higher trophic positions accumulate concentrations of THg (Hop et al., 2002). In our study, we found no evidence of biomagnification between *D. hudsoni* and L. *lorigera*, with a muscle tissue BMF of 0.54 which was indicative of the much higher THg concentrations found in *D.hudsoni* despite its lower trophic position. However, there was clear evidence of biomagnification between *M. ventralis* to L. *lorigera* (1.45). Our BMF values are much lower than those reported in other marine ecosystems. For example, in the North Pacific Ocean BMFs have been shown to range from 2.0 to 6.5 (Gupta and Yadav, 2024; Kim et al., 2023; Wang et al., 2021). This discrepancy may reflect distinct ecological dynamics in our study system, including variations in feeding behavior, trophic structure, and Hg (especially MeHg) bioavailability. Recent research underscores the complexity of Hg bioaccumulation and biomagnification in marine food webs (Dutton and Fisher, 2014; Kidd et al., 2012; Kim et al., 2023). The most substantial bioconcentration of MeHg occurs at the base of the food web, where phytoplankton can accumulate MeHg from the aqueous phase by up to 5–6 orders of magnitude, and trophic transfer through higher trophic positions typically results in 3- to 10-fold increases per level (Lee et al., 2016; Lee and Fisher, 2016), which aligns with the patterns observed in our study, from *M. ventralis* to *L. lorigera*.

To obtain a broader food web perspective on THg biomagnification, we examined relationships between THg concentrations and $\delta^{13}C$, $\delta^{15}N$, and size/length across the three mesopelagic species in our study (Fig. 1). We also calculated trophic magnification factors (TMFs) to test the extent of magnification compared to other food web studies. Patterns of magnification up the food web were shown to differ between muscle

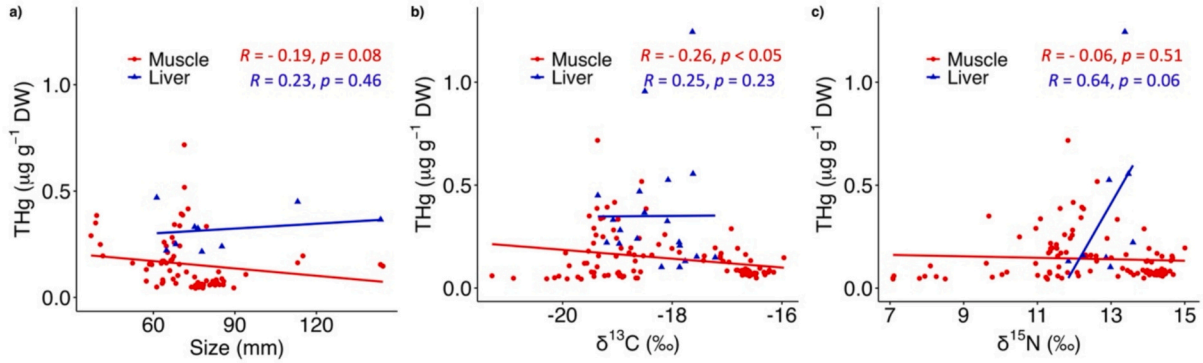

Fig. 1. Correlations between total mercury concentrations (THg; μg g^{-1} dry weight: DW) and a) body size, b) bulk $\delta^{13}C$ values, and c) bulk $\delta^{15}N$ values for the three mesopelagic species examined in this study.

and liver tissues (Fig. 1). In muscle tissue, THg exhibited weak negative correlations with trophic indicators ($\delta^{13}C$, $\delta^{15}N$) and size, with only $\delta^{13}C$ showing a significant relationship ($p < 0.05$) with THg (Fig. 1b). This resulted in the calculation of a TMF of 0.78 in muscle tissue, indicating no or very limited magnification across the trophic positions. In contrast, liver THg was more strongly correlated with isotopic trophic indicators, particularly $\delta^{15}N$ (Fig. 1c), reflecting a higher degree of mercury magnification (TMF = 1.89) up the food web. However, none of the factors ($\delta^{13}C$, $\delta^{15}N$, and size) were significantly correlated with THg ($p > 0.05$) in liver tissue. The observed relationships in liver THg for two fish species should be interpreted with caution due to the small sample size, which may limit the representativeness of these findings. Further investigation with higher sample size is warranted to confirm and expand upon these initial trends and to provide a more robust assessment of population-level effects.

The weak associations between THg and isotopic trophic indicators observed here differed to other studies that have reported stronger relationships (Chen et al., 2008). TMFs for THg have been shown to range from −0.19 to 7.8 in various fish species and food webs (Kim et al., 2023; Lavoie et al., 2013), indicating that mesopelagic ecosystem within the Tasman Sea may see comparatively reduced biomagnification from lanternfish to mesopelagic squid. A higher TMF of 4.8 was reported in a deep-sea shark THg biomagnification study off south-east Australia. Another possible reason is that the relatively low THg concentrations observed in the studied squid species contribute to the lower calculated TMF. Despite their intermediate trophic position, Hg concentrations are considered moderately low, which is noteworthy given the squid's potential for bioaccumulation (Minet et al., 2021). This can be attributed to their short lifespan of approximately two years, which limits the duration of mercury accumulation in their tissues (Chouvelon et al., 2011; Lacoue-Labarthe et al., 2009). In addition to this, the extent of mercury biomagnification is also influenced by the efflux rates of inorganic Hg and MeHg from organisms (Reinfelder et al., 1998). Future investigations incorporating Hg elimination rates would enhance understanding of the physiological and ecological processes regulating Hg accumulation and distribution in mesopelagic biota.

3.5. Spatial variations in trophic ecology and THg concentrations

Significant regional differences in THg concentrations in muscle tissue were observed among the studied species. For *M. ventralis*, THg was significantly higher in the eastern site (0.07 μg g^{-1} DW) compared to the western site (0.05 μg g^{-1} DW; Mann-Whitney test, U = 128, $p = 0.01$; Fig. 2a). Similarly, $\delta^{13}C$ and $\delta^{15}N$ values were more enriched in the east (−19.33 ‰ and 10.54 ‰, respectively) than in the west (−19.60 ‰ and 9.70 ‰, respectively; Fig. 2b and c). For *D. hudsoni*, THg concentrations were higher in the east (0.33 μg g^{-1} DW) than in the west (0.22 μg g^{-1} DW), though not significantly different. $\delta^{13}C$ and $\delta^{15}N$ showed minimal spatial variation, with slightly enriched $\delta^{13}C$ (−18.96 ‰) and $\delta^{15}N$ (12.28 ‰) in the east compared to the west (−19.00 ‰ and 11.53 ‰, respectively). In L. *lorigera*, THg concentrations varied significantly across regions, highest in the east (0.17 μg g^{-1} DW) compared to the central (0.14 μg g^{-1} DW) and western sites (0.09 μg g^{-1} DW; Kruskal-Wallis test, H = 15.62, $p < 0.001$). $\delta^{13}C$ values were less negative in the central (−16.66 ‰) and western (−16.70 ‰) regions than in the east (−17.18 ‰), while $\delta^{15}N$ values were highest in the east (14.43 ‰) and similar between the central (13.93 ‰) and western sites (14.11 ‰).

Spatial comparisons of THg in mesopelagic fish suggest that concentrations observed in this study fall within the lower global range (0.02–11.74 μg g^{-1} DW), but correspond to the higher end of concentrations previously reported for whole fish from the Tasman Sea (Zhang et al., 2024) (0.02–0.48 μg g^{-1} DW). The observed spatial differences in THg align with previous findings by Zhang et al. (2024) and support the trends reported by Flynn and Kloser (2012), who noted higher $\delta^{13}C$

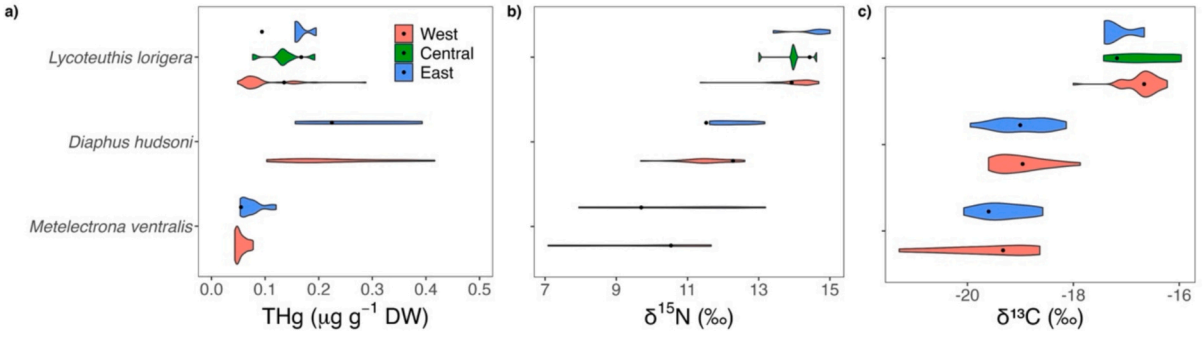

Fig. 2. Violin plots of a) total mercury (THg μg g^{-1}; dry weight: DW), b) bulk $\delta^{15}N$ values, and c) bulk $\delta^{13}C$ values across different locations (west, central, east) from mesopelagic fish and squid muscle tissue in the Tasman Sea.

values in the west and enriched $\delta^{15}N$ values in the east for *D. hudsoni* and *M. ventralis*. Enriched $\delta^{13}C$ values in the eastern sites for *M. ventralis* and L. *lorigera* may reflect shifts in carbon sources or food web structure (Wada, 2009). For L. *lorigera*, limited studies exist on its stable isotope composition and trophic position. However, its role as prey for petrels in New Zealand waters (Imber, 1975) and albacore tuna in Australian waters (Romanov et al., 2020) is well-documented. THg concentrations in this species were consistent with values reported by Pethybridge et al. (2010b), including 0.2 μg g^{-1} WW (0.8 μg g^{-1} DW; conversion factor: 0.75) in liver and 0.09 μg g^{-1} WW (0.36 μg g^{-1} DW; conversion factor: 0.75) in mantle. These findings align with broader studies highlighting spatial variations in Hg concentrations driven by local pollution sources, oceanographic conditions, and food web structures. Such complexities underscore the importance of considering multiple factors in bioaccumulation studies (Dunton, 2001; Madigan et al., 2018; Seco et al., 2021).

4. Conclusion

This study investigates Hg bioaccumulation and trophic dynamics in the mesopelagic ecosystem of the Tasman Sea, revealing species-specific patterns that both align with and challenge existing research. This study represents the first comprehensive examination of SIA and Hg concentrations across various tissues in myctophid fish species and *L. lorigera*, offering valuable baseline data and insights into the functional roles of different body parts in relation to Hg dynamics. Notably, the smaller myctophid *Diaphus hudsoni* exhibited higher THg concentrations, particularly in liver tissue, underscoring the influence of physiological and ecological factors on Hg accumulation. Biomagnification rates were weaker when assessed in muscle than liver tissue, highlighting the importance of multi-tissue analyses for a comprehensive understanding of Hg dynamics. However, inconsistent relationships between THg concentrations and isotopic trophic indicators suggest complex mercury cycling within the food web. While our findings provide valuable insights, the limited sample size for liver tissue warrants cautious interpretation of the relationships observed for this tissue. Future studies should include larger liver tissue sample sizes to strengthen and extend insights into Hg accumulation in mesopelagic organisms. This study provides the novel amino acid-specific stable isotope analysis data for two mesopelagic fish species, offering a valuable baseline for future investigations into trophic dynamics. Comprehensive resolution of mesopelagic food web structure remains a priority for future work.

CRediT authorship contribution statement

Bowen Zhang: Writing – original draft, Validation, Investigation, Data curation, Conceptualization. **Heidi Pethybridge:** Writing – review & editing, Validation, Supervision, Resources, Investigation. **Yunkai Li:** Writing – review & editing, Methodology, Data curation.

Declaration of competing interest

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

Acknowledgement

We gratefully acknowledge the valuable contributions of our colleagues from CSIRO Environment, in particular Elizabeth Brewer who conducted the experiment and managed the instrument facilities of amino acid compound stable isotope analysis and Caroline Sutton who collected, stored and supplied the fish and squid samples. We also acknowledge Tristan Verhoeff for identifying the squid samples and assisting sub-sampling, and Kim Jye Lee Chang for fish sample storage and guidance. We thank the assistance of Yu Ding and Leixu Ye from Shanghai Ocean University in conducting the mercury and bulk stable isotope measurements. This work was funded by a PhD scholarship to BZ provided by China Scholarship Council (CSC) Grant, University of Tasmania tuition fee scholarship and Commonwealth Scientific and Industrial Research Organisation (CSIRO) Julius Award to HP. We are thankful for contributions from the CSIRO ResearchPlus Postgraduate Top-Up Scholarship Grants and the Holsworth Wildlife Research Endowment.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2025.118209.

Data availability

Data will be made available on request.

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