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Mercury concentrations in cephalopods from the Pacific sector of the Southern Ocean in relation to their biology, habitat and trophic position

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ABSTRACT

Mercury (Hg) can negatively affect marine biota through uptake from prey and from the surrounding environment. Cephalopods constitute a major prey group in Southern Ocean ecosystems, yet little is known about Hg concentrations in these taxa and how biological and ecological factors can influence Hg body burdens. By combining stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) and Hg concentrations in beaks from 25 cephalopod species from the Pacific sector of the Southern Ocean, we studied 1) habitats and trophic positions; 2) Hg concentrations; and 3) how Hg concentrations relates to lower rostral length, habitat and trophic position of the studied species. Our results showed that $\delta^{13}C$ values indicated that species inhabited various water masses, with *Alluroteuthis antarcticus* inhabiting further north than previously reported. Additionally, $\delta^{15}N$ values of these cephalopod species showed that cephalopods in the Pacific sector of the Southern Ocean occupy two to three trophic levels with Hg concentrations among studied cephalopod species increasing from southern to northern habitats. Mercury concentrations in cephalopod beaks ranged from 0.003 μg g^{-1} (*Filippovia knipovitchi*) to the highest concentration ever recorded in cephalopod beaks (0.590 μg g^{-1} in *Histioteuthis atlantica*), with Hg concentrations increasing with the lower rostral length in *H. atlantica* but decreasing in *Moroteuthopsis ingens*. Our results suggest that Hg concentrations in Southern Ocean cephalopods may be driven by species-specific factors rather than a general pattern across species. This study emphasizes the need for cephalopod species-specific research on Hg bioaccumulation and biomagnification to better understand its impact on Southern Ocean marine food webs.

1. Introduction

Cephalopods (Mollusca: Cephalopoda) play an important ecological role in the Southern Ocean, being the main prey of several predators (Boyle and Rodhouse, 2005; Xavier & Cherel 2009; Xavier et al., 2015) including seabirds (Cherel and Klages, 1998, 1999; Xavier et al., 2014; Alvito et al., 2015), marine mammals (Clarke et al., 1980; Rodhouse et al., 1992; Negri et al., 2016) and fish (Smale, 1996; Xavier et al.,

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2002; Seco et al., 2016).

Fifty-four cephalopod species are known to occur south of the Antarctic Polar Front (APF; Xavier et al., 2018). However, they are difficult to study as most adult stages of cephalopods easily avoid scientific nets, and there are no local Southern Ocean cephalopod fisheries south of the APF to obtain information on cephalopods. Thus, much of their ecology, life-history and contaminant burden remains poorly known, particularly in the Pacific sector of the Southern Ocean (PSSO; Goldsworthy et al., 2002; Xavier et al., 2014; Cherel, 2020; Queirós et al., 2021; Queirós et al., 2021).

In order to study cephalopod ecology, their beaks (chitinous mandibles) have been widely used to obtain considerable information on, but not limited to, the identification of species, and the size and mass of individuals (Xavier et al., 2022). Cephalopod beaks may resist digestion and can remain in predator stomachs for long periods (i.e., from days to months depending on predator species), which allows studies to be carried out through both direct (e.g., stomach contents of their predators) and indirect methods (e.g., seabirds boluses; Ashmole and Ashmole, 1967; Duffy and Jackson, 1986; Xavier et al., 2005). Cephalopod beaks can also provide information on species ecology via chemical analyses, e.g., using stable isotopes (Seco et al., 2016; Abreu et al., 2020) and/or concentrations of trace elements including mercury (Hg; Xavier et al., 2015; Northern et al., 2019; Queirós et al., 2020).

Stable isotope values of carbon (δ^{13}C), reflecting the primary carbon source within the food web, generally do not increase with trophic level (though a small increase of ~1.0 ‰ can occur), and thus can be used as a proxy for habitat (Cherel and Hobson, 2005; Jaeger et al., 2010). In the Southern Ocean, δ^{13}C values are correlated with latitude (Cherel and Hobson, 2007), and allow to investigate the north-south gradient of foraging habitat of individuals across the Southern Ocean (Cherel and Hobson, 2005; Jaeger et al., 2010). In contrast, stable isotope ratios of nitrogen (δ^{15}N) increase with trophic level, with consumers being enriched compared to prey (~3.4 ‰ per trophic level; Peterson and Brian, 1987; Hobson et al., 1994; McCutchan et al., 2003).

Within the various threats to Southern Ocean ecosystems (Convey and Peck, 2019; Chown et al., 2022), Hg is considered to be a major threat to Antarctic marine biota (Bargagli, 2008; Seco et al., 2020). Previous studies showed that the Southern Ocean has some of the highest concentrations of Hg ever recorded in open waters (2.76 pmol. L^{-1}, Cossa et al., 2011). Cephalopods incorporate Hg in their tissue via two main pathways: seawater and/or food (Lacoue-Labarthe et al., 2009; Minet et al., 2022). Intake can occur directly from seawater through the gills during respiration, yet diet is considered to be the main intake pathway (Lacoue-Labarthe et al., 2009; Minet et al., 2022). After being absorbed by the animal, a fraction of the uptaken Hg is incorporated in the beak throughout its lifespan (Xavier et al., 2016; Matias et al., 2019; Queirós et al., 2020). Due to the high affinity of Hg to proteins, Hg tends to accumulate within organisms, often referred to as bioaccumulation (Wolfe et al., 1998; Karagas et al., 2012; Kershaw and Hall, 2019; Queirós et al., 2020). Furthermore, Hg biomagnifies within food webs with top predators consequently presenting the highest Hg concentrations (Cherel et al., 2018; Queirós et al., 2020). The central position of cephalopods in Southern Ocean food webs and their relatively short lifespan (generally up to 1-2 years; Rodhouse, 1998), with some species living 3 to 8 years (Schwarz et al., 2019; Queirós et al., 2021), make them good bioindicators of ecosystem contamination, as cephalopods will quickly reflect any environmental change (Collins and Paul, 2006; Seco et al., 2020, 2021; Lopes-Santos et al., 2025).

In cephalopods, Hg exhibits varying distribution and accumulation characteristics among different tissues that may also vary among species. Generally, Hg concentrations increase from beaks, gills, muscle to digestive gland (Bustamante et al., 2006). Such a pattern is due to the low content of protein in beaks, the high affinity of Hg with sulfhydryl groups of proteins present in myocytes and the main incorporation pathway being via digestion (Raimundo et al., 2010; Xavier et al., 2015; Penicaud et al., 2017; Matias et al., 2020). Consistently, in all previous studies, the beak was always the tissue with the lowest Hg concentration. Thus, a high Hg concentration in beaks would suggest an even higher concentration in soft tissues.

Using beaks of cephalopods collected from the diet of Antipodean (*Diomedea antipodensis*) and Gibson's (*D. gibsoni*) wandering albatrosses foraging in the PSSO (Walker et al., 2006), the main objectives of this study are to: (1) assess the habitat (δ^{13}C) and trophic position (δ^{15}N) of 25 cephalopod species from the PSSO; (2) determine Hg concentrations in the beak of these 25 cephalopod species; and, (3) evaluate which biological (size of the beak) and ecological (habitat and trophic position) factors influence Hg concentration.

2. Materials & methods

2.1. Collection and identification of beaks

Cephalopod beaks were collected and sorted from boluses of *D. antipodensis* and *D. gibsoni* chicks breeding at Antipodes Island (49°S, 178°W) and Adams Island (Auckland Islands group, 51°S, 166°E), respectively. The beaks were collected during the 2000 and 2001 breeding seasons (see Xavier et al. (2014) for further details on beak collection). The chicks are fed by their parents, which are known to forage east of New Zealand (*D. antipodensis*) and between Australia and New Zealand (*D. gibsoni*), across Subtropical, Subantarctic and, to a lesser extent, Antarctic waters (Walker et al., 2006; Walker and Elliott, 2022). The use of these predators as biological samplers has made it possible to sample cephalopods inhabiting the PSSO. As cephalopod beaks were recovered from 2 different species of wandering albatrosses boluses, the assemblage analysed reflects predator foraging selectivity and may not fully represent the regional cephalopod community. The boluses were transported to the New Zealand Institute for Earth Science (Earth Sciences NZ), Wellington (New Zealand), stored frozen and extracted beaks were preserved in 70% ethanol. Lower beaks were identified to species level using Xavier and Cherel (2021) and beak collections at Earth Sciences NZ, at the British Antarctic Survey (United Kingdom) and at the University of Coimbra (Portugal). After species identification, the lower rostral length (LRL, mm) for squid species or the lower hood length (LHL, mm) for octopod species was measured with vernier callipers to 0.1 mm. A total of 251 lower beaks from 24 squid species and nine lower beaks from a single pelagic octopod species (*Ocythoe tuberculata)* were used to analyse δ^{13}C and δ^{15}N values, and Hg concentrations. Scientific names of cephalopod species were verified using WoRMS (https://www.marinespecies.org/index.php) as a reference.

2.2. Estimated mantle length and mass

To estimate cephalopod mantle length (ML, mm) and mass (M, g) we used allometric equations from Xavier and Cherel (2021), since ML and M are a function of LRL. When no species-specific equation was available, family level equations were applied. For sex-dependent equations, mean values from males and females were averaged. Since no equations are available in the literature for *O. tuberculata* octopod, no estimation were performed for its LHL, ML and M.

2.3. Stable isotope analysis

Lower beaks were cleaned with 70% ethanol and dried overnight in an oven at 60 °C. Dried beaks were reduced to a fine powder using a mixer mill (Retsch® MM400) for 10 min at a 30 Hz frequency. Approximately 0.35 mg of milled powder from each beak was weighed into a tin capsule. Values of δ^{13}C and δ^{15}N were measured using a continuous flow isotope ratio mass spectrometer (CFIRMS) at Laboratório MAREFOZ, Figueira da Foz, Portugal. Results are presented using δ notation, in ‰, and were calculated using the equation:

$\delta X = [(Rsample - Rstandard - 1)*1000]$

where X represents C or N, and R the ratios of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Isotope values for carbon and nitrogen are presented relative to Vienna PeeDee Belemnite (VPDB) and atmospheric N_2 (air), respectively. Throughout the analyses, internal reproducibility was measured as < 0.1 ‰ for $\delta^{13}C$ and <0.3 ‰ for $\delta^{15}N$, using acetanilide as a standard.

2.4. Stable isotopes literature

The distribution of cephalopod species was determined on the basis of estimated isoscapes (i.e., isotopic geographical gradients) of the Antarctic Polar Front (APF) and Subtropical Front (STF) estimated using blood and plasma analyses of penguins and albatrosses monitored by satellite tracking (Cherel and Hobson, 2007; Jaeger et al., 2010). As there are no isoscapes based on analyses of cephalopod beaks, a conservative approach was adopted following Guerreiro et al. (2015). Samples presenting values of $\delta^{13}C$ lower than −22.9 ‰ were considered to belong to individuals living in Antarctic waters, whereas values higher than −19.5 ‰ were considered to belong to individuals living in Subtropical waters (Cherel and Hobson, 2007; Jaeger et al., 2010). Individuals with $\delta^{13}C$ values between −22.9 ‰ and −19.5 ‰ were considered to inhabit Subantarctic waters. Changes in cephalopod trophic positions were analysed using ~3.4 ‰ $\delta^{15}N$ variation as a reference value for one trophic level increase according to Hobson and Cherel (2006). Bulk $\delta^{15}N$ values measured in whole beaks should be interpreted cautiously as proxies of trophic position because beaks are chitinous structures and their $\delta^{15}N$ values can vary with chitinisation and overall composition. Bulk $\delta^{15}N$ values and C:N ratio of the whole beak are therefore major limits in our interpretation.

2.5. Habitat clustering

In addition to $\delta^{13}C$ values to identify isoscapes and cluster habitats (see above), since stable isotopes baselines vary across water masses, we clustered cephalopod species by habitat following Cherel (2020). It enabled a more detailed distinction of species living in Southern Ocean habitats when compared to $\delta^{13}C$ values. Habitats were classified, from south to north, as follows: Antarctic Zone – Polar Front Zone (AZ-PFZ), Antarctic Zone – Polar Front Zone – Subantarctic Zone (AZ-PFZ-SAZ), Polar Front Zone – Subantarctic Front (PFZ-SAF), Polar Front Zone – Subantarctic Zone (PFZ-SAZ), Subantarctic Zone (SAZ) and North of the Subtropical Front (North STF). *O. tuberculata* was not included by Cherel (2020) review and was thus assigned to the North STF habitat following Nesis (2003).

2.6. Mercury analysis

Approximately 98 ± 5 mg of sample was analysed for Hg concentration by thermal decomposition atomic absorption spectrometry with gold amalgamation, using a LECO AMA-254 (Advanced Mercury Analyser) following Coelho et al. (2008) at the Chemistry department of the University of Aveiro, Portugal. Analyses were performed at least in duplicate, and the coefficient of variation between replicates never exceeded 10% (additional replicates were performed if the variation was >10%). Certified reference material TORT-3 lobster hepatopancreas from the National Research Council Canada was used to validate Hg analyses, with a recovery of 95 ± 10% (n = 59) of the certified value. The limit of detection for the AMA was 0.01 ng of Hg. All concentrations are expressed in $\mu g.g^{-1}$ as a function of dry weight (dw).

2.7. Statistical analysis

Statistical tests were performed, and graphs generated, using R software (TeamR. Core, 2022), using "*ggplot2*" and "*stats*" packages (Wickham, 2011). "*Stats*" package was used to perform Shapiro-Wilk normality test and Bartlett's test to test the normality and homogeneity of variance of the different variables. A Kruskal-Wallis test followed by a Dunn's multiple comparison test was used to test differences in habitat, LRL/LHL, estimated ML, estimated M, $\delta^{13}C$ and $\delta^{15}N$ values, and Hg concentrations between the different species. Spearman rank correlations were used to assess relationships between Hg concentrations and LRL/LHL, and $\delta^{13}C$ and $\delta^{15}N$ values to assess the influence of these factors on Hg concentrations in cephalopod beaks. All values are presented as mean ± 1 standard deviation. The significance level for statistical analyses was set at $\alpha = 5$ %. Graphical outputs were produced with the "*ggplot2*" package.

3. Results

3.1. Lower rostral length, lower hood length and estimated mantle length and mass

The species with the longest LRL was *Octopoteuthis* sp. (13.26 ± 1.02 mm) whereas the species with the smallest LRL was *Histioteuthis eltaninae* (3.22 ± 0.31 mm, Table S1). Interspecific significant differences in LRL were observed (Kruskal-Wallis, H = 200.4, p < 0.0001; Table S1). Only one species of pelagic octopod (*O. tuberculata*) was found and its LHL ranged from 5.77 mm to 7.51 mm (6.62 ± 0.70 mm, Table S1).

Significant interspecific differences were observed in estimated ML (Kruskal-Wallis, H = 230.2, p < 0.0001; Table S1). Estimated M also varied significantly depending on the species (Kruskal-Wallis, H = 224.9, p < 0.0001; Table S1).

3.2. $\delta^{13}C$ and $\delta^{15}N$ values in cephalopod beaks

The species with the lowest $\delta^{13}C$ values was *Filippovia knipovitchi* (−23.65 ± 0.91 ‰) whereas the highest $\delta^{13}C$ values were found in *Chiroteuthis veranii* (−17.96 ± 0.29 ‰, Fig. 1, Table S1). Overall, significant inter-specific differences were observed for $\delta^{13}C$ values (Kruskal-Wallis, H = 159.8, p < 0.0001; Table S1).

Beaks with the lowest $\delta^{15}N$ were found in *Galiteuthis glacialis* (5.71 ± 0.51 ‰) and the highest $\delta^{15}N$ values were found in *C. veranii* (11.96 ± 1.09 ‰, Fig. 1, Table S1). Significant differences among species were also observed for $\delta^{15}N$ values (Kruskal-Wallis, H = 200.4, p < 0.0001; Table S1).

3.3. Hg concentrations in cephalopod beaks and potential influencing factors

Mercury concentrations in cephalopod lower beaks varied by a factor of 6.5 times across species, ranging from 0.043 ± 0.024 $\mu g\ g^{-1}$ for *Moroteuthopsis ingens* to 0.282 ± 0.121 $\mu g\ g^{-1}$ for *H. macrohista* (Fig. 2, Table S1) and Hg concentrations were significantly different between species (Kruskal-Wallis, H = 96.77, p < 0.0001; Fig. 2, Table S1; Table S3).

Spearman correlations between Hg concentration and LRL or LHL, $\delta^{13}C$ and $\delta^{15}N$ values showed contrasting results (Table 1). Hg concentrations were only positively correlated to the LRL for *H. atlantica* and negatively correlated to the LRL for *M. ingens* (Table 1). Secondly, Hg concentrations were negatively correlated to $\delta^{13}C$ values for *H. atlantica* and for *T. notalia* (Table 1). Finally, there were no significant correlations between Hg concentration and $\delta^{15}N$ values (Table 1).

When species were grouped according to their main habitat, following Cherel (2020), a clear northward increase in Hg concentrations in the beak was observed (Fig. 3). Cephalopods inhabiting the AZ – PFZ and the AZ – PFZ – SZ exhibited significantly lower Hg concentration in the beak than those inhabiting North STF (Kruskal-Wallis, H = 17.36, p = 0.004; Fig. 3). Hg concentrations in cephalopods from the PFZ – SF, PFZ – SZ and SZ were not significantly different from each other or when compared to other groups.

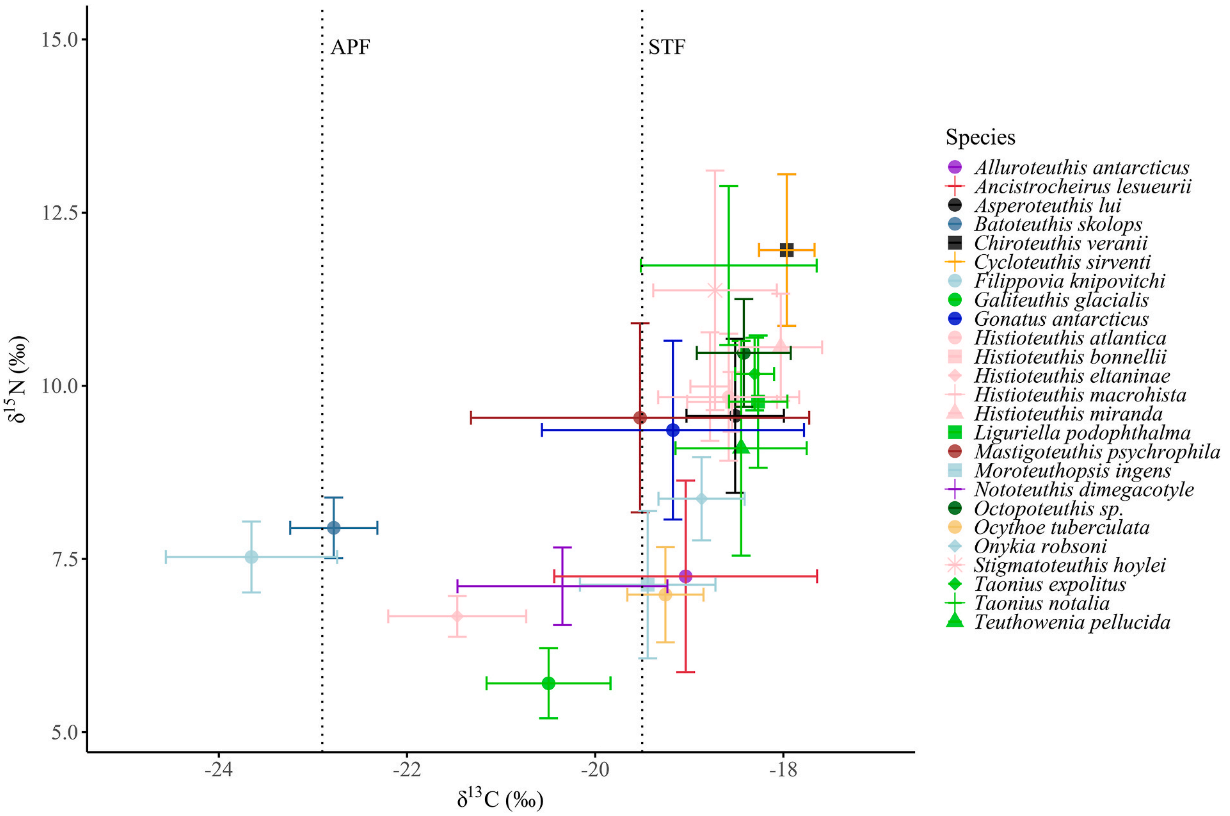

Fig. 1. Beak δ^{15}N (‰) as function of beak δ^{13}C (‰) of cephalopod species of the Pacific sector of the Southern Ocean. Species are colour depending on the family. Symbols represent the species mean ± standard deviation. The two vertical dashed lines indicate the approximate positions of the Antarctic Polar Front (APF; −22.9 ‰) and the Subtropical Front (STF; −19.5 ‰) following Cherel and Hobson (2007). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

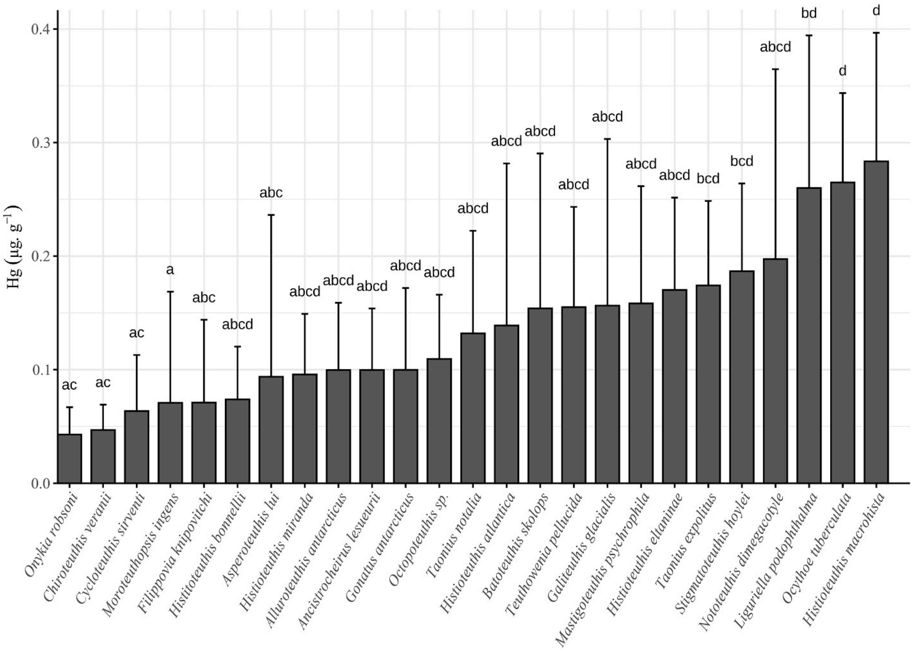

Fig. 2. Mercury (Hg) concentration (mean + 1 standard deviation; µg.g^{-1} dw) measured from beaks of different cephalopod species from the Pacific sector of the Southern Ocean, ranked from the lowest to the highest mean Hg concentration. Different letters above the bars indicate significant differences between species (Dunn's post hoc test, $p < 0.05$).

Table 1
Spearman correlations between mercury (Hg, µg.g^{-1} dw) and lower rostral length (LRL, mm) or lower hood length (LHL, mm), stable isotopes of carbon ($\delta^{13}C$, ‰) and nitrogen ($\delta^{15}N$, ‰) for each cephalopod species. Statistically significant correlations for $\delta^{13}C$, $\delta^{15}N$, LRL and Hg between species are expressed with the p-value showing significant values calculated from a spearman correlation ($p < 0.05$ = *, $p < 0.01$ = **, $p < 0.001$ = ***, NS = non-significant).

Family	Species	Hg ~ LRL or LHL (ρ; p-value)		Hg ~ $\delta^{13}C$ (ρ; p-value)		Hg ~ $\delta^{15}N$ (ρ; p-value)	
Ancistrocheiridae	*Ancistrocheirus lesueurii*	0.21	NS	−0.19	NS	−0.04	NS
Batoteuthidae	*Batoteuthis skolops*	−0.47	NS	−0.60	NS	0.11	NS
Chiroteuthidae	*Asperoteuthis lui*	0.34	NS	−0.09	NS	−0.20	NS
Chiroteuthidae	*Chiroteuthis veranii*	−0.36	NS	0.14	NS	0.05	NS
Cranchiidae	*Galiteuthis glacialis*	0.30	NS	0.05	NS	−0.32	NS
Cranchiidae	*Liguriella podophthalma*	0.18	NS	−0.21	NS	0.49	NS
Cranchiidae	*Taonius expolitus*	0.01	NS	0.56	NS	−0.54	NS
Cranchiidae	*Taonius notalia*	0.14	NS	**−0.64**	**0.05***	−0.39	NS
Cranchiidae	*Teuthowenia pellucida*	0.02	NS	−0.43	NS	−0.14	NS
Cycloteuthidae	*Cycloteuthis sirventi*	0.28	NS	0.05	NS	0.25	NS
Gonatidae	*Gonatus antarcticus*	0.30	NS	0.35	NS	0.32	NS
Histioteuthidae	*Histioteuthis atlantica*	**0.72**	**0.001****	**−0.56**	**0.02***	−0.42	NS
Histioteuthidae	*Histioteuthis bonnellii*	0.32	NS	−0.13	NS	0.63	NS
Histioteuthidae	*Histioteuthis eltaninae*	−0.06	NS	−0.69	NS	0.43	NS
Histioteuthidae	*Histioteuthis macrohista*	0.44	NS	−0.24	NS	0.67	NS
Histioteuthidae	*Histioteuthis miranda*	−0.24	NS	−0.09	NS	−0.02	NS
Histioteuthidae	*Stigmatoteuthis hoylei*	−0.19	NS	−0.07	NS	0.52	NS
Mastigoteuthidae	*Mastigoteuthis psychrophila*	−0.83	NS	−0.49	NS	−0.15	NS
Neoteuthidae	*Alluroteuthis antarcticus*	0.21	NS	0.21	NS	0.29	NS
Neoteuthidae	*Nototeuthis dimegacotyle*	0.05	NS	−0.55	NS	0.05	NS
Octopoteuthidae	*Octopoteuthis sp.*	−0.24	NS	−0.39	NS	0.05	NS
Ocythoidae	*Ocythoe tuberculata*	−0.35	NS	−0.33	NS	0.15	NS
Onychoteuthidae	*Filippovia knipovitchi*	−0.22	NS	−0.05	NS	−0.32	NS
Onychoteuthidae	*Moroteuthopsis ingens*	**−0.49**	**0.05***	−0.24	NS	−0.02	NS
Onychoteuthidae	*Onykia robsoni*	No beak measured	No beak measured	−0.54	NS	−0.54	NS

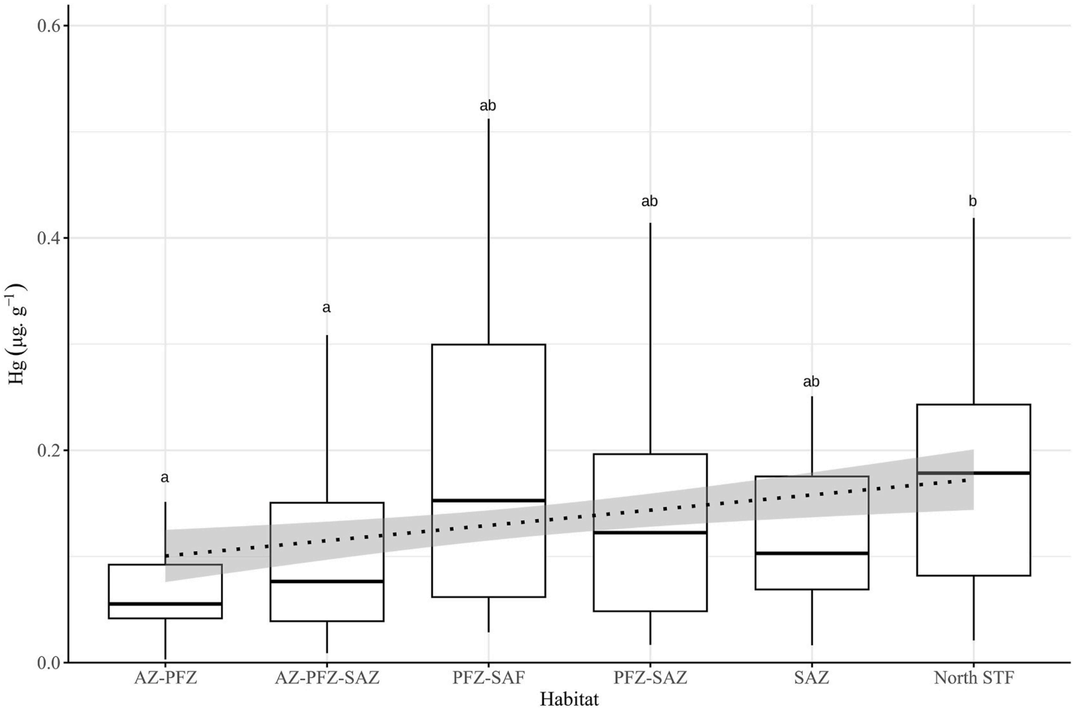

Fig. 3. Mercury (Hg) concentration (µg.g^{-1} dw) measured in cephalopod beak from the Pacific sector of the Southern Ocean according to the Habitat based on Cherel (2020) and Nesis (2003). The habitats are ranked from the southern (AZ-PFZ) to the northern (North STF). The central thick line represents the median, boxes indicate the interquartile range (25th-75th percentile), whiskers extend to 1.5x the interquartile range. Different letters indicating statistical differences between Habitats (Dunn's post hoc test, $p < 0.05$). The black dotted line represents the overall northward increase in Hg concentration ±95% interval.

4. Discussion

To our knowledge, this is the first study to analyse Hg concentrations and bioaccumulation in cephalopods from the PSSO, providing important baseline Hg information on these organisms from this region. Furthermore, we report the highest Hg concentration ever measured in cephalopod beaks. Few studies, mostly focused on the Atlantic sector of the Southern Ocean, have characterised Hg concentrations in cephalopods (Xavier et al., 2015; Seco et al., 2020; Queirós et al., 2020), complementing the information acquired here.

4.1. Habitat of cephalopods from the Pacific sector of the Southern Ocean

Using information from cephalopod beaks, beak δ^{13}C values ranged widely from *F. knipovitchi* (−25.05 ‰) to *H. atlantica* (−17.29 ‰, Table S2), suggesting that cephalopod species found in the diet of *D. antipodensis* and *D. gibsoni* chicks are inhabiting various water masses from Subtropical to Antarctic waters, agreeing with studies that Southern Ocean cephalopods have a wide range of distribution (Xavier et al. 1999, 2014). The relatively enriched δ^{13}C values of *A. antarcticus* (−19.04 ± 1.39 ‰) suggest that this species associated to the AZ-PFZ habitat (Cherel, 2020), would also forage in North STF habitat (Fig. 1).

Overall, δ^{13}C values were approximately 1 ‰ higher compared to previous studies that analysed δ^{13}C in cephalopod beaks in other sectors of the Southern Ocean, suggesting that many of the species studied forage at lower latitudes in the PSSO (e.g., *A. antarcticus, A. lui, B. skolops, G. antarcticus, G. glacialis, H. atlantica, H. eltaninae, L. podophthalma, T. expolitus* and *T. notalia*; Alvito et al., 2015; Guerreiro et al., 2015). Such enrichment may reflect regional alteration of the δ^{13}C baseline level from different water masses (Morée et al., 2018), driven by phytoplanktonic composition, as diatom-dominated ecosystems exhibit enriched δ^{13}C values (Rau et al., 1992; Francois et al., 1993; Laws et al., 1995, 1997; Popp et al., 1998).

Our study showed that some Southern Ocean cephalopod species had relatively elevated δ^{13}C values, and most species studied here are known to be pelagic and live at great depth in the open ocean without water mass-associated variation in foraging depth (Cherel, 2020). Thus, the most logical explanations for this overall increase in δ^{13}C values of cephalopod beaks collected in the PSSO are 1) that *A. antarcticus* inhabits northern water masses (Cherel and Hobson, 2005; Newsome et al., 2007; Cherel, 2020); and 2) that δ^{13}C baseline values driven by primary productivity might be associated with more diatoms-enriched phytoplankton communities (Rau et al., 1992; Francois et al., 1993; Goericke and Fry, 1994).

Additionally, we found intra-specific δ^{13}C values variations. *H. atlantica* showed a significant difference in the habitat areas associated with the size of the beak, with smaller individuals exhibiting higher δ^{13}C values (mean = −18.14 ‰ for the ten individuals with the smallest LRL and mean = −19.02 ‰ for the ten individuals with the largest LRL), suggesting ontogenetic shifts and a change in habitat towards southern latitudes as *H. atlantica* grow, similar to those reported by Jp Queirós et al. (2021). These results underscore the complexity of cephalopod habitat use in the Southern Ocean. Such spatial and ontogenetic variations likely influence the trophic structure of cephalopods.

4.2. Trophic position of cephalopods from the Pacific sector of the Southern Ocean

Similar to δ^{13}C, δ^{15}N values showed a wide range, suggesting that cephalopods from the PSSO occupy diverse trophic positions, agreeing with previous studies from other sectors (Cherel and Hobson, 2005; Guerreiro et al., 2015) and in the same sector (Queirós et al., 2021) of the Southern Ocean. Varying from *G. glacialis* (5.04 ‰) to *S. hoylei* (13.99 ‰, Table S2), δ^{15}N values showed that cephalopod species occupy between two to three trophic levels (~3.4 ‰ per trophic level, Peterson and Brian, 1987; Hobson et al., 1994; McCutchan et al., 2003). Interestingly, an increase between δ^{13}C and δ^{15}N values was observed (Fig. 1), suggesting either that species foraging in northern waters tend to occupy higher trophic positions or that increasing δ^{15}N values might be associated with baseline effect between water masses.

Compared with previous stable isotope studies on squid beaks in the Southern Ocean, our δ^{15}N values are generally lower (~1 ‰, e.g., *A. antarcticus, A. lui, B. skolops, G. antarcticus, G. glacialis, H. atlantica, H. eltaninae, L. podophthalma, T. expolitus* and *T. notalia*; Guerreiro et al., 2015; Alvito et al., 2015). These different δ^{15}N values among sectors suggest differences in baseline δ^{15}N across water masses (Guerreiro et al., 2015; Woods et al., 2022), as it is unlikely that cephalopods of the same species vary their diets significantly across water masses. Alternatively, it is possible that the cephalopod beaks analysed here had a lower chitin content than beaks previously studied, leading to a bias in the characterisation of trophic position (Hobson and Cherel, 2006; Ruiz-Cooley et al., 2006; Cherel et al., 2009). Beaks are chitinous structures, thus impoverished in ^{15}N compared to other cephalopod tissues as chitin has lower nitrogen content than muscles (mantle: 11.3 ± 1.2 ‰, arms: 10.9 ± 1.2 ‰, buccal mass: 10.4 ± 1.2 ‰, lower beak: 7.6 ± 1.5 ‰; Cherel et al., 2009). In our dataset, C:N ratio ranged between 1.11 and 6.12 (Table S2) indicating high variability of chitin content in beaks, depleting beaks in ^{15}N (the older beaks, darker and larger, contain less chitin, Clarke, 1986). This could affect the determination of the trophic position (Clarke, 1996; Cherel et al., 2009). Thus, beaks with different chitin percentages will differ in the δ^{15}N values and trophic position estimation (Hobson and Cherel, 2006; Ruiz-Cooley et al., 2006; Cherel et al., 2009). However, the hypothesis led by a lower chitin content in the cephalopod beaks studied is unlikely, as cephalopods from the same species are susceptible to developing the same way within the Southern Ocean.

The use of compound-specific isotope analysis of amino-acids would allow to the effect of variability in chitin content to be accounted for and should allow for better estimation of trophic position (Cherel et al., 2019). However, it is not expected that chitinisation of beaks differ for the same species depending on the water mass (Xavier et al., 2022). Combined with habitat, the trophic position is essential to understand Hg concentrations variations across cephalopod species.

4.3. Hg concentrations in cephalopod beaks

Mercury concentrations showed a wide range of values and revealed interspecific differences that appear to depend on the ecology of each species. As samples were collected during 2000–2001, our results should be considered a historical baseline, as environmental changes may have altered Hg bioavailability over the past decades (Zhou et al., 2025; Lopes-Santos et al., 2025). We measured Hg concentrations varying from 0.003 μg g^{-1} (*F. knipovitchi*) to 0.590 μg g^{-1} (*H. atlantica*; Table S2). To the best of our knowledge, our results represent the highest Hg concentrations ever recorded in cephalopod beaks by 12 times (0.047 μg g^{-1}; Xavier et al., 2016). Furthermore, for *F. knipovitchi, G. antarcticus* and *G. glacialis*, we measured Hg concentrations 2.8, 7.7 and 19.5 times higher than those previously recorded, respectively (Xavier et al., 2016). These results suggest that the bioavailability of Hg for cephalopods in the PSSO is higher than previously reported in other Southern Ocean water masses (Xavier et al. 2015, 2016; Matias et al., 2019; Queirós et al., 2020; Seco et al., 2020).

In the Southern Ocean, dissolved Hg concentrations increase with depth (Cossa et al., 2011). Although there has been no specific study of Hg concentrations in marine organisms as a function of depth in the Southern Ocean, various studies carried out in contrasting environments have shown that epipelagic species have lower Hg concentrations than species living at depth (e.g., Monteiro et al., 1996; Choy et al., 2009; Chouvelon et al., 2012). Accordingly, our results suggest that individuals with relatively high Hg concentrations may have been foraging on deep-sea prey compared to other cephalopods from different sectors of the Southern Ocean. However, current knowledge about the feeding ecology of the four species exhibiting the highest Hg concentrations (*H. atlantica, H. macrohista, O. tuberculata* and *L. podophthalma*) suggests that they perform diel vertical migrations at night to feed in shallower waters on small fishes and crustaceans that are known to live during the day between 200 and 1500 m deep (Xavier et al., 2018). Since most of the species in this study are pelagic and feed on vertical migratory prey, shift in vertical habitat seems unlikely.

4.3.1. Intrinsic factors influencing contamination

As expected, Hg concentrations increased with increasing LRL in *H. atlantica*. As the beak is constantly growing during the lifespan of the individual, larger cephalopods will have longer LRL and higher Hg concentrations reflecting a level of contamination over the individual's life-span (Penicaud et al., 2017; Lischka et al. 2018, 2019). Though, as the beak growth pattern is influenced by many other factors such as the habitat (Seco et al., 2020), this could explain why we only observed it on one species and not in others (Queirós et al., 2020). In contrast, Hg concentrations decreased with increasing LRL in *M. ingens*. It seems that the relation between LRL and Hg in the beak may be species dependent, as previous studies report, the link between cephalopod size and Hg concentration varies among species (Seco et al., 2020). Further work is required to better understand Hg burden during the lifespan of cephalopod species of the Southern Ocean.

Two hypotheses already mentioned in previous studies could explain these contradictory results; the first is tissue dilution, whereby cephalopods with larger beaks may have a higher total Hg body burden but a lower Hg concentration compared to smaller cephalopods (Lacoue-Labarthe et al., 2009). The second relates to ontogenetic shift in energy allocation, in which cephalopods with larger beaks (close to reaching their maximum size), feed only to maintain their body equilibrium, while smaller cephalopods must invest energy in growing (Boyle and Rodhouse, 2005). Smaller individuals are therefore expected to have a higher food intake, that could lead to a greater Hg incorporation (Bustamante et al., 2006; Xavier et al., 2016). This would suggest that with individuals growing, *H. atlantica* individuals would face increasing Hg concentration in soft tissues, whereas in *M. ingens* individuals, would have decreasing Hg concentrations with increasing LRL size. Hg burden in various tissues of these cephalopod species should therefore be investigated.

4.3.2. Extrinsic factors influencing contamination

Habitat use, through $\delta^{13}C$ as a proxy, exhibits contradictory results when accounting for Hg concentrations. Hg concentrations were negatively correlated to $\delta^{13}C$ values for *H. atlantica* and *T. notalia,* indicating that individuals foraging in northern waters tend to accumulate less Hg. On the contrary, the use of known foraging habitat showed an increase in Hg concentration in beaks of cephalopods from northern groups (Fig. 3). When species were grouped by habitat, we found an increase in Hg concentrations in the group foraging North STF compared to AZ-PFZ and AZ-PFZ-SAZ groups inhabiting waters closer to Antarctica (Fig. 3). This northward gradient of increasing Hg concentrations has been previously reported for seabirds (Blévin et al., 2013; Carravieri et al., 2013, 2016). This gradient could be related to the relatively high productivity around Antarctica (Ainley and Douglas, 2013), leading to the dilution of Hg in the biomass and to lower Hg concentrations in cephalopod prey compared to ecosystems further to the north, and to reduced bioaccumulation and biomagnification in Antarctic-associated habitats. Several biotic and abiotic factors could influence this northward enrichment in Hg concentrations, possibly linked to increasing Hg deposition, organic matter concentration, microbial activity and temperature resulting in an increase in Hg methylation towards northern latitudes (Fitzgerald et al., 2007). In addition, food web structure with a shortening toward southern latitudes, could contribute to the decrease in biomagnification of Hg with trophic levels (Cabana and Rasmussen, 1994; Point et al., 2011).

As Hg biomagnifies through the food web, cephalopods occupying a higher trophic position cephalopods can be expected to have correspondingly higher Hg concentrations (Chouvelon et al., 2011). The absence of such a result might stem from methodological and ecological factors. This lack of correlation may be due to the fact that we analysed the whole beak, which would have incorporated $\delta^{15}N$ values and Hg concentrations over the whole lifetime, whereas cephalopods are expected to switch targeted prey as they grow (Villanueva et al., 2017). As mentioned before, other factors such as habitat, size or a combination of factors could further complicate the interpretation of Hg concentrations. Species-specific ecology and life history can independently affect Hg concentrations, regardless of trophic position (Queirós et al., 2020; Lopes-Santos et al., 2025). Our results suggest that Hg concentrations in Southern Ocean cephalopod species vary according to the species and a general pattern with Hg varying with size, $\delta^{13}C$ and $\delta^{15}N$ does not exist.

Both Lopes-Santos et al. (2025) and Xavier et al. (2016) found no relationship between Hg concentration and LRL in *M. longimana* beaks (analyses performed on entire beaks). When using subsections of beaks of *M. longimana*, Queirós et al. (2020) were able to find a positive relationship between Hg concentration and LRL. As the analyses of the entire beak integrate all life stages of the individual, including potentially significant ontogenetic changes. This could explain why studying the whole beak accounted for only a small part of Hg concentrations, reflecting total Hg contamination throughout the individual's life stage, unlike Hg concentrations in muscles, which reflect more recent contamination (Lopes-Santos et al., 2025).

Our study highlights the complex interactions between LRL, habitat and trophic ecology in shaping Hg concentration in Southern Ocean cephalopods. The high degree of variability in $\delta^{13}C$ and $\delta^{15}N$ values suggests that these species occupy diverse habitats and trophic positions. Notably, we identified the highest Hg concentrations ever recorded in cephalopod beaks, suggesting even higher concentrations in their soft tissues. These high Hg concentrations are associated with the foraging habitat of the animal, species associated with northern habitats having higher Hg concentrations in the beak compared to Antarctic-associated species. These findings suggest that cephalopods in the PSSO may be exposed to elevated Hg bioavailability compared to other regions, potentially due to differences in baseline contamination levels. This underlines that the Southern Ocean should not be treated as a homogenous water mass and given that cephalopods are key prey for a wide range of top predators, including large fish, seabirds, and marine mammals, these relatively high Hg concentrations raise concerns about the potential for trophic transfer and its toxicological consequences. Further studies should explore regional, temporal and structural variations in Hg concentration in beaks, as well as its implications for predator health and ecosystem stability. Understanding these dynamics is crucial for developing effective conservation strategies for vulnerable species in the changing Southern Ocean.

CRediT authorship contribution statement

Marius Lespinas: Conceptualization, Data curation, Formal analysis, Investigation, Software, Visualization, Writing – original draft. **José C. Xavier:** Funding acquisition, Writing – review & editing. **Paco Bustamante:** Writing – review & editing. **José P. Queirós:** Formal analysis, Writing – review & editing. **David R. Thompson:** Writing – review & editing. **Pedro Coelho:** Methodology, Writing – review & editing. **Maria Eduarda Pereira:** Funding acquisition. **José Seco:** Project administration, Supervision, Validation, Writing – review & editing.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2026.108173.

Data availability

Data will be made available on request.

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