



## Decreasing mercury concentrations in beaks of the giant warty squid *Moroteuthopsis longimana* in the Scotia Sea (Southern Ocean) since the 1970s

Sara Lopes-Santos<sup>a,\*</sup>, José C. Xavier<sup>a,b,1</sup>, José Abreu<sup>a,b</sup>, José Seco<sup>a</sup>, João P. Coelho<sup>c</sup>, Eduarda Pereira<sup>d</sup>, Richard A. Phillips<sup>b</sup>, José P. Queirós<sup>a,b,2</sup>

<sup>a</sup> University of Coimbra, Marine and Environmental Sciences Centre (MARE)/Aquatic Research Network (ARNET), Department of Life Sciences, 3000-456 Coimbra, Portugal

<sup>b</sup> British Antarctic Survey (BAS), Natural Environment Research Council (NERC), High Cross, Madingley Road, CB3 0ET Cambridge, United Kingdom

<sup>c</sup> Laboratory for Innovation and Sustainability of Marine Biological Resources (ECOMARE), Centre for Environmental and Marine Studies (CESAM), Department of Biology, University of Aveiro, Estrada do Porto de Pesca Costeira, 3830-565 Gafanha da Nazaré, Portugal

<sup>d</sup> Departamento de Química & Laboratório Central de Análises, Laboratório Associado para a Química Verde (LAQV – REQUIMTE), Universidade de Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal

### ARTICLE INFO

#### Keywords:

Antarctic  
Cephalopods  
Contaminants  
Metal  
Onychoteuthidae  
Trace elements

### ABSTRACT

The giant warty squid *Moroteuthopsis longimana* is an important prey of top predators in the Southern Ocean. It is therefore a major link in the pathway of contaminants like mercury (Hg) to higher levels in food webs. In this study, we evaluated changes in Hg concentrations in beaks of adult *M. longimana* collected from the boluses (pellets) of wandering albatross *Diomedea exulans* chicks at Bird Island (South Georgia) over five decades (1976, 1984, 1995, 2006 and 2016). A steep decrease in Hg concentrations was observed in *M. longimana* from 1984 to 1995 ( $0.086 \pm 0.021 \mu\text{g.g}^{-1}$  to  $0.017 \pm 0.013 \mu\text{g.g}^{-1}$ ), with concentrations remaining low thereafter, likely reflecting the effects of international regulations and the global reductions in Hg emissions and usage initiated in the 1970s. Hg concentrations were not related to the squid size,  $\delta^{15}\text{N}$  nor  $\delta^{13}\text{C}$  values (proxies for trophic position and habitat, respectively), providing no evidence of bioaccumulation nor biomagnification in this squid species. Our results suggest that Hg concentrations in the beaks may be related to Hg bioavailability in the ecosystem, which makes *M. longimana* a potential biomonitor of Hg concentrations in pelagic environments of the Southern Ocean. However, further investigations are needed to confirm this finding.

Mercury (Hg) is a trace metal that occurs naturally in the environment, although its concentrations are increasing due to anthropogenic activities (Streets et al., 2017, 2019). As Hg is toxic and can bioaccumulate in organisms and biomagnify through food webs, it poses a threat to wildlife (Scheuhammer et al., 2007; Kidd et al., 2011; Lavoie et al., 2013; Murillo-Cisneros et al., 2018; Ordiano-Flores et al., 2021). Thus, long-lived top predators usually exhibit the highest Hg concentrations (Lehnherr, 2014). In response to such concerns, the Minamata Convention on Mercury (2013) was signed, aiming to reduce Hg levels and protect the environment (Minamata Convention on Mercury, 2023).

However, Hg concentrations in biota are still increasing in some regions, reinforcing the need for long-term monitoring (Selin et al., 2018; Médieu et al., 2023).

Although the Southern Ocean is often regarded as pristine and isolated from anthropogenic impacts, Hg levels are high in some regions (Aronson et al., 2011; Cossa et al., 2011). These concentrations are likely influenced by long-range atmospheric and oceanic transport, and glacial melt driven by climate change (Bargagli, 2008; Pérez-Rodríguez et al., 2019; Chown et al., 2022). Hg concentrations have been assessed in many Antarctic biota, from zooplankton to top predators (Seco et al.,

\* Corresponding author.

E-mail address: [sara.santos@student.uc.pt](mailto:sara.santos@student.uc.pt) (S. Lopes-Santos).

<sup>1</sup> Current address: Centre for Functional Ecology – Science for People & the Planet (CFE), Associate Laboratory TERRA, Department of Life Sciences, University of Coimbra, Calçada Martim de Freitas, Coimbra 3000-456, Portugal.

<sup>2</sup> Current address: CIIMAR/ CIMAR LA - Interdisciplinary Centre of Marine and Environmental Research, University of Porto, Terminal de Cruzeiros do Porto de Leixões, 4450-208, Matosinhos, Portugal.

2019; Queirós et al., 2020b; Charapata et al., 2023; Padilha et al., 2023; Mills et al., 2024; Espejo et al., 2024). Several studies have also assessed Hg concentrations in cephalopods, but no study has fully evaluated the use of squid as potential biomonitors of Hg concentrations in the Southern Ocean (Anderson et al., 2009; Matias et al., 2019; Xavier et al., 2016).

Cephalopods play a pivotal role as mid and upper-trophic-level predators in Southern Ocean ecosystems (Collins and Rodhouse, 2006; Rodhouse, 2013). They are prey to numerous top predators, playing an important role in the biomagnification process, especially as they tend to bioaccumulate Hg throughout their life (Xavier et al., 2018; Queirós et al., 2020a). These species are widely distributed in the Southern Ocean, from Antarctic to subtropical waters, and have a short life span (~1 to 2 years) (Collins and Rodhouse, 2006; Cherel, 2020). As such, levels of contaminants in their tissues reflect exposure over a relatively short and well-constrained time period. These biological and ecological characteristics suggest that cephalopods may be useful biomonitors of Hg levels in the Southern Ocean.

Cephalopods, in particular oceanic squid, are difficult to catch due to net avoidance behaviour and high swimming speeds (Santos et al., 2001; Rodhouse, 2013). To overcome this, studies often focus on their chitinous beaks, which are indigestible and can be recovered from stomachs of predators (Clarke, 1986; Trasviña-Carrillo et al., 2018; Xavier et al., 2022). Beaks grow continuously throughout the life of the individuals and accumulate trace elements, including Hg (Xavier et al., 2016; Matias et al., 2019; Queirós et al., 2020a). They can be preserved using different methodologies, e.g. frozen, ethanol 70%, without affecting the concentration of these elements, enabling their use in long-term studies (Golikov et al., 2024; Dimkovikj et al., 2025). Recent studies have shown that beaks preserve stable isotope values even after decades in storage (Dimkovikj et al., 2025). Combined with the strong binding affinity of Hg to protein thiol groups (Bustamante et al., 2006), it supports the assumption that Hg concentrations remain stable in archived beak samples. Within the Southern Ocean cephalopod community, *Moroteuthopsis longimana* is an important prey for many top predators, including the wandering albatross *Diomedea exulans* (Xavier et al., 2003; Collins and Rodhouse, 2006). This squid species presents an ontogenetic, likely size-related shift in its diet, feeding on crustaceans as juvenile and changing to fish and squid as adult, reflecting an increase of one trophic level (Nemoto et al., 1985; Queirós et al., 2018). Previous studies showed that Hg concentrations in *M. longimana* are 10 to 100-fold higher in the muscle than in beaks (Anderson et al., 2009; Xavier et al., 2016; Queirós et al., 2020a; Lopes-Santos et al., 2025). These studies also evaluated Hg bioaccumulation in this squid species, however, with contrasting results. While Queirós et al. (2020a) showed that adults have 2-fold higher Hg concentrations than juveniles, this pattern was only observed when comparing Hg concentrations for different life periods of the same individual. No bioaccumulation was found when comparing entire beaks from different individuals (Lopes-Santos et al., 2025).

This study aims to evaluate long-term temporal trends of Hg concentrations in *M. longimana* and investigate the potential of this species as a biomonitor for Hg concentrations in the Southern Ocean. To achieve this, Hg concentrations were measured in lower beaks of *M. longimana* collected from the boluses of wandering albatrosses *D. exulans* chicks. Beaks were collected at Bird Island (South Georgia) in 1976, 1984, 1995, 2006, and 2016 (see sampling details in Abreu et al., 2020). All boluses were frozen at  $-20^{\circ}\text{C}$  immediately after collection and kept frozen until analysis.

Beaks were cleaned, and lower beaks identified using a cephalopod beak guide (Xavier and Cherel, 2009). Ten lower beaks of *M. longimana* were randomly selected per study year, and the lower rostral length (LRL) measured using a digital calliper ( $\pm 0.01$  mm). Ten beaks were selected per year to guarantee consistency and to allow reliable annual comparisons. Furthermore, ten beaks was considered representative of the *M. longimana* population due to the low variation observed among

individuals sampled per year and between years, and it is consistent with other ecological studies using stable isotopes in cephalopods and seabird diets (Cherel and Hobson, 2005; Guerreiro et al., 2015). All beaks were of similar size and adult stage (Clarke, 1986). Mantle length (ML, in mm) and mass (M, in g) were estimated using allometric equations on Brown and Klages (1987). Beaks were further dried in an oven at  $60^{\circ}\text{C}$  for 24 h and ground into a fine powder using a mixer mill for 10 min with a  $30\text{ s}^{-1}$  frequency. Stable isotope values of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  in these beaks were previously determined by Abreu et al. (2020) using a continuous-flow isotope ratio mass spectrometer at the Laboratório MAREFOZ (MARE – Figueira da Foz). Analytical precision was monitored using certified reference material (acetanilide – Thermo), with internal measurement errors  $<0.1\text{ ‰}$  for  $\delta^{13}\text{C}$  and  $<0.3\text{ ‰}$  for  $\delta^{15}\text{N}$  (Abreu et al., 2020).

Mercury concentrations were determined in a LECO AMA-245 Advanced Mercury Analyzer through thermal decomposition atomic absorption spectrometry with gold amalgamation, with a detection threshold of  $0.00001\text{ }\mu\text{g.g}^{-1}$  (LECO Corporation, United States). This methodology does not require a pre-treatment or digestion of the samples (Costley et al., 2000). For each beak, approximately 25 mg of sample was used to determine Hg concentration. Samples were analysed in duplicate or triplicate, with the coefficient of variation always lower than 10%. Recovery efficiency ( $104 \pm 8\%$ ) was determined using ERM-CE278K mussel *Mytilus edulis* tissue (Joint Research Centre) as certified reference material. All concentrations are presented as mean  $\pm$  standard deviation in  $\mu\text{g.g}^{-1}$  dry weight.

Statistical analyses were performed in GraphPad Prism v9.0.0 considering an  $\alpha = 5\%$ . Normal distribution of Hg concentrations was tested using a Shapiro-Wilk test. A Kruskal-Wallis test followed by a Dunn's multiple comparison test was used to assess differences in Hg concentrations between years. In R software v4.2.2 (R Core Team, 2020), we evaluated how Hg concentrations changed over time and with squid size using a generalized linear model (GLM; family: Gamma, link function: identity) using year (1976 as reference) and LRL as explanatory variables. We also implemented a GLM (family: Gamma, link function: identity), with year (1976 as reference), LRL,  $\delta^{13}\text{C}$  values (proxy for habitat, (Cherel and Hobson, 2005) and  $\delta^{15}\text{N}$  values (proxy for trophic position, (Peterson and Fry, 1987)), and the interactions LRL:  $\delta^{13}\text{C}$  values and LRL:  $\delta^{15}\text{N}$  values as explanatory variables, to test for Hg bioaccumulation or biomagnification. Collinearity between explanatory variables was tested ahead of both GLMs using the Variation Inflation Factor (VIF), calculated using the *vif* function from the *car* package (Fox and Weisberg, 2018). No collinearity was found between variables (all  $\text{VIF} < 5$ ).

The LRL of the studied individuals ranged from 11.2 mm (1995 and 2006) to 16.3 mm (1984), corresponding to ML of 395.6 to 585.9 mm, and mass M of 1446 to 4720 g, respectively (Table 1). Mean LRL (and respective ML and M) was highest in 1984 ( $13.5 \pm 1.4$  mm), and lowest in 1995 ( $12.6 \pm 0.8$  mm) (Table 1).

Overall, mean Hg concentrations varied between  $0.010 \pm 0.007\text{ }\mu\text{g.g}^{-1}$  in 2016 and  $0.086 \pm 0.021\text{ }\mu\text{g.g}^{-1}$  in 1984, with the highest concentrations observed in the earliest sampled years (Table 1). Hg concentrations decreased in the following order  $1984 > 1976 >> 1995 > 2006 > 2016$ , with Hg concentrations in 1984 approximately 8-fold higher than those in 2016 (Table 1; Fig. 1). Significant differences were found in Hg concentrations between years ( $H = 35.14$ ,  $p < 0.0001$ ), with Dunn's multiple comparison test showing significant differences between 1976 and 1984 with 1995, 2006 and 2016 (Table 1). Results from the GLMs also indicated that Hg concentrations in beaks collected in 1995, 2006 and 2016 were significantly lower than in 1976 and 1984, suggesting a steep decrease in Hg concentrations after the mid-1980s (Table 2). The decrease in Hg concentrations is not associated with shifts in either habitat or trophic level, as the second GLM showed that LRL,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values do not explain the variation in Hg concentrations in the lower beaks of *M. longimana* (Table 3). Moreover, no significant changes in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values over the years indicate consistency in trophic level and habitat use (Abreu et al., 2020). This

**Table 1**

Mean ( $\pm$  standard deviation) mercury concentrations (Hg;  $\mu\text{g}\cdot\text{g}^{-1}$  dry weight), lower rostral length (LRL), mantle length (ML), mass (M),  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in the giant warty squid *M. longimana* sampled over five decades. Mean Hg concentrations in years with the same letters (<sup>a</sup> and <sup>b</sup>) are not statistically different.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values from Abreu et al. (2020).

Year	n	Hg ( $\mu\text{g}\cdot\text{g}^{-1}$ )	LRL (mm)	ML (mm)	M (g)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
1976	10	0.059 $\pm$ 0.036 <sup>a</sup>	13.1 $\pm$ 0.9	464.7 $\pm$ 31.9	2372.0 $\pm$ 476.9	-22.7 $\pm$ 0.9	6.1 $\pm$ 0.4
1984	10	0.086 $\pm$ 0.021 <sup>a</sup>	13.5 $\pm$ 1.4	480.7 $\pm$ 53.3	2686.9 $\pm$ 1000.6	-21.9 $\pm$ 2.0	6.5 $\pm$ 1.0
1995	10	0.017 $\pm$ 0.013 <sup>b</sup>	12.6 $\pm$ 0.8	446.7 $\pm$ 29.6	2105.8 $\pm$ 406.5	-21.8 $\pm$ 1.1	6.3 $\pm$ 0.4
2006	10	0.013 $\pm$ 0.004 <sup>b</sup>	13.3 $\pm$ 1.1	473.2 $\pm$ 42.1	2527.9 $\pm$ 643.5	-22.4 $\pm$ 1.6	6.5 $\pm$ 0.6
2016	10	0.010 $\pm$ 0.007 <sup>b</sup>	13.2 $\pm$ 0.6	468.4 $\pm$ 22.4	2413.7 $\pm$ 343.5	-22.4 $\pm$ 1.2	5.9 $\pm$ 0.6

suggests that the observed Hg decline reflects environmental rather than biological factors.

The reduction in Hg concentrations may reflect international efforts to reduce Hg pollution, as global Hg usage and atmospheric release have declined by  $\sim 60\%$  and  $\sim 30\%$ , respectively, since the 1970s, driven by international conventions such as the International Convention on the Prevention of Marine Pollution by Dumping of Wastes and Other Matter (1972) (Selin and Selin, 2006; Horowitz et al., 2014). The  $\sim 88\%$  decrease observed in *M. longimana* between 1984 and 2016 is consistent with this global trend, though the greater magnitude may reflect the cumulative effects of international regulatory measures and declining atmospheric deposition over time, particularly in remote environments like the Southern Ocean (Bargagli, 2016). Similar declines have been observed in other squids, such as *Loligo vulgaris* ( $\sim 40\%$ ) and *L. forbesi* ( $\sim 60\%$ ) (Monteiro et al., 1992; Bustamante et al., 2006; Vieira et al., 2020; Minet et al., 2021). The recent worldwide increase in Hg emissions ( $\sim 1.8\%$  between 2010 and 2015; Streets et al., 2019) was not reflected in the Hg concentrations of *M. longimana* lower beaks, suggesting that increasing emissions are not immediately reflected in the Southern Ocean biota (Bargagli, 2016). Previous studies recorded a decreasing trend in Hg concentrations in two other Antarctic squid

species, *Galiteuthis glacialis* and *Slosarczykovia circumantartica*, over a shorter timescale (2006 to 2016; Seco et al., 2020a, 2020b). This recent decrease was not observed in our results, which showed similar Hg concentrations in beaks of *M. longimana* sampled in 2006 and 2016. This may relate to the type of tissue analysed, i.e. beaks in our study and muscle in Seco et al. (2020a, 2020b). The ratio of Hg in beak:muscle varies between cephalopod species and, as the two tissues may exhibit different accumulation patterns, a subtle change in Hg may be less detectable in beaks, in which concentrations are generally much lower (Matias et al., 2020; Lopes-Santos et al., 2025).

Unlike squid, some Southern Ocean top predators have shown increasing Hg trends over recent decades: Antarctic toothfish

**Table 2**

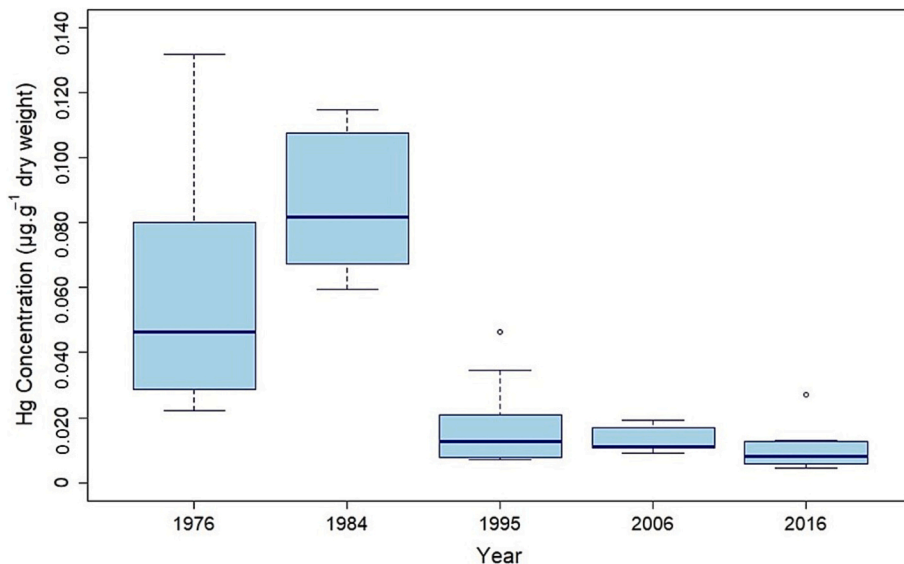
Effects of year and lower rostral length (LRL) of the generalized linear model (GLM) of Hg concentrations in lower beaks of giant warty squid *M. longimana* sampled over five decades. SE: Standard Error. **Bold** indicates statistically significant years.

Variable	Estimate	SE	t-value	p-value
(intercept)	41.12	22.01	1.86	0.068
Year				
1984	25.64	17.87	1.43	0.158
1995	-41.36	10.62	-3.89	<b>&lt;0.001</b>
2006	-46.36	10.41	-4.46	<b>&lt;0.001</b>
2016	-49.03	10.32	-4.75	<b>&lt;0.001</b>
LRL	1.39	1.50	0.93	0.360

**Table 3**

Effects of the year, lower rostral length (LRL),  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, and their interactions in a generalized linear model (GLM) of Hg concentrations in lower beaks of giant warty squid *M. longimana* sampled over five decades. SE: Standard Error. **Bold** indicates years in which values were significantly different.

Variable	Estimate	SE	t-value	p-value
(intercept)	-4.26	453.64	-0.009	0.99
Year				
1984	25.58	17.31	1.48	0.15
1995	-41.98	10.17	-4.13	<b>&lt;0.001</b>
2006	-46.15	10.21	-4.52	<b>&lt;0.001</b>
2016	-48.03	9.92	-4.84	<b>&lt;0.001</b>
LRL	1.46	34.78	0.04	0.97
$\delta^{15}\text{N}$	-8.73	34.36	-0.25	0.80
$\delta^{13}\text{C}$	-4.59	14.65	-0.31	0.76
LRL * $\delta^{13}\text{C}$	0.29	1.12	0.26	0.80
LRL * $\delta^{15}\text{N}$	0.99	2.64	0.37	0.71



**Fig. 1.** Boxplot of mercury (Hg) concentrations in the lower beaks of the giant warty squid *M. longimana* sampled over 5 decades.

(*Dissostichus mawsoni*) (~300%), grey-headed albatrosses (*Thalassarche chrysostoma*) (~200%), and elephant seals (*Mirounga leonina*) (~400%) (De Moreno et al., 1997; Queirós et al., 2020b; Mills et al., 2020; Barragán-Barrera et al., 2023). These contrasting results likely reflect differences in lifespan and trophic position, as squid are short-lived and accumulate Hg over ~2 years, making them more sensitive to short-term environmental changes than long-lived top predators which accumulate Hg over longer periods (Boyle and Rodhouse, 2007; Murillo-Cisneros et al., 2018; Queirós et al., 2020b; Ordiano-Flores et al., 2021). Additionally, climate change may increase the food chain length in the Southern Ocean, which would increase Hg biomagnification, resulting in higher Hg burdens in top predators (Seco et al., 2021; Queirós et al., 2025). For these reasons, short-lived species at mid-trophic levels, such as squid, can potentially be more efficient environmental biomonitors.

In our study, no evidence of Hg bioaccumulation or biomagnification was detected in *M. longimana*. This may be due to the small size range of studied beaks, as well as the similar trophic level of the squid in the studied years (Abreu et al., 2020). Hg concentrations in whole beaks of adult squid will reflect bioavailability in the environment throughout their lifespan (Queirós et al., 2023). Considering its short lifespan and hence its sensitivity to short-term changes in Hg exposure, along with its widespread distribution, abundance, and the ease of sampling of its beaks, *M. longimana* is well-suited as a biomonitor of Hg concentrations in the Southern Ocean. In addition, analysing the entire beak provides information on Hg intake over two to three years, enabling straightforward comparisons among individuals and locations. From this perspective, *M. longimana* appears to be an effective biomonitor for Hg concentrations in the Southern Ocean. However, this should be confirmed by further investigations.

#### CRedit authorship contribution statement

**Sara Lopes-Santos:** Visualization, Methodology, Investigation, Formal analysis, Writing – original draft. **José C. Xavier:** Supervision, Conceptualization, Writing – original draft. **José Abreu:** Methodology, Writing – original draft. **José Seco:** Methodology, Writing – original draft. **João P. Coelho:** Writing – original draft. **Eduarda Pereira:** Resources, Funding acquisition, Writing – original draft. **Richard A. Phillips:** Supervision, Writing – original draft. **José P. Queirós:** Visualization, Supervision, Methodology, Conceptualization, Writing – original draft.

#### Funding sources

This study represents a contribution to the Ecosystems component of the British Antarctic Survey Polar Science for a Sustainable Planet Programme funded by the Natural Environment Research Council. JA salary was supported by FCT through a PhD Scholarship (2020.07291.BD). JS salary was supported by FCT through an Individual Scientific Employment (2021/00624/CEECIND). JPC salary was supported by FCT through an Individual Scientific Employment (2020/01778/CEECIND). JPQ salary was supported by FCT through a PhD Scholarship co-financed by FSE (SFRH/BD/144320/2019) and the extraordinary scholarship to mitigate COVID-19 impacts in research activities (COVID/BD/153444/2024). This work had the support of FCT through national funds granted to MARE (UIDB/04292/2020 and UIDP/04292/2020) and to Associate Laboratory ARNET (LA/P/0069/2020).

#### 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.

#### Acknowledgements

The authors would like to thank the field teams of the British Antarctic Survey for collecting the wandering albatross boluses at Bird Island. We would like to thank FCT for supporting JA with a PhD Scholarship (2020.07291.BD); JS and JPC by an Individual Scientific Employment (2021/00624/CEECIND and 2020/01778/CEECIND); and JPQ with a PhD Scholarship co-financed by FSE (SFRH/BD/144320/2019) and for the extraordinary scholarship to mitigate COVID-19 impacts in research activities (COVID/BD/153444/2024).

#### Data availability

Data produced during this study is available at <https://doi.org/10.5281/zenodo.14996427>.

#### References

- Abreu, J., Phillips, R.A., Ceia, F.R., Ireland, L., Paiva, V.H., Xavier, J.C., 2020. Long-term changes in habitat and trophic level of Southern Ocean squid in relation to environmental conditions. *Sci. Rep.* <https://doi.org/10.1038/s41598-020-72103-6>.
- Anderson, O.R.J., Phillips, R.A., McDonald, R.A., Shore, R.F., McGill, R.A.R., Bearhop, S., 2009. Influence of trophic position and foraging range on mercury levels within a seabird community. *Mar. Ecol. Prog. Ser.* 375, 277–288. <https://doi.org/10.3354/meps07784>.
- Aronson, R.B., Thatje, S., McClintock, J.B., Hughes, K.A., 2011. Anthropogenic impacts on marine ecosystems in Antarctica. *Ann. N. Y. Acad. Sci.* 1223, 82–107. <https://doi.org/10.1111/j.1749-6632.2010.05926.x>.
- Bargagli, R., 2008. Environmental contamination in Antarctic ecosystems. *Sci. Total Environ.* 400, 212–226. <https://doi.org/10.1016/j.scitotenv.2008.06.062>.
- Bargagli, R., 2016. Moss and lichen biomonitoring of atmospheric mercury: a review. *Sci. Total Environ.* 572, 216–231. <https://doi.org/10.1016/j.scitotenv.2016.07.202>.
- Barragán-Barrera, D.C., Riet-Sapirza, F.G., Mojica-Moncada, D.F., Negrete, J., Curtosi, A., Bustamante, P., Caballero, S., Luna-Acosta, A., 2023. Sex-specific mercury levels in skin samples of Southern Elephant Seals (*Mirounga leonina*) at Isla 25 de Mayo (King George Island), Antarctic Peninsula. *Mar. Mamm. Sci.* <https://doi.org/10.1111/mms.13058>.
- Boyle, P., Rodhouse, P. (2007) Cephalopods: Ecology and Fisheries. *Cephalopods: ecology and fisheries* 1–452. <https://doi.org/10.1002/9780470995310>.
- Brown, C.R., Klages, N.T., 1987. Seasonal and annual variation in diets of macaroni (*Eudyptes chrysolophus chrysolophus*) and southern rockhopper (*E. chrysocome chrysocome*) penguins at sub-Antarctic Marion Island. *J. Zool.* 212, 7–28. <https://doi.org/10.1111/j.1469-7998.1987.tb05111.x>.
- Bustamante, P., Lahaye, V., Durnez, C., Churlaud, C., Caurant, F., 2006. Total and organic hg concentrations in cephalopods from the north eastern Atlantic waters: influence of geographical origin and feeding ecology. *Sci. Total Environ.* 368, 585–596. <https://doi.org/10.1016/j.scitotenv.2006.01.038>.
- Charapata, P., Clark, C.T., Miller, N., Kienle, S.S., Costa, D.P., Goebel, M.E., Gunn, H., Sperou, E.S., Kanatous, S.B., Crocker, D.E., Borrás-Chavez, R., Trumble, S.J., 2023. Whiskers provide time-series of toxic and essential trace elements, Se:Hg molar ratios, and stable isotope values of an apex Antarctic predator, the leopard seal. *Sci. Total Environ.* 854, 158651. <https://doi.org/10.1016/j.scitotenv.2022.158651>.
- Cherel, Y., 2020. A review of Southern Ocean squids using nets and beaks. *Mar. Biodivers.* 50, 98. <https://doi.org/10.1007/s12526-020-01113-4>.
- Cherel, Y., Hobson, K.A., 2005. Stable isotopes, beaks and predators: a new tool to study the trophic ecology of cephalopods, including giant and colossal squids. *Proc. R. Soc. B Biol. Sci.* 272, 1601–1607. <https://doi.org/10.1098/rspb.2005.3115>.
- Chown, S.L., Leihy, R.I., Naish, T.R., Brooks, C.M., Convey, P., Henley, B.J., Mackintosh, A.N., Phillips, L.M., 2022. Antarctic climate change and the environment: a decadal synopsis and recommendations for action.
- Clarke, M.R., 1986. *A Handbook for the Identification of Cephalopod Beaks*. Clarendon Press, Oxford.
- Collins, M.A., Rodhouse, P.G.K., 2006. Southern Ocean Cephalopods. In: *Advances in Marine Biology*, pp. 191–265.
- Cossa, D., Heimbürger, L.E., Lannuzel, D., Rintoul, S.R., Butler, E.C.V., Bowie, A.R., Averty, B., Watson, R.J., Remenyi, T., 2011. Mercury in the Southern Ocean. *Geochim. Cosmochim. Acta* 75, 4037–4052. <https://doi.org/10.1016/j.gca.2011.05.001>.
- Costley, C.T., Mossop, K.F., Dean, J.R., Garden, L.M., Marshall, J., Carroll, J., 2000. Determination of mercury in environmental and biological samples using pyrolysis atomic absorption spectrometry with gold amalgamation. *Anal. Chim. Acta* 405, 179–183. [https://doi.org/10.1016/S0003-2670\(99\)00742-4](https://doi.org/10.1016/S0003-2670(99)00742-4).
- De Moreno, J.E.A., Gerpe, M.S., Moreno, V.J., Vodopivec, C. (1997) Heavy metals in Antarctic organisms. Springer-Verlag.
- Dimkovikj, V.H., Staudinger, M.D., Leggett, H.D., France, C.A.M., Vecchione, M., 2025. Using museum specimens of northern shortfin squid (*Illex illecebrosus*) to evaluate long-term ecological changes in the northeast U.S. continental shelf large marine ecosystem. *Mar. Biol.* 172, 10. <https://doi.org/10.1007/s00227-024-04571-7>.
- Espejo, W., Celis, J.E., O'Driscoll, N.J., Sandoval, M., 2024. Total mercury and methylmercury levels in blood of Adélie penguins (*Pygoscelis adeliae*) from the



- Antarctic peninsula area. *Mar. Pollut. Bull.* 209, 117239. <https://doi.org/10.1016/j.marpolbul.2024.117239>.
- Fox, J., Weisberg, S., 2018. *An R Companion to Applied Regression*. Sage publications.
- Golkov, A.V., Xavier, J.C., Ceia, F.R., Queirós, J.P., Bustamante, P., Couperus, B., Guillou, G., Larionova, A.M., Sabirov, R.M., Somes, C.J., Hoving, H.-J., 2024. Insights on long-term ecosystem changes from stable isotopes in historical squid beaks. *BMC Ecol. Evol.* 24, 90. <https://doi.org/10.1186/s12862-024-02274-7>.
- Guerreiro, M., Phillips, R.A., Cherel, Y., Ceia, F.R., Alvito, P., Rosa, R., Xavier, J.C., 2015. Habitat and trophic ecology of Southern Ocean cephalopods from stable isotope analyses. *Mar. Ecol. Prog. Ser.* 530, 119–134. <https://doi.org/10.3354/meps11266>.
- Horowitz, H.M., Jacob, D.J., Amos, H.M., Streets, D.G., Sunderland, E.M., 2014. Historical mercury releases from commercial products: global environmental implications. *Environ. Sci. Technol.* 48, 10242–10250. <https://doi.org/10.1021/es501337j>.
- Kidd, K., Clayden, M., Jardine, T., 2011. Bioaccumulation and Biomagnification of Mercury through Food Webs. In: *Environmental Chemistry and Toxicology of Mercury*. Wiley, pp. 453–499.
- Lavoie, R.A., Jardine, T.D., Chumchal, M.M., Kidd, K.A., Campbell, L.M., 2013. Biomagnification of mercury in aquatic food webs: a worldwide meta-analysis. *Environ. Sci. Technol.* 47, 13385–13394. <https://doi.org/10.1021/es403103t>.
- Lehnher, I., 2014. Methylmercury biogeochemistry: a review with special reference to Arctic aquatic ecosystems. *Environ. Rev.* 22, 229–243. <https://doi.org/10.1139/er-2013-0059>.
- Lopes-Santos, S., Xavier, J.C., Seco, J., Coelho, J.P., Hollyman, P.R., Pereira, E., Phillips, R.A., Queirós, J.P., 2025. Squid beaks as a proxy for mercury concentrations in muscle of the giant warty squid *Moroteuthopsis longimana*. *Mar. Environ. Res.* 204, 106841. <https://doi.org/10.1016/j.marenvres.2024.106841>.
- Matias, R.S., Gregory, S., Ceia, F.R., Baeta, A., Seco, J., Rocha, M.S., Fernandes, E.M., Reis, R.L., Silva, T.H., Pereira, E., Piatkowski, U., Ramos, J.A., Xavier, J.C., 2019. Show your beaks and we tell you what you eat: different ecology in sympatric Antarctic benthic octopods under a climate change context. *Mar. Environ. Res.* <https://doi.org/10.1016/j.marenvres.2019.104757>.
- Matias, R.S., Seco, J., Gregory, S., Belchier, M., Pereira, M.E., Bustamante, P., Xavier, J.C., 2020. Antarctic octopod beaks as proxy for mercury concentrations in soft tissues. *Mar. Pollut. Bull.* <https://doi.org/10.1016/j.marpolbul.2020.111447>.
- Médieu, A., Point, D., Sonke, J.E., Angot, H., Allain, V., Bodin, N., Adams, D.H., Bignert, A., Streets, D.G., Buchanan, P.B., Heimbürger-Boavida, L.E., Pethybridge, H., Gillikin, D.P., Ménard, F., Choy, C.A., Itai, T., Bustamante, P., Dhurmea, Z., Ferriss, B.E., Bourlès, B., Habasque, J., Verheyden, A., Munaron, J.M., Laffont, L., Gauthier, O., Lorrain, A., 2023. Stable tuna mercury concentrations since 1971 illustrate marine inertia and the need for strong emission reductions under the Minamata convention. *Environ. Sci. Technol. Lett.* <https://doi.org/10.1021/acs.estlett.3c00949>.
- Mills, W.F., Bustamante, P., McGill, R.A.R., Anderson, O.R.J., Bearhop, S., Cherel, Y., Votier, S.C., Phillips, R.A., 2020. Mercury exposure in an endangered seabird: long-term changes and relationships with trophic ecology and breeding success. *Proc. R. Soc. Lond. B Biol. Sci.* 287, 20202683. <https://doi.org/10.1098/rspb.2020.2683>.
- Mills, W.F., Bustamante, P., Ramírez, F., Forero, M.G., Phillips, R.A., 2024. Mercury concentrations in feathers of albatrosses and large petrels at South Georgia: contemporary patterns and comparisons with past decades. *Arch. Environ. Contam. Toxicol.* 86, 363–374. <https://doi.org/10.1007/s00244-024-01067-9>.
- Minamata Convention on Mercury, 2023. *Minamata Convention on Mercury: text and annexes*.
- Minet, A., Manceau, A., Valada-Mennuni, A., Brault-Favrou, M., Churlaud, C., Fort, J., Nguyen, T., Spitz, J., Bustamante, P., Lacoue-Labarthe, T., 2021. Mercury in the tissues of five cephalopods species: first data on the nervous system. *Sci. Total Environ.* 759, 143907. <https://doi.org/10.1016/j.scitotenv.2020.143907>.
- Monteiro, L.R., Porteiro, F., Gonçalves, J. Inter- and intra-specific variation of mercury levels in muscle of cephalopods from the Azores. *Arquipélago Life Earth Sci.* 10A:13–22, 1992.
- Murillo-Cisneros, D.A., O'Hara, T.M., Castellini, J.M., Sánchez-González, A., Elorriaga-Verplancken, F.R., Marmolejo-Rodríguez, A.J., Marín-Enríquez, E., Galván-Magaña, F., 2018. Mercury concentrations in three ray species from the Pacific coast of Baja California Sur, Mexico: variations by tissue type, sex and length. *Mar. Pollut. Bull.* 126, 77–85. <https://doi.org/10.1016/j.marpolbul.2017.10.060>.
- Nemoto, T., Okiyama, M., Takahashi, M., 1985. Aspects of the roles of squid in food chains of marine Antarctic ecosystems. In: *Antarctic Nutrient Cycles and Food Webs*. Springer, pp. 415–420.
- Ordiano-Flores, A., Galván-Magaña, F., Sánchez-González, A., Soto-Jiménez, M.F., Páez-Osuna, F., 2021. Mercury, selenium, and stable carbon and nitrogen isotopes in the striped marlin *Kajika audax* and blue marlin *Makaira nigricans* food web from the Gulf of California. *Mar. Pollut. Bull.* <https://doi.org/10.1016/j.marpolbul.2021.112657>.
- Padilha, J.A.G., Souza-Kasprzyk, J., Pinzone, M., Bighetti, G.P., Espejo, W., Leite, A., Santos, S., Cunha, L.S.T., Costa, E.S., Pessôa, A.R., Torres, J.P.M., Lepoint, G., Das, K., Dorneles, P.R., 2023. Mercury exposure in Antarctic seabirds: assessing the influence of trophic position and migration patterns. *Chemosphere* 340, 139871. <https://doi.org/10.1016/j.chemosphere.2023.139871>.
- Pérez-Rodríguez, M., Biester, H., Aboal, J.R., Toro, M., Martínez Cortizas, A., 2019. Thawing of snow and ice caused extraordinary high and fast mercury fluxes to lake sediments in Antarctica. *Geochim. Cosmochim. Acta* 248, 109–122. <https://doi.org/10.1016/j.gca.2019.01.009>.
- Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* 18, 293–320. <https://doi.org/10.1146/annurev.es.18.110187.001453>.
- Queirós, J.P., Cherel, Y., Ceia, F.R., Hilário, A., Roberts, J., Xavier, J.C., 2018. Ontogenic changes in habitat and trophic ecology in the Antarctic squid *Kondakovia longimana* derived from isotopic analysis on beaks. *Polar Biol.* 41, 2409–2421. <https://doi.org/10.1007/s00300-018-2376-4>.
- Queirós, J.P., Bustamante, P., Cherel, Y., Coelho, J.P., Seco, J., Roberts, J., Pereira, E., Xavier, J.C., 2020a. Cephalopod beak sections used to trace mercury levels throughout the life of cephalopods: the giant warty squid *Moroteuthopsis longimana* as a case study. *Mar. Environ. Res.* <https://doi.org/10.1016/j.marenvres.2020.105049>.
- Queirós, J.P., Hill, S.L., Pinkerton, M., Vacchi, M., Coelho, J.P., Pereira, E., Ramos, J.A., Seco, J., Stevens, D.W., Xavier, J.C., 2020b. High mercury levels in Antarctic toothfish *Dissostichus mawsoni* from the Southwest Pacific sector of the Southern Ocean. *Environ. Res.* <https://doi.org/10.1016/j.envres.2020.109680>.
- Queirós, J.P., Bartolomé, A., Piatkowski, U., Xavier, J.C., Perales-Raya, C., 2023. Age and growth estimation of Southern Ocean squid *Moroteuthopsis longimana*: can we use beaks collected from predators' stomachs? *Mar. Biol.* <https://doi.org/10.1007/s00227-022-04156-2>.
- Queirós, J.P., Hollyman, P.R., Bustamante, P., Vaz, D., Belchier, M., Xavier, J.C., 2025. Deep-sea food-web structure at South Sandwich Islands (Southern Ocean): net primary production as a main driver for interannual changes. *Ecography*. <https://doi.org/10.1111/ecog.07263>.
- R Core Team, 2020. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rodhouse, P.G.K., 2013. Role of squid in the Southern Ocean pelagic ecosystem and the possible consequences of climate change. *Deep Sea Res. 2 Top. Stud. Oceanogr.* 95, 129–138. <https://doi.org/10.1016/j.dsr2.2012.07.001>.
- Santos, M.B., Clarke, M.R., Pierce, G.J., 2001. Assessing the importance of cephalopods in the diets of marine mammals and other top predators: problems and solutions. *Fish. Res.* 52, 121–139. [https://doi.org/10.1016/S0165-7836\(01\)00236-3](https://doi.org/10.1016/S0165-7836(01)00236-3).
- Scheuhammer, A.M., Meyer, M.W., Sandheinrich, M.B., Murray, M.W., 2007. Effects of environmental methylmercury on the health of wild birds, mammals, and fish. *Ambio* 36, 12–18. [https://doi.org/10.1579/0044-7447\(2007\)36\[12:eoemot\]2.0.co;2](https://doi.org/10.1579/0044-7447(2007)36[12:eoemot]2.0.co;2).
- Seco, J., Xavier, J.C., Coelho, J.P., Pereira, B., Tarling, G., Pardal, M.A., Bustamante, P., Stowasser, G., Brierley, A.S., Pereira, M.E., 2019. Spatial variability in total and organic mercury levels in Antarctic krill *Euphausia superba* across the Scotia Sea. *Environ. Pollut.* 247, 332–339. <https://doi.org/10.1016/j.envpol.2019.01.031>.
- Seco, J., Xavier, J.C., Bustamante, P., Coelho, J.P., Saunders, R.A., Ferreira, N., Fielding, S., Pardal, M.A., Stowasser, G., Viana, T., Tarling, G.A., Pereira, E., Brierley, A.S., 2020a. Main drivers of mercury levels in Southern Ocean lantern fish *Myctophidae*. *Environ. Pollut.* 264, 114711. <https://doi.org/10.1016/j.envpol.2020.114711>.
- Seco, J., Xavier, J.C., Brierley, A.S., Bustamante, P., Coelho, J.P., Gregory, S., Fielding, S., Pardal, M.A., Pereira, B., Stowasser, G., Tarling, G.A., Pereira, E., 2020b. Mercury levels in Southern Ocean squid: variability over the last decade. *Chemosphere* 239, 124785. <https://doi.org/10.1016/j.chemosphere.2019.124785>.
- Seco, J., Aparício, S., Brierley, A.S., Bustamante, P., Ceia, F.R., Coelho, J.P., Philips, R.A., Saunders, R.A., Fielding, S., Gregory, S., Matias, R., Pardal, M.A., Pereira, E., Stowasser, G., Tarling, G.A., Xavier, J.C., 2021. Mercury biomagnification in a Southern Ocean food web. *Environ. Pollut.* 275, 116620. <https://doi.org/10.1016/j.envpol.2021.116620>.
- Selin, H., Keane, S.E., Wang, S., Selin, N.E., Davis, K., Bally, D., 2018. Linking science and policy to support the implementation of the Minamata convention on mercury. *Ambio* 47, 198–215. <https://doi.org/10.1007/s13280-017-1003-x>.
- Selin, N.E., Selin, H., 2006. Global politics of mercury pollution: the need for multi-scale governance. *Rev. Eur. Comp. Int. Environ. Law* 15, 258–269. <https://doi.org/10.1111/j.1467-9388.2006.00529.x>.
- Streets, D.G., Horowitz, H.M., Jacob, D.J., Lu, Z., Levin, L., Ter Schure, A.F.H., Sunderland, E.M., 2017. Total mercury released to the environment by human activities. *Environ. Sci. Technol.* 51, 5969–5977. <https://doi.org/10.1021/acs.est.7b00451>.
- Streets, D.G., Horowitz, H.M., Lu, Z., Levin, L., Thackray, C.P., Sunderland, E.M., 2019. Global and regional trends in mercury emissions and concentrations, 2010–2015. *Atmos. Environ.* 201, 417–427. <https://doi.org/10.1016/j.atmosenv.2018.12.031>.
- Trasviña-Carrillo, L.D., Hernández-Herrera, A., Torres-Rojas, Y.E., Galván-Magaña, F., Sánchez-González, A., Aguiñiga-García, S., 2018. Spatial and trophic preferences of jumbo squid *Dosidicus gigas* (D'Orbigny, 1835) in the Central Gulf of California: ecological inferences using stable isotopes. *Rapid Commun. Mass Spectrom.* 32, 1225–1236. <https://doi.org/10.1002/rcm.8147>.
- Vieira, H.C., Rendón-von Osten, J., Soares, A.M.V.M., Morgado, F., Abreu, S.N., 2020. Mercury bioaccumulation in the long-fin squid *Loligo forbesi* near the mid-Atlantic ridge: implications to human exposure. *Ecotoxicol. Environ. Saf.* <https://doi.org/10.1016/j.ecoenv.2020.110957>.
- Xavier, J.C., Cherel, Y., 2009. *Cephalopod beak guide for the Southern Ocean*.
- Xavier, J.C., Croxall, J.P., Trathan, P.N., Rodhouse, P.G., 2003. Inter-annual variation in the cephalopod component of the diet of the wandering albatross, *Diomedea exulans*, breeding at Bird Island, South Georgia. *Mar. Biol.* 142, 611–622. <https://doi.org/10.1007/s00227-002-0962-y>.
- Xavier, J.C., Ferreira, S., Tavares, S., Santos, N., Mieiro, C.L., Trathan, P.N., Lourenço, S., Martinho, F., Steinke, D., Seco, J., Pereira, E., Pardal, M., Cherel, Y., 2016. The significance of cephalopod beaks in marine ecology studies: can we use beaks for

- DNA analyses and mercury contamination assessment? *Mar. Pollut. Bull.* 103, 220–226. <https://doi.org/10.1016/j.marpolbul.2015.12.016>.
- Xavier, J.C., Cherel, Y., Allcock, L., Rosa, R., Sabirov, R.M., Blicher, M.E., Golikov, A.V., 2018. A review on the biodiversity, distribution and trophic role of cephalopods in the Arctic and Antarctic marine ecosystems under a changing ocean. *Mar. Biol.* 165, 93. <https://doi.org/10.1007/s00227-018-3352-9>.
- Xavier, J.C., Golikov, A.V., Queirós, J.P., Perales-Raya, C., Rosas-Luis, R., Abreu, J., Bello, G., Bustamante, P., Capaz, J.C., Dimkovikj, V.H., González, A.F., Guímaro, H., Guerra-Marrero, A., Gomes-Pereira, J.N., Hernández-Urcera, J., Kubodera, T., Laptikhovsky, V., Lefkadiou, E., Lishchenko, F., Luna, A., Liu, B., Pierce, G.J., Pissarra, V., Reveillac, E., Romanov, E.V., Rosa, R., Roscian, M., Rose-Mann, L., Rouget, I., Sánchez, P., Sánchez-Márquez, A., Seixas, S., Souquet, L., Varela, J., Vidal, E.A.G., Cherel, Y., 2022. The significance of cephalopod beaks as a research tool: an update. *Front. Physiol.* <https://doi.org/10.3389/fphys.2022.1038064>.