Ecotoxicology
https://doi.org/10.1007/s10646-023-02709-9

Circumpolar assessment of mercury contamination: the Adélie penguin as a bioindicator of Antarctic marine ecosystems

Fanny Cusset[1,2] · Paco Bustamante[1,3] · Alice Carravieri[1,2] · Clément Bertin[1] · Rebecka Brasso[4] · Ilaria Corsi[5] · Michael Dunn[6] · Louise Emmerson[7] · Gaël Guillou[1] · Tom Hart[8] · Mariana Juáres[9,10] · Akiko Kato[2] · Ana Laura Machado-Gaye[11] · Candice Michelot[2,12] · Silvia Olmastroni[5,13] · Michael Polito[14] · Thierry Raclot[15] · Mercedes Santos[9] · Annie Schmidt[16] · Colin Southwell[7] · Alvaro Soutullo[11] · Akinori Takahashi[17] · Jean-Baptiste Thiebot[17,18] · Phil Trathan[6] · Pierre Vivion[1] · Claire Waluda[6] · Jérôme Fort[1] · Yves Cherel[2]

Accepted: 11 October 2023

Abstract

Due to its persistence and potential ecological and health impacts, mercury (Hg) is a global pollutant of major concern that may reach high concentrations even in remote polar oceans. In contrast to the Arctic Ocean, studies documenting Hg contamination in the Southern Ocean are spatially restricted and large-scale monitoring is needed. Here, we present the first circumpolar assessment of Hg contamination in Antarctic marine ecosystems. Specifically, the Adélie penguin (*Pygoscelis adeliae)* was used as a bioindicator species, to examine regional variation across 24 colonies distributed across the entire Antarctic continent. Mercury was measured on body feathers collected from both adults ($n = 485$) and chicks ($n = 48$) between 2005 and 2021. Because penguins' diet represents the dominant source of Hg, feather $\delta^{13}C$ and $\delta^{15}N$ values were measured as proxies of feeding habitat and trophic position. As expected, chicks had lower Hg concentrations (mean ± SD: $0.22 \pm 0.08\ \mu g \cdot g^{-1}$) than adults ($0.49 \pm 0.23\ \mu g \cdot g^{-1}$), likely because of their shorter bioaccumulation period. In adults, spatial variation in feather Hg concentrations was driven by both trophic ecology and colony location. The highest Hg concentrations were observed in the Ross Sea, possibly because of a higher consumption of fish in the diet compared to other sites (krill-dominated diet). Such large-scale assessments are critical to assess the effectiveness of the Minamata Convention on Mercury. Owing to their circumpolar distribution and their ecological role in Antarctic marine ecosystems, Adélie penguins could be valuable bioindicators for tracking spatial and temporal trends of Hg across Antarctic waters in the future.

✉ Fanny Cusset
cussetfanny@gmail.com

1 Littoral, Environnement et Sociétés (LIENSs), UMR 7266 CNRS - La Rochelle Université, 2 Rue Olympe de Gouges, 17000 La Rochelle, France

2 Centre d'Études Biologiques de Chizé (CEBC), UMR 7372 du CNRS - La Rochelle Université, 79360 Villiers-en-Bois, France

3 Institut Universitaire de France (IUF), 1 rue Descartes, 75005 Paris, France

4 Department of Zoology, Weber State University, Ogden, UT, USA

5 Department of Physical, Earth and Environmental Sciences, University of Siena, 53100 Siena, Italy

6 British Antarctic Survey, Cambridge, UK

7 Department of Climate Change, Energy, the Environment and Water, Australian Antarctic Division, Canberra, ACT, Australia

8 Department of Biological and Medicinal Sciences, Oxford Brooke University, Oxford, UK

9 Departamento Biología de Predadores Tope, Instituto Antártico Argentino, Buenos Aires, Argentina

10 Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Ciudad Autónoma de Buenos Aires, Buenos Aires, Argentina

11 Centro Universitario Regional del Este, Universidad de la República, Maldonado, Uruguay

12 Institut Maurice-Lamontagne, Pêches et Océans Canada, Mont-Joli, QC, Canada

13 Museo Nazionale dell'Antartide, Siena, Italy

14 Louisiana State University, Baton Rouge, LA, USA

15 Institut Pluridisciplinaire Hubert Curien, UMR 7178 du CNRS, Université de Strasbourg, 67087 Strasbourg, France

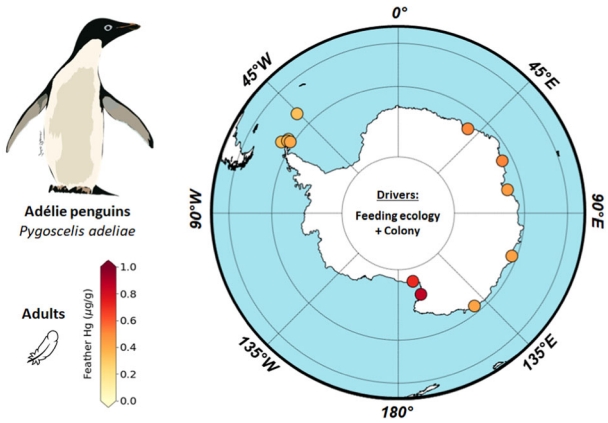
16 Point Blue Conservation, Petaluma, CA, USA

17 National Institute of Polar Research, 10-3 Midori-cho, Tachikawa, Tokyo 190-8518, Japan

18 Graduate School of Fisheries Sciences, Hokkaido University, Minato-cho 3-1-1, Hakodate 041-8611, Japan

Published online: 25 October 2023

Graphical Abstract



Keywords Feathers · Hg · Marine food web · Seabirds · Stable Isotopes · Southern Ocean

Highlights

- Adélie penguins are relevant bioindicators of Hg contamination in Antarctic marine ecosystems.
- Feather Hg concentrations were measured in 24 breeding colonies (adults and chicks).
- The highest Hg concentrations were found in the Ross Sea.
- Both trophic ecology and colony location drove feather Hg concentrations.

Introduction

Mercury (Hg) is a global pollutant of both natural and anthropogenic origin (Sonke et al. 2023). Since the Industrial Revolution, anthropogenic activities, such as chemical manufacturing, gold-mining and coal combustion (Streets et al. 2017), have released considerable amounts of Hg into the environment, resulting in a three- to five-fold increase of Hg globally (Lamborg et al. 2014; Selin 2009). Yet, this non-essential and toxic metal is of global concern due to its adverse effects on wildlife and human health (NRC/NAS 2000; Ackerman et al. 2016; Dietz et al. 2019; Roman et al. 2011; Scheuhammer et al. 2012; Tan et al. 2009). As a reaction, the Minamata Convention on Mercury was adopted in 2013 (implemented in 2017) by more than 140 countries, to protect human health and the environment worldwide. Today, large-scale monitoring of environmental Hg contamination is required to assess the effectiveness of this international treaty and guide its future directions.

Mercury disperses worldwide mainly through atmospheric currents and deposits even in the most remote oceanic regions, such as polar oceans (UN-Environment 2019). These oceans are facing significant modifications due to climate change, which alters the biogeochemical cycle of Hg (Chételat et al. 2022; McKinney et al. 2022) and ultimately its transfer in marine food webs (Zhou et al. 2023). In the Arctic Ocean, Hg contamination has been extensively documented over large temporal and spatial scales (e.g., Albert et al. 2021; Bond et al. 2015; Desforges et al. 2022; Dietz et al. 2022). In the Southern Ocean (*sensu lato,* i.e., water masses south of the Subtropical Front; Carter et al. 2008; Orsi et al. 1995), studies are more spatially restricted mainly due to logistical constraints, with a focus on local and/or regional scales (but see Brasso et al. 2015; Carravieri et al. 2017; Cherel et al. 2018). This is particularly the case in the Antarctic Zone (i.e., water masses south of the Polar Front; Carter et al. 2008; Orsi et al. 1995). This critical gap in sampling areas can be filled by using bioindicator species that closely rely on marine food webs from these specific areas, such as seabirds (e.g., Burger and Gochfeld 2004; Furness and Camphuysen 1997). As meso- to top predators, seabirds are abundant consumers of the world's marine resources. Due to biomagnification processes, they reflect Hg contamination of their marine food webs (Braune et al. 2015; Fort et al. 2016; Piatt et al. 2007). Food intake is the major source of Hg in seabirds, and thus assessing their feeding ecology and spatial distribution is needed to disentangle ecological drivers of Hg contamination (Carravieri et al. 2014b; Cherel et al. 2018). Specifically, accounting for feeding ecology is key to identify whether spatial variation in Hg contamination is linked to dietary differences (Brasso et al. 2015;

Carravieri et al. 2014c; Gatt et al. 2020) and/or to other environmental factors (Foster et al. 2019; Furtado et al. 2021; Tartu et al. 2022).

Once assimilated by seabirds, Hg is distributed *via* blood to internal tissues where it bioaccumulates (i.e., Hg concentrations increase over time) between moulting periods. During moult, stored Hg is remobilised and up to 90% of the total Hg body burden is excreted into growing feathers (Honda et al. 1986), where it binds to keratin proteins (Crewther et al. 1965). Hence, moult represents the main excretion pathway for Hg in seabirds (Thompson et al. 1990; Thompson and Furness 1989). Feathers incorporate the cumulative signal of Hg exposure between two moulting episodes (i.e., over several weeks/months to up to one year in most species; Albert et al. 2019). Sampling seabird feathers thus represent a powerful monitoring opportunity to investigate Hg contamination in marine food webs over large temporal and spatial scales, especially in the remote Southern Ocean.

Penguins constitute the largest seabird biomass in the Southern Ocean and consume several million tons of marine resources annually (Knox 2006; Southwell et al. 2017; Williams 1995). Available evidence suggests that they exploit similar marine resources over both the short-term (breeding season) and the long-term (non-breeding season; Cherel et al. 2007; Polito et al. 2016; Tierney et al. 2009). Therefore, penguins are adequate bioindicator species to monitor Hg contamination in Antarctic marine food webs (Brasso et al. 2015; Carravieri et al. 2013). Among seabirds, penguins present a unique moulting pattern. Following a pre-moult foraging period of hyperphagia at sea, they renew their entire plumage annually while fasting ashore or on sea ice (a few weeks; Cherel et al. 1994; Emmerson et al. 2019), less frequently at the breeding colonies (Ainley 2002). All body feathers are thus moulted simultaneously every year. Within each individual penguin, all body feathers have thus the same chemical signature, including Hg concentrations and stable isotope values (Brasso et al. 2013; Carravieri et al. 2014a). Since the 1980s, 20 studies documented Hg contamination in feathers of eight penguin species from the Southern Ocean, including species breeding both in the Subantarctic (i.e., water masses between the Subtropical and Polar Fronts) and Antarctic Zones (see Table S1 for a complete review). Whereas contamination from subantarctic islands has been well documented, spatial coverage is limited to local and regional investigations in the Antarctic. For example, out of the 14 studies on Hg in the Antarctic Zone, nine (64%) were carried out in the South Shetland Islands only (e.g. Álvarez-Varas et al. 2018; Becker et al. 2016; Brasso et al. 2015; Matias et al. 2022; Souza et al. 2020). Other documented regions include the coasts of Queen Maud Land, Adélie Land and Victoria Land (Ross Sea) (Bargagli et al. 1998; Carravieri et al. 2016; Pilcher et al. 2020; Yamamoto et al. 1996). To date, most Antarctic regions where penguins breed remain unexplored. Large-scale sampling of penguin feathers is thus needed to identify potential hotspots of Hg contamination and determine the toxicological risk to Antarctic marine biodiversity, which is simultaneously threatened by other anthropogenic stressors, including climate change (Barbraud et al. 2012; Clucas et al. 2014; Lee et al. 2017; Morley et al. 2019).

The Adélie penguin (*Pygoscelis adeliae*) is an ideal candidate to reflect Hg contamination in Antarctic marine food webs. With its circumpolar distribution, it is the most common and abundant penguin species in both continental and maritime (Antarctic Peninsula and adjacent archipelagos) Antarctica. Adélie penguins forage in Antarctic waters year-round (Ballard et al. 2010; Takahashi et al. 2018; Thiebot et al. 2019) and consistently use similar feeding resources (Ainley 2002; Jafari et al. 2021; Juáres et al. 2016). The Adélie penguin is an indicator species for the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) for the Ecosystem Monitoring Program (Agnew 1997). The latter aims (i) to ensure that krill fisheries consider the needs of krill-predators, such as seals and seabirds, and (ii) to distinguish between environmental and fishery-related changes in the Southern Ocean. Here, we take advantage of a large, international field-based scientific network, to provide the first circumpolar assessment of Hg contamination in Antarctic marine ecosystems, using feathers of Adélie penguins that breed across both continental and maritime Antarctica. The aims of this study were four-fold. The first aim was to quantify current Hg contamination of Antarctic marine food webs, by focussing on this key higher-order indicator species at a circumpolar scale. Given the unique oceanographic features of the Southern Ocean (i.e., circumpolar circulation), relatively homogenous Hg concentrations were expected across all Adélie penguin colonies. The second aim was to identify potential Hg hotspots by assessing Hg contamination over different spatial and temporal scales, using pre-fledging chick feathers, which reflect short-term, local contamination (~two months during the breeding season only), and adult feathers, which integrate a geographically larger scale over one year (incorporating both the breeding and non-breeding seasons). Because of longer exposure to Hg, adults were expected to have higher Hg concentrations than chicks (Stewart et al. 1997; Thompson et al. 1991). The third aim was to investigate the influence of penguin trophic ecology on spatial patterns of Hg contamination, by using feather carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes, as proxies of feeding habitat and trophic position, respectively (Kelly 2000; Newsome et al. 2007). Mercury and stable isotopes are uncoupled in feathers (Bond 2010), yet provide relevant information on

feeding ecology for the understanding of Hg contamination. As for other species and regions, trophic ecology was expected to be a major driver of spatial differences of Hg contamination in Antarctic marine ecosystems (e.g., Becker et al. 2002; Bustamante et al. 2016; Carravieri et al. 2014c; Mills et al. 2020). Finally, the last aim was to investigate sex differences in both Hg contamination and trophic ecology using a subset of adult Adélie penguins from various colonies.

Material and methods

Feather collection and preparation

This comprehensive assessment brings together published and new Hg concentrations for Adélie penguin feathers (Tables 1 and 2). Overall, 538 individuals of Adélie penguins (490 breeding adults and 48 pre-fledging chicks) were sampled between 2005 and 2021, in 24 colonies around Antarctica ($n = 5$–40 individuals per colony; Fig. 1). Sample sizes for each colony are provided in Table 1 (adults) and 2 (chicks), and geographical coordinates of sampled colonies are detailed in the Supplementary Material (Table S2). For both adults and chicks, body feathers were sampled for two reasons: (i) they are generally considered to be the best feather type to sample (Furness et al. 1986) and (ii) in penguins, they represent the majority of the plumage (no flight feather). Therefore, 1–5 body feathers from the breast or the back were collected for each individual, because of their complete and drastic moulting strategy (Brasso et al. 2013; Cherel et al. 1994). In a limited number of colonies, where no other pygoscelid penguin breeds, freshly molted feathers were also collected from the ground (i.e., in Shirley Island, Brown Bluffs, Madder Cliffs and Paulet Island; feather sampling locations in each of these colonies were at least several nests away from each other to avoid pseudoreplication; minimum distance = 15 m). Feathers were then stored in either plastic bags or paper envelopes and kept at room temperature until laboratory analyses.

In adults, feather moult starts when the penguins are still at sea, building body reserves during the pre-moulting period (Cherel et al. 1993, 1994; Croxall 1982). The part of the feather that grows at this time (i.e., the tip) thus reflects the pre-moult feeding period at sea. In contrast, the remaining feather that grows during moult reflects the fasting period on sea ice or ashore, and hence the dietary signature from accumulated body reserves. Given the difference in integration of dietary information (stable isotopes) during these two periods, feather's tip (i.e., 5 mm) was cut and discarded. Both Hg and stable isotopes were analysed in the remaining feather. In order to avoid any external contamination, feathers were cleaned with a chloroform:methanol mixture (2:1), sonicated for 3 min, rinsed twice with methanol and dried at 45 °C for 48 h. Given the homogenous chemical composition of body feathers in penguins (Brasso et al. 2013; Carravieri et al. 2014a), measurements were made on a single randomly-selected feather for each bird, which was cut with precision (stainless steel) scissors to obtain a homogenous powder to be analysed for both Hg and stable isotopes.

Mercury analyses

Total Hg (THg) includes both inorganic and organic Hg (mainly methyl-Hg, MeHg). In feathers, >90% of THg is in the form of MeHg (Renedo et al. 2017), the most toxic and bioavailable form that bioaccumulates and biomagnifies in marine food webs (Cossa 2013). Therefore, we used THg as a proxy of MeHg in Adélie penguin feathers.

Mercury analyses were performed on feather homogenates (0.5–1.5 mg) in duplicate, using an Advanced Mercury Analyser (AMA 254, Altech). When the relative standard deviation (RSD) between duplicates was <10%, Hg concentrations were averaged for each sample. When the RSD was >10%, an additional sample of the homogenate was analysed, and the duplicates guaranteeing the lowest RSD were kept for average calculations. The AMA quantification limit was 0.1 ng. Blanks and two certified reference materials (TORT3 – Lobster hepatopancreas, DOLT5 – Fish liver, NRC Canada) were analysed during each analytical session to guarantee accuracy (Table S3). Recovery values were 100.6 ± 2.3 and 96.7 ± 2.6%, respectively. Concentrations are expressed as $\mu g \cdot g^{-1}$ dry weight (dw).

Stable isotope analyses

Carbon and nitrogen stable isotope analyses were performed on feather homogenates (0.2–0.8 mg), loaded into tin cups (8 × 5 mm; Elemental Microanalysis Ltd, Okehampton, UK) using a microbalance (XPRUD5, Mettler Toledo, Greifensee, Switzerland). Values of $\delta^{13}C$ and $\delta^{15}N$ were determined with a continuous flow isotope ratio mass spectrometer (Delta V Plus with a Conflo IV Interface, Thermo Scientific, Bremen, Germany) coupled to an elemental analyzer (Flash 2000 or Flash IRMS EA Isolink CN, Thermo Scientific, Milan, Italy). Results are expressed in the usual δ unit notation relative to Vienna PeeDee Belemnite for $\delta^{13}C$ (‰) and atmospheric N_2 for $\delta^{15}N$ (‰), following the formula:

$$\delta^{13}C \text{ or } \delta^{15}N = \left[\left(R_{sample}/R_{standard}\right) - 1\right] \times 10^3$$

Table 1 Mercury concentrations and stable isotope values from adult Adélie penguins (*Pygoscelis adeliae*) sampled around Antarctica, from both this study (included in the analyses) and literature review (for comparison; not included in the analyses)

Sites, colonies	Season	*n*	Feather Hg (μg·g^{-1} dw)	Feather δ^{13}C (‰)	Feather δ^{15}N (‰)	References	Included
Continental Antarctica							
Queen Maud Land							
Hukuro Cove	2010/2011	27	0.51 ± 0.15 (0.32–0.92)	−23.9 ± 1.5 (−25.7, −22.9)	10.1 ± 1.4 (8.6–12.1)	This study	Yes
	1990/1991	10	0.09 ± 0.05	–	–	Yamamoto et al. (1996)	No
Rumpa Island	1981/1982	10	0.17 ± 0.05 (0.11–0.27)	–	–	Honda et al. (1986)	No
Mac. Robertson Land							
Welch Island	2019/2020	15	0.40 ± 0.11 (0.21–0.59)	−25.0 ± 0.4 (−25.8, −24.4)	9.7 ± 0.5 (8.8–10.8)	This study	Yes
Macey Island	2019/2020	15	0.63 ± 0.19 (0.31–0.98)	−25.0 ± 0.3 (−25.3, −24.2)	10.5 ± 0.8 (9.6–12.3)	This study	Yes
Princess Elizabeth Land							
Hop Island	2019/2020	5	0.36 ± 0.13 (0.22–0.50)	−24.7 ± 0.5 (−25.4, −24.2)	9.8 ± 0.9 (8.8–10.9)	This study	Yes
Magnetic Island	2019/2020	5	0.53 ± 0.22 (0.29–0.76)	−24.5 ± 0.4 (−24.9, −24.0)	10.0 ± 0.8 (8.9–10.8)	This study	Yes
Un-named Island IS 73413*	2019/2020	5	0.46 ± 0.15 (0.29–0.69)	−24.6 ± 0.4 (−25.1, −24.0)	10.1 ± 0.5 (9.5–10.6)	This study	Yes
Wilkes Land							
Shirley Island	2020/2021	40	0.43 ± 0.15 (0.19–0.79)	−24.9 ± 0.5 (−25.8, −23.9)	9.5 ± 0.6 (8.5–10.8)	This study	Yes
Adélie Land							
Dumont d'Urville	2006/2007	10	0.66 ± 0.20 (0.41–1.06)	−23.4 ± 0.4 (−24.2, −23.0)	10.7 ± 0.6 (9.7–11.3)	Carravieri et al. (2016)	Yes
	2011/2012	10	0.40 ± 0.09 (0.25–0.52)	−24.3 ± 0.7 (−25.6, −23.3)	10.8 ± 0.7 (9.8–11.9)	Carravieri et al. (2016)	Yes
	2017/2018	15	0.41 ± 0.11 (0.25–0.60)	−24.9 ± 0.4 (−25.7, −24.4)	8.9 ± 0.3 (8.4–9.7)	This study	Yes
Cape Bienvenue	2017/2018	14	0.42 ± 0.13 (0.27–0.77)	−24.5 ± 0.6 (−25.7, −23.6)	9.2 ± 0.4 (8.5–10.1)	This study	Yes
Cape Jules	2017/2018	15	0.44 ± 0.14 (0.23–0.68)	−25.3 ± 0.7 (−26.6, −24.3)	9.1 ± 0.5 (8.2–10.2)	This study	Yes
Victoria Land (Ross Sea)							
Terra Nova Bay							
Adélie Cove	2017/2018	15	0.92 ± 0.25 (0.49–1.35)	−24.4 ± 0.8 (−25.6, −22.5)	11.0 ± 1.0 (9.9–12.8)	This study	Yes
Inexpressible Island	2017/2018	15	0.83 ± 0.26 (0.50–1.33)	−24.5 ± 0.9 (−25.6, −22.8)	10.9 ± 1.0 (9.0–12.8)	This study	Yes
Edmonson Point	2017/2018	15	0.83 ± 0.18 (0.50–1.18)	−24.5 ± 0.7 (−25.8, −23.6)	10.6 ± 0.6 (9.8–11.6)	This study	Yes
Ross Island							
Cape Crozier	2019/2020	15	0.62 ± 0.12 (0.46–0.92)	−25.9 ± 0.3 (−26.5, −25.4)	9.8 ± 0.5 (9.1–10.9)	This study	Yes
Cape Royds	2019/2020	15	0.80 ± 0.19 (0.56–1.08)	−25.4 ± 0.8 (−25.9, −22.8)	10.3 ± 0.8 (9.2–11.9)	This study	Yes
Cape Bird	2004–2016	154	0.59 ± 0.17	–	–	Pilcher et al. (2020)	No
Cape Hallett, Cape Adare	2004–2016	20	0.50 ± 0.10	–	–	Pilcher et al. (2020)	No
Multiple sites							
Cape Bird, Cape Hallett, Cape Adare	2004–2016	174	0.59 ± 0.02	−25.3 ± 0.6	9.0 ± 0.7	Pilcher et al. (2020)	No

Table 1 (continued)

Sites, colonies	Season	*n*	Feather Hg (μg·g^{-1} dw)	Feather $\delta^{13}C$ (‰)	Feather $\delta^{15}N$ (‰)	References	Included
Maritime Antarctica							
King George/25 de Mayo Island							
Ardley Island	2021/2022	11	0.32 ± 0.06 (0.24–0.41)	−24.9 ± 0.3 (−25.3, −24.4)	9.3 ± 0.2 (9.0–9.7)	This study	Yes
Admiralty Bay	2005/2006	20	0.35 ± 0.16 (0.20–0.90)	−24.9 ± 0.7 (−25.7, −23.3)	8.8 ± 0.4 (8.1–9.7)	Brasso et al. (2013, 2014, 2015)	Yes
	2006/2007	20	0.25 ± 0.12 (0.16–0.70)	−25.0 ± 0.3 (−25.7, −24.6)	8.7 ± 0.3 (8.1–9.6)	Brasso et al. (2013, 2014, 2015)	Yes
	2007/2008	20	0.38 ± 0.11 (0.21–0.65)	−24.8 ± 0.5 (−25.3, −23.9)	8.9 ± 0.3 (8.5–9.7)	Brasso et al. (2013, 2014, 2015)	Yes
	2008/2009	16	0.35 ± 0.08 (0.18–0.47)	−24.6 ± 0.5 (−25.3, −23.8)	8.9 ± 0.5 (8.3–10.5)	Brasso et al. (2013, 2014, 2015)	Yes
	2009/2010	22	0.35 ± 0.14 (0.18–0.69)	−23.9 ± 0.8 (−25.4, −22.4)	9.1 ± 0.4 (8.0–10.1)	Brasso et al. (2013, 2014, 2015)	Yes
	2010/2011	22	0.35 ± 0.14 (0.18–0.69)	−24.1 ± 1.1 (−27.4, −22.4)	9.1 ± 0.4 (8.0–10.1)	Brasso et al. (2013, 2014, 2015), Polito et al. (2016)	Yes
	2005–2011	120	0.34 ± 0.13 (0.16–0.90)	−24.5 0.8 (−27.4, −22.4)	8.9 ± 0.4 (8.0–10.5)	Brasso et al. (2013, 2014, 2015)	Yes
Carlini (Stranger Point)	2019/2020	10	0.39 ± 0.09 (0.23–0.57)	−25.2 ± 0.5 (−26.3, −24.7)	9.0 ± 0.3 (8.5–9.7)	This study	Yes
Hennequin Point, Hannah Point	2013/2014	31	0.40 ± 0.13 (0.16–0.69)	–	–	Souza et al. (2020)	No
Antarctic Peninsula							
Esperanza/Hope Bay	2019/2020	10	0.37 ± 0.10 (0.17–0.51)	−23.2 ± 1.3 (−24.3, −20.1)	8.7 ± 0.3 (8.4–9.3)	This study	Yes
Brown Bluffs	2019/2020	13	0.37 ± 0.30 (0.11–1.22)	−21.8 ± 1.8 (−24.7, −19.9)	9.7 ± 1.1 (8.5–9.7)	This study	Yes
Seymour Island							
Marambio	2019/2020	10	0.41 ± 0.09 (0.29–0.54)	−22.7 ± 0.7 (−24.1, −21.9)	8.8 ± 0.3 (8.0–9.2)	This study	Yes
Joinville Island Group							
Madder Cliffs	2019/2020	15	0.23 ± 0.12 (0.09–0.48)	−22.5 ± 1.5 (−25.9, −20.9)	9.8 ± 0.9 (8.7–12.0)	This study	Yes
Paulet Island	2019/2020	15	0.18 ± 0.11 (0.06–0.40)	−22.9 ± 1.4 (−25.5, −20.7)	9.3 ± 0.3 (8.6–10.0)	This study	Yes
Signy Island							
Gourlay	2021/2022	30	0.33 ± 0.10 (0.21–0.62)	−25.6 ± 0.4 (−26.1, −24.4)	8.9 ± 0.3 (8.3–10.1)	This study	Yes

n indicates sample sizes. Feather $\delta^{13}C$ and $\delta^{15}N$ values are proxies of penguin feeding habitat and trophic position, respectively. Values are expressed as means ± SD with ranges in parentheses

– No available data (stable isotopes)

*Alpha-numeric identifier in Southwell et al. (2021)

Table 2 Mercury concentrations and stable isotope values from Adélie penguin chicks sampled around Antarctica, from both this study (included in the analyses) and a literature review (for comparison; not included in the analyses)

Sites, colonies	Season	*n*	Feather Hg (μg·g^{-1} dw)	Feather $\delta^{13}C$ (‰)	Feather $\delta^{15}N$ (‰)	References	Included
Continental Antarctica							
Queen Maud Land							
Hukuro Cove	1990/1991	12	0.04 ± 0.02	–	–	Yamamoto et al. (1996)	No
Princess Elizabeth Land							
Un-named Island IS 73413*	2019/2020	5	0.25 ± 0.06 (0.19–0.32)	−23.3 ± 1.0 (−24.8, −21.9)	12.0 ± 0.7 (11.3–12.9)	This study	Yes
Magnetic Island	2019/2020	4	0.23 ± 0.03 (0.18–0.25)	−23.4 ± 0.2 (−23.6, −23.2)	11.1 ± 0.2 (10.8–11.3)	This study	Yes
Hop Island	2019/2020	4	0.20 ± 0.08 (0.14–0.32)	−24.3 ± 1.6 (−25.6, −22.2)	10.1 ± 0.8 (9.4–11.1)	This study	Yes
Adélie Land							
Dumont d'Urville	2006/2007	10	0.19 ± 0.06 (0.07–0.27)	−23.5 ± 0.2 (−23.9, −23.2)	10.7 ± 0.4 (10.1–11.3)	Carravieri et al. (2016)	Yes
	2011/2012	10	0.34 ± 0.04 (0.30–0.40)	−22.9 ± 0.5 (−23.2, −21.6)	11.5 ± 0.3 (11.1–12.0)	Carravieri et al. (2016)	Yes
Victoria Land (Ross Sea)							
Edmonson Point	1989–1991	11	0.37 ± 0.15	–	–	Bargagli et al. (1998)	No
Maritime Antarctica							
King George/25 de Mayo Island							
Carlini (Stranger Point)	2019/2020	5	0.12 ± 0.02 (0.09–0.14)	−25.0 ± 0.2 (−25.2, −24.9)	7.6 ± 0.3 (7.2–8.1)	This study	Yes
Hennequin Point + Hannah Point	2013/2014	10	0.10 ± 0.01 (0.07–0.13)	–	–	Souza et al. (2020)	No
Antarctic Peninsula							
Esperanza/Hope Bay	2013/2014	18	0.32 ± 0.14 (0.14–0.63)	−23.7 ± 0.7 (−24.6, −22.0)	8.0 ± 0.5 (7.5–9.7)	McKenzie et al. (2021)	No
	2019/2020	5	0.16 ± 0.01 (0.14–0.18)	−23.5 ± 0.4 (−23.9, −23.0)	7.5 ± 0.3 (7.2–7.8)	This study	Yes
Seymour Island							
Penguin Point	2013/2014	20	0.57 ± 0.20 (0.23–1.05)	−20.0 ± 1.2 (−23.2, −18.9)	11.2 ± 1.1 (7.8–13.4)	McKenzie et al. (2021)	No
Marambio	2019/2020	5	0.23 ± 0.02 (0.19–0.25)	−20.6 ± 0.6 (−21.7, −20.2)	9.1 ± 0.4 (8.6–9.4)	This study	Yes

n indicates sample sizes. Feather $\delta^{13}C$ and $\delta^{15}N$ values are proxies of penguin feeding habitat and trophic position, respectively. Values are means ± SD with ranges in parentheses

– No available data (stable isotopes)

*Alpha-numeric identifier in Southwell et al. (2021)

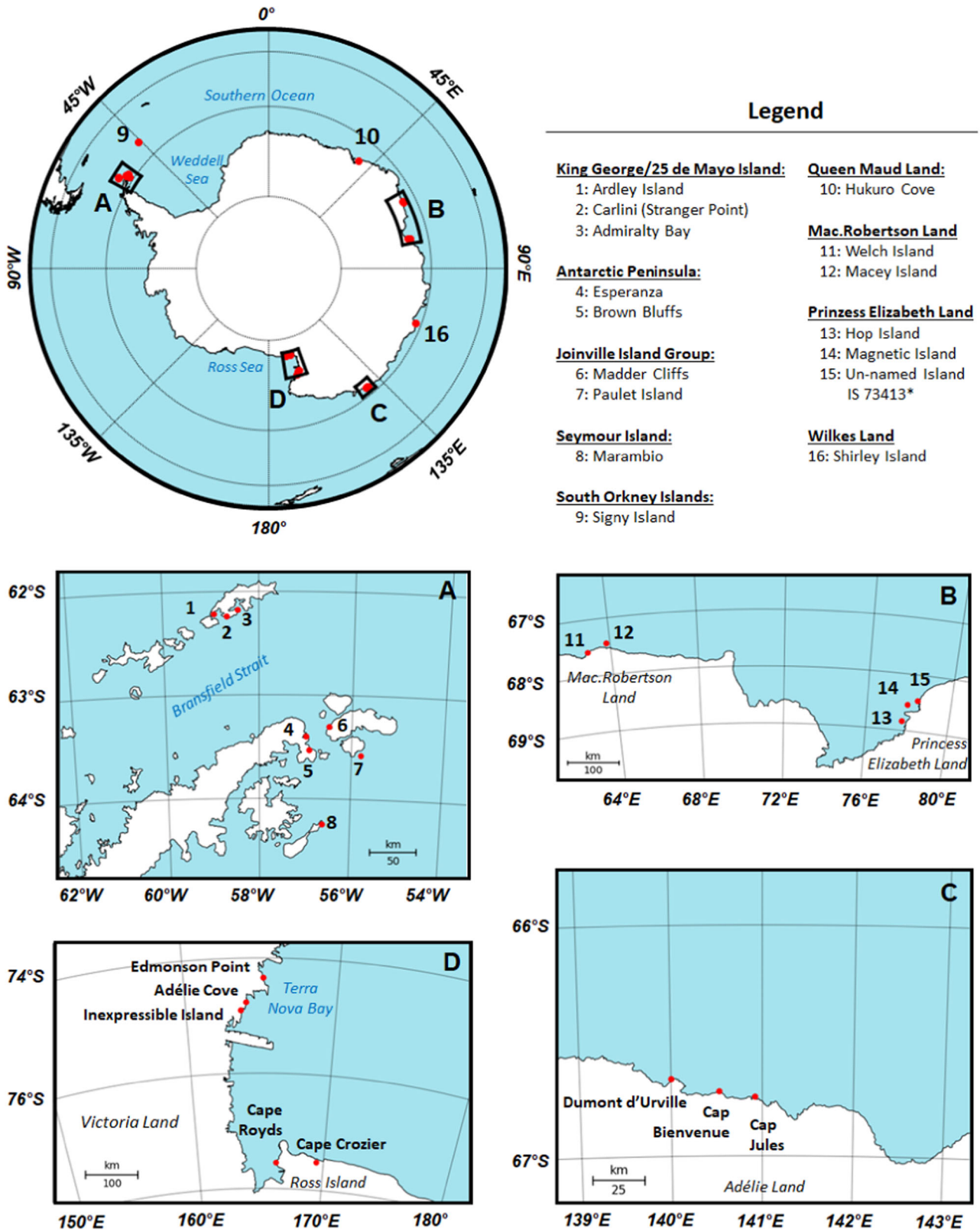


Fig. 1 Sampling colonies of the present study ($n = 24$), where feathers of Adélie penguins (*Pygoscelis adeliae;* both adults and chicks) were collected during the breeding season, between 2005 and 2021 (see Tables 1 and 2 for further details)

where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively. Replicate measurements of reference materials (USGS-61 and USGS-63, US Geological Survey) indicated measurement uncertainties <0.10‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. Further methodological details are provided in the Supplementary Material.

Combining feather Hg and stable isotopes

While Hg and stable isotopes are both incorporated during feather growth, their integration period is temporally uncoupled in adult seabirds (Bond 2010). Feathers indicate Hg accumulation in the whole body since the previous moult (i.e., integration period: one year in adult penguins), a temporal period that includes different stages of their life cycle (i.e., non-breeding, migration/return to colony, breeding, post-breeding dispersal and moult). In contrast, stable isotopes represent the diet during feather synthesis (i.e., integration period: a few weeks corresponding to the pre-moult foraging period). However, available evidence suggests that Adélie penguins consistently use similar feeding resources during the non-breeding period (Polito et al. 2016; Tierney et al. 2009). Thus, stable isotopes are still relevant to understand the ecological drivers of Hg contamination in adult Adélie penguins. In large fledging chicks, there is no such temporal mismatch between Hg concentrations and stable isotopes, as both are incorporated during the growth of body feathers and reflect local contamination and diet during the same period (chick-rearing period; ~two months in summer).

Statistical analyses

Data analyses and representation («ggplot2» package; Wickham 2016) were carried out with R (Version 4.2.2, R Core Team 2022).

During data exploration, five feather samples showed extremely high $\delta^{13}C$ values, which are theoretically associated with either a coastal/benthic or a northern environment instead of offshore/pelagic Antarctic $\delta^{13}C$ values, as expected (Carravieri et al. 2014b; Cherel and Hobson 2007). Feather Hg and stable isotope values for these five individuals are presented in Supplementary Material (Table S4). Following a conservative approach, these values were considered to be outliers and were therefore excluded from statistical analyses and figures.

Spatial variation in Hg contamination and trophic ecology

Unifactorial analyses were performed to investigate independently differences in feather Hg concentrations and $\delta^{13}C$ and $\delta^{15}N$ values between colonies. Residual normality and homoscedasticity were examined with Shapiro-Wilk and Breusch-Pagan tests («lmtest» package; Zeileis and Hothorn 2002), respectively. Since test assumptions were not met, a non-parametric (Kruskal-Wallis) test was used, followed by a multiple comparisons (Pairwise-Wilcoxon) test.

Drivers of Hg contamination and its spatial variation

Multifactorial analyses were performed to investigate simultaneously the influence of trophic ecology, colony location, sex and age class on Hg contamination. Prior to model definition, relationships between continuous variables (i.e., $\delta^{13}C$, $\delta^{15}N$) were tested using a correlation matrix to validate the simultaneous inclusion of non-collinear explanatory variables. Models were Generalized Linear Models (GLMs) with a Gaussian distribution and either identity or inverse link-functions, built using the «nlme» R package (Pinheiro et al. 2022).

We used three datasets: adults only ($n = 485$), adults of known sex ($n = 231$), and adults and pre-fledging chicks sampled at the same colony ($n = 113$), to test for different effects with the larger available sample size. Initial models for each dataset were the following: (1) Hg ~ $\delta^{13}C + \delta^{15}N$ + Colony, (2) Hg ~ $\delta^{13}C + \delta^{15}N$ + Colony * Sex and (3) Hg ~ $\delta^{13}C + \delta^{15}N$ + Colony * Age class.

Model selection was based on Akaike's Information Criterion adjusted for small sample sizes (AIC_c) for the three datasets. All potential combinations of variables for each dataset are presented in Table 3. Models were ranked using the «dredge» function («MuMIn» package; Bartoń 2022). Following Burnham and Anderson (2002), the model with the lowest AIC_c value and a difference of AIC_c (ΔAIC_c) > 2 when compared with the next best model was considered to be the best. Following Johnson and Omland (2004), model performance was assessed using Akaike weights (w_i). Model assumptions (residual normality, homogeneity, independence) were checked with diagnostic functions («plot» and «qqnorm»). The degree of model fit was reported by using the McFadden's R-Squared metric. Differences between colonies were then identified with Estimated Marginal Means (EMMs; «emmeans» package; Length 2023) following Bond and Diamond (2009a). Finally, partial residuals were extracted from each best model to obtain predictor effect plots («effects» package; Fox and Weisberg 2018, 2019). This allowed us to quantify and visualise Hg spatial variation by controlling variation due to both $\delta^{13}C$ and $\delta^{15}N$ values. Year was not included as an explanatory factor for two reasons: (i) year and colony were confounded for most colonies (92%) and (ii) inter-annual differences in Hg concentrations are expected to be negligible over the short term at remote locations (Brasso et al. 2014; Carravieri et al. 2016). To confirm this, we

Table 3 AICc model ranking from statistical analyses of feather Hg concentrations from Adélie penguins

Models	k	AIC_c	ΔAIC_c	w_i
(1) All adults ($n = 485$)				
$\delta^{13}C + \delta^{15}N$ + Colony	**27**	**−596.6**	**0.00**	**1.00**
$\delta^{15}N$ + Colony	26	−574.6	21.94	0.00
$\delta^{13}C$ + Colony	26	−538.8	57.94	0.00
Colony	25	−534.1	62.48	0.00
$\delta^{15}N$	3	−393.8	202.73	0.00
$\delta^{13}C$	3	−204.8	391.79	0.00
NULL	2	−181.0	415.54	0.00
(2) Sexed adults ($n = 231$)*				
$\delta^{13}C + \delta^{15}N$ + Colony	**11**	**−258.4**	**0.00**	**0.58**
$\delta^{13}C + \delta^{15}N$ + Colony + Sex	**12**	**−257.2**	**1.20**	**0.32**
$\delta^{15}N$ + Colony	10	−253.8	4.54	0.06
$\delta^{15}N$ + Colony + Sex	11	−253.2	5.13	0.04
$\delta^{13}C + \delta^{15}N$ + Colony * Sex	19	−246.6	11.80	0.00
$\delta^{13}N$ + Colony * Sex	18	−242.5	15.90	0.00
Colony + Sex	10	−236.5	21.89	0.00
Colony	9	−235.4	22.92	0.00
$\delta^{13}C$ + Colony + Sex	11	−234.4	23.95	0.00
$\delta^{13}C$ + Colony	10	−233.4	24.94	0.00
(3) Adults and pre-fledging chicks from the same colony ($n = 113$)*				
$\delta^{13}C + \delta^{15}N$ + Colony * Age class	**19**	**−232.7**	**0.00**	**0.97**
$\delta^{15}N$ + Colony * Age class	18	−226.0	6.69	0.03
$\delta^{13}C$ + Colony *Age class	18	−213.5	19.17	0.00
Colony * Age class	17	−213.4.	19.28	0.00
$\delta^{13}C + \delta^{15}N$ + Age class	5	−200.9	31.80	0.00
$\delta^{15}N$ + Age class	4	−200.8	31.86	0.00
$\delta^{15}N$ + Colony + Age class	11	−196.7	35.98	0.00
$\delta^{13}C + \delta^{15}N$ + Colony + Age class	12	−194.6	38.07	0.00
Colony + Age class	10	−174.5	58.20	0.00
$\delta^{13}C$ + Colony + Age class	11	−173.0	59.71	0.00

Models are Generalized Linear Models (GLMs) with Gamma distribution, and identity (all adults) or inverse (sexed adults and both age classes) link-functions. Models with $\Delta AIC_c < 2$ represent very plausible models (in bold). A model with $\Delta AIC_c = 0$ is interpreted as the best model among all the selected ones. Weights are cumulative (sum to 1)

k number of parameters, AIC_c Akaike's Information Criterion adjusted for small sample size, w_i AIC_c weights

*Only the first 10 models are showed in this table

quantified inter-annual variation in adult feather Hg concentrations of Adélie penguins at Admiralty Bay (King George/25 de Mayo Island), which were sampled across six consecutive years (between 2005 and 2011). Annual mean feather Hg concentrations ranged from 0.25 to 0.35 $\mu g \cdot g^{-1}$, a low 0.10 $\mu g \cdot g^{-1}$ scope that translated into a marginal statistical significance (one-way ANOVA, $F_{5,114} = 2.31$, $p = 0.048$).

Visual representation of Hg contamination in the presumed spatial distribution of Adélie penguins

In penguins, body feather Hg concentrations reflect exposure over a large temporal and spatial scale (see previous sections for further details; Brasso et al. 2014; Carravieri et al. 2014a). As a spatial assessment, this study aimed to match visually this year-round Hg accumulation with the presumed, year-round spatial distribution of Adélie penguins. Since the individuals sampled in this study were not tracked precisely with geolocators, their maximum distribution (i.e., including all individual tracks) during the non-breeding season was extracted from published studies (Fig. S1). Tracking data were available for six Antarctic colonies (Ballard et al. 2010; Clarke et al. 2003; Davis et al. 1996; Dunn et al. 2011; Erdmann et al. 2011; Hinke et al. 2015; Takahashi et al. 2018; Thiébot et al. 2019), resulting in a large geographical coverage that can be associated with feather Hg concentrations (Fig. S1). In addition, we used three regionally important habitat characteristics that shape penguins' spatial distribution:

(i) the Antarctic Polar Front (PF). The PF represents an ecologically meaningful limit for the distribution of Adélie penguins (northernmost limit), as they exploit marine resources within the Antarctic Zone, remaining solely south of the PF. Following Freeman and Lovenduski (2016), the PF was defined here as the average of its weekly positions during the 2002–2014 period, with a resolution of 0.25°.

(ii) the Marginal Ice Zone (MIZ). Within the Antarctic Zone, Adélie penguins are closely tied to sea ice, which is their main habitat year-round; they migrate to the MIZ (i.e., the transitional zone between consolidated pack ice and open water) to forage during the non-breeding season (Ballard et al. 2010; Dunn et al. 2011; Takahashi et al. 2018). Therefore, the position of the MIZ can be expected to reflect the birds' presumed distribution during their non-breeding period. Following previous work (Bliss et al. 2019; Meier et al., 2014), the MIZ was defined here as areas included within the maximum annual sea ice extent (i.e., in September) covered by at least 15% of ice, averaged on daily sea-ice concentrations over the 2003–2022 period (which encompasses our sampling years; AMSR-E/ASMR2, 3.125 km resolution, downloaded in March 2023 on https://www.seaice.uni-bremen.de; Spreen et al. 2008).

(iii) the 1000 m isobath. To distinguish between neritic (i.e., over the deep Antarctic shelf) and oceanic (i.e., open-ocean) environments that Adélie penguins may exploit, the 1000 m isobath appeared to be a key habitat feature (data downloaded in March 2020 from

https://www.ncei.noaa.gov/products/etopo-global-relief-model; Bed Rock ETOPO1; 1 arc-min resolution; Amante and Eakins 2009).

Maps representing these three environmental characteristics with the averaged Hg concentrations for both adults and chicks were computed using Python (Version 3.7.6).

Results

Spatial differences in feather Hg concentrations and isotopic values (unifactorial analyses)

In adult Adélie penguins, individual feather Hg concentrations ranged from 0.06 to 1.35 μg·g^{-1} dw (Table 1). Unifactorial analyses revealed that mean values were significantly different between colonies (Kruskal-Wallis, $\chi^2(23) = 255.7$, $p < 0.0001$, $n = 485$). Specifically, seven colonies differed from all others (Pairwise Wilcoxon, $p < 0.001$): five colonies from Terra Nova Bay and Ross Island (i.e., highest averaged concentrations; mean: 0.80, range: 0.46–1.35 μg·g^{-1}) and two colonies from Joinville Island Group (i.e., lowest averaged concentrations; mean: 0.21, range: 0.06–0.48 μg·g^{-1}) (Fig. 2a).

Individual feather δ^{13}C values ranged from −27.4 to −19.9‰ (Table 1) and mean values differed among colonies (Kruskal-Wallis, $\chi^2(23) = 226.53$, $p < 0.0001$, $n = 485$), with those from the Antarctic Peninsula, Seymour Island and Joinville Island Group (mean: −22.6, range: −25.9, −19.9 ‰) differing from the others (mean: −24.8, range: −27.4, −22.4 ‰; Fig. 2b). Individual feather δ^{15}N values ranged from 8.0 to 12.8‰ (Table 1) and mean values differed among colonies (Kruskal-Wallis, $\chi^2(23) = 249.9$, $p < 0.0001$, $n = 485$), with the lowest and highest δ^{15}N values recorded in Seymour Island (mean: 8.83, range: 8.0–9.2 ‰) and Terra Nova Bay (mean: 10.9, range: 9.0–12.8 ‰), respectively (Fig. 2c).

Drivers of feather Hg concentrations (multifactorial analyses)

Results from model selections are presented in Table 3. For all adults ($n = 485$), the best model included δ^{13}C and δ^{15}N values and the colony as significant predictors (Table 3), and explained 61% of the observed variation in feather Hg concentrations (Table 4). Feather Hg concentrations decreased and increased with δ^{13}C (β ± SE: −0.03 ± 0.006; CI: −0.05, −0.02) and δ^{15}N values (β ± SE: 0.09 ± 0.01, CI: 0.06–0.11), respectively. When accounting for δ^{13}C and δ^{15}N values, the colony effect plot showed that: (i) most colonies (71%) exhibited feather Hg concentrations close to the circumpolar average (i.e., 0.45 μg·g^{-1}; all colonies combined), and (ii) colonies from the Ross Sea had higher Hg concentrations than all other sites (Fig. 5). These results are reinforced by the EMMs (Table 5).

For sexed adults ($n = 231$), two models met the selection criteria for the best model (i.e., $\Delta AIC_c < 2$), weighing together 90% of all models (Table 3). The first best model ($\Delta AIC_c = 0$) included δ^{13}C and δ^{15}N values and colony, but did not include sex as a significant predictor (Table 3). The second best model ($\Delta AIC_c = 1.2$) included δ^{13}C and δ^{15}N values, colony and sex (Table 3). Because it was 1.8 times more powerful than the second one, the first best model was selected as the final best model. This model explained 67% of the measured variation in feather Hg concentrations (Table 4). Feather Hg concentrations strongly decreased and increased with δ^{13}C (β ± SE: 0.14 ± 0.06; CI: 0.03–0.26; Gamma inverse) and δ^{15}N values (β ± SE: −0.29 ± 0.06; CI: –0.40, –0.17; Gamma inverse), respectively. Spatial differences are provided with the EMMs in Table S6. Despite no statistical difference between sexes (see Table S5 for more details), differences were observed for Hg concentrations, δ^{13}C and δ^{15}N values (Fig. S2). Regarding Hg concentrations, females had lower concentrations than males at six colonies (Queen Maud Land: Hukuro Cove, and the Ross Sea: Adélie Cove, Edmonson Point, Inexpressible Island, Cape Crozier and Cape Royds). In contrast, females had higher concentrations than males at two other colonies (Adélie Land and King George/25 de Mayo Island), respectively. Regarding δ^{13}C values (Fig. S2), there was no clear difference between sexes in five colonies. Compared to males, females had lower values in one colony (Edmonson Point) and higher values in two colonies from the Ross Sea (Adélie Cove and Cape Royds). For δ^{15}N values, females and males had similar values in two colonies (Cape Crozier and Admiralty Bay), but females had lower mean values in five colonies (Hukuro Cove, Adélie Cove, Edmonson Point, Inexpressible Island and Cape Royds) and higher mean values in one colony (Dumont d'Urville) compared to males (Fig. S2).

For the dataset including fledging chicks and adults from the same colonies ($n = 113$), the best model included δ^{13}C and δ^{15}N values, colony, age class and their interaction as significant predictors (Table 3), explaining 79% of the observed variation in feather Hg concentrations (GLM, Table 4). Feather Hg concentrations were strongly and positively driven by δ^{15}N values (β ± SE: −0.58 ± 0.13; CI: −0.84, −0.33; Gamma inverse). In contrast, δ^{13}C values were positively but only marginally related to feather Hg concentrations (small effect size, Table 4). In chicks, individual Hg concentrations ranged from 0.07 to 0.63 μg·g^{-1} (Table 2), which is 1.8–3.5 times lower than those measured in adults at any colony (Table 1), with the exception of Dumont d'Urville in 2011/2012 (Fig. 3a, Table 6). Chick feather δ^{13}C values ranged from −25.6 to −20.2 ‰, with outlying values in Marambio (Seymour Island) compared to other colonies (Fig. 3b). Chick δ^{15}N values varied

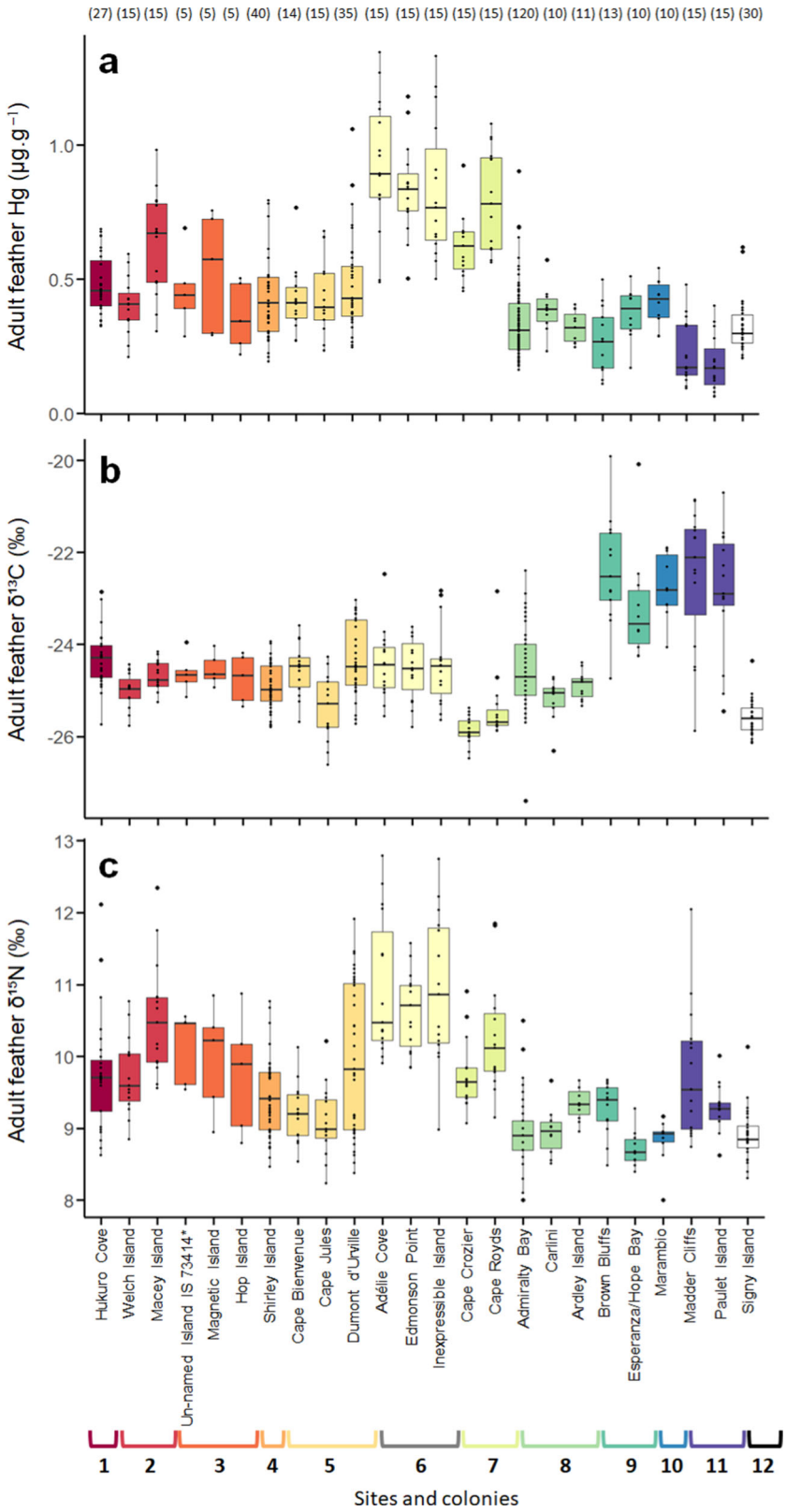


Fig. 2 Spatial comparison of feather (**a**) Hg concentrations, (**b**) $\delta^{13}C$ and (**c**) $\delta^{15}N$ values in adult Adélie penguins (*Pygoscelis adeliae*) collected in 24 Antarctic colonies, represented by a clockwise colour gradient (from East-Antarctica in dark red to South Orkney Islands in grey). Feather $\delta^{13}C$ and $\delta^{15}N$ values are proxies for penguin feeding habitat and trophic position, respectively. Numbers in brackets (top) represent sample sizes for each colony. Numbers (bottom) refer to the sites where the sampling colonies are located: (1) Queen Maud Land, (2) Mac.Robertson Land, (3) Princess Elizabeth Land, (4) Wilkes Land, (5) Adélie Land, Victoria Land: (6) Terra Nova Bay, (7) Ross Island; (8) King George/25 de Mayo Island, (9) Antarctic Peninsula, (10) Seymour Island, (11) Joinville Island Group and (12) South Orkney Islands. Individual values (smaller dots) are presented with boxplots, representing median values (midlines), errors bars (whiskers) and outliers (black dots outside whiskers)

Table 4 Estimated parameters of variables included in the best model for each dataset: (1) adults ($n = 485$), (2) sexed adults ($n = 231$) and (3) both age classes (i.e., adults and pre-fledging chicks from the same colony; $n = 113$)

	Datasets		
	(1) Adults	(2) Sexed adults	(3) Both age classes
Model specification			
Distribution	Gamma	Gamma	Gamma
Link-function	Identity	Inverse	Inverse
Variables			
Intercept	−1.15 [−1.58, −0.72] ± 0.21	8.42 [4.87, 11.97] ± 1.81	16.28 [9.66–23.02] ± 3.41
$\delta^{15}N$	0.09 [0.06–0.11] ± 0.01	−0.29 [−0.40, −0.17] ± 0.06	−0.58 [−0.84, −0.33] ± 0.13
$\delta^{13}C$	−0.03 [−0.05, −0.02] ± 0.006	0.14 [0.03, 0.26] ± 0.06	0.33 [0.11–0.56] ± 0.11
Colony	+	+	+
Age class			2.49 [1.45–3.60] ± 0.55
McFadden's R^2	0.61	0.67	0.79

Values are estimates [CI] ± SE. Models are Generalized Linear Models (GLMs) with Gamma distribution and identity or inverse link-function. Results are on the response scale for (1) and the inverse scale for (2) and (3). McFadden's R^2 indicates the degree of model fit (i.e., from low and high model fit indicated from 0 to 1, respectively). Feather $\delta^{13}C$ and $\delta^{15}N$ values are proxies of the penguin feeding habitat and trophic position, respectively. When specified, the «+» symbol indicates when the colony (categorical factor) is included in the best model for each dataset. Results for site comparisons (estimated marginal means) are provided in Table 5 (all adults), Table S6 (sexed adults) and Table 6 (both age classes)

CI confidence interval (95%), *SE* standard error

from 7.2 to 12.9 ‰ (Table 2), with an average 3 ‰ difference between East and West Antarctic colonies (Fig. 3c).

Discussion

The Southern Ocean hosts some of the most extreme and least accessible environments on Earth. As such, it has commonly been considered to be a pristine ocean, free from substantial anthropogenic contamination. Nevertheless, latitudinal gradients in persistent contaminants, such as Hg, were previously described across the Southern Ocean (Carravieri et al. 2014b; Renedo et al. 2020), posing potential threats for its marine ecosystems. Specifically, lower Hg concentrations were observed in Antarctic compared to subantarctic and subtropical seabirds. Whether this Hg gradient is locally restricted or widespread in the Southern Ocean is still unknown. Here, we studied the Adélie penguin as a circumpolar bioindicator species to reveal ocean-wide patterns in Hg contamination across Antarctic marine ecosystems. To the best of our knowledge, this study is the first to use a single bioindicator and document Hg contamination over such a large spatial scale, encompassing a total of 24 colonies around Antarctica (both continental and maritime). This circumpolar assessment revealed notable variation in feather Hg concentrations of Adélie penguins, with a hotspot in the Ross Sea (Victoria Land). Drivers of this spatial variation involved both the trophic ecology and colony location.

Circumpolar Hg contamination in adult Adélie penguins

Overall, feather Hg concentrations found in this study were similar to those reported by previous studies on Adélie penguins (Table 1). In the Antarctic Zone, Adélie penguins exhibited lower Hg concentrations (0.45 $\mu g \cdot g^{-1}$) compared to chinstrap (*Pygoscelis antarcticus*; 0.71 $\mu g \cdot g^{-1}$), gentoo (*P. papua*; 1.34 $\mu g \cdot g^{-1}$) and emperor (*Aptenodytes forsteri*) penguins (1.37 $\mu g \cdot g^{-1}$) on average (Table S1). This was also the case when comparing with other penguin species elsewhere in the Southern Ocean (Table S1), such as the southern rockhopper (*Eudyptes chrysocome*; 2.03 $\mu g \cdot g^{-1}$), king (*A. patagonicus*; 2.19 $\mu g \cdot g^{-1}$) and macaroni (*E. chrysolophus*; 2.73 $\mu g \cdot g^{-1}$) penguins; and with other flying seabirds from the Southern Ocean, including storm petrels (5.47 $\mu g \cdot g^{-1}$; Pacyna et al. 2019) or albatrosses (22.14 $\mu g \cdot g^{-1}$; Bustamante et al. 2016). Our results thus confirm that the overall Hg concentrations are consistent around the Antarctic continent. We propose that the Adélie penguin, which is also a relevant indicator species for CCAMLR, is a good indicator for Hg contamination in Antarctic marine food webs.

In adult Adélie penguins, body feather Hg concentrations reflect a large temporal and spatial scale of exposure (see Material and Methods for further details; Brasso et al. 2014; Carravieri et al. 2014a). During the breeding season, Adélie penguins are central place foragers (Ainley 2002): they forage in a restricted area immediately adjacent to the colony, within a few hundred kilometres (Ainley et al. 2004; Davis and Miller 1992; Michelot et al. 2021; Riaz et al.

Table 5 Estimated marginal mean (EMM) feather Hg concentrations for adult Adélie penguins ($n = 485$) from 24 Antarctic colonies

Colony	EMM	SE	95% CI		Group
			Lower	Upper	
Hukuro Cove	0.46	0.029	0.41	0.52	A
Welch Island	0.37	0.033	0.30	0.43	A
Macey Island	0.52	0.052	0.42	0.62	AB
Un-named Island*	0.39	0.065	0.26	0.52	A
Magnetic Island	0.46	0.071	0.32	0.60	AB
Hop Island	0.32	0.049	0.23	0.42	A
Shirley Island	0.41	0.021	0.37	0.46	A
Dumont d'Urville	0.45	0.026	0.40	0.50	A
Cape Bienvenue	0.46	0.037	0.38	0.53	A
Cape Jules	0.44	0.036	0.37	0.51	A
Adélie Cove	0.78	0.077	0.63	0.93	B
Edmonson Point	0.73	0.070	0.60	0.87	B
Inexpressible Island	0.69	0.068	0.56	0.82	AB
Cape Crozier	0.55	0.052	0.45	0.66	AB
Cape Royds	0.70	0.066	0.57	0.83	AB
Admiralty Bay	0.39	0.012	0.37	0.41	A
Carlini	0.41	0.039	0.33	0.49	A
Ardley Island	0.32	0.031	0.26	0.38	A
Brown Bluffs	0.35	0.029	0.30	0.41	A
Esperanza/Hope Bay	0.48	0.039	0.40	0.55	AB
Marambio	0.53	0.044	0.44	0.61	A
Madder Cliffs	0.29	0.023	0.25	0.34	AC
Paulet Island	0.27	0.021	0.23	0.31	AC
Signy Island	0.34	0.021	0.30	0.38	A

Estimates were derived from the best-ranked generalized linear model (GLM with Gamma distribution and identity link-function) defined as follows: Hg ~ $\delta^{13}C + \delta^{15}N$ + Colony (see Table 3 for further details)

Differences were considered significant when confidence intervals of each colony did not overlap with those of others. Colonies sharing the same Group letters were not significantly different from each other. Colonies with two letters were not significantly different from either group

CI confidence interval, *SE* standard error

Un-named Island refers to Un-named Island IS 73413

2021). During the non-breeding period, they travel several hundred to thousand of kilometres away from their breeding grounds (e.g., 500–2500 km on average; Ballard et al. 2010; Clarke et al. 2003; Davis et al. 1996; Dunn et al. 2011; Erdmann et al. 2011; Hinke et al. 2015; Takahashi et al. 2018; Thiébot et al. 2019) and are assumed to forage in the MIZ (Dunn et al. 2011; Wilson et al. 2001). In the absence of precise tracking positions, feather Hg concentrations could be qualitatively associated with a large spatial region, encompassing most of the Antarctic Zone from the Antarctic Peninsula to the Ross Sea, thanks to published tracking studies (Fig. S1). At the circumpolar scale, our results revealed spatial variation in feather Hg concentrations, which were the lowest in West Antarctica (i.e., maritime Antarctica: King George/25 de Mayo, Seymour and Joinville Islands, and the Antarctic Peninsula), intermediate in East Antarctica, and the highest in the Ross Sea (Figs. 2a, 4).

As expected, penguin feeding ecology was a major driver of among colony variation, as indicated by the results of model selection (Table 3). Trophic position was a significant predictor of feather Hg concentrations, as showed by the higher $\delta^{15}N$ values in the Ross Sea (Fig. 2c). This suggests that penguins foraged at higher trophic position at these locations. Adélie penguins are strongly associated with sea-ice environments, both during the breeding (Emmerson and Southwell 2008; Guen et al. 2018; Kokubun et al. 2021) and non-breeding seasons (Emmerson and Southwell 2011). They feed preferentially in waters covered by 10 to 80% sea ice, but also in the open sea (Ballard et al. 2019; Cottin et al. 2012; Guen et al. 2018; Michelot et al. 2020). In these habitats, their diet comprises different euphausiid crustaceans, mainly the Antarctic krill (*Euphausia superba*) and smaller amounts of the ice krill (*Euphausia crystallorophias*) (Tierney et al. 2009). Their diet also includes fish species such as the Antarctic silverfish (*Pleuragramma antarcticum)* in different proportions according to colony location and season (Ainley et al. 1998; Ainley 2002). Thus, their diet may vary significantly according to the geographical localization of the colony, but also the year (Tierney et al. 2009). For example, Adélie penguins feed almost exclusively on Antarctic krill along the Antarctic Peninsula and in the Scotia Sea (Coria et al. 1995; Juáres et al. 2018; Lynnes et al. 2004). In East Antarctica, they have a mixed diet depending on feeding habitat: fish and ice krill in neritic waters (continental shelf) versus Antarctic krill in pelagic waters (shelf break; Green and Johnstone 1988; Kent et al. 1998; Puddicombe and Johnstone 1988; Watanuki et al. 1997; Wienecke et al. 2000). In contrast, Adélie penguins from the Ross Sea consume higher proportions of Antarctic silverfish (Ainley et al. 1998; Olmastroni et al. 2020), which are abundant in continental shelf waters (Gon and Heemstra 1990). Yet, the silverfish is also a zooplankton predator itself and thus exhibits a higher trophic position than krill (Everson 2000; Hodum and Hobson 2000; Polito et al. 2011). Hence, a higher consumption of silverfish could explain the higher Hg concentrations observed in Adélie penguins from Victoria Land (Ross Sea). This is supported by previous studies showing that Hg concentrations in several species of Antarctic fish, including the Antarctic silverfish, were 4 to 20 times higher than in different krill species (Polito et al. 2016; Seco et al. 2021, 2019; Sontag et al. 2019).

Nevertheless, the diet of adult Adélie penguins (as detailed above) has been studied mainly determined during the chick-rearing season, when individuals are directly

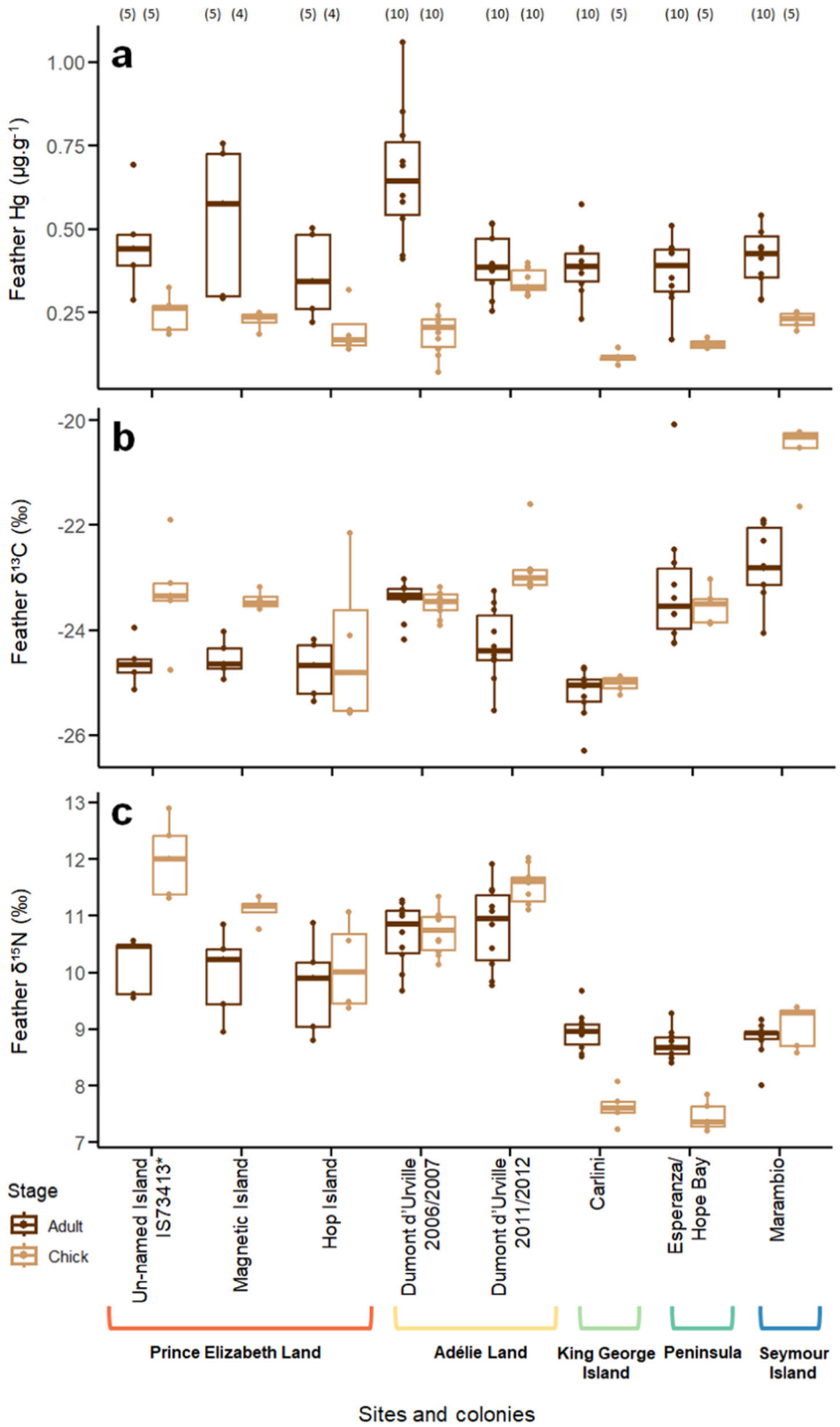


Fig. 3 Adult and chick comparison in feather (**a**) Hg concentrations, and (**b**) $\delta^{13}C$ and (**c**) $\delta^{15}N$ values in Adélie penguins (*Pygoscelis adeliae*) from eight Antarctic colonies. Adult and chicks are represented in dark and light brown, respectively. Feather $\delta^{13}C$ and $\delta^{15}N$ values are proxies for penguin feeding habitat and trophic position, respectively. Individual values (smaller dots) are presented with boxplots, representing median values (midlines), errors bars (whiskers) and outliers (black dots outside whiskers). Numbers in brackets indicate sample sizes for each age class and colony

accessible on land, but scarcely during the non-breeding season (also the period of Hg exposure). Given the lack of dietary information available for the non-breeding period, we assumed here that Adélie penguins use similar marine resources during both periods (Polito et al. 2016; Tierney et al. 2009). However, seasonal variation in feeding ecology

Table 6 Estimated marginal mean (EMM) feather Hg concentrations for adults and pre-fledging chicks of Adélie penguins from the same Antarctic colonies ($n = 113$)

Age class	Adults				Chicks				
			95% CI				95% CI		Age class
Colonies	EMM	SE	Lower	Upper	EMM	SE	Lower	Upper	Difference
Un-named Island*	0.38	0.037	0.32	0.47	0.19	0.019	0.16	0.24	yes
Magnetic Island	0.44	0.044	0.36	0.54	0.20	0.022	0.16	0.25	yes
Hop Island	0.33	0.033	0.27	0.41	0.19	0.021	0.15	0.24	yes
Dumont d'Urville 1	0.52	0.044	0.45	0.63	0.17	0.013	0.15	0.20	yes
Dumont d'Urville 2	0.30	0.024	0.26	0.36	0.27	0.023	0.24	0.33	no
Carlini	0.39	0.041	0.32	0.49	0.13	0.016	0.10	0.17	yes
Esperanza/Hope Bay	0.52	0.070	0.41	0.71	0.20	0.031	0.15	0.29	yes
Marambio	0.65	0.11	0.49	0.96	0.34	0.073	0.24	0.59	yes

Estimates were derived from the best-ranked generalized linear model (GLM with Gamma distribution and inverse link-function) defined as follows: Hg ~ $\delta^{13}C + \delta^{15}N$ + Colony * Age class (see Table 3 for further details)

Differences were considered significant when confidence intervals of adults and chicks from the same colony do not overlap. Dumont d'Urville 1 and 2 refers to samples from 2006/2007 and 2011/2012, respectively

CI confidence interval, *SE* standard error

Un-named Island refers to Un-named Island IS 73413

of Adélie penguins cannot be excluded and could thus influence feather Hg concentrations.

Five penguins from Hukuro Cove and Brown Bluffs were excluded from analyses (Table S4) because they had unexpected high positive $\delta^{13}C$ values for Antarctic environments (Carravieri et al. 2014b; Cherel and Hobson 2007) and high $\delta^{15}N$ values for this species. Since it is unlikely that these individuals were associated with northern ecosystems, such values would rather indicate that the birds had foraged in more coastal/benthic habitats (Cherel et al. 2011), possibly resulting in high feather Hg concentrations. One way to better understand why these five individuals had different isotopic signatures would be to perform Compound-Specific Stable Isotope Analysis of Amino-Acids (CSIA-AA). Indeed, CSIA-AA enables to distinguish between source (i.e., baseline) and trophic $\delta^{15}N$ values. In other words, it could clarify whether the $\delta^{15}N$ baseline is different (environmental driver) or whether the diet is the major driver (trophic driver). Similarly, CSIA-AA analyses are likely to help clarify whether the differences in $\delta^{15}N$ values observed in the Ross Sea came from different $\delta^{15}N$ baseline, trophic position or both, and how this could translate into a higher Hg contamination.

Regional colony location was also associated with feather Hg concentrations (Table 3), suggesting that environmental factors are also involved in explaining spatial differences in feather Hg concentrations. When accounting for feeding ecology (i.e., $\delta^{13}C$ and $\delta^{15}N$ values), colonies from Victoria Land (Ross Sea) still appeared to have higher Hg concentrations than all other colonies (Fig. 5). Hence, penguins in the Ross Sea have a disproportionately higher Hg concentrations than would be expected on the basis of their diet alone. Two non-exclusive factors could explain this result: (1) volcanism and (2) katabatic winds. The West-Antarctic Rift System runs from the base of the Antarctic Peninsula through the Weddell Sea to the Ross Sea (Rocchi et al. 2003), resulting in numerous volcanoes present in Western versus Eastern Antarctica. Despite low activity levels, two main active volcanoes border the coast of the Ross Sea: Mount Erebus and Mount Melbourne, which are located on Ross Island and in Terra Nova Bay, respectively (Behrendt 1990; Edwards and Smellie 2016; Ferraccioli et al. 2000; Global Volcanism Program 2022). Since volcanoes represent a primary source of Hg to the atmosphere (Grasby et al. 2019), they are likely to constitute a local source of Hg for the ocean and associated marine food webs as well. On the other hand, katabatic winds may also influence Hg deposition in the Ross Sea. Katabatic winds are strong winds that blow from the large and elevated Antarctic ice sheets toward the coast and represent a major environmental feature in Antarctica (Parish 1988; Parish and Cassano 2003) that can transport dust and debris. The Ross Sea is strongly exposed to katabatic winds (Turner 2015) and in Terra Nova Bay, regions exposed to strong katabatic winds showed enhanced Hg deposition on the coast (Bargagli 2008, 2016). Consequently, by carrying air masses originating from the Antarctic continent towards coastal regions, katabatic winds could represent a local natural source of Hg in marine ecosystems of the Ross Sea. Still, the biochemical cycle of Hg is complex and includes several chemical processes and biological transformations with both abiotic and biotic interactions (Chételat et al. 2022; McKinney et al. 2022): methylation/demethylation, redox reactions, MeHg

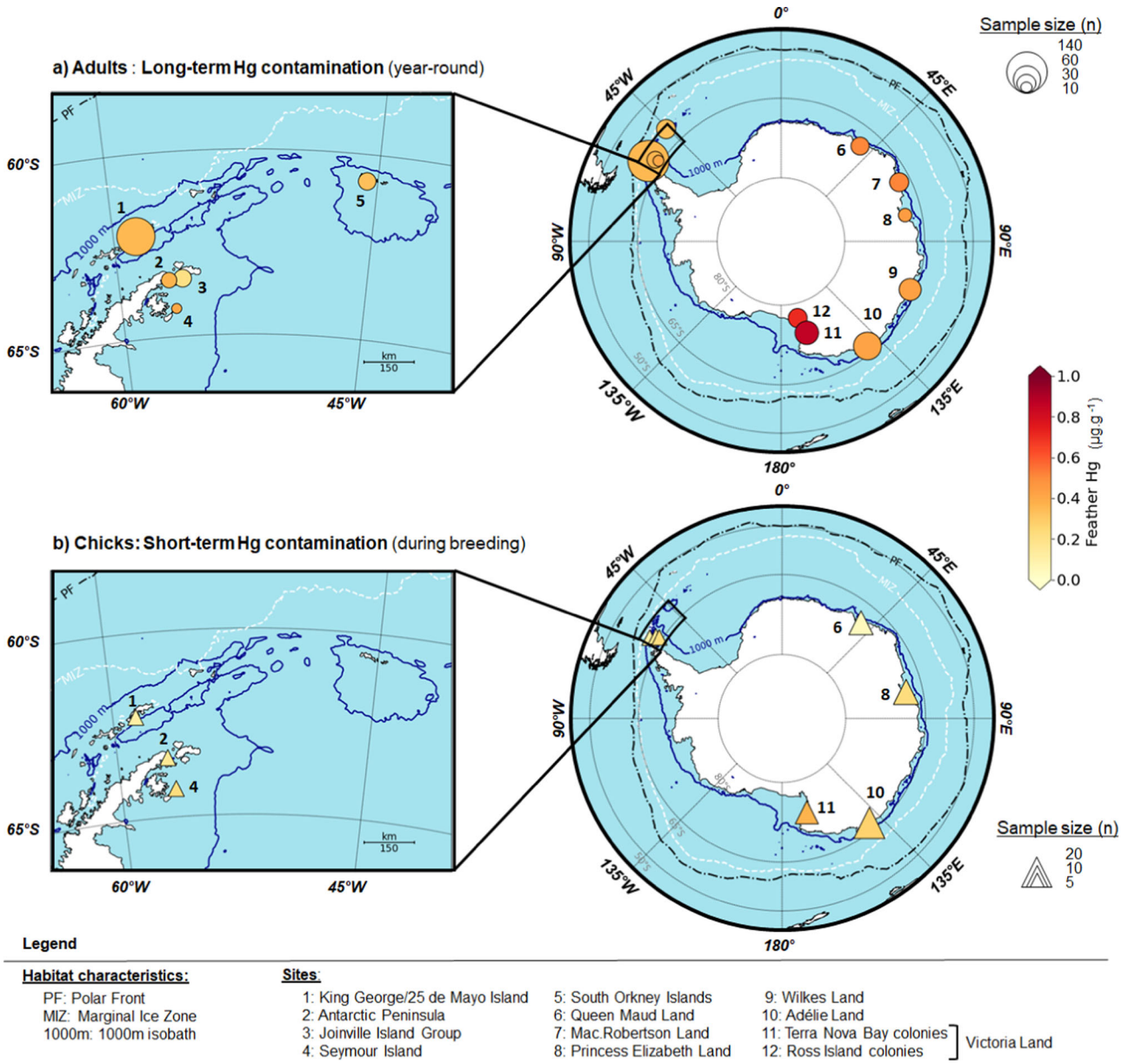


Fig. 4 Spatial variation in feather Hg concentrations of (**a**) adult and (**b**) chick Adélie penguins (*Pygoscelis adeliae*) across 24 Antarctic colonies. The colour gradient represents increasing Hg concentrations. Sample sizes (n) are indicated by the size of circles and triangles. The averaged position of the Polar Front (PF, dashed black line) reflects the northernmost limit of Adélie penguin distribution, whereas the Marginal Ice Zone (MIZ, dashed white line) reflects the presumed northern limit of their non-breeding distribution (i.e., maximum sea ice cover extent in September; see Material and Methods for further details). The darkblue line indicates the 1000 m isobath

production, bioavailability and transfer through marine food webs, especially in polar environments with the influence of sea ice (Cossa et al. 2011). The presence of sea ice, which harbour microbial sources of MeHg in the Southern Ocean (Gionfriddo et al. 2016; Yue et al. 2023), may thus influence Hg contamination in Antarctic marine food webs. Further research is needed to disentangle the biochemical processes at the circumpolar scale, but also those that could result in higher year-round Hg exposure in Adélie penguins from the Ross Sea.

Because sample collection is challenging in Antarctic environments, feathers in this study were collected across a relatively large time period (between 2005 and 2021). Even if interannual variations were very low in one colony where adult Hg concentrations were available for six consecutive years (i.e., Admiralty Bay, King George/25 de Mayo Island), observed spatial variation could result from the combination of both spatial and temporal variations. It is worth noting that Hg concentrations in two colonies were different from those reported previously. In

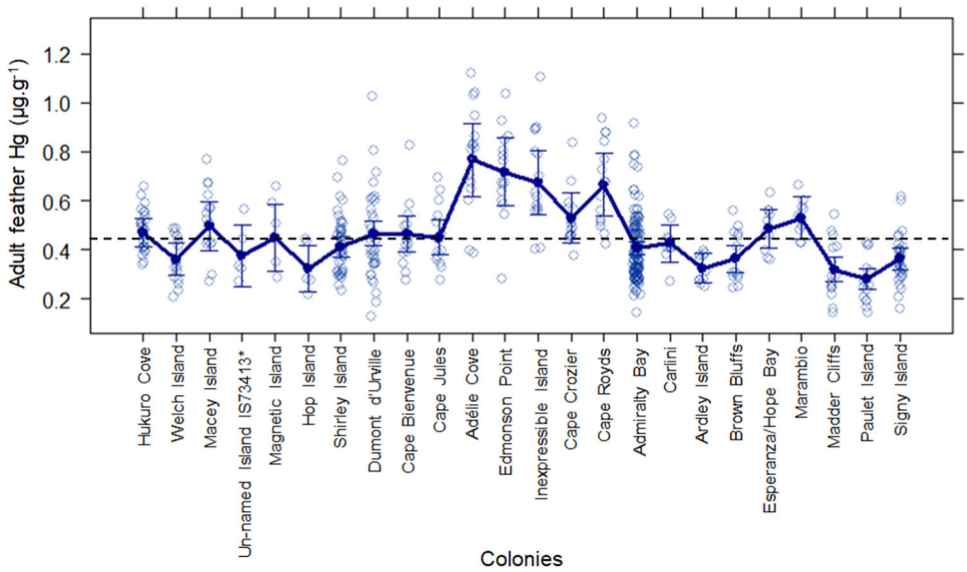


Fig. 5 Spatial comparison in feather Hg concentrations in adult Adélie penguins (*Pygoscelis adeliae*) from 24 Antarctic colonies ($n = 485$) when controlled by their feeding ecology (feather $\delta^{13}C$ and $\delta^{15}N$ values). Relationships result from the extraction of partial residuals of the best Generalized Linear Model (GLM; see Table 3 and Material and Methods for further details). Individual data are represented in light blue (open circle). Points (filled circle) are means ± SD. The dark blue line links all mean Hg concentrations. The dashed black line indicates the circumpolar average Hg concentrations (i.e., 0.45 $\mu g \cdot g^{-1}$, all pooled data from all colonies)

Queen Maud Land, feather Hg concentrations in the 2010s were five times higher than in the 1980s and the 1990s (Honda et al. 1986; Yamamoto et al. 1996; Table 1). In Adélie Land, feather Hg concentrations dropped by 30% between 2006 and the following years (2011 and 2017; Carravieri et al. 2016; this study; Table 1). However, this temporal difference (0.2 $\mu g \cdot g^{-1}$) is still low compared to the spatial difference measured among adult Hg concentrations (1.2 $\mu g \cdot g^{-1}$). Further studies should thus investigate mid- and long-term Hg trends in Antarctic food webs, for instance by increasing the temporal resolution in Hg monitoring.

Potential sex-specific Hg concentrations

In seabirds, sexual segregation in diet has been suggested as a strategy to reduce intra-specific competition (Bearhop et al. 2006; Forero et al. 2002; González-Solís et al. 2000; Phillips et al. 2011). In Adélie penguins, diet segregation between sexes was observed during the breeding season: females foraged for more krill than fish in more offshore, pelagic waters, in contrast to males which fed equally on both prey types in more inshore, benthic waters (Clarke et al. 1998; Colominas-Ciuró et al. 2018). In theory, such sexual segregation in diet should therefore be reflected in stable isotopes and then in Hg concentrations. In our study, no clear sexual segregation could be deduced from the observed feather $\delta^{13}C$ and $\delta^{15}N$ values (Fig. S2b, c). However, differences between sexes in feather Hg concentrations could be noticed when differences in either $\delta^{13}C$ or $\delta^{15}N$ values or both were present. Feather Hg concentrations were similar between sexes at Adélie Cove (Terra Nova Bay) and Admiralty Bay (King George/25 de Mayo Island), as previously reported (Polito et al. 2016). In contrast, females had lower Hg concentrations in Queen Maud Land (Hukuro Cove) and the Ross Sea, including Edmonson Point and Inexpressible Island (Terra Nova Bay), and Cape Crozier and Cape Royds (Ross Island). These results were similar to previous studies on Adélie penguins from the Ross Sea (Pilcher et al. 2020), but also in other penguin species (i.e., gentoo and macaroni penguins) from South Georgia/Islas Georgias del Sur (Becker et al. 2002, Pedro et al. 2015). Although moult is the major process responsible for Hg elimination in males, egg production represents an additional route (Bond and Diamond 2009b; Braune and Gaskin 1987), that could lead to lower Hg concentrations in females.

Despite these potential differences between sexes, sex did not significantly drive spatial variation in adult Hg contamination, according to the first best model (Table 3). Indeed, this model included $\delta^{13}C$ and $\delta^{15}N$ values and colony location. However, a second model met the selection criteria for the best model (although its weight was lower), which included sex as a predictor in addition to $\delta^{13}C$ and $\delta^{15}N$ values and colony location (Table 3). Unfortunately, information on penguin sex was not available for all individuals. Models were thus run on a dataset that only included half of the total sample size. Complete sexing analyses, either determined through morphological or molecular approaches, should help to further investigate differences in Hg contamination between sexes and its drivers (either extrinsic or intrinsic), on a circumpolar scale. Whether sexual segregation in diet and Hg contamination are related during the breeding and the non-breeding season warrants further research.

Comparing Hg contamination on different spatio-temporal scales with adult and chick feathers

Chick and adult feathers reflect different temporal and spatial scales: local accumulation during a few months

during the breeding season *versus* year-round accumulation including their entire distribution (breeding and non-breeding), respectively. In general, chicks exhibit lower feather Hg concentrations relative to adults, as a result of their shorter exposure period (Carravieri et al. 2014c). Our results were coherent with this explanation, with feather concentrations in chicks being 1.8 to 3.6 times lower than in adults on average (Fig. 3).

Feather Hg concentrations were driven by the age class (adult or fledging chick), the trophic ecology (indicated by $\delta^{13}C$ and $\delta^{15}N$ values) and colony location (Table 3). In most colonies, chicks exhibited equivalent or higher feather $\delta^{15}N$ values than adults, suggesting that they were fed with similar prey or with prey of higher trophic position across colonies (for example with higher proportions of fish compared to krill; Cherel 2008). There was one exception to this pattern: in Dumont d'Urville (Adélie Land; in 2011), average feather Hg concentrations were similar between adults and chicks (Table 6), translating into a similar contamination status between age classes. In 2011, sea ice was quite high around the colony (60%) during the chick-rearing period and quite homogenous at a larger scale (Michelot et al. 2021). Whether these sea-ice conditions could be associated with higher Hg exposure for both adults and chicks would deserve further research.

Importantly, Terra Nova Bay (and hence the Ross Sea) exhibited the highest feather Hg concentrations in both chicks and adults (Fig. 4), which reinforces the higher exposure year-round in this region compared to other areas. Since foraging trips are shorter during the chick-rearing period, this also suggests that Hg contamination may be local.

Conclusions and perspectives

This study provides a unique assessment of Hg contamination in Antarctic marine food webs, by using the Adélie penguin as a circum-Antarctic bioindicator. Feathers represent a valuable, non-destructive and non-invasive monitoring tool, in complete agreement with Antarctic Treaty protocols, to examine the variation in Hg contamination across temporal and spatial scales. Feather Hg concentrations detected in Adélie penguins (<2 $\mu g \cdot g^{-1}$) were below toxicity thresholds recognized for seabird feathers (1.6–10 $\mu g \cdot g^{-1}$; Ackerman et al. 2016; Chastel et al. 2022). Currently, this suggests low risks of toxicity for this species, although toxic effects may arise at low Hg concentrations, particularly in combination with other stressors (e.g., other contaminants, environmental changes, diseases; Grunst et al., 2023; Provencher et al., 2016). At the circumpolar scale, Hg contamination was relatively homogeneous across regions. This is consistent with the circumpolar structure of the Southern Ocean, which is characterized by a unique stratification of annular fronts and water masses encircling the Antarctic Continent (Carter et al. 2008). This reinforces the suitability of Adélie penguins as bioindicator species for Antarctic marine ecosystems.

Trophic ecology (indicated by feeding habitat and trophic position) was crucial to explain spatial variation of Hg contamination. The Hg hotspot observed in the Ross Sea was associated with higher trophic position of Adélie penguins, probably due to a higher proportion of fish in their diet. This reinforces the need to account systematically for the diet when monitoring Hg contamination in seabirds, especially at such large spatial scales.

Thanks to published tracking studies, feather Hg concentrations could be qualitatively associated with a large spatial region, encompassing most of the Antarctic Zone, from the Antarctic Peninsula to the Ross Sea. However, detailed spatial information of penguin movements during their annual cycle is essential to quantify precisely the spatial variation in their Hg exposure. The Arctic Monitoring and Assessment Program (AMAP) provides a circumpolar and long-term assessment of Hg contamination in marine ecosystems for the entire Arctic Ocean. In this program, Hg contamination was associated to the spatial and seasonal distributions of seabirds thanks to biologging. In a similar way, such work in the Southern Ocean would be substantially improved by the deployment of individual tracking devices, allowing connection to be made between spatial and seasonal distributions of penguins, at the individual level, with contaminants at the ocean scale.

Through Adélie penguins, this work documented circumpolar Hg contamination in the epipelagic compartment of the Southern Ocean. A complementary approach could investigate the mesopelagic compartment, where high MeHg concentrations were recorded (Cossa et al. 2011), by studying the circumpolar breeding emperor penguin (*Aptenodytes forsteri*), which mainly feeds on prey of higher trophic position in both epipelagic and mesopelagic waters (Cherel 2008; Wienecke and Robertson 1997). Such large-scale monitoring is fundamental for international monitoring programs, such as the Global Mercury Assessment from the United Nations, to assess the effectiveness of the Minamata Convention on Mercury. Renewing a large-scale assessment, such as that presented here, on a regular basis (every few years or decade for example) is highly recommended to monitor the contamination status of Antarctic marine food webs over time and to further investigate global trends, especially in the context of climate change.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1007/s10646-023-02709-9.

Acknowledgements The authors are thankful to all people involved in fieldwork, sample preparation and shipment in all Antarctic research stations. In addition, we thank the Mawson seabird field team and Casey station expeditioners for collecting samples, and Marcus Salton

for organising sample transport. Special thanks are due to Yan Ropert-Coudert for his help in the construction of collaborations in the Antarctic research community and to Frédéric Angelier. The authors are grateful to (i) Maud Brault-Favrou and Carine Churlaud from the Plateforme Analyses Élémentaires of the LIENSs for their support during Hg analyses, as well as (ii) Sandy Pascaud for her support in sample preparation in the laboratory, and to (iii) Julie Charrier for the penguin drawings in the figures. The IUF (Institut Universitaire de France) is acknowledged for its support to Paco Bustamante as a Senior Member. This study is also a contribution to the Excellence Chair in Marine Ecology ECOMM funded by the Région Nouvelle Aquitaine (France). This work/review benefitted from the French GDR Aquatic Ecotoxicology framework which aims at fostering stimulating scientific discussions and collaborations for more integrative approaches.

Author contributions Conceptualization: FC, PB, JF, YC. Methodology: FC, PB, AC, YC. Software: FC, AC, CB. Investigation: FC, PV. Formal analysis: FC, AC. Visualization: FC, CB. Writing - original draft preparation: FC, PB, AC, YC. Writing - review and editing: FC, PB, AC, CB, RB, IC, MD, LE, GG, TH, MJ, AK, ALM-G, CM, SO, MP, TR, MS, AS, CS, AS, AT, JBT, PT, CW, JF and YC. Project administration: FC. Funding acquisition: PB, Resources: AC, RB, IC, MD, LE, TH, MJ, ALM-G, CM, SO, MP, TR, MS, AS, CS, AS, AT, JBT, PT, CW. Supervision: PB, JF, YC.

Funding This work relied on several national and international existing monitoring programs in Antarctica, implying several funding sources associated with the logistical support to all research stations. (i) The circumpolar monitoring program led by Jean-Baptiste Thiebot was funded by National Geographic Society grant WW-24R-17. (ii) Samples from Mac.Robertson Land (Mawson station), Princess Elizabeth Land (Davis station) and Wilkes Land (Casey station) were collected through Australian Antarctic Division support to AAS 4518. (iii) Sampling in Adélie Land was supported financially and logistically by IPEV (Programmes N°109 ORNITHOECO, C. Barbraud, and N°1091 AMMER, A. Kato and T. Raclot) and WWF-UK. (iv) Sampling in Terra Nova Bay was funded by the Ministry and Research (MUR) and National Research Council Italy (CNR) through project #PNRA2016_004 Penguin ERA. (v) Sampling in Ross Island was funded by the National Science Foundation (OPP Award, #1543498). (vi) Fieldwork in Ardley Island was supported by Instituto Antártico Uruguato (IAU), Ecos Sud Program (project PU20B01/U20B03), Commission for the Conservation of Antarctic Marine Living Ressources (CCAMLR) General Capacity Building Fund and Scientific Scholarship Scheme, Agencia Nacional de Investigación e Innovación's (ANII) Clemente Estable Fund (project FCE 1 2021 1 166587), National System of Researchers and National Postgraduate Scholarship Programme, and Basic Science Development Programme (PEDECIBA). (vii) The Instituto Antártico Argentino – Dirección Nacional del Antártico (PINST-05) provided financial and logistical support to carry out the Argentine Antarctic campaign. Finally, funding was provided by CPER (Contrat de Plan Etat-Région) and the FEDER (Fonds Européen de Développement Régional) for the AMA and the IRMS of LIENSs laboratory.

Compliance with ethical standards

Conflict of interest The authors declare no competing interests.

Ethics approval In this work, feather sampling relied on several existing monitoring programs and were carried out at all sites under appropriate permits. More specifically, (i) animal handling and sample collection for Australian stations (Mawson, Davis and Casey stations) were approved by the Australian Antarctic Division animal ethics committee and ATEP environmental approvals. (ii) Fieldwork in Adélie Land was approved by the Conseil des Programmes Scientifiques et Technologies Polaires of the Institut Polaire Français Paul Emile Victor (IPEV), and procedures were approved by the Animal Ethics Committee of IPEV. (iii) Fieldwork in Terra Nova Bay was approved under permission released from the Programma Nazionale di Ricerche in Antartide (PNRA). All sampling followed SCAR's Code of Conduct for the Use of Animals for Scientific Purposes in Antarctica (https://www.scar.org/policy/scar-codes-of-conduct). (iv) The Instituto Antártico Argentino – Dirección Nacional del Antártico (PINST-05) provided financial and logistical support to carry out the Argentine Antarctic campaign. The field work was carried out under the permit granted by the Dirreción Nacional del Antártico (Environmental Management Office). (v) Animal handling and sample collection at Signy Island was approved by the British Antarctic Survey Animal Welfare and Ethical Review Board, and permission was granted by the British Foreign and Commonwealth Office on behalf of HM Secretary of State, under Sections 12 and 13 of the Antarctic Act, 1994, 2013.

References

Ackerman JT, Eagles-Smith CA, Herzog MP, Hartman CA, Peterson SH, Evers DC, Jackson AK, Elliott JE, Vander Pol SS, Bryan CE (2016) Avian mercury exposure and toxicological risk across western North America: a synthesis. Sci Total Environ 568:749–769. https://doi.org/10.1016/j.scitotenv.2016.03.071

Agnew DJ (1997) Review—the CCAMLR ecosystem monitoring programme. Antarct Sci 9:235–242. https://doi.org/10.1017/S095410209700031X

Ainley DG (2002) The Adélie Penguin: Bellwether of Climate Change. Columbia University Press. https://doi.org/10.7312/ainl12306

Ainley DG, Ribic CA, Ballard G, Heath S, Gaffney I, Karl BJ, Barton KJ, Wilson PR, Webb S (2004) Geographic structure of Adélie penguin populations: overlap in colony-specific foraging areas. Ecol Monogr 74:159–178. https://doi.org/10.1890/02-4073

Ainley DG, Wilson PR, Barton KJ, Ballard G, Nur N, Karl B (1998) Diet and foraging effort of Adélie penguins in relation to pack-ice conditions in the southern Ross Sea. Polar Biol 20:311–319. https://doi.org/10.1007/s003000050308

Albert C, Helgason HH, Brault-Favrou M, Robertson GJ, Descamps S, Amélineau F, Danielsen J, Dietz R, Elliott K, Erikstad KE, Eulaers I, Ezhov A, Fitzsimmons MG, Gavrilo M, Golubova E, Grémillet D, Hatch S, Huffeldt NP, Jakubas D, Kitaysky A, Kolbeinsson Y, Krasnov Y, Lorentsen S-H, Lorentzen E, Mallory ML, Merkel B, Merkel FR, Montevecchi W, Mosbech A, Olsen B, Orben RA, Patterson A, Provencher J, Plumejeaud C, Pratte I, Reiertsen TK, Renner H, Rojek N, Romano M, Strøm H, Systad GH, Takahashi A, Thiebot J-B, Thórarinsson TL, Will AP, Wojczulanis-Jakubas K, Bustamante P, Fort J (2021) Seasonal variation of mercury contamination in Arctic seabirds: a pan-Arctic assessment. Sci Total Environ 750:142201. https://doi.org/10.1016/j.scitotenv.2020.142201a

Albert C, Renedo M, Bustamante P, Fort J (2019) Using blood and feathers to investigate large-scale Hg contamination in Arctic seabirds: a review. Environ. Res. 177:108588. https://doi.org/10.1016/j.envres.2019.108588

Amante, C., Eakins, B.W., (2009). ETOPO1 1 Arc-Minute Global Reflief Model: Procedures, data sources and analysis. NOAA Technical Memorandum NESDIS NGDC-24. National Geophysical Data Center, NOAA, Boulder, Colorado, USA.

Álvarez-Varas R, Morales-Moraga D, González-Acuña D, Klarian SA, Vianna JA (2018) Mercury exposure in Humboldt (*Spheniscus*

humboldti) and chinstrap (*Pygoscelis antarcticus*) penguins throughout the Chilean coast and Antarctica. Arch Environ Contam Toxicol 75:75–86. https://doi.org/10.1007/s00244-018-0529-7

Ballard G, Schmidt AE, Toniolo V, Veloz S, Jongsomjit D, Arrigo KR, Ainley DG (2019) Fine-scale oceanographic features characterizing successful Adélie penguin foraging in the SW Ross Sea. Mar Ecol Prog Ser 608:263–277. https://doi.org/10.3354/meps12801

Ballard G, Toniolo V, Ainley DG, Parkinson CL, Arrigo KR, Trathan PN (2010) Responding to climate change: Adélie penguins confront astronomical and ocean boundaries. Ecology 91:2056–2069. https://doi.org/10.1890/09-0688.1

Barbraud C, Rolland V, Jenouvrier S, Nevoux M, Delord K, Weimerskirch H (2012) Effects of climate change and fisheries bycatch on Southern Ocean seabirds: a review. Mar. Ecol. Prog. Ser. 454:285–307

Bargagli R (2016) Atmospheric chemistry of mercury in Antarctica and the role of cryptogams to assess deposition patterns in coastal ice-free areas. Chemosphere 163:202–208. https://doi.org/10.1016/j.chemosphere.2016.08.007

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, Monaci F, Sanchez-Hernandez JC, Cateni D (1998) Biomagnification of mercury in an Antarctic marine coastal food web. Mar Ecol Prog Ser 169:65–76. https://doi.org/10.3354/meps169065

Bartoń K (2022). _MuMIn: Multi-Model Inference_. R package version 1.47.1, https://CRAN.R-project.org/package=MuMIn

Bearhop S, Phillips RA, McGill R, Cherel Y, Dawson DA, Croxall JP (2006) Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. Mar Ecol Prog Ser 311:157–164. https://doi.org/10.3354/meps311157

Becker PH, González-Solís J, Behrends B, Croxall J (2002) Feather mercury levels in seabirds at South Georgia: influence of trophic position, sex and age. Mar Ecol Prog Ser 243:261–269. https://doi.org/10.3354/meps243261

Becker PH, Goutner V, Ryan PG, González-Solís J (2016) Feather mercury concentrations in Southern Ocean seabirds: variation by species, site and time. Environ Pollut 216:253–263. https://doi.org/10.1016/j.envpol.2016.05.061

Behrendt JC (1990) Ross Sea. Antarct. Res. Ser. 48:89–90

Bliss AC, Steele M, Peng G, Meier WN, Dickinson S (2019) Regional variability of Arctic sea ice seasonal change climate indicators from a passive microwave climate data record. Environ Res Lett 14:045003. https://doi.org/10.1088/1748-9326/aafb84

Bond AL (2010) Relationships between stable isotopes and metal contaminants in feathers are spurious and biologically uninformative. Environ Pollut 158:1182–1184. https://doi.org/10.1016/j.envpol.2010.01.004

Bond AL, Diamond AW (2009a) Mercury concentrations in seabird tissues from Machias Seal Island, New Brunswick, Canada. Sci Total Environ 407:4340–4347. https://doi.org/10.1016/j.scitotenv.2009.04.018

Bond AL, Diamond AW (2009b) Total and methyl mercury concentrations in seabird feathers and eggs. Arch Environ Contam Toxicol 56:286–291. https://doi.org/10.1007/s00244-008-9185-7

Bond AL, Hobson KA, Branfireun BA (2015) Rapidly increasing methyl mercury in endangered ivory gull (*Pagophila eburnea*) feathers over a 130 year record. Proc Biol Sci 282:1–8

Brasso RL, Chiaradia A, Polito MJ, Raya Rey A, Emslie SD (2015) A comprehensive assessment of mercury exposure in penguin populations throughout the Southern Hemisphere: using trophic calculations to identify sources of population-level variation. Mar Pollut Bull 97:408–418. https://doi.org/10.1016/j.marpolbul.2015.05.059

Brasso RL, Drummond BE, Borrett SR, Chiaradia A, Polito MJ, Rey AR (2013) Unique pattern of molt leads to low intraindividual variation in feather mercury concentrations in penguins. Environ Toxicol Chem 32:2331–2334. https://doi.org/10.1002/etc.2303

Brasso RL, Polito MJ, Emslie SD (2014) Multi-tissue analyses reveal limited inter-annual and seasonal variation in mercury exposure in an Antarctic penguin community. Ecotoxicology 23:1494–1504. https://doi.org/10.1007/s10646-014-1291-x

Braune B, Chételat J, Amyot M, Brown T, Clayden M, Evans M, Fisk A, Gaden A, Girard C, Hare A, Kirk J, Lehnherr I, Letcher R, Loseto L, Macdonald R, Mann E, McMeans B, Muir D, O'Driscoll N, Poulain A, Reimer K, Stern G (2015) Mercury in the marine environment of the Canadian Arctic: review of recent findings. Sci Total Environ Special Issue: Mercury Canada's North 509–510:67–90. https://doi.org/10.1016/j.scitotenv.2014.05.133

Braune BM, Gaskin DE (1987) Mercury levels in Bonaparte's gulls (*Larus Philadelphia*) during autumn molt in the Quoddy region, New Brunswick, Canada. Arch Environ Contam Toxicol 16:539–549. https://doi.org/10.1007/BF01055810

Burger J, Gochfeld M (2004) Marine birds as sentinels of environmental pollution. EcoHealth 1:263–274. https://doi.org/10.1007/s10393-004-0096-4

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information - theoretic approach, second ed. Springer, US

Bustamante P, Carravieri A, Goutte A, Barbraud C, Delord K, Chastel O, Weimerskirch H, Cherel Y (2016) High feather mercury concentrations in the wandering albatross are related to sex, breeding status and trophic ecology with no demographic consequences. Environ Res 144:1–10. https://doi.org/10.1016/j.envres.2015.10.024

Carravieri A, Bustamante P, Churlaud C, Cherel Y (2013) Penguins as bioindicators of mercury contamination in the Southern Ocean: birds from the Kerguelen Islands as a case study. Sci Total Environ 454–455:141–148. https://doi.org/10.1016/j.scitotenv.2013.02.060

Carravieri A, Bustamante P, Churlaud C, Fromant A, Cherel Y (2014a) Moulting patterns drive within-individual variations of stable isotopes and mercury in seabird body feathers: Implications for monitoring of the marine environment. Mar Biol 161:963–968. https://doi.org/10.1007/s00227-014-2394-x

Carravieri A, Bustamante P, Tartu S, Meillère A, Labadie P, Budzinski H, Peluhet L, Barbraud C, Weimerskirch H, Chastel O, Cherel Y (2014b) Wandering Albatrosses document latitudinal variations in the transfer of persistent organic pollutants and mercury to Southern Ocean predators. Environ Sci Technol 48:14746–14755. https://doi.org/10.1021/es504601m

Carravieri A, Cherel Y, Blévin P, Brault-Favrou M, Chastel O, Bustamante P (2014c) Mercury exposure in a large subantarctic avian community. Environ Pollut 190:51–57. https://doi.org/10.1016/j.envpol.2014.03.017

Carravieri A, Cherel Y, Brault-Favrou M, Churlaud C, Peluhet L, Labadie P, Budzinski H, Chastel O, Bustamante P (2017) From Antarctica to the subtropics: contrasted geographical concentrations of selenium, mercury, and persistent organic pollutants in skua chicks (*Catharacta* spp.). Environ Pollut 228:464–473. https://doi.org/10.1016/j.envpol.2017.05.053

Carravieri A, Cherel Y, Jaeger A, Churlaud C, Bustamante P (2016) Penguins as bioindicators of mercury contamination in the southern Indian Ocean: geographical and temporal trends. Environ. Pollut. Barking Essex 1987 213:195–205. https://doi.org/10.1016/j.envpol.2016.02.010

Carter L, McCave IN, Williams MJM (2008) Chapter 4 Circulation and water masses of the Southern Ocean: a review, in: Florindo, F., Siegert, M. (Eds), Developments in Earth and Environmental Sciences, Antarctic Climate Evolution. Elsevier, pp. 85–114. https://doi.org/10.1016/S1571-9197(08)00004-9

Chastel O, Fort J, Ackerman JT, Albert C, Angelier F, Basu N, Blévin P, Brault-Favrou M, Bustnes JO, Bustamante P, Danielsen J, Descamps S, Dietz R, Erikstad KE, Eulaers I, Ezhov A, Fleishman AB, Gabrielsen GW, Gavrilo M, Gilchrist G, Gilg O, Gíslason S, Golubova E, Goutte A, Grémillet D, Hallgrimsson GT, Hansen ES, Hanssen SA, Hatch S, Huffeldt NP, Jakubas D, Jónsson JE, Kitaysky AS, Kolbeinsson Y, Krasnov Y, Letcher RJ, Linnebjerg JF, Mallory M, Merkel FR, Moe B, Montevecchi WJ, Mosbech A, Olsen B, Orben RA, Provencher JF, Ragnarsdottir SB, Reiertsen TK, Rojek N, Romano M, Søndergaard J, Strøm H, Takahashi A, Tartu S, Thórarinsson TL, Thiebot J-B, Will AP, Wilson S, Wojczulanis-Jakubas K, Yannic G (2022) Mercury contamination and potential health risks to Arctic seabirds and shorebirds. Sci. Total Environ. 156944. https://doi.org/10.1016/j.scitotenv.2022.156944

Cherel Y (2008) Isotopic niches of emperor and Adélie penguins in Adélie Land, Antarctica. Mar Biol 154:813–821. https://doi.org/10.1007/s00227-008-0974-3

Cherel Y, Barbraud C, Lahournat M, Jaeger A, Jaquemet S, Wanless RM, Phillips RA, Thompson DR, Bustamante P (2018) Accumulate or eliminate? Seasonal mercury dynamics in albatrosses, the most contaminated family of birds. Environ Pollut 241:124–135. https://doi.org/10.1016/j.envpol.2018.05.048

Cherel Y, Charrassin JB, Challet E (1994) Energy and protein requirements for molt in the king penguin Aptenodytes patagonicus. Am J Physiol 266:R1182–1188. https://doi.org/10.1152/ajpregu.1994.266.4.R1182

Cherel Y, Charrassin J-B, Handrich Y (1993) Comparison of body reserve buildup in prefasting chicks and adults of King Penguins (*Aptenodytes patagonicus*). Physiol Zool 66:750–770. https://doi.org/10.1086/physzool.66.5.30163822

Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Mar Ecol Prog Ser 329:281–287. https://doi.org/10.3354/meps329281

Cherel Y, Hobson KA, Guinet C, Vanpe C (2007) Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. J Anim Ecol 76:826–836. https://doi.org/10.1111/j.1365-2656.2007.01238.x

Cherel Y, Koubbi P, Giraldo C, Penot F, Tavernier E, Moteki M, Ozouf-Costaz C, Causse R, Chartier A, Hosie G (2011) Isotopic niches of fishes in coastal, neritic and oceanic waters off Adélie land, Antarctica. Polar Sci 5:286–297. https://doi.org/10.1016/j.polar.2010.12.004

Chételat J, McKinney MA, Amyot M, Dastoor A, Douglas TA, Heimbürger-Boavida L-E, Kirk J, Kahilainen KK, Outridge PM, Pelletier N, Skov H, St. Pierre K, Vuorenmaa J, Wang F (2022) Climate change and mercury in the Arctic: Abiotic interactions. Sci Total Environ 824:153715. https://doi.org/10.1016/j.scitotenv.2022.153715

Clarke J, Kerry K, Fowler C, Lawless R, Eberhard S, Murphy R (2003) Post-fledging and winter migration of Adélie penguins *Pygoscelis adeliae* in the Mawson region of East Antarctica. Mar Ecol Prog Ser 248:267–278. https://doi.org/10.3354/meps248267

Clarke J, Manly B, Kerry K, Gardner H, Franchi E, Corsolini S, Focardi S (1998) Sex differences in Adélie penguin foraging strategies. Polar Biol 20:248–258. https://doi.org/10.1007/s003000050301

Clucas GV, Dunn MJ, Dyke G, Emslie SD, Levy H, Naveen R, Polito MJ, Pybus OG, Rogers AD, Hart T (2014) A reversal of fortunes: climate change 'winners' and 'losers' in Antarctic Peninsula penguins. Sci Rep 4:5024. https://doi.org/10.1038/srep05024

Colominas-Ciuró R, Santos M, Coria N, Barbosa A (2018) Sex-specific foraging strategies of Adélie penguins (*Pygoscelis adeliae*): females forage further and on more krill than males in the Antarctic Peninsula. Polar Biol 41:2635–2641. https://doi.org/10.1007/s00300-018-2395-1

Coria NR, Spairani H, Vivequin S, Fontana R (1995) Diet of Adélie penguins *Pygoscelis adeliae* during the post-hatching period at Esperanza Bay, Antarctica, 1987/88. Polar Biol 15:415–418. https://doi.org/10.1007/BF00239717

Cossa D (2013) Methylmercury manufacture. Nat Geosci 6:810–811. https://doi.org/10.1038/ngeo1967

Cossa D, Heimbürger L-E, Lannuzel D, Rintoul SR, Butler ECV, Bowie AR, Averty B, Watson RJ, Remenyi T (2011) Mercury in the Southern Ocean. Geochim. Cosmochim. Acta 75:4037–4052. https://doi.org/10.1016/j.gca.2011.05.001

Cottin M, Raymond B, Kato A, Amélineau F, Le Maho Y, Raclot T, Galton-Fenzi B, Meijers A, Ropert-Coudert Y (2012) Foraging strategies of male Adélie penguins during their first incubation trip in relation to environmental conditions. Mar Biol 159:1843–1852. https://doi.org/10.1007/s00227-012-1974-x

Crewther WG, Fraser RD, Lennox FG, Lindley H (1965) The chemistry of keratins. Adv Protein Chem 20:191–346. https://doi.org/10.1016/s0065-3233(08)60390-3

Croxall JP (1982) Energy costs of incubation and moult in petrels and penguins. J Anim Ecol 51:177–194. https://doi.org/10.2307/4318

Davis LS, Boersma PD, Court GS (1996) Satellite telemetry of the winter migration of Adélie penguins (*Pygoscelis adeliae*). Polar Biol 16:221–225. https://doi.org/10.1007/BF02329210

Davis LS, Miller GD (1992) Satellite tracking of Adélie penguins. Polar Biol 12:503–506. https://doi.org/10.1007/BF00238189

Desforges J-P, Outridge P, Hobson KA, Heide-Jørgensen MP, Dietz R (2022) Anthropogenic and climatic drivers of long-term changes of mercury and feeding ecology in Arctic Beluga (*Delphinapterus leucas*) populations. Environ Sci Technol 56:271–281. https://doi.org/10.1021/acs.est.1c05389

Dietz R, Letcher RJ, Desforges J-P, Eulaers I, Sonne C, Wilson S, Andersen-Ranberg E, Basu N, Barst BD, Bustnes JO, Bytingsvik J, Ciesielski TM, Drevnick PE, Gabrielsen GW, Haarr A, Hylland K, Jenssen BM, Levin M, McKinney MA, Nørregaard RD, Pedersen KE, Provencher J, Styrishave B, Tartu S, Aars J, Ackerman JT, Rosing-Asvid A, Barrett R, Bignert A, Born EW, Branigan M, Braune B, Bryan CE, Dam M, Eagles-Smith CA, Evans M, Evans TJ, Fisk AT, Gamberg M, Gustavson K, Hartman CA, Helander B, Herzog MP, Hoekstra PF, Houde M, Hoydal K, Jackson AK, Kucklick J, Lie E, Loseto L, Mallory ML, Miljeteig C, Mosbech A, Muir DCG, Nielsen ST, Peacock E, Pedro S, Peterson SH, Polder A, Rigét FF, Roach P, Saunes H, Sinding M-HS, Skaare JU, Søndergaard J, Stenson G, Stern G, Treu G, Schuur SS, Víkingsson G (2019) Current state of knowledge on biological effects from contaminants on arctic wildlife and fish. Sci Total Environ 696:133792. https://doi.org/10.1016/j.scitotenv.2019.133792

Dietz R, Wilson S, Loseto LL, Dommergue A, Xie Z, Sonne C, Chételat J (2022) Special issue on the AMAP 2021 assessment of mercury in the Arctic. Sci Total Environ 157020. https://doi.org/10.1016/j.scitotenv.2022.157020

Dunn MJ, Silk JRD, Trathan PN (2011) Post-breeding dispersal of Adélie penguins (*Pygoscelis adeliae*) nesting at Signy Island, South Orkney Islands. Polar Biol 34:205–214. https://doi.org/10.1007/s00300-010-0870-4

Edwards BR, Smellie JL (Eds) (2016) Distribution of glaciovolcanism on Earth, in: Glaciovolcanism on Earth and Mars: Products, Processes and Palaeoenvironmental Significance. Cambridge

University Press, Cambridge, p 15–56. https://doi.org/10.1017/CBO9781139764384.003

Emmerson L, Southwell C (2011) Adélie penguin survival: age structure, temporal variability and environmental influences. Oecologia 167:951–965. https://doi.org/10.1007/s00442-011-2044-7

Emmerson L, Southwell C (2008) Sea ice cover and its influence on Adélie penguin reproductive performance. Ecology 89:2096–2102. https://doi.org/10.1890/08-0011.1

Emmerson L, Walsh S, Southwell C (2019) Nonbreeder birds at colonies display qualitatively similar seasonal mass change patterns as breeders. Ecol Evol 9:4637–4650. https://doi.org/10.1002/ece3.5067

Erdmann ES, Ribic CA, Patterson-Fraser DL, Fraser WR (2011) Characterization of winter foraging locations of Adélie penguins along the Western Antarctic Peninsula, 2001–2002. Deep Sea Res. Part II Top. Stud. Oceanogr., Understanding the linkages between Antarctic food webs and the environment: a synthesis of Southern Ocean GLOBEC studies 58:1710–1718. https://doi.org/10.1016/j.dsr2.2010.10.054

Everson I (2000) Roles of krill in marine food webs: The Southern Ocean, in: Everson, I. (Ed.), Blackwell Science, Oxford, pp. 194–201.

Ferraccioli F, Armadillo E, Bozzo E, Privitera E (2000) Magnetics and gravity image tectonic framework of the Mount Melbourne volcano area (Antarctica). Phys Chem Earth Part Solid Earth Geod 25:387–393. https://doi.org/10.1016/S1464-1895(00)00061-2

Forero MG, Hobson KA, Bortolotti GR, Donázar JA, Bertellotti M, Blanco G (2002) Food resource utilisation by the Magellanic penguin evaluated through stable-isotope analysis: Segregation by sex and age and influence on offspring quality. Mar Ecol Prog Ser 234:289–299. https://doi.org/10.3354/meps234289

Fort J, Grémillet D, Traisnel G, Amélineau F, Bustamante P (2016) Does temporal variation of mercury levels in Arctic seabirds reflect changes in global environmental contamination, or a modification of Arctic marine food web functioning? Environ Pollut 211:382–388. https://doi.org/10.1016/j.envpol.2015.12.061

Foster KL, Braune BM, Gaston AJ, Mallory ML (2019) Climate influence on mercury in Arctic seabirds. Sci Total Environ 693:133569. https://doi.org/10.1016/j.scitotenv.2019.07.375

Fox J, Weisberg S (2018) Visualizing fit and lack of fit in complex regression models with predictor effect plots and partial residuals. J Statis Software 87(9):1–27. https://doi.org/10.18637/jss.v087.i09

Fox J, Weisberg S (2019) An R Companion to Applied Regression, 3rd Edition. Thousand Oaks, CA. https://socialsciences.mcmaster.ca/jfox/Books/Companion/index.html

Freeman NM, Lovenduski NS (2016) Mapping the Antarctic Polar Front: weekly realizations from 2002 to 2014. Earth Syst Sci Data 8:191–198. https://doi.org/10.5194/essd-8-191-2016

Furness RW, Camphuysen KCJ (1997) Seabirds as monitors of the marine environment ICES J Mar Sci 54:726–737. https://doi.org/10.1006/jmsc.1997.0243

Furness RW, Muirhead SJ, Woodburn M (1986) Using bird feathers to measure mercury in the environment: relationships between mercury content and moult. Mar Pollut Bull 17:27–30. https://doi.org/10.1016/0025-326X(86)90801-5

Furtado R, Granadeiro JP, Gatt MC, Rounds R, Horikoshi K, Paiva VH, Menezes D, Pereira E, Catry P (2021) Monitoring of mercury in the mesopelagic domain of the Pacific and Atlantic oceans using body feathers of Bulwer's petrel as a bioindicator. Sci Total Environ 775:145796. https://doi.org/10.1016/j.scitotenv.2021.145796

Gatt MC, Reis B, Granadeiro JP, Pereira E, Catry P (2020) Generalist seabirds as biomonitors of ocean mercury: the importance of accurate trophic position assignment. Sci Total Environ 740:140159. https://doi.org/10.1016/j.scitotenv.2020.140159

Gionfriddo CM, Tate MT, Wick RR, Schultz MB, Zemla A, Thelen MP, Schofield R, Krabbenhoft DP, Holt KE, Moreau JW (2016) Microbial mercury methylation in Antarctic sea ice. Nat Microbiol 1:1–12. https://doi.org/10.1038/nmicrobiol.2016.127

Global Volcanism Program (2022) Report on Erebus (Antarctica) (Venzke, E., ed.). Bulletin of the Global Volcanism Network, 47:2. Smithsonian Institution. https://doi.org/10.5479/si.GVP.BGVN202202-390020

Gon O, Heemstra PC (1990) Fishes of the Southern Ocean, First edition. ed. J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa

González-Solís J, Croxall JP, Wood AG (2000) Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. Oikos 90:390–398. https://doi.org/10.1034/j.1600-0706.2000.900220.x

Grasby SE, Them TR, Chen Z, Yin R, Ardakani OH (2019) Mercury as a proxy for volcanic emissions in the geologic record. Earth Sci Rev 196:102880. https://doi.org/10.1016/j.earscirev.2019.102880

Green K, Johnstone GW (1988) Changes in the diet of Adélie penguins breeding in East-Antarctica. Wildl Res 15:103–110. https://doi.org/10.1071/wr9880103

Grunst AS, Grunst ML, Grémillet D, Kato A, Bustamante P, Albert C, Brisson-Curadeau É, Clairbaux M, Cruz-Flores M, Gentès S, Perret S, Ste-Marie E, Wojczulanis-Jakubas K, Fort J (2023) Mercury contamination challenges the behavioral response of a keystone species to Arctic climate change. Environ Sci Technol 57(5):2054–2063. https://doi.org/10.1021/acs.est.2c08893

Guen CL, Kato A, Raymond B, Barbraud C, Beaulieu M, Bost C-A, Delord K, MacIntosh AJJ, Meyer X, Raclot T, Sumner M, Takahashi A, Thiebot J-B, Ropert-Coudert Y (2018) Reproductive performance and diving behaviour share a common sea-ice concentration optimum in Adélie penguins (*Pygoscelis adeliae*). Glob Change Biol 24:5304–5317. https://doi.org/10.1111/gcb.14377

Hinke JT, Polito MJ, Goebel ME, Jarvis S, Reiss CS, Thorrold SR, Trivelpiece WZ, Watters GM (2015) Spatial and isotopic niche partitioning during winter in chinstrap and Adélie penguins from the South Shetland Islands. Ecosphere 6:art125. https://doi.org/10.1890/ES14-00287.1

Hodum PJ, Hobson KA (2000) Trophic relationships among Antarctic fulmarine petrels: insights into dietary overlap and chick provisioning strategies inferred from stable-isotope ($\delta^{15}N$ and $\delta^{13}C$) analyses. Mar Ecol Prog Ser 198:273–281. https://doi.org/10.3354/meps198273

Honda K, Yamamoto Y, Hidaka H, Tatsukawa R (1986) Heavy metal accumulations in Adelie penguin, *Pygoscelis adeliae*, and their variations with the reproductive processes 40, 443–453.

Jafari V, Maccapan D, Careddu G, Sporta Caputi S, Calizza E, Rossi L, Costantini ML (2021) Spatial and temporal diet variability of Adélie (*Pygoscelis adeliae*) and Emperor (*Aptenodytes forsteri*) penguin: a multi tissue stable isotope analysis. Polar Biol 44:1869–1881. https://doi.org/10.1007/s00300-021-02925-1

Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends Ecol Evol 19:101–108. https://doi.org/10.1016/j.tree.2003.10.013

Juáres MA, Casaux R, Corbalán A, Blanco G, Pereira GA, Perchivale PJ, Coria NR, Santos MM (2018) Diet of Adélie penguins (*Pygoscelis adeliae*) at Stranger Point (25 de Mayo/King George Island, Antarctica) over a 13-year period (2003–2015). Polar Biol 41:303–311. https://doi.org/10.1007/s00300-017-2191-3

Juáres MA, Santos M, Mennucci JA, Coria NR, Mariano-Jelicich R (2016) Diet composition and foraging habitats of Adélie and

gentoo penguins in three different stages of their annual cycle. Mar Biol 163:105. https://doi.org/10.1007/s00227-016-2886-y

Kelly JF (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Can J Zool 78:1–27. https://doi.org/10.1139/z99-165

Kent S, Seddon J, Robertson G, Wienecke BC (1998) Diet of Adélie penguins *Pygoscelis adeliae* at Shirley Island, East Antarctica, January 1992. Mar Ornithol 26:7–10

Knox GA (2006) Biology of the Southern Ocean (2nd ed.). CRC Press, Boca Raton, USA. https://doi.org/10.1201/9781420005134, https://www.taylorfrancis.com/books/mono/10.1201/9781420005134/biology-southern-ocean-george-knox

Kokubun N, Emmerson L, McInnes J, Wienecke B, Southwell C (2021) Sea-ice and density-dependent factors affecting foraging habitat and behaviour of Adélie penguins throughout the breeding season. Mar Biol 168:97. https://doi.org/10.1007/s00227-021-03899-8

Lamborg CH, Hammerschmidt CR, Bowman KL, Swarr GJ, Munson KM, Ohnemus DC, Lam PJ, Heimbürger L-E, Rijkenberg MJA, Saito MA (2014) A global ocean inventory of anthropogenic mercury based on water column measurements. Nature 512:65–68. https://doi.org/10.1038/nature13563

Lee JR, Raymond B, Bracegirdle TJ, Chadès I, Fuller RA, Shaw JD, Terauds A (2017) Climate change drives expansion of Antarctic ice-free habitat. Nature 547:49–54. https://doi.org/10.1038/nature22996

Length R (2023) _emmeans: Estimated Marginal Means, aka Least-Squares Means_. R package version 1.8.5, https://CRAN.R-project.org/package=emmeans

Lynnes AS, Reid K, Croxall JP (2004) Diet and reproductive success of Adélie and chinstrap penguins: linking response of predators to prey population dynamics. Polar Biol 27:544–554. https://doi.org/10.1007/s00300-004-0617-1

Matias RS, Guímaro HR, Bustamante P, Seco J, Chipev N, Fragão J, Tavares S, Ceia FR, Pereira ME, Barbosa A, Xavier JC (2022) Mercury biomagnification in an Antarctic food web of the Antarctic Peninsula. Environ Pollut 304:119199. https://doi.org/10.1016/j.envpol.2022.119199

McKenzie AC, Silvestro AM, Marti LJ, Emslie SD (2021) Intraspecific variation in mercury, δ^{15}N, and δ^{13}C Among three Adélie Penguin (*Pygoscelis adeliae*) populations in the Northern Antarctic Peninsula Region. Environ Toxicol Chem 40:2791–2801. https://doi.org/10.1002/etc.5166

McKinney MA, Chételat J, Burke SM, Elliott KH, Fernie KJ, Houde M, Kahilainen KK, Letcher RJ, Morris AD, Muir DCG, Routti H, Yurkowski DJ (2022) Climate change and mercury in the Arctic: biotic interactions. Sci Total Environ 834:155221. https://doi.org/10.1016/j.scitotenv.2022.155221

Meier WN et al. (2014) Arctic sea ice in transformation: A review of recent observed changes and impacts on biology and human activity. Rev. Geophys. 51:185–217. https://doi.org/10.1002/2013RG000431

Michelot C, Kato A, Raclot T, Ropert-Coudert Y (2021) Adélie penguins foraging consistency and site fidelity are conditioned by breeding status and environmental conditions. PLOS ONE 16:e0244298. https://doi.org/10.1371/journal.pone.0244298

Michelot C, Kato A, Raclot T, Shiomi K, Goulet P, Bustamante P, Ropert-Coudert Y (2020) Sea-ice edge is more important than closer open water access for foraging Adélie penguins: evidence from two colonies. Mar Ecol Prog Ser 640:215–230. https://doi.org/10.3354/meps13289

Mills WF, Bustamante P, McGill RAR, Anderson ORJ, Bearhop S, Cherel Y, Votier SC, Phillips RA (2020) Mercury exposure in an endangered seabird: long-term changes and relationships with trophic ecology and breeding success. Proc R Soc B Biol Sci 287:20202683. https://doi.org/10.1098/rspb.2020.2683

Morley SA, Barnes DKA, Dunn MJ (2019) Predicting which species succeed in climate-forced polar seas. Front Mar Sci 5

NRC/NAS (2000) Toxicological Effects of Methylmercury. National Research Council/National Academy of Sciences, Washington, DC

Newsome SD, del Rio CM, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. Front Ecol Environ 5:429–436

Olmastroni S, Fattorini N, Pezzo F, Focardi S (2020) Gone fishing: Adélie penguin site-specific foraging tactics and breeding performance. Antarct Sci 32:199–209. https://doi.org/10.1017/S0954102020000085

Orsi AH, Whitworth T, Nowlin WD (1995) On the meridional extent and fronts of the Antarctic circumpolar current. Deep Sea Res Part Oceanogr Res Pap 42:641–673. https://doi.org/10.1016/0967-0637(95)00021-W

Pacyna AD, Jakubas D, Ausems ANMA, Frankowski M, Polkowska Ż, Wojczulanis-Jakubas K (2019) Storm petrels as indicators of pelagic seabird exposure to chemical elements in the Antarctic marine ecosystem. Sci Total Environ 692:382–392. https://doi.org/10.1016/j.scitotenv.2019.07.137

Parish TR (1988) Surface winds over the Antarctic continent: a review. Rev Geophys 26:169–180. https://doi.org/10.1029/RG026i001p00169

Parish TR, Cassano JJ (2003) The role of katabatic winds on the Antarctic surface wind regime. Mon Weather Rev 131:317–333. https://doi.org/10.1175/1520-0493(2003)131<0317:TROKWO>2.0.CO;2

Pedro S, Xavier JC, Tavares S, Trathan PN, Ratcliffe N, Paiva VH, Medeiros R, Vieira RP, Ceia FR, Pereira E, Pardal MA (2015) Mercury accumulation in gentoo penguins *Pygoscelis papua*: spatial, temporal and sexual intraspecific variations. Polar Biol 38:1335–1343. https://doi.org/10.1007/s00300-015-1697-9

Phillips RA, McGill RAR, Dawson DA, Bearhop S (2011) Sexual segregation in distribution, diet and trophic level of seabirds: Insights from stable isotope analysis. Mar Biol 158:2199–2208. https://doi.org/10.1007/s00227-011-1725-4

Piatt JF, Harding AMA, Shultz M, Speckman SG, Pelt TI, van, Drew GS, Kettle AB (2007) Seabirds as indicators of marine food supplies: Cairns revisited. Mar Ecol Prog Ser 352:221–234. https://doi.org/10.3354/meps07078

Pilcher N, Gaw S, Eisert R, Horton TW, Gormley AM, Cole TL, Lyver PO (2020) Latitudinal, sex and inter-specific differences in mercury and other trace metal concentrations in Adélie and Emperor penguins in the Ross Sea, Antarctica. Mar. Pollut. Bull. 154:111047. https://doi.org/10.1016/j.marpolbul.2020.111047

Pinheiro J, Bates D, R Core Team (2022) _nlme: Linear and Nonlinear Mixed Effects Models_. R package version 3. 1–160, https://CRAN.R-project.org/package=nlme

Polito MJ, Brasso RL, Trivelpiece WZ, Karnovsky N, Patterson WP, Emslie SD (2016) Differing foraging strategies influence mercury (Hg) exposure in an Antarctic penguin community. Environ Pollut 218:196–206. https://doi.org/10.1016/j.envpol.2016.04.097

Polito MJ, Lynch HJ, Naveen R, Emslie SD (2011) Stable isotopes reveal regional heterogeneity in the pre-breeding distribution and diets of sympatrically breeding *Pygoscelis spp*. penguins. Mar Ecol Prog Ser 421:265–277. https://doi.org/10.3354/meps08863

Provencher JF, Gilchrist HG, Mallory ML, Mitchell GW, Forbes MR (2016) Direct and indirect causes of sex differences in mercury concentrations and parasitic infections in a marine bird. Sci Total Environ 551–552:506–512. https://doi.org/10.1016/j.scitotenv.2016.02.055

Puddicombe RA, Johnstone GW (1988) The breeding season diet of Adélie penguins at the Vestfold Hills, East Antarctica. In: Ferris JM, Burton HR, Johnstone GW, Bayly IAE Eds.) Biology of the Vestfold Hills, Antarctica, Developments in Hydrobiology.

Springer Netherlands, Dordrecht, p 239–253. https://doi.org/10.1007/978-94-009-3089-6_25

R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, https://www.R-project.org/URL

Renedo M, Bustamante P, Cherel Y, Pedrero Z, Tessier E, Amouroux D (2020) A "seabird-eye" on mercury stable isotopes and cycling in the Southern Ocean. Sci Total Environ 742:140499. https://doi.org/10.1016/j.scitotenv.2020.140499

Renedo M, Bustamante P, Tessier E, Pedrero Z, Cherel Y, Amouroux D (2017) Assessment of mercury speciation in feathers using species-specific isotope dilution analysis. Talanta 174:100–110. https://doi.org/10.1016/j.talanta.2017.05.081

Riaz J, Bestley S, Wotherspoon S, Emmerson L (2021) Horizontal-vertical movement relationships: Adélie penguins forage continuously throughout provisioning trips. Mov Ecol 9:43. https://doi.org/10.1186/s40462-021-00280-8

Rocchi S, Storti F, Di Vincenzo G, Rossetti F (2003) Intraplate strike-slip tectonics as an alternative to mantle plume activity for the Cenozoic rift magmatism in the Ross Sea region, Antarctica. Geol Soc Lond Spec Publ 210:145–158. https://doi.org/10.1144/GSL.SP.2003.210.01.09

Roman HA, Walsh TL, Coull BA, Dewailly É, Guallar E, Hattis D, Mariën K, Schwartz J, Stern AH, Virtanen JK, Rice G (2011) Evaluation of the cardiovascular effects of methylmercury exposures: Current evidence supports development of a dose–response function for regulatory benefits analysis. Environ Health Perspect 119:607–614. https://doi.org/10.1289/ehp.1003012

Scheuhammer AM, Basu N, Evers DC, Heinz GH, Sandheinrich MB, Bank MS (2012) Ecotoxicology of mercury in fish and wildlife: Recent advances, in: Bank, M. (Ed.), Mercury in the environment: Pattern and Process. University of California Press, p. 0. https://doi.org/10.1525/california/9780520271630.003.0011

Seco J, Aparício S, Brierley AS, Bustamante P, Ceia FR, Coelho JP, Philips RA, Saunders RA, Fielding S, Gregory S, Matias R, Pardal MA, Pereira E, Stowasser G, Tarling GA, Xavier JC (2021) Mercury biomagnification in a Southern Ocean food web. Environ Pollut 275:116620. https://doi.org/10.1016/j.envpol.2021.116620

Seco J, Xavier JC, Coelho JP, Pereira B, Tarling G, Pardal MA, Bustamante P, Stowasser G, Brierley AS, Pereira ME (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

Selin NE (2009) Global biogeochemical cycling of mercury: a review. Annu Rev Environ Resour 34:43–63. https://doi.org/10.1146/annurev.environ.051308.084314

Sonke JE, Angot H, Zhang Y, Poulain A, Björn E, Schartup A (2023) Global change effects on biogeochemical mercury cycling. Ambio. https://doi.org/10.1007/s13280-023-01855-y

Sontag PT, Steinberg DK, Reinfelder JR (2019) Patterns of total mercury and methylmercury bioaccumulation in Antarctic krill *(Euphausia superba*) along the West Antarctic Peninsula. Sci Total Environ 688:174–183. https://doi.org/10.1016/j.scitotenv.2019.06.176

Southwell C, Emmerson L, Takahashi A, Barbraud C, Delord K, Weimerskirch H (2017) Large-scale population assessment informs conservation management for seabirds in Antarctica and the Southern Ocean: a case study of Adélie penguins. Glob Ecol Conserv 9:104–115. https://doi.org/10.1016/j.gecco.2016.12.004

Southwell C, Smith D, Bender A, Emmerson L (2021) A spatial reference and identification system for coastal ice-free land in East Antarctica. Polar Rec 57:e30. https://doi.org/10.1017/S0032247421000280

Souza JS, Kasper D, da Cunha LST, Soares TA, de Lira Pessoa AR, de Carvalho GO, Costa ES, Niedzielski P, Torres JPM (2020) Biological factors affecting total mercury and methylmercury levels in Antarctic penguins. Chemosphere 261:127713. https://doi.org/10.1016/j.chemosphere.2020.127713

Spreen G, Kaleschke L, Heygster G (2008) Sea ice remote sensing using AMSR-E 89-GHz channels. J Geophys Res Oceans 113. https://doi.org/10.1029/2005JC003384

Stewart F, Phillips R, Catry P, Furness R (1997) Influence of species, age and diet on mercury concentrations in Shetland seabirds. Mar Ecol Prog Ser 151:237–244. https://doi.org/10.3354/meps151237

Streets DG, Horowitz HM, Jacob DJ, Lu Z, Levin L, ter Schure AFH, Sunderland EM (2017) Total mercury released to the environment by human activities. Environ Sci Technol 51:5969–5977. https://doi.org/10.1021/acs.est.7b00451

Takahashi A, Ito M, Nagai K, Thiebot J-B, Mitamura H, Noda T, Trathan PN, Tamura T, Watanabe YY (2018) Migratory movements and winter diving activity of Adélie penguins in East Antarctica. Mar Ecol Prog Ser 589:227–239. https://doi.org/10.3354/meps12438

Tan SW, Meiller JC, Mahaffey KR (2009) The endocrine effects of mercury in humans and wildlife. Crit Rev Toxicol 39:228–269. https://doi.org/10.1080/10408440802233259

Tartu S, Blévin P, Bustamante P, Angelier F, Bech C, Bustnes JO, Chierici M, Fransson A, Gabrielsen GW, Goutte A, Moe B, Sauser C, Sire J, Barbraud C, Chastel O (2022) A U-turn for mercury concentrations over 20 Years: How do environmental conditions affect exposure in Arctic seabirds? Environ Sci Technol 56:2443–2454. https://doi.org/10.1021/acs.est.1c07633

Thiebot J-B, Ropert-Coudert Y, Raclot T, Poupart T, Kato A, Takahashi A (2019) Adélie penguins' extensive seasonal migration supports dynamic Marine Protected Area planning in Antarctica. Mar Policy 109:103692. https://doi.org/10.1016/j.marpol.2019.103692

Thompson DR, Furness RW (1989) The chemical form of mercury stored in South Atlantic seabirds. Environ Pollut 60:305–317. https://doi.org/10.1016/0269-7491(89)90111-5

Thompson DR, Hamer KC, Furness RW (1991) Mercury accumulation in Great Skuas *Catharacta skua* of known age and sex, and its effects upon breeding and survival. J Appl Ecol 28:672–684. https://doi.org/10.2307/2404575

Thompson DR, Stewart FM, Furness RW (1990) Using seabirds to monitor mercury in marine environments: the validity of conversion ratios for tissue comparisons. Mar Pollut Bull 21:339–342. https://doi.org/10.1016/0025-326X(90)90795-A

Tierney M, Emmerson L, Hindell M (2009) Temporal variation in Adélie penguin diet at Béchervaise Island, east Antarctica and its relationship to reproductive performance. Mar Biol 156:1633–1645. https://doi.org/10.1007/s00227-009-1199-9

Turner J (2015) ARCTIC AND ANTARCTIC | Antarctic Climate. In: North GR, Pyle J, Zhang F (Eds.) Encyclopedia of Atmospheric Sciences (Second Edition). Academic Press, Oxford, p 98–106. https://doi.org/10.1016/B978-0-12-382225-3.00044-X

UN Environment (2019) Global Mercury Assessment 2018. UN-Environment Programme, Chemicals and Health Branch, Geneva, Switzerland, p 59

Watanuki Y, Kato A, Naito Y, Robertson G, Robinson S (1997) Diving and foraging behaviour of Adélie penguins in areas with and without fast sea-ice. Polar Biol 17:296–304. https://doi.org/10.1007/PL00013371

Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York

Wienecke BC, Lawless R, Rodary D, Bost C-A, Thomson R, Pauly T, Robertson G, Kerry KR, LeMaho Y (2000) Adélie penguin foraging behaviour and krill abundance along the Wilkes and

Adélie land coasts, Antarctica. Deep Sea Res Part II Top Stud Oceanogr 47:2573–2587. https://doi.org/10.1016/S0967-0645(00)00036-9

Wienecke BC, Robertson G (1997) Foraging space of emperor penguins *Aptenodytes forsteri* in Antarctic shelf waters in winter. Mar Ecol Prog Ser 159:249–263. https://doi.org/10.3354/meps159249

Williams TD (1995) The penguins: Spheniscidae, Bird families of the world. Oxford University Press, Oxford

Wilson PR, Ainley DG, Nur N, Jacobs SS, Barton KJ, Ballard G, Comiso JC (2001) Adélie penguin population change in the Pacific sector of Antarctica: relation to sea-ice extent and the Antarctic Circumpolar Current. Mar Ecol Prog Ser 213:301–309. https://doi.org/10.3354/meps213301

Yamamoto Y, Kanesaki S, Kuramochi T, Miyazaki N, Watanuki Y, Naito Y (1996) Comparison of trace element concentrations in tissues of the chick and adult Adelie penguins. Proc NIPR Symp Polar Biol Natl Inst Polar Res 253–262

Yue F, Li Y, Zhang Y, Wang L, Li Dan, Wu P, Liu H, Lin L, Li Dong, Hu J, Xie Z (2023) Elevated methylmercury in Antarctic surface seawater: the role of phytoplankton mass and sea ice. Sci Total Environ 882:163646. https://doi.org/10.1016/j.scitotenv.2023.163646

Zeileis A, Hothorn T (2002) Diagnostic checking in regression relationships. R News 2(3):7–10. https://CRAN.R-project.org/doc/Rnews/

Zhou Z, Wang H, Li Y (2023) Mercury stable isotopes in the ocean: analytical methods, cycling, and application as tracers. Sci Total Environ 874:162485. https://doi.org/10.1016/j.scitotenv.2023.162485