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Mercury concentration in Antarctic krill varies in time and space and with individual size

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Environmental context. Several predators that eat Antarctic krill may be unintentionally ingesting toxic substances. Studying aspects of krill life to understand the effects of potential increases in Antarctic mercury (Hg) availability revealed that seasons, locations and individual size influence krill Hg concentration. Despite increasing human presence (potential Hg sources) in Antarctica, krill Hg content remains stable, and evidence suggests that Hg accumulates in predators by both short (krill-based) and longer food chains.

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ABSTRACT

Rationale. Mercury (Hg) is passively assimilated from the water by phytoplankton, accumulated by lower trophic levels species, and biomagnified along food chains. Any increases in its bioavailability in Antarctic waters could endanger the survival of vulnerable top predators. With Antarctic food webs reliant on krill, we must understand the temporal, spatial and biological variability in their Hg concentration to forecast ecosystem-wide impacts of rising Hg levels. **Methodology.** We sampled krill fortnightly from South Georgia, South Orkney Islands and West Antarctic Peninsula between December 2013 and September 2019 (excluding October and November months). Individuals were weighed, sexed and analysed for Hg. We assessed the importance of biological (krill size, sex and life stage) and environmental (location, time and chlorophyll-*a* concentration) parameters on krill Hg concentrations with generalised linear models, analyses of variance, Gaussian linear models and vector autoregressive modelling. **Results.** Temporal variation explained most of the differences in krill Hg concentrations, with location and individual size also contributing to the variability. Subsurface chlorophyll-*a* concentrations and the affinity of methylmercury to sulfhydryl groups of some proteins, rather than krill fatty acid content, were likely the drivers of observed annual cycles. **Discussion.** Antarctic krill Hg concentrations have remained stable since the 1990s, although our measurements were lower than most. Such a historic baseline is indispensable for continued monitoring of Antarctic ecosystems. Krill is considered a key prey species, but our findings and those of biomagnification studies suggest that there may be a gap in our understanding of trophic transfer and accumulation of Hg in some top predators. Future biomagnification studies would benefit from conducting mass balance models.

Keywords: chlorophyll-*a*, euphausiids, fatty acids, food web, maturity stage, mercury, phytoplankton, Southern Ocean.

Introduction

Long-range atmospheric transport and deposition processes have resulted in mercury (Hg) from natural and anthropogenic sources being widely distributed in the oceans. This is the case even in areas away from major urban developments and in remote locations such as Antarctica (Dommergue *et al.* 2010), where some of the highest open water Hg concentrations have been recorded (Cossa *et al.* 2011). Light and temperature conditions in polar zones make for unique Hg cycling in these regions. A synthesis of the available

Collection: Mercury in the environment

information on Hg cycling in Antarctica, with a focus on key Hg species, is presented in Fig. 1. Mercury is recycled between the ocean surface and the lower troposphere by oxidation and reduction reactions, and is actively scavenged by particulate matter (Mason and Gill 2005; Cossa *et al.* 2011). Atmospheric Hg^0 (elemental Hg) is rapidly oxidised to Hg^{II} (inorganic Hg) in the spring by sea-salt-derived bromine that is released into the atmosphere during sea-ice formation (Schroeder *et al.* 1998; Lindberg *et al.* 2001; Ariya *et al.* 2002; Yue *et al.* 2021). These reactive Hg species can be deposited onto snow and transferred to the ocean upon thawing (Lindberg *et al.* 2001; Brooks *et al.* 2008). Once in the water, Hg^{II} species can be reduced to Hg^0, re-emitted into the troposphere, bound to minerals or organic matter, or incorporated into phytoplankton within the photic zone (Cossa *et al.* 2011). Hg^{II} transported to the deeper ocean while attached to particles can be biomethylated in the water column, the rate of which will depend on the microbial activity associated with the degradation of phytoplankton (Heimbürger *et al.* 2010). Biological and photochemical demethylation can occur concurrently in the water column, snow packs and sediment, such that monomethylmercury (MeHg) concentrations reflect the net methylation–demethylation processes (Cossa *et al.* 2011). Overall, the distribution of Hg in the ocean is characterised by surface depletion and elevated concentrations at depth in the regeneration zone (Cossa *et al.* 2011). Net Hg methylation by microbial activity is thought to take place in low oxygen regions, driven by the decomposition of sinking organic matter (Heimbürger *et al.* 2010; Cossa *et al.* 2011). The sediment is the final compartment for Hg in the open ocean environment, where it can be transformed into MeHg by biomethylation. Monomethylmercury can then be released back into the water column, where upwelling currents may transport it to surface waters. Deep-sea cold seeps can be a sink for Hg and a source of MeHg in the ocean floor (Li *et al.* 2024). Proximity to bird or penguin colonies may also influence Hg concentrations in the water column and in the Antarctic food web, as their excreta is enriched with Hg (Bargagli *et al.* 1998; Chiang *et al.* 2021).

The Antarctic food web is heavily reliant on Antarctic krill (*Euphausia superba*) (Locarnini and Presley 1995; Everson 2000). Several interconnected biotic and abiotic factors, including diet composition, geographic location, topographical features, depth of feeding and physiological state, can influence the concentration of Hg in krill. Although these crustaceans feed on phytoplankton and zooplankton (Perissinotto *et al.* 2000), the former is their primary source of food and, thus, of Hg. Phytoplankton blooms vary in time and space in the Southern Ocean (Cuzin-Roudy 2000; Atkinson *et al.* 2006), such that seasonal shifts in the proportion of phytoplankton and zooplankton in krill diets, as well as spatially variable (location-dependent) food dynamics and availability, may affect Hg intake and bioaccumulation in krill (Chen and Folt 2005; Sontag *et al.* 2019; Korejwo *et al.* 2023). The concentration of Hg in surface snow is greater at the sea-ice edge, adjacent to the freezing ocean surface, and its concentration in surface waters increases poleward (Brooks *et al.* 2008; Cossa *et al.* 2011). This pattern should be reflected in phytoplankton in these areas. Krill feed where thawing of sea-ice occurs in spring and summer, and could thus consume phytoplankton with

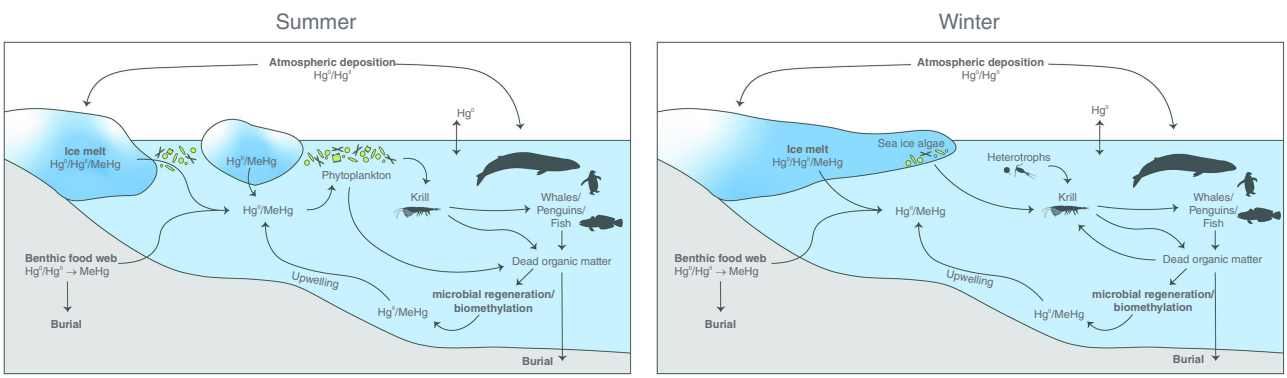

Fig. 1. Processes involved in mercury (Hg) cycling in Antarctica during summer months (left panel) and winter months (right panel), with a focus on key Hg species (elemental mercury, Hg^0; inorganic mercury, Hg^{II}; and methylmercury, MeHg). Arrows indicate the transfer of Hg species between different compartments and reservoirs. Burial can happen at shallower and deeper waters, depending on local hydrodynamics and biological activity in the sediment. Guano Hg input from bird colonies in coastal zones, as well as cold seep influences (Hg sink and MeHg source) are not included. Biological processes influencing Hg cycling are illustrated if directly related to Antarctic krill. The feeding ecology of this species varies with seasons; individuals feed primarily on phytoplankton during the summer, whereas during the winter krill larvae feed on ice algae and juveniles and adults opportunistically feed on heterotrophs (e.g. small copepods and flagellates) or marine snow when these are available, or consume their energy reserves (i.e. storage lipids) when food is unavailable. Phytoplankton, krill, and higher trophic level species (exemplified herein by whales, penguins and fish) contribute to the dead organic matter pool (including marine snow) with frustules, excretion and egestion (i.e. faeces) products, moults and dead bodies, among others.

higher Hg content. A similar trend could be expected for krill feeding in areas with high land or submarine volcanic activity and hydrothermal vents that emit heavy metals (e.g. Dick 1991; Bargagli *et al.* 1998; Tovar-Sanchez *et al.* 2009; Tomiyasu *et al.* 2023). Elsewhere, adult krill, which primarily feed in surface waters, likely consume phytoplankton with lower Hg concentrations. Juvenile krill, which develop and feed while ascending through mesopelagic depths, will encounter prey where environmental Hg concentrations may be higher. It is also possible that Hg can be lost once assimilated by adult female krill. Indeed, Seco *et al.* (2019) observed higher concentrations in eggs than in somatic tissue and proposed spawning as a potential mechanism for Hg elimination in krill.

Krill are a major food source for cephalopods, fish, seals, baleen whales and seabirds in Antarctica. Some seal and whale species feed exclusively on krill (Seco *et al.* 2019). Just as krill are the energy transfer link between primary producers and higher trophic levels, they also play a key role in the transfer, bioaccumulation and biomagnification of Hg in Antarctic food webs (e.g. Matias *et al.* 2022). Mercury is a non-essential metal that can be toxic even in low concentrations (e.g. it interferes with hormone regulation; as reviewed by Tan *et al.* 2009), and its presence in aquatic habitats is commonly seen as a global toxicity problem (Jackson 1998). It can also bioaccumulate and biomagnify in food webs primarily as MeHg (Bengtson Nash *et al.* 2021; Seco *et al.* 2021), a neurotoxic Hg species whose seawater concentration is controlled by biological methylation and both biotic and abiotic demethylation reactions (Cossa *et al.* 2011; Cipro *et al.* 2017; Maher *et al.* 2020). Mercury concentrations in Southern Ocean biota are expected to increase with climate change, as higher global temperatures lead to enhanced Hg methylation and bioavailability in subsurface waters where oxygen is depleted (Cossa *et al.* 2011). This is expected to affect Antarctic food webs at structural and functional levels, possibly endangering the reproduction and survival of more vulnerable top predator populations (e.g. Goutte *et al.* 2014; Mills *et al.* 2020).

A thorough understanding of trends and patterns in krill Hg content and its potential effects on the Antarctic food web, especially under changing climate conditions, requires comprehensive sampling at spatial and temporal scales. The costs and difficulty of frequently accessing Southern Ocean environments, however, have prevented scientists from establishing such long-term data sets. In this study, we collaborated with AkerBiomarine, a Norwegian krill fishing and biotech company, to obtain a scientifically unique and almost continuous (fortnightly between December and September) source of krill samples from late 2013 until 2019. Our objective was to establish a baseline (for past and future comparison) of Hg concentrations in female and male adult krill sampled from fishing locations in the South Orkney Islands (SOI), South Georgia (SG) and the West Antarctic Peninsula (WAP). We also investigated whether biological (size, sex and life stage) and abiotic (geographic location and temporal variation in food supply) variables had any influence on Hg concentrations in krill.

Experimental

Study sites and sample collection

Krill were collected by the vessel FV *Saga Sea* (Aker BioMarine, Oslo, Norway) during six fishing seasons (Fig. 2): December 2013–September 2014, December 2014–September 2015, December 2015–September 2016, January–August 2017, December 2017–August 2018 and January–September 2019 (hereafter referred to as fishing years 2014 through 2019 respectively; seasons are mentioned for the Southern Hemisphere which, in Australia, start on the first day of the respective months). Spring samples could only be obtained for the beginning of the season as FV *Saga Sea* concluded fishing in mid-September (fishing resumed in early December or in January the following year).

Fishing took place within the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Convention Area at WAP, SOI and SG (Food and Agriculture Organization (FAO) statistical subareas 48.1, 48.2 and 48.3 respectively; Supplementary material Fig. S1). The vessel predominantly fished at the WAP and SOI during summer and autumn, and at SG in winter and early spring. It moved between locations when sea-ice presence deterred fishing (WAP and SOI) or upon reaching subarea-specific maximum allowable catch quotas (WAP) or production goals (SG); fishing locations at a certain date therefore varied on a yearly basis.

A continuous catch system (Eco-Harvesting technology, Aker BioMarine) was used, which ensured that krill remained alive and intact while steadily pumped for 24 h from a mid-water trawl net onto FV *Saga Sea*. Twenty individuals were randomly sampled from the catch (there was no selection by size or maturity stage) every day by a fisheries observer. These were divided into two packages (either aluminium foil or a vacuum-sealed transparent plastic packet stored inside a dark package) and immediately frozen at −20°C for 4 h, being subsequently transferred to −80°C storage until shipping. Packages were transported on dry ice to the Institute for Marine and Antarctic Studies (Hobart, Australia), where they were stored in freezers at either −80 or −20°C until analysis.

Mercury analysis

An average of three samples for each male and female krill were chosen per fortnight for total Hg analysis, together with a few samples of juveniles (total $n = 451$; Fig. 2; Franco-Santos *et al.* 2025). Thawed individuals were sexed with a dissecting microscope and measured ('Standard 1' measurement from the tip of the rostrum to the tip of the uropod) according to

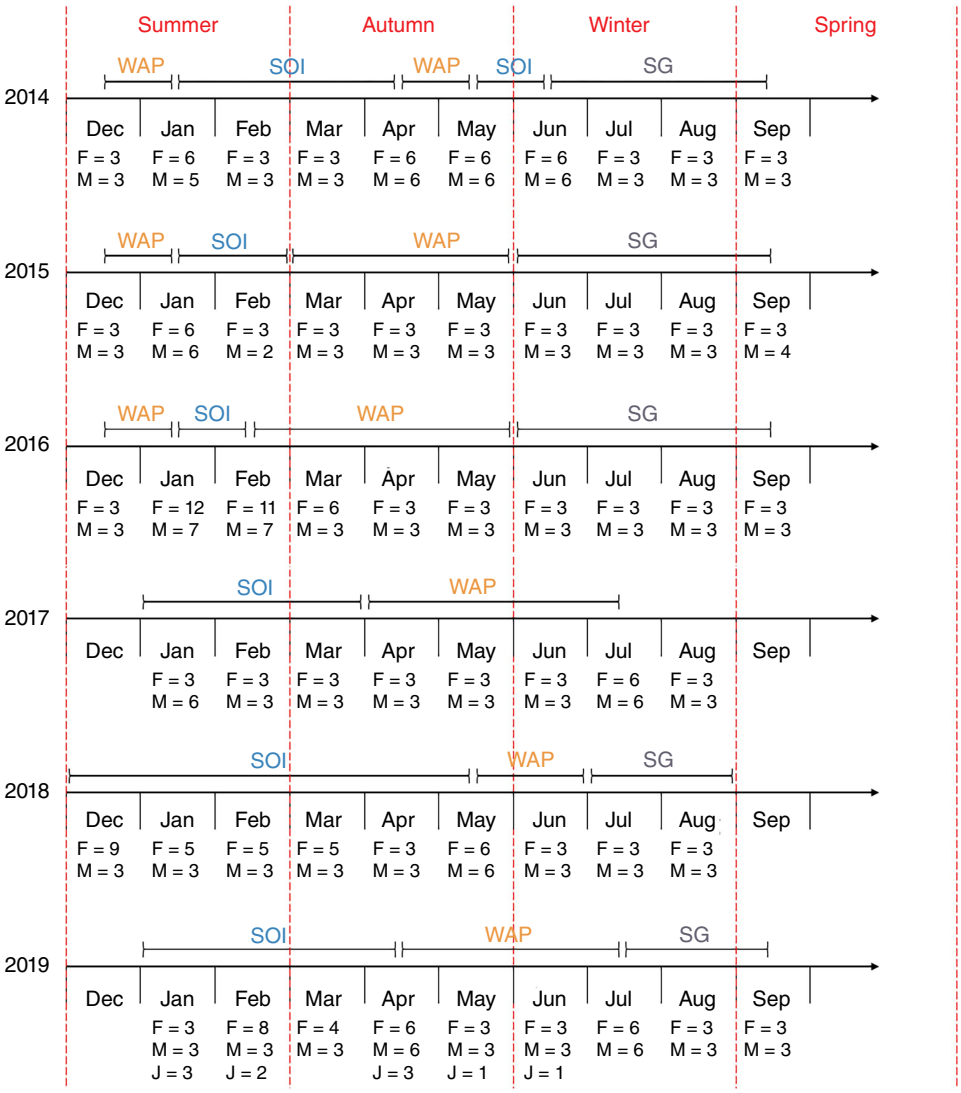

Fig. 2. Timing (December 2013–September 2019), location and number of juvenile (J), female (F) and male (M) krill samples obtained for total mercury analysis. Each line corresponds to a fishing year, starting in December of the previous year and ending in September of the year indicated for each line (e.g. the first line presents data from fishing year 2014, which ran from December 2013 until September 2014). The timing (months and years) of krill fishing is indicated for each of the colour-coded locations (dark blue, South Georgia, SG; light blue, South Orkney Islands, SOI; and orange, Western Antarctic Peninsula, WAP). The red dashed vertical bars separate the months by season.

Kirkwood (1982). They were then freeze-dried for 24 h and subsequently weighed (dry mass, DM); length and mass measurements were used as proxies for krill size. Most samples for Hg analysis pooled two to four individuals of the same sex and life stage, with sample length and weight representing the average of measurements from each pooled individual. A few samples pooled adults and subadults of the same sex (n = 31) and were considered as a third life stage category (adult only and subadult only were the other two) for statistical analyses.

Samples were homogenised to a fine powder (20–100 μm) using an IKA A11 Analytical micromill (MEDOS, Australia). Mercury analysis was conducted using a Milestone Direct Mercury Analyser (DMA-80 Tri-Cell; Milestone, Bergamo, Italy). The instrument was calibrated with an aqueous Hg standard for atomic absorption spectroscopy (AAS) (1000 mg L^{-1} of Hg in nitric acid; Sigma–Aldrich TraceCERT). A calibration curve was constructed by plotting the absorbances of standards against Hg concentrations in nanograms with an R^2 value of 0.99 or higher. Samples were analysed using the US EPA Method 7473 (United States Environmental Protection Agency 1998); two blanks and three reference materials were analysed for every 40 samples. Approximately 100 mg of the sample was weighed in nickel boats. After every tenth sample, a replicate sample was analysed. When replicate recovery exceeded a variance of 10% compared to the original sample, a third replicate was run. Measured values for NIST SRM 1515 Apple leaves, NIST SRM1566b Oyster tissue and MURST-ISSA2 Antarctic Krill (42 ± 2 ng g^{-1}, n = 33; 34 ± 4 ng g^{-1}, n = 43; and 13 ± 1 ng g^{-1}, n = 7 respectively) were in agreement with certified values (43.2 ± 2.3, 37.1 ± 1.3 and 13 ± 3 ng g^{-1} respectively).

Statistical analyses

To assess the overall importance of biological (size, sex and life stage), as well as abiotic (location and time – fishing year and month) variables on krill Hg concentrations, we

fitted several generalised linear models (GLMs) to the data. We fitted separate models using length or mass as measures of individual size. Juveniles were not included in the analyses as their sample size was low ($n = 10$). We modelled the data with two different approaches for every combination of predictor variables, GLMs including main effects only and GLMs including main effects and a month–year interaction term, to allow for interannual variation in seasonal patterns. We used months rather than seasons for the interaction term because the former provided a better fit for the data regarding intraannual variation. The GLMs, including those without biological factors as predictor variables (the unbalanced study design resulted in a lack of statistical power for these factors), were compared using the Akaike information criterion (AIC). The comparison revealed that the main effects model with the month–year interaction term had optimal explanatory power, so these are the results we report. Given the high explanatory power of abiotic factors as predictor variables, we did not perform GLMs without them for comparison with the AIC. As data for December and September were missing for 2 out of 6 years, model predictions for those months are biased toward the years in which there are data. Other interaction terms were not included due to insufficient data coverage across all predictor variables (e.g. locations were not sampled over the same time periods – see Fig. 2). By excluding interactions, we assume that each variable's effect operates independently of others, allowing us to capture broad trends across the dataset. As an example, seasonal patterns are treated as consistent across different locations, and differences in Hg concentrations associated with either sex or life stage are assumed to be stable regardless of other factors. Furthermore, given the right-skewed distribution of the data (Supplementary Fig. S2), we square root-transformed Hg concentrations and fitted the data using a scaled *t*-distribution (degrees of freedom and scaling parameters were estimated through maximum likelihood estimation), which is more robust to heavy tails and outliers than the normal distribution. Assessment of Q–Q plots and residual vs fitted plots confirmed model validity (using the scaled *t*-distribution for the residuals). An analysis of variance (ANOVA) was performed on each model to assess the significance of the main effects (length and mass, sex, stage, month, year and location) on square root-transformed Hg concentrations, using a scaled *t*-distribution for the residuals. The significance of each model term was assessed using a Wald test, as implemented in the *R* package *mgcv* (ver. 1(29), S. Wood, see https://cran.r-project.org/package=mgcv/). Wald tests are analogous to Type III ANOVA, in that they are useful for analysing imbalanced data and assessing the significance of each effect while accounting for the presence of other terms in the model. Pairwise comparisons were made using the Sidak method for adjusting *P* values for multiple comparisons and the *R* package *emmeans* (ver. 1.8.8, R. Lenth, see https://cran.r-project.org/package=emmeans/).

To further account for the incomplete coverage of biological metrics across other factors in the dataset, we also fitted Gaussian linear models to square root-transformed data with a two-way interaction between sex and life stage, focusing on the summer and autumn data from SOI and WAP, where all combinations of male and female and adult and subadult krill were sampled. For these, we excluded data from the mixed stage group (adult + subadults). Two-way ANOVAs were carried out using Type III Sum of Squares to account for data imbalance, but as the results were not statistically significant, we did not perform subsequent pairwise comparisons. We also conducted linear regressions between krill length and mass and Hg concentrations for each combination of location and season available in our data set.

Lastly, we obtained chlorophyll-*a* concentrations from Ocean Colour (Plymouth Marine Laboratory, see https://www.oceancolour.org/) to contrast trends with krill Hg. We downloaded the 5-day CCI_ALL-v6.0 chlorophyll data product (Sathyendranath *et al.* 2019) and averaged pixels to develop a time series. We then employed Vector Autoregressive Modelling (VAR) to examine the dynamic interrelationships between chlorophyll-*a* concentration and krill Hg across all sampling locations over time. By applying the VAR framework, we modelled the bi-directional influence of these variables, capturing both direct and lagged responses. An impulse response function was then generated to quantify how shocks to either chlorophyll-*a* or Hg concentrations propagate through the system over time, allowing us to visualise temporal effects and their statistical significance. Chlorophyll-*a* and Hg data were compared as concurrent 8-day averages. Modelling and diagnostics used to determine the number of lag terms were conducted using the *R* package *vars* (ver. 1.6-1, see https://cran.r-project.org/package=vars/; Pfaff 2008).

Data analyses and visualisation were performed in *R* (ver. 4.2.1, R Foundation for Statistical Computing, Vienna, Austria, see https://www.r-project.org/). Data manipulation was conducted using tools from the *tidyverse* package (ver. 2.0.0, see https://cran.r-project.org/package=tidyverse; Wickham *et al.* 2019).

Results and discussion

Baseline mercury data

Mercury concentrations in krill averaged 5 ± 4 ng g^{-1} (w/w DM) and ranged from 0.05 to 21 ng g^{-1}, with two additional high-concentration individuals containing 30 and 36 ng g^{-1} (Tables 1 and 2, Supplementary Fig. S2). Approximately half of our samples had Hg concentrations below 4 ng g^{-1}. These data align with the lower range of previously reported values (Table 1). This likely reflects the higher proportion of our samples collected during autumn and winter (60%), when Hg concentrations are lower, compared to other studies that sample mostly during summer

Table 1. Published mercury (Hg) concentrations for Antarctic krill *Euphausia superba*.

Year	Location	Hg (ng g^{-1} DM)	Reference
1978[A]	Scotia Sea	<100[B]	Stoeppler and Brandt (1979)
1989–1991[A]	Ross Sea	**77** ± 26 (50–105)	Bargagli *et al.* (1998)
1993	West Antarctic Peninsula	**31.7** ± 26.3 (16.1–40.9)	Locarnini and Presley (1995)
1993–1994	Ross Sea	**35** ± 5[B]	Caroli *et al.* (1998)
1994–1995	Marguerite Bay (WAP)	**40** ± 20[B]	Caroli *et al.* (1998)
1994–1995	Livingston Island (WAP)	**25** ± 5[B]	Caroli *et al.* (1998)
2004[A]	Admiralty Bay (WAP)	**34.6**	dos Santos *et al.* (2006)
2004–2008[A]	King George Island (WAP)	**18** ± 5	Cipro *et al.* (2017)
2006[A]	SW Indian Ocean sector of Southern Ocean (60–70°S, 30–80°E)	Sa = **42** ± 37 (12–84); Ad = **53** ± 11 (45–65); F_{SP} = **20** ± 0 (20–20)	Bengtson Nash *et al.* (2021)
2007–2008[A]	South Georgia	E = **15** ± 2; F = **8** ± 3	Seco *et al.* (2019)
		40 ± 20	Seco *et al.* (2021*a*)
2007–2008 and 2010–2011	Palmer Long-Term Ecological Research study area (WAP)	**16** ± 2	Brault (2012)
2009[A]	Admiralty Bay (WAP)	**10** ± 5 (5–10)[B]	Polito *et al.* (2016)
2011–2015[A]	Anvers Island (WAP)	Ad = (4.04–12.6); J = (7.85–19.4)	Sontag *et al.* (2019)
2015–2016[A]	South Orkney Islands	Ad = **51** ± 15 (F = **54** ± 18, M = **48** ± 11); J = **71** ± 24	Seco *et al.* (2019)
	Scotia Sea	**40** ± 10	Seco *et al.* (2021*b*)
2016–2017[A]	South Georgia	Ad = **7** ± 2 (F = **6** ± 2, M = **7** ± 2); J = **14** ± 5	Seco *et al.* (2019)
	Polar Front	J = **17** ± 6	Seco *et al.* (2019)
	South Georgia	**10** ± 3	Seco *et al.* (2021*a*)
2018[C]	West Antarctic Peninsula	**20** (Ad = **18**, J = **34**), median = 10	Korejwo *et al.* (2023)
2020[A]	Weddell Sea	**30** (19.5–53)	Mirzoeva *et al.* (2022)
2013–2019	South Georgia	**3** ± 2 (0.05- 12.0) F_S = **3** ± 2 (0–11); M = **3** ± 2 (0–7); M_S = **4** ± 3 (1–12)	This study
2013–2019	South Orkney Islands	**6** ± 5 (0.3–35.5) F = **8** ± 5 (2–36); F_S = **4** ± 3 (1–10); M = **5** ± 4 (1–18); M_S = **6** ± 5 (0–30); J = **4** ± 2 (2–8)	This study
2013–2019	West Antarctic Peninsula	**4** ± 4 (0.05–20.1) F = **7** ± 4 (1–20); F_S = **3** ± 3 (1–15); M = **7** ± 4 (1–13); M_S = **4** ± 4 (0–18); J = **1** ± 1 (0–2)	This study

Where available, and unless stated otherwise, Hg concentrations are reported as nanograms per gram of dry mass (ng g^{-1} DM) and presented as mean (in bold) ± 1 standard deviation, with the range in parentheses if available. Where available, letter coding indicated sex and life stage of individuals analysed: F, female; F_S, subadult female; F_{SP}, spent female; M, male; M_S, subadult male; Ad, adults; Sa, subadults; E, eggs; J, juveniles; WAP, Western Antarctic Peninsular. Studies providing Hg values for krill obtained from predator stomach contents were not included.

[A]Sampled during summer months.

[B]Hg reported on a wet mass basis was converted into dry mass by multiplying by a factor of 5.

[C]Sampled during autumn months.

(see seasonality discussion below). Our concentrations exhibited a positively skewed distribution (Supplementary Fig. S2) typical of inherent variability attributed to genetics, age and other factors that may result in the variable uptake and retention of Hg (Lobel and Wright 1982; Lobel *et al.* 1982). Comparing data collected over the last 25 years (Table 1, Fig. 3), no substantial increase in krill Hg concentration is evident, despite increasing global Hg inputs and human activities in the Antarctic. The higher value recorded by Stoeppler and Brandt (1979) likely reflects the analytical capability at the time (lower instrument precision, greater likelihood of sample contamination during sampling, transport or analysis) rather than truly higher Hg concentrations.

The influence of biological metrics (size, sex and life stage) on mercury concentrations in krill

Krill ranged in length from 28 to 58 mm and in weight from 44 to 479 mg DM (mean ± 1 standard deviation: 44 ± 5 mm and 174 ± 70 mg DM; Table 2). The GLM showed that

Table 2. Antarctic krill *Euphausia superba* length (mm), dry mass (DM, mg) and mercury concentrations (Hg, ng g^{-1} DM) in relation to individual sex and life stage, location, and season and year.

Location	Season and year	Juveniles			Subadult females			Subadult males			Adult females			Adult males		
		Length	DM	Hg	Length	DM	Hg	Length	DM	Hg	Length	DM	Hg	Length	DM	Hg
SG	Sp 2014				41 ± 2 (40)	94 ± 13 (88)	4 ± 2 (5)	39	79	8				44 ± 0 (44)	129 ± 4 (129)	5 ± 3 (5)
	W 2014				37 ± 3 (36)	85 ± 26 (78)	4 ± 1 (3)	39 ± 2 (39)	109 ± 11 (109)	2 ± 0 (2)				42	116	3
	Sp 2015				45 ± 1 (45)	142 ± 18 (138)	5 ± 1 (5)							46 ± 3 (45)	158 ± 32 (154)	5 ± 1 (5)
	W 2015				44 ± 3 (43)	160 ± 44 (151)	2 ± 1 (2)	48 ± 2 (46)	214 ± 29 (212)	2 ± 0 (2)				48 ± 0 (48)	223 ± 25 (223)	2 ± 3 (2)
	Sp 2016				41 ± 2 (40)	107 ± 17 (110)	6 ± 3 (7)	41 ± 3 (40)	111 ± 26 (111)	8 ± 2 (8)						
	W 2016				42 ± 4 (43)	139 ± 25 (142)	5 ± 4 (4)	44 ± 2 (45)	185 ± 40 (187)	3 ± 4 (2)				46	190	4
	W 2017				38 ± 2 (37)	93 ± 18 (91)	3 ± 1 (2)	36 ± 4 (37)	91 ± 28 (86)	3 ± 2 (3)				44	155	2
	W 2018				46 ± 2 (45)	177 ± 37 (174)	1 ± 1 (0)							48 ± 3 (48)	216 ± 48 (207)	1 ± 2 (1)
	Sp 2019				40 ± 2 (40)	87 ± 21 (87)	6 ± 2 (6)	41	98	4						
	W 2019				39 ± 3 (40)	121 ± 29 (127)	2 ± 1 (2)	36 ± 3 (36)	83 ± 17 (84)	3 ± 1 (3)				45 ± 2 (45)	188 ± 29 (188)	2 ± 1 (2)
SOI	Su 2013–2014							47 ± 2 (47)	260 ± 53 (260)	8 ± 1 (8)	48 ± 3 (48)	237 ± 58 (256)	7 ± 5 (6)	49 ± 5 (48)	283 ± 105 (252)	4 ± 1 (4)
	A 2014				44 ± 3 (44)	151 ± 23 (142)	2 ± 1 (2)	44 ± 3 (44)	170 ± 53 (146)	3 ± 1 (3)	47 ± 0 (47)	244 ± 12 (244)	4 ± 0 (4)	45	277	4
	W 2014				43 ± 2 (43)	146 ± 37 (135)	3 ± 1 (2)							51	280	1
	Su 2014–2015				38 ± 2 (38)	123 ± 15 (131)	8 ± 2 (9)	41 ± 2 (41)	135 ± 23 (129)	7 ± 2 (6)	44	137	9			
	Su 2015–2016							47 ± 3 (48)	274 ± 74 (286)	10 ± 5 (10)	49 ± 3 (49)	234 ± 38 (241)	12 ± 8 (10)	46 ± 1 (46)	204 ± 17 (204)	7 ± 1 (7)
	Su 2016–2017							40 ± 2 (40)	114 ± 20 (122)	6 ± 2 (6)	50 ± 3 (49)	198 ± 44 (178)	8 ± 4 (8)	52 ± 2 (52)	259 ± 97 (253)	7 ± 6 (5)
	A 2017				44 ± 2 (44)	105 ± 23 (105)	9 ± 3 (9)	41 ± 3 (40)	147 ± 29 (145)	6 ± 2 (5)						
	Su 2017–2018				42 ± 1 (42)	171 ± 17 (166)	5 ± 1 (4)	44 ± 4 (43)	196 ± 53 (162)	6 ± 3 (5)	44 ± 5 (45)	197 ± 67 (186)	6 ± 4 (5)			
	A 2018				46 ± 2 (46)	220 ± 46 (217)	3 ± 2 (2)	47 ± 1 (47)	231 ± 20 (230)	5 ± 10 (2)	52 ± 3 (52)	253 ± 37 (260)	4 ± 1 (4)			
	Su 2018–2019	37 ± 2 (37)	107 ± 27 (115)	5 ± 2 (5)				41 ± 5 (41)	162 ± 73 (136)	5 ± 1 (6)	47 ± 4 (48)	170 ± 79 (156)	6 ± 3 (6)	51	339	5
	A 2019	42 ± 2 (42)	163 ± 9 (163)	2 ± 0 (2)	50 ± 3 (51)	264 ± 57 (273)	3 ± 3 (2)	45 ± 4 (47)	220 ± 89 (220)	4 ± 4 (2)	52	321	5	51	273	1

(*Continued on next page*)

Table 2. (*Continued*)

Location	Season and year	Juveniles			Subadult females			Subadult males			Adult females			Adult males		
		Length	DM	Hg	Length	DM	Hg	Length	DM	Hg	Length	DM	Hg	Length	DM	Hg
WAP	Su 2013–2014				48	208	5	45 ± 4 (45)	170 ± 88 (159)	10 ± 4 (10)	43 ± 2 (42)	131 ± 50 (108)	10 ± 6 (8)	42	107	12
	A 2014				40 ± 2 (40)	105 ± 18 (101)	2 ± 2 (2)	43 ± 3 (43)	145 ± 34 (155)	2 ± 1 (2)	51	187	2			
	Su 2014–2015							44 ± 3 (44)	183 ± 40 (163)	7 ± 1 (7)	43 ± 1 (43)	158 ± 41 (159)	7 ± 1 (7)	44	163	9
	A 2015				41 ± 3 (41)	134 ± 25 (137)	5 ± 5 (3)	40 ± 1 (41)	127 ± 12 (128)	6 ± 6 (5)	47	222	2	49 ± 2 (49)	221 ± 8 (221)	2 ± 0 (2)
	Su 2015–2016							45 ± 4 (44)	187 ± 91 (159)	11 ± 5 (10)	47 ± 5 (46)	230 ± 101 (208)	8 ± 4 (8)	48 ± 2 (49)	313 ± 47 (326)	7 ± 1 (7)
	A 2016				48 ± 2 (48)	244 ± 45 (236)	2 ± 1 (1)	47 ± 6 (50)	251 ± 92 (291)	2 ± 2 (2)	50 ± 6 (51)	253 ± 95 (253)	4 ± 4 (3)	49	276	1
	A 2017				45 ± 3 (45)	177 ± 45 (183)	2 ± 2 (1)	46 ± 0 (46)	201 ± 32 (205)	1 ± 1 (1)						
	W 2017				42 ± 4 (40)	146 ± 33 (125)	2 ± 1 (2)	40 ± 1 (40)	138 ± 7 (139)	3 ± 2 (3)						
	A 2018				38 ± 2 (38)	133 ± 27 (125)	1 ± 0 (1)	41 ± 2 (42)	142 ± 8 (144)	1 ± 1 (1)						
	W 2018				43 ± 2 (44)	151 ± 25 (163)	2 ± 0 (2)	44 ± 2 (43)	172 ± 31 (165)	4 ± 4 (2)						
	A 2019	37 ± 3 (37)	98 ± 20 (98)	1 ± 2 (1)	42 ± 4 (41)	136 ± 48 (127)	3 ± 1 (2)	42 ± 3 (41)	149 ± 35 (139)	2 ± 1 (1)				46	155	13
	W 2019	28	47	1	40 ± 4 (40)	109 ± 31 (105)	4 ± 4 (2)	36 ± 2 (35)	88 ± 17 (80)	3 ± 2 (3)						

Values are reported as mean ± 1 standard deviation, with the median in parentheses. Samples without replicates only have a mean value. Empty cells indicate combinations of categories for which we did not have samples. Data for samples pooling adults and subadults are not included. SG, South Georgia; SOI, South Orkney Islands; WAP, Western Antarctic Peninsular; A, autumn; Sp, spring; Su, summer; W, winter.

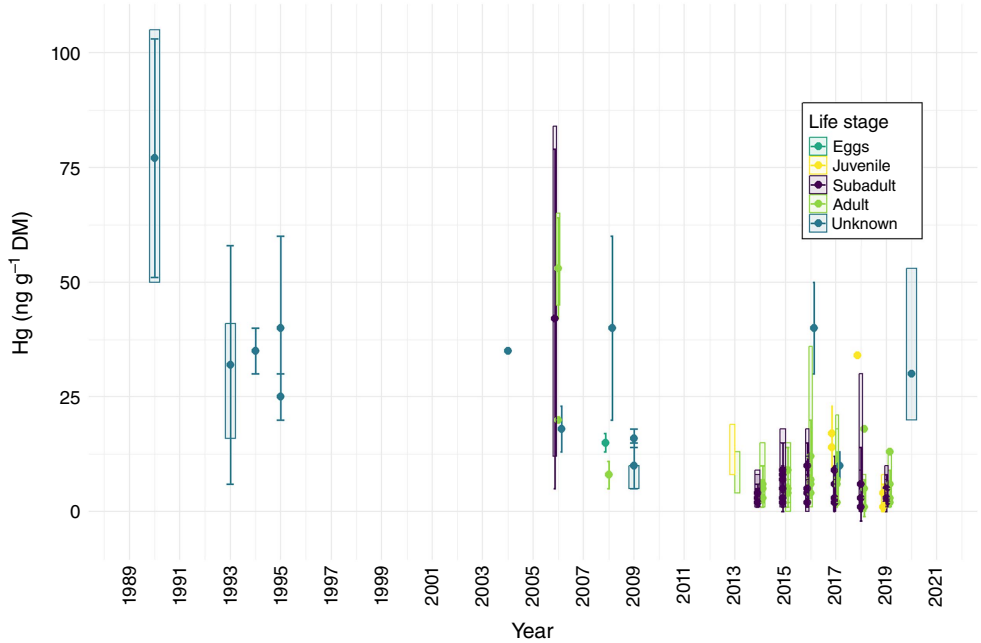

Fig. 3. Compilation of historical and current (1989–2020) mercury (Hg) concentration (ng g^{-1} dry mass, DM) in krill sampled from various locations around Antarctica (see Table 1 for site names and publication references; values from Stoeppler and Brandt (1979) are excluded due to likely lower instrument precision). Circles, vertical bars and shaded rectangles represent mean, standard deviation and range values, when available. Life stages, when known, are indicated by different colours: dark green, eggs; yellow, juveniles; purple, subadults; light green, adults; and dark blue, individuals of unknown life stage.

length had a significant, although minor, negative effect on Hg concentrations (Wald test: $\chi^2 = 7.5$, $P = 0.006$), contributing to only 0.9% of the total (53.8%) deviance explained by the GLM. We obtained a similar result when the data were categorised by location and season: significant negative correlations, but only for SG krill in the winter and WAP krill in the summer (Fig. 4*a*; $R^2 = 0.17$ and 0.21, $P < 0.001$ and $= 0.001$). Even then, only 17 and 21% of the variance was explained by the regression. The relationship between krill dry mass and Hg concentrations (Fig. 4*b*) was similar to that described for krill length. Dry mass had greater predictive power than length as an explanatory variable in the GLM, with a significant and slightly negative effect on Hg concentrations (Wald test: $\chi^2 = 26.0$, $P < 0.001$), explaining 3.8% of the total (55%) deviance. We also observed significant negative correlations between DM and Hg in SG krill during winter and WAP krill during summer (Fig. 4*b*; $R^2 = 0.12$ and 0.26, $P < 0.001$), as well as in SOI and WAP krill during autumn ($R^2 = 0.07$ and 0.10, $P = 0.047$ and 0.005). Linear regressions only explained 7–26% of the variability in the data. Given the superior performance of the mass models (in comparison to length), we only report mass-based GLM results henceforth, with results for length-based models reported in Supplementary Table S1. It should be noted that any conclusions about bioaccumulation based on length or mass could be confounded by the fact that female and male krill reach maturity at different lengths (35–36 and 43–44 mm respectively) (Siegel and Loeb 1994; this study), although we did not find evidence for the latter (Supplementary Fig. S3).

A two-orders of magnitude range is typically required to obtain clear relationships of metal and metalloid concentration with animal biomass (Boyden 1977), which could explain the minor role of dry mass in our results. As krill grow and age, their Hg concentrations are likely to decrease because their growth rate exceeds the rate at which they accumulate Hg (Korejwo *et al.* 2023). Although we observed a trend of slightly lower Hg concentrations in larger krill, this relationship was not as pronounced or statistically significant as that reported in many other studies (Locarnini and Presley 1995; Corbisier *et al.* 2004; Seco *et al.* 2019; Sontag *et al.* 2019; Bengtson Nash *et al.* 2021; Korejwo *et al.* 2023). The lack of strong relationships between krill size (length and mass) and Hg concentrations in our study is most likely explained by the lack of juvenile samples (i.e. smaller individuals with higher Hg concentrations) in the dataset. Furthermore, length and mass are not necessarily good indicators of age as, depending on food availability, female krill can shrink in winter and increase in size during reproduction (Tarling *et al.* 2016; Korejwo *et al.* 2023). Both male and female krill also lose mass during winter food shortages as they consume their lipid reserves to supplement

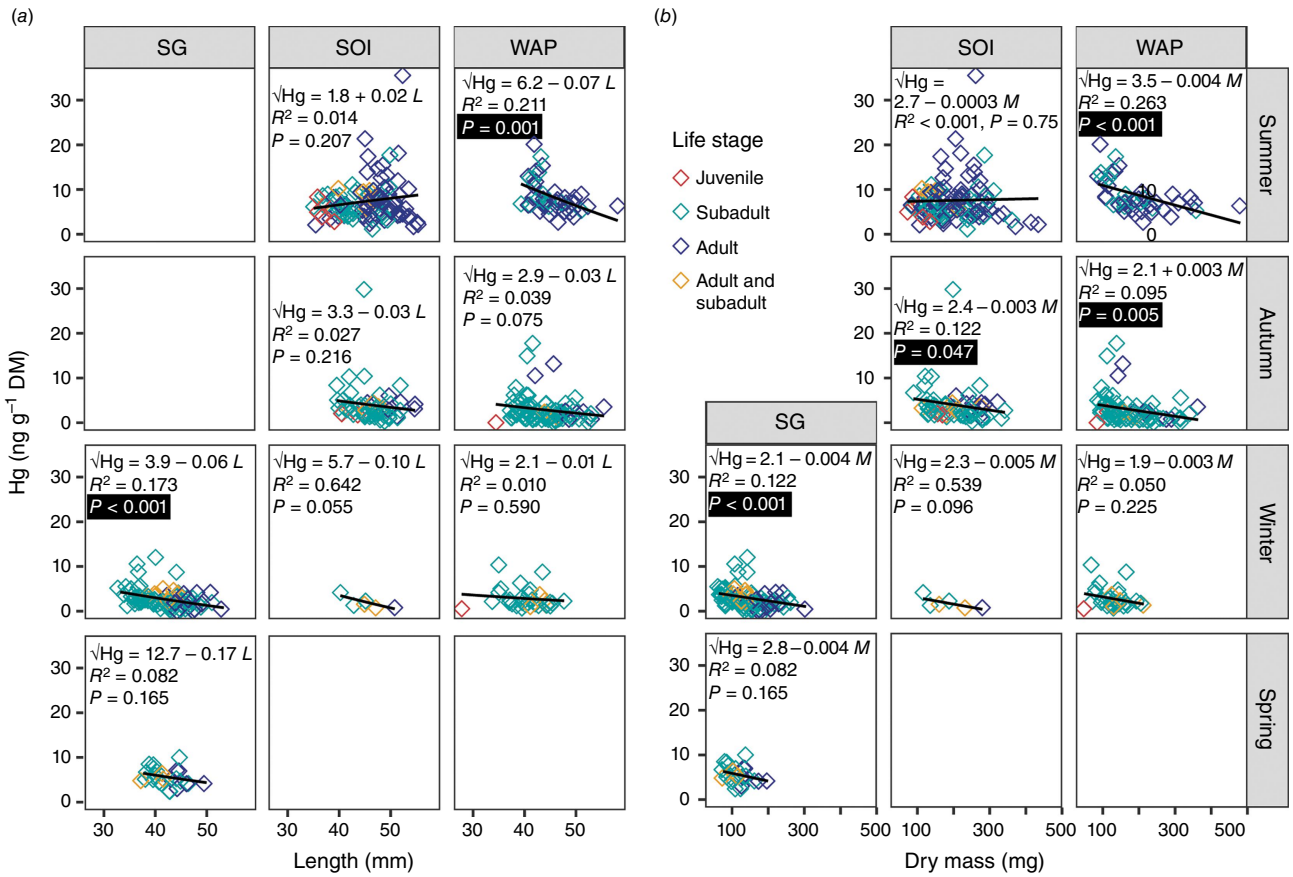

Fig. 4. Scatter plots of krill mercury (Hg) concentrations (ng g^{-1} dry mass, DM) against krill (*a*) length (mm) and (*b*) dry mass (mg). Life stages are colour-coded, with the samples pooling adult and subadult data making up their own category. Linear regressions for the relationship between the square-root of Hg and length (*L*) or dry mass (*M*) and their determination coefficients (R^2) and *P* values are shown in each graph, this is within levels of location (vertical facets; SG, South Georgia; SOI, South Orkney Islands; WAP, Western Antarctic Peninsula) and season (horizontal facets). Statistically significant results ($\alpha = 0.05$) are indicated by black boxes around *P* values.

nutrition from opportunistic feeding (if any) (e.g. Torres *et al.* 1994).

Predicting Hg concentrations in krill based on their life and maturity stage was also not straightforward. The effect of sex was not statistically significant in the GLM (Wald test: $\chi^2 = 0.4$, $P = 0.51$), nor could we find clear differences when comparing between seasons within locations or throughout the dataset (Table 2; Supplementary Fig. S4 and S5). Results were similar for summer and autumn data for the SOI and WAP, both within adult and subadult life stages (Supplementary Tables S2 and S3). The pattern revealed by our GLM, plots and ANOVAs (krill sex is unrelated to Hg concentrations) is expected, given the lack of evidence for sex-specific differences in krill food intake (Polito *et al.* 2013); this also agrees with previous results from published studies for adult krill (e.g. Seco *et al.* 2019; Korejwo *et al.* 2023). Krill life stage also had no significant influence on Hg concentrations (Table 2) in our GLM (Wald test: $\chi^2 = 3.6$, $P = 0.17$) and ANOVAs for the SOI and SG during summer and spring (Supplementary Tables S2 and S3). Juvenile krill often exhibit a wide range of Hg concentrations; in our study, they were not significantly higher than those of subadult and adult krill. Our low juvenile sample size may have only captured individuals at the lower range, so we could not meaningfully verify this trend. Studies that revealed different Hg concentrations between juveniles and adult krill often condensed various maturity stages into one adult stage category. When these maturity stages are disentangled, differences in Hg concentrations to juveniles may not be significant. Korejwo *et al.* (2023) reported statistically significant differences in Hg concentrations between juveniles and adults, but non-significant results were observed between juveniles, subadults and two adult maturity stages. The latter agrees with our findings, and both show that a finer resolution within the adult substages better represents the gradual changes in Hg concentration with krill development.

The influence of abiotic metrics (location and season) on mercury concentrations in krill

Many factors are believed to contribute to geographical differences in krill Hg concentrations, which may vary

temporally. All our samples were obtained by the same fishing vessel, and locations were sampled at different times of the year. This led to an unbalanced dataset in which the timing of fishing was location-dependent (during summer–autumn, autumn–winter and winter–spring in SOI, WAP and SG respectively; Fig. 2). Of the 56 unique month and year combinations for which we have data, only 11 contained samples from two locations, and none from all three sites. Although the GLM revealed statistically significant differences (Wald test: $\chi^2 = 11.2$, $P < 0.01$), it estimated the effect of each location as a separate coefficient, extrapolating across months and years during which locations were not sampled. This translated into a lack of statistical power for geographic location as a predictor variable (e.g. only 1.7% of the 55% total deviance was explained by the GLM), preventing us from speculating about its influence on krill Hg concentrations. Where comparisons were available between locations for a given month (Fig. 5, Tables 1 and 2), values appeared to be similar, providing some confidence that any seasonal variations discussed below are not confounded by an effect of location. Volcanic activity had no influence on Hg concentrations in our study, as none of the WAP sites showed significantly elevated Hg concentrations.

Mean Hg concentrations in our study were considerably and consistently lower in autumn and winter (3 ± 4 and 3 ± 2 ng g^{-1}) than in spring and summer (6 ± 2 and 8 ± 4 ng g^{-1}) (Fig. 5, Table 2). When results were looked at on a yearly basis, this pattern still held, although with month-specific variations (Fig. 5*a*). For example, December concentrations were higher in 2013, 2015 and 2016 than in 2014, 2017 and 2018, and March concentrations at times resembled values from summer. The GLM revealed that the month (Wald test: $\chi^2 = 138$, $P < 0.001$) and month–year interaction (Wald test: $\chi^2 = 135$, $P < 0.001$) terms had the strongest influence on Hg concentrations in krill, explaining 20 and 20.6% of the model deviance (55% in total). The fishing year also had a significant influence (Wald test: $\chi^2 = 58$, $P \leq 0.001$) and explained 8.6% of the deviance in Hg concentration data. Estimated marginal mean concentrations averaged across years within the GLM were significantly higher in summer months (December to February) relative to other sampled months (Supplementary Table S4),

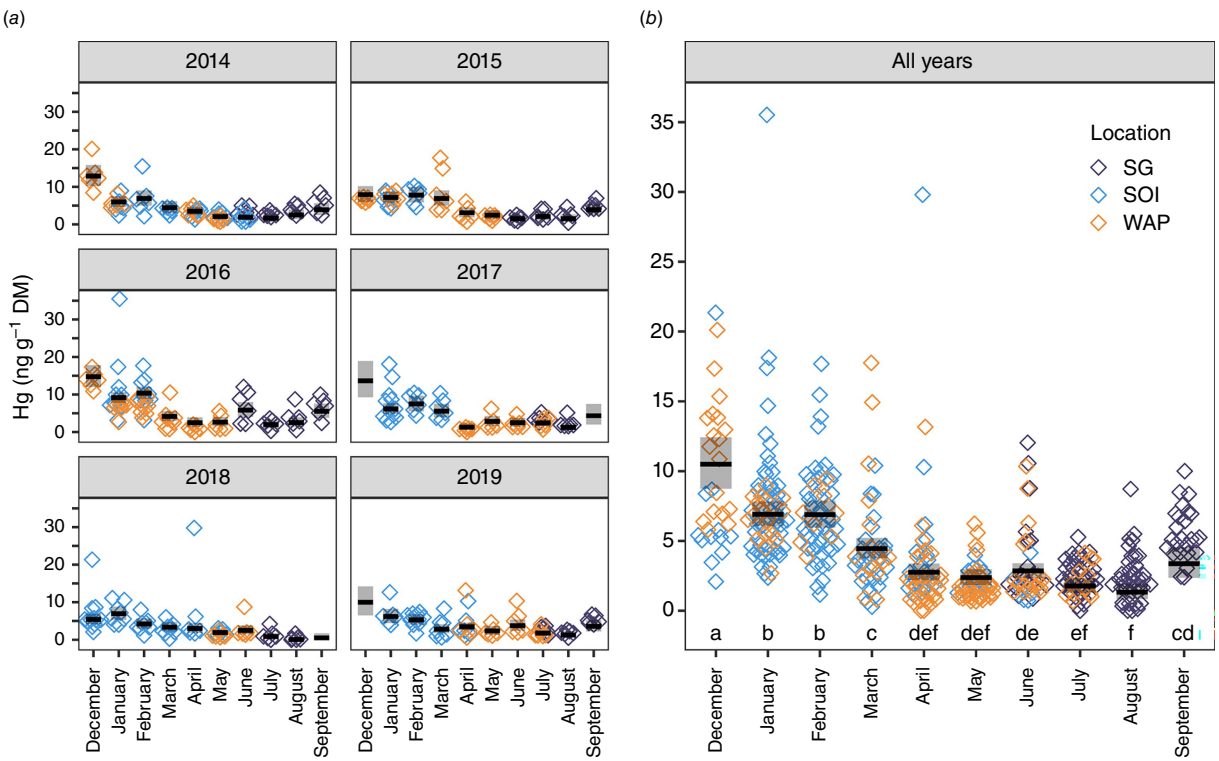

Fig. 5. Monthly average influence of seasonality (by sampling month) on krill mercury (Hg) concentrations (ng g^{-1} dry mass, DM) per year sampled (*a*) and over all years (*b*). Months in (*a*) begin in December of the previous year to facilitate visualisation in terms of seasons as well as months. Colours indicate sampling locations (purple for South Georgia, SG; light blue for South Orkney Islands, SOI; orange for Western Antarctic Peninsula, WAP). The horizontal black bars are estimated marginal means from a GLM including main effects with interannual variability in seasonal effects (month–year interaction term). Shaded rectangles represent the 95% confidence intervals on the estimated marginal means. Months with different letters (a through f) at the bottom of the plot in (*b*) had significantly different Hg concentrations based on estimated marginal means averaged over all other factors in the GLM.

with Hg concentrations in December higher than those in January and February (Fig. 5*b*; Sidak-adjusted pairwise comparison: *t*-ratios = 4.13 and 3.95 respectively, *P* values <0.01). Estimated mean concentrations in March were significantly lower than those in summer and higher than other autumn and winter months (Supplementary Table S4), highlighting March as a period from which krill Hg concentrations start decreasing. Similarly, the estimated mean concentrations in September were significantly higher than those for July and August but were statistically indistinguishable from those between March and June (Fig. 5*b*, Supplementary Table S4). The latter highlighted September as a period in which krill Hg concentrations were increasing again towards an early summer maximum.

Ecological processes and mercury concentrations in krill

The best GLM fitted to our data revealed that krill size, as well as the location and timing of sampling, all contribute to explaining Hg concentrations in individuals, with the latter showing the highest prediction power (Supplementary Table S1). Ecological processes interlink these variables and need to be considered jointly to understand Hg intake and accumulation in krill. Different krill life stages tend to inhabit different open ocean (deep and shallow water) and coastal (ice covered and ice free) locations (Fig. 1). Krill spawn offshore in areas where high export of phytoplankton to depth and subsequent organic matter remineralisation promotes biomethylation of Hg to MeHg (Cossa *et al.* 2011; Blum *et al.* 2013; Sontag *et al.* 2019), which they readily bioaccumulate. Larval populations develop in this environment and, as such, juvenile krill are expected to develop amid higher MeHg concentrations, resulting in higher Hg concentrations in their tissues – a pattern we could not verify due to our small juvenile sample size. Larvae and juveniles migrate toward coastal areas where ice forms, being thus subject to glacial inputs (Canário *et al.* 2017; Chiang *et al.* 2021; Matias *et al.* 2022), where higher biomethylation and MeHg concentrations are also expected (Bargagli *et al.* 1998; Sontag *et al.* 2019). Adult krill feed less during winter due to their reduced metabolic rate (both may be triggered by photoperiod; Meyer 2012 and references therein), while juveniles continue to feed, accumulating Hg in their tissues (Meyer *et al.* 2009, 2010; Schaafsma *et al.* 2017; Korejwo *et al.* 2023). The above-mentioned processes are all linked to light and temperature, which vary spatially and temporally in the Southern Ocean, making it difficult to differentiate the influence of krill life stages on Hg concentrations from that of location and time.

Based on our results, which contained several adult maturity substages (Supplementary Fig. S6 and S7), and on the literature, we propose that krill undergo three major changes in Hg concentration pattern during the juvenile-to-adult transition. The first is a decrease in Hg concentration from the juvenile to the subadult stage, as juveniles are expected to accumulate more Hg than (sub)adults due to their higher metabolic demands (i.e. they eat more) and to greater Hg availability in the environment they occupy. As they become subadults, accumulated Hg is 'diluted' by a larger body mass, and krill Hg intake and assimilation decrease comparatively (Karimi *et al.* 2007; Korejwo *et al.* 2023). Concentrations then increase as subadults gradually mature into adults and decrease again when gravid females spawn and males release spermatophores (as suggested by Seco *et al.* 2019).

Seasonal and interannual variations in light and temperature at a location also lead to highly variable phytoplankton production and microbial communities (Clarke and Leakey 1996; Bargagli *et al.* 1998). Some studies have suggested a shift in the proportion of phytoplankton-to-zooplankton intake during krill development might affect Hg bioaccumulation (Polito *et al.* 2013; Sontag *et al.* 2019). Antarctic summers are characterised by higher light availability and water temperatures (than winters), such that primary production is highly seasonal in the Southern Ocean. The summer phytoplankton biomass results in krill selectively grazing on diatoms. The seasonality of primary production in Antarctica is also reflected in consumer over-wintering strategies (Bargagli *et al.* 1998). As krill grow and the availability of summer phytoplankton decreases, larger individuals may adjust their diet and foraging range, transitioning to consuming heterotrophs such as small copepods and protozoans (Polito *et al.* 2013) (Fig. 1). During winter, adult krill feeding activity is reduced considerably in comparison to spring (14% of spring feeding rates), although it is still sufficient to avoid shrinkage or to survive the season (Torres *et al.* 1994; Meyer *et al.* 2010). Owing to the food shortage, krill primarily sustain themselves by extensively using their lipid reserves (Hagen *et al.* 2001; O'Brien *et al.* 2011), at a rate of ~10% body lipid dry mass^{-1} month^{-1} (Meyer 2012), with the lipid content decreasing to 25% of its maximum content (Hagen *et al.* 1996).

Several studies have linked lipid stores to the bioaccumulation of toxic organic substances (reviewed by Kainz and Fisk 2009), prompting us to look for relationships between Hg and total fatty acid (TFA) concentrations in krill (Ericson *et al.* 2018; Hellessey *et al.* 2018; R. M. Franco-Santos, P. D. Nichols and P. Virtue unpubl. data). When these variables are plotted (Fig. 6*a*), the mismatch between their highest and lowest concentrations is evident – Hg peaks in early summer (in the absence of late spring data), and is less than half that content by April–May (autumn). In comparison, TFA concentations peak in autumn and reduce significantly during winter to the lowest in spring. We offer three possible explanations for this pattern, although further studies are needed to fully confirm them. The first would involve the physiological elimination mechanisms previously mentioned (Seco *et al.* 2019). Lipids are a major component of eggs and sperm; if Hg bioaccumulates within lipid stores, we can expect an immediate decrease in Hg concentration when krill release sperm and spawn. Krill gonad maturation starts

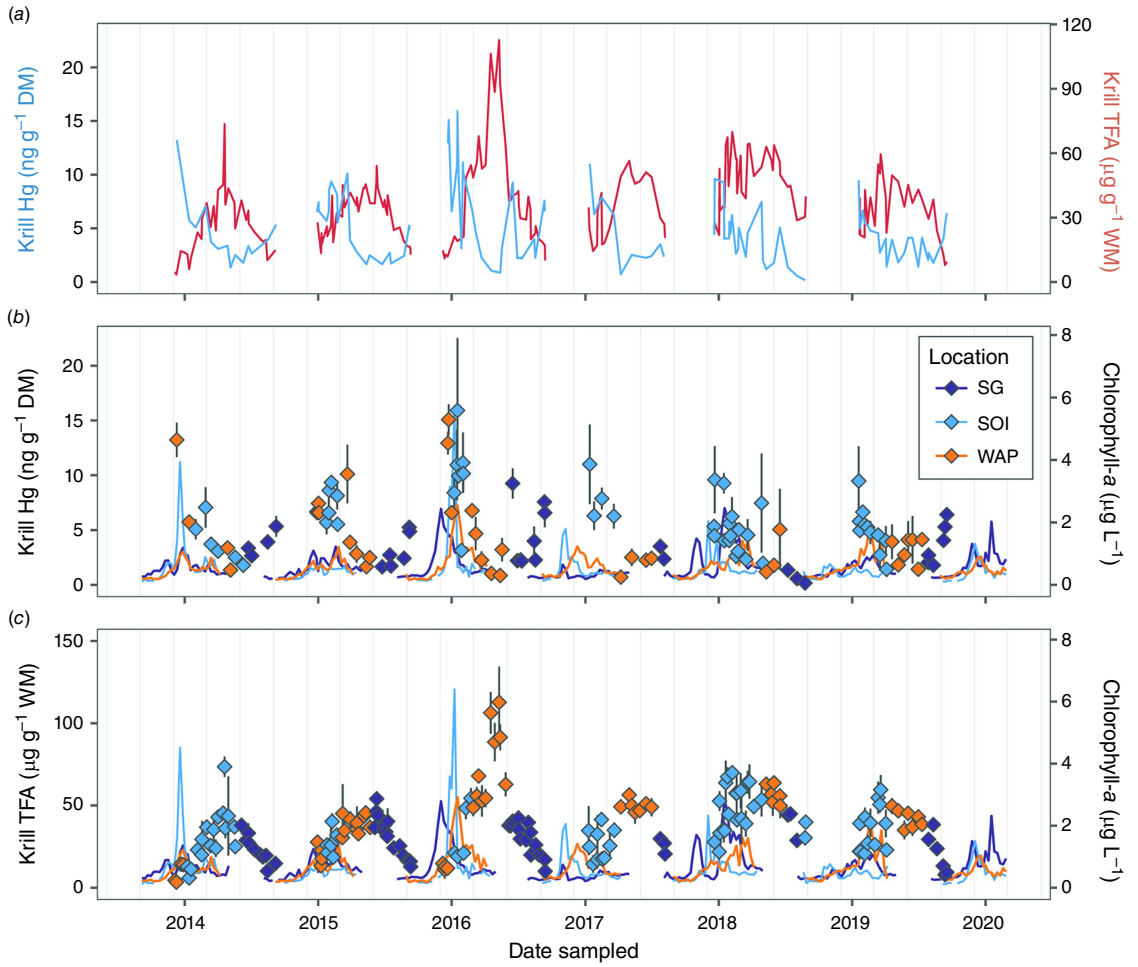

Fig. 6. Relationships between mercury (Hg) concentration (ng g^{-1} dry mass, DM) and total fatty acid (TFA) content (µg g^{-1} wet mass, WM) in krill with satellite-derived sea surface chlorophyll-*a* concentrations (µg L^{-1}). The average comparison between Hg concentration (blue line) and FA content (red line) over the sampling period (from different individuals collected by the same sampling effort; Ericson *et al.* 2018; Hellessey *et al.* 2018; Franco-Santos *et al.*, unpubl. data) is shown in (*a*), whereas (*b*) and (*c*) present time series (diamond points; error bars are ±1 s.d.) of daily mean krill Hg concentration and FA content overlayed with 8-day average (lines) chlorophyll-*a* concentrations (respectively). Colours indicate the sampling location (purple for South Georgia, SG; light blue for South Orkney Islands, SOI; orange for Western Antarctic Peninsula, WAP).

in spring, with reproduction occurring between mid-November and March (Witek *et al.* 1980). Most (68%) of our adult female samples had yet to develop eggs during summer (December–February), indicating that spawning in the sampled locations occurred towards the end of the reproductive period. Our data might have provided evidence for such a relationship if we knew the timing of spawning events. The potentially lagged response of Hg concentration (lowest in April to May) to reproduction (November to March) suggests that this mechanism had a minor role in explaining our results.

Another explanation for the mismatch between Hg and TFA concentrations would consider lipid and protein dynamics in krill, as these and other dietary components have a physiological interaction with Hg (Olsvik *et al.* 2011). Were Hg in lipids, we would expect the former to peak in autumn, together with TFAs, rather than to bottom out, as was observed (Fig. 6). Lavoie *et al.* (2010) propose that lipid-rich organisms are expected to have a low Hg concentration for a Canadian food web. This would be due to (1) MeHg having a high chemical affinity to sulfhydryl groups from certain proteins (Wolfe *et al.* 1998), as seen for fish (Bloom 1992) and cephalopods (Bustamante *et al.* 2006), and (2) the proportion of proteins being inversely related to that of lipids (i.e. only one is metabolised for energy). Previous studies report lower protein content in adult krill in autumn than in winter and summer (Meyer *et al.* 2010; Kim *et al.* 2014), potentially following its metabolism during the summer while lipids are accumulated (Meyer 2012), and negligible use of proteins for energy provision in winter (~3% body $protein^{-1}$ DM $month^{-1}$;

Meyer *et al.* 2010; Meyer 2012). The MeHg–protein association could potentially explain our results. We know that protein-affinitive organic Hg (i.e. MeHg) in adult krill accounts for 5–37% of total Hg (Seco *et al.* 2019; Sontag *et al.* 2019; Korejwo *et al.* 2023). In addition, the significant drop in Hg concentration between summer and mid-late autumn and subsequent increase between autumn and winter follows the same seasonal pattern described for protein content in adult krill.

In our study, total Hg concentrations appear to be synchronised with phytoplankton bloom intensity, as evidenced by increased sea-surface chlorophyll-*a* concentrations (Fig. 6*b*, *c*). Korejwo *et al.* (2023) reported that an average of 48% of the Hg fraction in *E. superba* (April, WAP) is labile (inorganic) Hg-halides. The latter are known to be an important fraction of Hg species in microorganisms, including phytoplankton (Bełdowska *et al.* 2018), and their presence in large amounts in krill, therefore, signifies feeding on phytoplankton. The impulse response function based on the Vector Autoregressive Modelling of chlorophyll-*a* and krill Hg concentrations demonstrates that there is a 32–40-day lag between an increase in the former and peak values for the latter, with the resulting increase in krill Hg (~0.1 ng g^{-1} DM) subsiding to baseline values after ~3 months (Fig. 7). We propose, therefore, that the seasonality in krill Hg concentrations is affected by both the dietary uptake of labile Hg-halides during the annual phytoplankton bloom period (spring through summer) and by the relationship between MeHg and certain proteins, with spawning potentially and partially explaining Hg loss during autumn. Hg-halides do not tend to biomagnify (Lawson and Mason 1998), but MeHg does, which could be problematic despite its lower concentrations (than the former). Future analyses of Hg speciation in krill may also shed light on the role of lipids in Hg assimilation.

Bioaccumulation and biomagnification

Antarctic phytoplankton passively assimilate inorganic Hg and MeHg from the surrounding water; the former mainly binds to algal cell membranes, whereas the latter accumulates in their cytoplasm (Mason *et al.* 1996). This physiological difference leads to a 4× greater assimilation of MeHg by primary consumers than inorganic Hg (Mason *et al.* 1995, 1996). The higher transfer efficiency of MeHg to higher trophic levels, coupled with differences in species' abilities to eliminate it, is the basis for its biomagnification potential in complex food webs (see Lavoie *et al.* 2013 for a summary of physical, chemical and biological controls on the process). Many food web studies have reported that bioaccumulation and biomagnification of toxic substances occur in Antarctic marine food webs, however, the role played by krill in this process is unclear (Stowasser *et al.* 2012). The krill-centred Antarctic food chain is relatively simple, comprising phytoplankton, filter-feeding krill and select vertebrate predators.

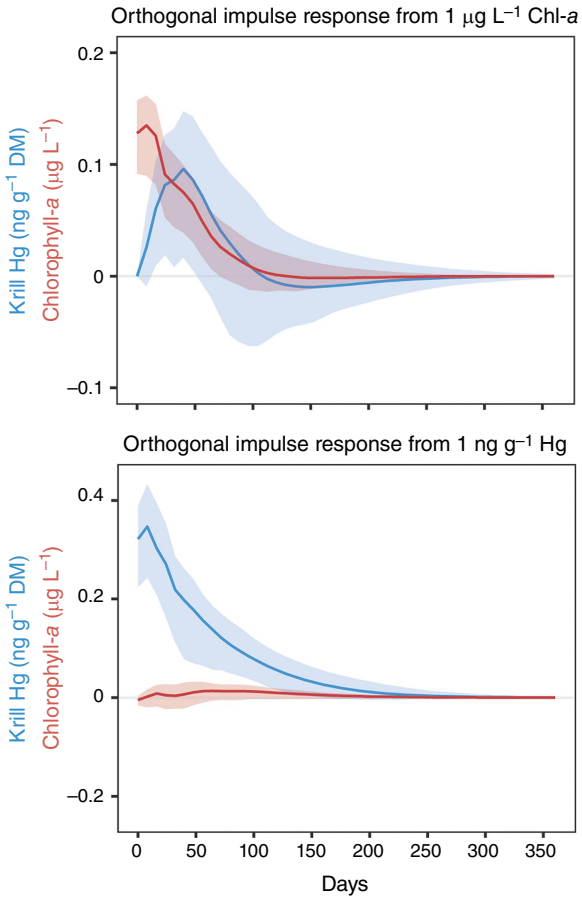

Fig. 7. Impulse Response Function based on a Vector Autoregressive Model of satellite-derived sea surface chlorophyll-*a* (μg L^{-1}) and krill Hg (ng g^{-1} dry mass, DM) concentrations (red and blue lines respectively; shaded areas represent 95% confidence intervals based on bootstrapping). The upper panel shows that an impulse of 1 μg L^{-1} chlorophyll-*a* leads to an increase in krill Hg concentration, which peaks ~32–40 days later. It then subsides ~80–100 days later. Note that, although the computed impulse for chlorophyll-*a* was 1 μg L^{-1}, a self-feedback mechanism led to a net change of only 0.05 μg L^{-1} at the next time step. The bottom panel shows that an increase in Hg does not influence chlorophyll-*a* concentrations, confirming that there is a clear response of Hg to chlorophyll-*a*.

Interannual shifts in prey availability may result in krill and higher trophic level species consuming alternate prey (Seco *et al.* 2021). When evaluating Hg biomagnification, it's important to carefully define and limit the scope of krill-based food webs, especially when the consumer species is migratory, and to provide evidence (e.g. mass balance calculations) for any biomagnification claims.

To verify if Hg biomagnification reflects the krill-based Antarctic food webs, we conducted simple mass balance calculations for Antarctic baleen (blue, fin and humpback) whales using the equation

$$W_{[\mathrm{MeHg}]} = \frac{I_{\mathrm{K}} \times I_{\mathrm{F}} \times \mathrm{LS} \times K_{[\mathrm{Hg}]} \times K_{[\mathrm{MeHg}]}}{W_{\mathrm{wm}}}$$

and available data on: whale-specific ingestion rates (I_K, g krill day^{-1}), feeding frequency (I_F, days year^{-1}), life span (LS, years) and average weight (W_{wm}, g wet mass, WM), and krill-specific Hg ($K_{[Hg]}$, μg g^{-1} WM) and MeHg ($K_{[MeHg]}$, as a percentage of total Hg) contents. The resulting range of values for whale MeHg concentration ($W_{[MeHg]}$, μg g^{-1} WM) was then compared to values reported in the literature (Table 3). Our mass balance results were within (although narrower than) the range reported in the literature. The proportion of MeHg (as a percentage of total Hg) in whales has been reported as 82% (Sanpera *et al.* 1993) and 106% (Maage *et al.* 2017); given the likelihood of errors in MeHg estimation in the early 1990s and the fact that total Hg and inorganic Hg are not readily transferred to higher trophic levels, we assumed the value to be 100%. It should be noted that Hg concentrations obtained for whales were not accompanied by the corresponding individual size and age.

We also extracted values from published food web studies that provided carbon and nitrogen stable isotope data (^{13}C and ^{15}N) along with Hg concentrations in various organisms that consume krill (Fig. 8). Little increase occurs from phytoplankton (diatoms) to krill. Inorganic Hg is not efficiently assimilated (Lawson and Mason 1998) and constitutes 90% of total Hg in phytoplankton (Silva-Filho *et al.* 2014). The remaining organic MeHg is assimilated by zooplankton with an efficiency of 65% (Mason *et al.* 1995), and makes up 5–37% of the krill total Hg content (Seco *et al.* 2019; Sontag *et al.* 2019; Korejwo *et al.* 2023). Transfer of Hg between krill and the next trophic level can be separated into two different patterns for whales and fish, both showing a large increase in Hg concentration. The increase in ^{15}N of whales (2–4‰) reflected the predicted values for two adjacent trophic levels (i.e. whales feeding on krill), as expected from our mass balance model calculations and also supported by ^{13}C values (e.g. Angel Romero *et al.* 2017). The ~6‰ increase in ^{15}N from krill to fish, however, suggested a missing intermediary trophic level, with ^{13}C values indicating feeding by fish on mixed food sources (e.g. Cipro *et al.* 2017). Values for other vertebrate species are also plotted in Fig. 8, but have not been considered as part of the fish food chain, as the former are migratory and, based on N isotope values, consume invertebrates other than krill and may not consume fish. Concentrations of Hg are so high in penguins, seals and flying birds (Endo *et al.* 2002; Bengtson Nash *et al.* 2021) that a large percentage of Hg needs to be present as MeHg. Such biomagnification can only occur in the presence of at least four trophic levels (Bowles *et al.* 2001), so Hg sources other than krill must be available to these vertebrates. This interpretation is based on phytoplankton, which contain only very low Hg concentrations (mostly inorganic Hg), being the organic matter source at the base of the food web. If other MeHg-rich primary producers are present, as could be expected in systems with guano input from bird colonies (Jarzynowska *et al.* 2023), our model would be invalid. In such a case, another model would have to be

Table 3. Parameters used for mass balance model exercise for biomagnification of mercury (Hg) in Antarctic blue, fin and humpback whales: whale feeding rate on krill (I_K, g day^{-1}), whale feeding frequency (I_F, days year^{-1}), life span (LS, years), krill Hg content ($K_{[Hg]}$, μg g^{-1} wet mass, WM; conversion of dry into wet mass used a 5:1 ratio), krill methylmercury (MeHg) content ($K_{[MeHg]}$, as a percentage of total Hg content) and whale weight (W_{wm}, g).

Whale species	I_K	I_F	LS	$K_{[Hg]}$	$K_{[MeHg]}$	W_{wm}	Range	$W_{[MeHg]}$
Blue	5.4–14.5 × 10^6 (Savoca *et al.* 2021; NOAA Fisheries 2023*a*)	120 (SeaWorld 2024)	80–90 (NOAA Fisheries 2023*a*)	2.2 × 10^{-3} (averaged means from Table 1 except Stoeppler and Brandt 1979)	5–37% (Seco *et al.* 2019; Sontag *et al.* 2019; Korejwo *et al.* 2023)	4.5–15 × 10^7 (NOAA Fisheries 2023*a*)	0.04–2.83	0.34 (Trumble *et al.* 2013)
Fin	≤ 1.8 × 10^6 (Oceanwide Expeditions 2024)	275 (NOAA Fisheries 2023*b*)	80–90 (NOAA Fisheries 2023*b*)			3.6–7.3 × 10^7 (NOAA Fisheries 2023*b*)	0.06–10.07	0.02–0.09 (Endo *et al.* 2012)
Humpback	4.6 × 10^5 (Owen *et al.* 2017)	275–365 (Owen *et al.* 2017)	80–90 (NOAA Fisheries 2024)			≤3.6 × 10^7 (NOAA Fisheries 2024)	0.03–0.34	0.001–1.3 (Bengtson Nash *et al.* 2021)

After calculating all possible results for a given species (Range), the resulting range in Hg concentration is compared with the whale MeHg content ($W_{[MeHg]}$, μg g^{-1} WM) reported from published studies. Value-specific references are given in parenthesis.

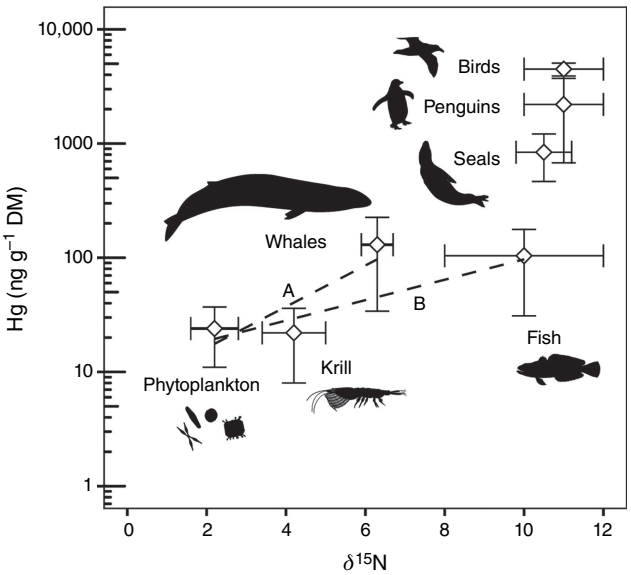

Fig. 8. Collation of concurrently published stable isotope and mercury (Hg) data (n = 128) on the bioaccumulation and biomagnification of Hg in krill-based Antarctic food webs. The graph presents Hg concentrations (ng g^{-1} dry mass, DM) and ^{15}N values (‰) for phytoplankton as primary producers, krill as primary consumer, fish or whales as secondary consumers, and other unknown consumer levels of migratory species (seals, penguins and flying birds). Data sources: Bargagli *et al.* (1998), Anderson *et al.* (2009), Aubail *et al.* (2011), Brault (2012), Endo *et al.* (2012), Carravieri *et al.* (2013), Angel Romero *et al.* (2017), Cipro *et al.* (2017), Seco *et al.* (2021*a*) and Matias *et al.* (2022).

proposed to explain the biomagnification of Hg to the levels reported in the literature for predators. We also did not take into account life span of modelled species, which could be related to their Hg concentrations.

Our study adds a considerable wealth of information, both data and metadata, to existing baseline records of krill Hg concentrations at various locations in the Southern Ocean. This dataset will be valuable for short- and long-term monitoring of climate change and other effects in the region. Although we observed yearly cycles, with Hg concentrations peaking in early austral summer together with sea surface chlorophyll-*a* concentrations and bottoming out in winter, on a decadal scale, concentrations appear fairly stable, with minor location-specific variations. It would be useful if future studies could compare decadal trends in Hg concentrations in various trophic levels with information on local anthropogenic emissions over the years. We also noted that krill Hg concentrations varied (a) between locations, although the unbalanced character of our data limited any further interpretations on this effect, and (b) by individual size, although our low juvenile sample size hindered any further investigation into this. Future studies should record individual sex and stage before Hg analysis to better understand the effects of physiology and diet on ontogenetic changes in Hg concentrations. Lastly, future studies on Hg biomagnification in Antarctic megafauna should strive to present Hg data for as many producers and consumers as potentially expected, together with stable isotope data to confirm trophic levels. When available, future studies should also gather relevant data to conduct mass balance models as a way of verifying biomagnification claims for specific food chains.

Supplementary material

Supplementary material is available online.

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Data availability. The data that support this study are available from the CSIRO Data Access Portal (DAP) (Franco-Santos *et al.* 2025). The *R* code used to analyse data for this study is publicly available from GitHub at https://github.com/sameggs/euphasia_antarctica_Hg.

Conflicts of interest. The krill used in this research were sampled from catches that are commercialised by Aker Biomarine as products for human health and nutrition. N. Hoem is the company's chief scientist and, as such, had a professional investment in the results of our research.

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