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Annual trends in mercury contamination are associated with changing trophic niches of giant petrels

William F. Mills [a,*,1], Danielle L. Buss [a,b], Paco Bustamante [c], Francisco Ramírez [d], Jaume Forcada [a], Manuela G. Forero [e], Richard A. Phillips [a]

[a] British Antarctic Survey, Natural Environment Research Council, Cambridge, CB3 0ET, UK
[b] NTNU University Museum, Norwegian University of Science and Technology, 7491, Trondheim, Norway
[c] Littoral Environnement et Sociétés (LIENSs), UMR 7266 CNRS-La Rochelle Université, 2 Rue Olympe de Gouges, 17000, La Rochelle, France
[d] Institut de Ciències Del Mar (ICM-CSIC), Departament de Recursos Marins Renovables, Passeig Marítim de la Barceloneta, 37-49, 08003, Barcelona, Spain
[e] Department of Conservation Biology, Estación Biológica de Doñana, Avda. Américo Vespucio, 26, Isla de la Cartuja, 41092, Sevilla, Spain

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ABSTRACT

Annual variation in prey availability can influence seabird diets and hence their exposure to pollutants, including mercury (Hg). Among seabirds, those species that scavenge carrion of marine mammals and other top predators may be especially vulnerable to accumulating high Hg concentrations. In this study, total Hg (THg) concentrations and carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope values were measured in chick feathers of northern giant petrels *Macronectes halli* and southern giant petrels *M. giganteus* at Bird Island, South Georgia (2013–2020). Both species are opportunistic predator-scavengers which feed mainly on penguins and Antarctic fur seal *Arctocephalus gazella* carrion, and to lesser extents on marine prey and other seabirds. THg concentrations were not significantly different between northern giant petrels and southern giant petrels (means ± SDs, 2.49 ± 0.92 μg g^{-1} dw and 2.34 ± 0.85 μg g^{-1} dw, respectively), but concentrations in both species declined significantly over time, as did $\delta^{13}C$ and $\delta^{15}N$ values. Annual feather THg concentrations of giant petrels were positively correlated with the number of dead Antarctic fur seal pups and their mortality rate at Bird Island, but not with population sizes or breeding success of penguins. Accordingly, these results suggest a shift away from carrion (associated with the decreasing size and productivity of the Antarctic fur seal population) and towards the consumption of prey from lower trophic levels (e.g., Antarctic krill *Euphausia superba*), with a corresponding reduction in dietary Hg exposure. Future work should investigate the consequences of changing prey availability for diets and pollutant exposure to other marine predators within the South Georgia and Scotia Sea marine ecosystems, given the ongoing environmental changes in the region.

1. Introduction

Chemical pollution (subsequently renamed as novel entities) was among nine planetary boundaries that were originally proposed to “define a safe operating space for humanity” (Rockström et al., 2009a, 2009b), and there is little doubt that pollutants such as mercury (Hg) represent an important threat to the biodiversity and health of the world’s oceans (Sigmund et al., 2023). Hg enters the environment due to natural process such as volcanism, geothermal actitivity and rock weathering (Outridge et al., 2018; Schneider et al., 2023); however, anthropogenic releases from the combustion of fossil fuels, artisanal and small-scale gold mining (ASGM), non-ferrous metals production and other processes have significantly increased environmental Hg levels (Streets et al., 2019; Fisher et al., 2023; Keane et al., 2023). As a result, the Hg content of ocean surface waters has tripled compared to the pre-industrial era (Lamborg et al., 2014). The atmosphere is the main distribution pathway for Hg, and the gaseous elemental form (Hg^0) has a long atmospheric residence time (3–6 months) and can be transported over large spatial scales (Cusset et al., 2023; Fisher et al., 2023; Schneider et al., 2023; Albert et al., 2019; Gimeno et al., 2024). For that reason, marine biota in the Antarctic and subantarctic are still exposed to Hg, despite being largely isolated from major sources of

* Corresponding author. Department of Geography and Environmental Science, University of Reading, Reading, UK.
E-mail address: w.f.mills@reading.ac.uk (W.F. Mills).
[1] **Present address:** Department of Geography and Environmental Science, University of Reading, Reading, UK.

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anthropogenic pollution (Cusset et al., 2023; Albert et al., 2019; Gimeno et al., 2024). Notwithstanding continued efforts to reduce emsissions (e.g., via the Minamata Convention on Mercury; minamataconvention.org), Hg remains a global threat to marine ecosystems.

Once Hg has entered the oceans, methyl-Hg (MeHg) is produced via the methylation of inorganic Hg (iHg), which is mediated principally by anaerobic microorganisms (Hsu-Kim et al., 2013). MeHg is a neurotoxin that bioaccumulates within organisms over time and biomagnifies up marine food chains, increasing with successive trophic levels (Chételat et al., 2020; Seco et al., 2021; Matias et al., 2022). Procellariiform seabirds (albatrosses and petrels), which are conspicuous components of Antarctic and subantarctic ecosystems, often occupy high trophic positions in marine food chains and so can potentially accumulate high levels of Hg via their diets (Bustamante et al., 2016; Moreno et al., 2016; Chételat et al., 2020; Mills et al., 2022, 2024a). Indeed, albatrosses and large petrels are among the most contaminated birds in terms of Hg (Cherel et al., 2018; Mills et al., 2024a), and species that scavenge on carrion of marine mammals and other top predators may be particularly at risk (Mills et al., 2022, 2024a). Given the relationship between Hg contamination and diet, annual variation in the availability of different prey can impact contamination levels of seabirds via changes in their trophic ecology (Chételat et al., 2020). At the subantarctic islands of South Georgia, for instance, reduced abundance of Antarctic krill *Euphausia superba*, which is a keystone species in the region, forces some seabird species to exploit alternative trophic pathways (e.g., myctophid fish or cephalopods) (Moreno et al., 2016), which may contain higher levels of Hg (Seco et al., 2021).

This study investigates Hg contamination of northern giant petrels *Macronectes halli* and southern giant petrels *M. giganteus* at South Georgia, where they are opportunistic predator-scavengers and breed in sympatry (Hunter, 1985; Mills et al., 2021). These species feed at high trophic levels, mainly on penguins (~50% by mass, primarily macaroni penguins *Eudyptes chrysolophus*) and Antarctic fur seal *Arctocephalus gazella* carrion, and to lesser extents on marine prey and other seabirds (Hunter, 1983; Mills et al., 2021). After extensive commercial exploitation during the 18th and 19th centuries, numbers of Antarctic fur seals increased substantially at South Georgia throughout the mid-20th century (Boyd, 1993; Forcada et al., 2023). However, since 2009 the Antarctic fur seal population has been in steep decline (Forcada et al., 2023), with potentially major implications for the diets of giant petrels and consequently their dietary exposure to Hg (Malcolm et al., 1994; Toro-Valdivieso et al., 2023). Understanding the factors driving changes in diet and pollutant exposure to marine predators is especially important at South Georgia, given the ongoing changes to marine food webs and the increasing evidence that Hg contamination has negative impacts on the behaviour, physiology and breeding success of other scavengers and procellariform seabirds in the region (Mills et al., 2020a; Ibañez et al., 2024). Importantly, Hg contamination can contribute to population declines of seabirds (Goutte et al., 2014a, 2014b). Accordingly, this study determined THg concentrations in chick feathers of northern giant petrels and southern giant petrels at South Georgia over an 8-year period (2013–2020). The objectives were to investigate interspecific differences and annual variation in Hg contamination, as well as the influences of feeding areas and trophic levels (inferred from stable isotope values of carbon and nitrogen), and the changing availability of different prey resources (local population trends and productivity of Antarctic fur seals and penguins).

2. Materials and methods

2.1. Study area, species and feather collection

This study focused on the giant petrel populations at Bird Island, South Georgia (54°00′S, 38°03′W), which is located on the Scotia Arc approximately 300 km south of the Antarctic Polar Front. The northern giant petrel and southern giant petrel populations at South Georgia are of global importance, constituting 71% and 17% of the global totals (15398 and 8803 breeding pairs), and increased by 74% and 27% between the mid-1980s and mid-2000s, respectively (Phillips et al., 2016; Poncet et al., 2020). Both species are typically annual breeders and lay a single egg without replacement in mid-September to mid-October, and November in northern giant petrels and southern giant petrels, respectively (Hunter, 1984; Brown et al., 2015; Gianuca et al., 2019). Incubation lasts ~60 days and chicks fledge in March and May in northern giant petrels and southern giant petrels, respectively, approximately 110–120 days after hatching. Fieldwork for this study was undertaken at Bird Island between the 2012/13 and 2019/20 breeding seasons, which are reported in this study as the years in which the giant petrel chicks fledged (for instance, 2019/20 is reported as 2020). Fully grown feathers were individually sampled from the lower back of randomly selected chicks of northern giant petrels ($n = 82$) and southern giant petrels ($n = 70$) that were ≥100 days old (i.e., within approximately 2–3 weeks of fledging). Mean laying and hatching dates of giant petrels are very consistent among years at Bird Island (Hunter, 1983; Brown et al., 2015; Keogan et al., 2018), and all chicks were sampled at a broadly similar age in all years. Feathers were then kept in envelopes or in sealed plastic bags at an ambient temperature before being returned to the United Kingdom (UK) for sample preparation and analysis.

2.1.1. Ethics statement

All handling and feather sampling of giant petrels was authorised by the British Antarctic Survey Animal Welfare and Ethics Review Body and undertaken under permits issued from the Government of South Georgia and the South Sandwich Islands.

2.2. Laboratory analyses

Prior to analyses, sample preparation of feathers followed previous studies at Bird Island (Moreno et al., 2016; Mills et al., 2020a, 2024a). External lipids and surface contaminants were removed from feathers using repeated rinses with chloroform:methanol solution (2:1 v/v) and ultrapure water (Milli-Q®). Cleaned feathers were subsequently dried in an oven at 40°C for 48 h. For each bird, multiple body feathers were pooled and homogenised by cutting into very fine pieces using stainless steel scissors (Moreno et al., 2016; Mills et al., 2020a, 2024a).

2.2.1. Total Hg analysis

Sequestration of ingested Hg into growing feathers is an important elimination route in seabirds (Braune and Gaskin, 1987; Kim et al., 1996). Total Hg concentrations (THg = iHg + MeHg) in seabird feathers (>90% of which is MeHg) are fixed after the feather is grown (Crewther et al., 1965; Appelquist et al., 1984; Renedo et al., 2017; Albert et al., 2019). Chick feather THg concentrations reflect dietary exposure during a discrete period, when all prey has been delivered by parents (Stewart et al., 1997; Blévin et al., 2013). The amount of Hg inherited via maternal transfer (i.e., excreted into the egg) in feathers of well-grown chicks (as sampled in this study) is very minor as it is mainly excreted into down and diluted with growth (Stewart et al., 1997; Blévin et al., 2013).

Feather THg concentrations were measured via an Advanced Mercury Analyser spectrophotometer (AMA-254 Altec®) in the laboratory Littoral Environnement et Sociétés (LIENSs) at La Rochelle Université (France), as previously reported by Chouvelon et al. (2009). All samples were analysed in duplicate or triplicate until the relative standard deviations among replicates were <10%, with aliquots ranging from 0.48 to 0.97 mg dry weight (dw). Two certified reference materials (CRMs) were used to determine the accuracy and reproducibility of the measurements. The CRMs were lobster hepatopancreas TORT-3 (National Research Centre, Canada; certified THg concentration: 0.29 ± 0.02 μg g^{-1} dw) and dogfish liver DOLT-5 (National Research Centre, Canada: 0.44 ± 0.18 μg g^{-1} dw). CRMs were analysed at the beginning and end of each sample run and after every tenth sample. Measured concentrations of the CRMs were 0.299 ± 0.005 μg g^{-1} dw (n = 42) for TORT-3 and 0.417 ± 0.004 μg g^{-1} dw (n = 9) for DOLT-5 indicating recoveries of 102.5 ± 1.9% and 94.8 ± 0.8%, respectively. Blanks were inserted at the start of each sample run. The detection limit of the AMA was 0.1 ng. Feather THg concentrations are expressed in μg g^{-1} dw.

2.2.2. Stable isotope analysis

Chick feather stable isotope ratios reflect diet during tissue formation, when all prey is delivered by parents, and the diet signal is preserved indefinitely (Cherel et al., 2000; Blévin et al., 2013). Carbon and nitrogen stable isotope values were measured in the same feathers as above at the Laboratorio de Isótopos Estables at Estación Biológica de Doñana (LIE-EBD) (https://www.ebd.csic.es/servicios/laboratorio-de-isotopos-estables) and LIENSs for samples collected from 2013 to 2018 and 2019–2020, respectively. At both facilities, subsamples were weighed (approximately 0.3 mg) into tin capsules (6 × 4 mm) using a microbalance. Results are reported using the conventional δ notification in parts per thousand (‰) relative to the international references Vienna PeeDee Belemnite for carbon and atmospheric N_2 (AIR) for nitrogen. Further details regarding the instrumentation at LIE-EBD and LIENSs have been described previously (e.g., Bustamante et al., 2023; Mills et al., 2024a). Briefly, at LIE-EBD, samples were combusted at 1020°C with a continuous flow isotope-ratio mass spectrometry system by means of Flash HT Plus elemental analyser coupled to a Delta-V Advantage isotope ratio mass spectrometer via a Conflo IV interface (ThermoFisher Scientific, Bremen, Germany). LIE-EBD standards, which had been calibrated with international standards from the International Atomic Energy Agency (IAEA, Vienna), were EBD-23 (cow horn, internal standard), LIE-BB (whale baleen, internal standard) and LIE-PA (razorbill feathers, internal standard). At LIENSs, isotopic analyses were conducted via a continuous flow isotope ratio mass spectrometer (Delta V Plus with a Conflo IV Interface, Thermo Scientific, Bremen, Germany) coupled to an elemental analyser (Flash, 2000or Flash IRMS EA Isolink CN, Thermo Scientific, Milan, Italy). Internal laboratory standards (caffeine USGS-61 and USGS-63) were used to check accuracy. At LIE-EBD and LIENSs, measurement errors were <0.20 ‰ for $\delta^{13}C$ and $\delta^{15}N$.

2.3. Annual prey availability metrics

Previous analyses of stomach contents showed that penguins and carrion of Antarctic fur seals are the two most common prey items for giant petrels (Hunter, 1983; Mills et al., 2021). Hence, the total numbers of Antarctic fur seal females, pups and dead pups, as well as the percentage mortality of pups, based on population monitoring on the designated Special Study Beach (SSB) on Bird Island, were included as annual proxies of food availability (Forcada et al., 2023). Although the species cannot always be identified from stomach contents, macaroni penguins are more numerous than other penguin species on Bird Island and the population is negatively impacted by giant petrel predation (Horswill et al., 2014, 2016). Although less abundant at Bird Island, gentoo penguins *Pygoscelis papua* also occur in giant petrel diets (Hunter, 1983; Mills et al., 2021). As such, the other proxies of prey availability included here were the total numbers of pairs and chicks of macaroni penguins at the Fairy Point colony on Bird Island and of gentoo penguins at all colonies (British Antarctic Survey, unpublished data).

2.4. Data analysis

All data processing and analysis for this study was undertaken using R (version 4.2.1) (R Core Team, 2022). Data were visualised using the ggplot2 package in R (Wickham, 2016). Shapiro-Wilks and Levene's tests were used to assess the assumptions of normality and homogeneity of variances, respectively, and chick feather THg concentrations were subsequently ln-transformed. General Linear Models (GLMs; Gaussian error distribution and identity link function) were then used to investigate variation in THg concentrations (ln-transformed), $\delta^{13}C$ and $\delta^{15}N$ values. Predictor variables in these GLMs were species, year and their two-way interaction (species × year). Model simplification was undertaken via the backwards stepwise deletion of non-significant terms, beginning with the interaction term. GLMs were also used to test whether relationships among THg concentrations (ln-transformed) and $\delta^{13}C$ and $\delta^{15}N$ values (with year included as a covariate) were significant. Lastly, a final set of GLMs (based on annual means) were used to assess relationships between chick feather THg concentrations, $\delta^{13}C$ and $\delta^{15}N$ values and the annual proxies of prey availability (see section 2.3). Significance was assumed at α = 0.05 in all cases. To aid the interpretation of $\delta^{13}C$ and $\delta^{15}N$ values, stable isotope ratios measured in prey of giant petrels were collated from studies that analysed samples collected at Bird Island or in the waters surrounding South Georgia (Stowasser et al., 2012; Seco et al., 2021).

3. Results

3.1. Variation in Hg contamination

Chick feather THg concentrations, $\delta^{13}C$ and $\delta^{15}N$ values were determined for 152 individual giant petrels at Bird Island (Table 1). The lowest (0.80 μg g^{-1} dw) and highest (4.80 μg g^{-1} dw) THg concentrations were from southern giant petrel chicks sampled in 2019 and 2014, respectively (Table 1). There was a significant effect of year on ln-transformed THg concentrations (GLM, $R^2 = 0.07$, $F_{1,150} = 11.54$, $p < 0.001$), reflecting a significant decrease in THg concentrations at 4.2% per year (estimate ± se, −0.04 ± 0.01) over the study period (Fig. 1a). Neither species nor the species × year interaction term were retained in the GLM following model simplification. This indicates that overall mean THg concentrations in chick feathers were similar in northern giant petrels (mean ± SD, 2.49 ± 0.92 μg g^{-1} dw) and southern giant petrels (2.34 ± 0.85 μg g^{-1} dw) (Table 1), and that the slope of the relationship with year did not depend on the species. Year also had a significant effect on $\delta^{13}C$ values ($R^2 = 0.13$, $F_{1,150} = 22.60$, $p < 0.0001$), indicating a significant decline over time (estimate ± se, −0.13 ± 0.03) (Fig. 1b). Neither the species term nor the species × year interaction were retained in the GLM after model simplification. Chick feather $\delta^{15}N$ values also showed a significant decrease (estimate ± se, −0.07 ± 0.02) with year ($R^2 = 0.10$, $F_{1,150} = 8.91$, $p < 0.01$) (Fig. 1c), and differed significantly among species ($F_{1,150} = 6.06$, $p < 0.05$) (Table 1). Feather $\delta^{15}N$ values of northern giant petrel were higher than southern giant petrels (Table 1 and Fig. 1d); however, the interaction term was not retained in the GLM. Feather $\delta^{15}N$ values were positively related (estimate ± se, 0.53 ± 0.05) to $\delta^{13}C$ values ($R^2 = 0.40$, $F_{1,150} = 100.01$, $p < 0.0001$) (Fig. 1d).

3.2. Relationships with diet and prey availability

There were significant positive relationships between chick feather THg concentrations (ln transformed) and both $\delta^{13}C$ ($R^2 = 0.14$, $F_{1,149} = 18.92$, $p < 0.001$) and $\delta^{15}N$ values ($R^2 = 0.09$, $F_{1,149} = 6.44$, $p < 0.05$) (Fig. 1e and Fig. 1f). THg concentrations showed significant positive corrrelations with the number of dead Antarctic fur seal pups ($R^2 = 0.61$, $F_{1,6} = 9.52$, $p < 0.05$) and the pup mortality rate ($R^2 = 0.58$, $F_{1,6} = 8.17$, $p < 0.05$) (Fig. 2). THg concentrations were not significantly related to the total number of fur seal females or pups, nor the annual breeding population sizes or productivity of macaroni or gentoo penguins (all $p > 0.05$). Stable isotope values were not significantly related to any of the annual proxies of Antarctic fur seal or penguin availability (all $p > 0.05$).

4. Discussion

4.1. Interspecific and geographic comparisons

Northern giant petrels and southern giant petrels occupy high

Table 1
Annual mean (±SD) total mercury (THg) concentrations (μg g^{-1} dw) (ranges in parentheses) and stable isotope values of carbon (δ^{13}C) and nitrogen (δ^{15}N) of chick feathers sampled from northern giant petrels *Macronectes halli* and southern giant petrels *M. giganteus* from Bird Island, South Georgia (southwest Atlantic Ocean) from 2013 to 2020.

	Northern giant petrel				Southern giant petrel			
Sampling year	n	THg (μg g^{-1} dw)	δ^{13}C (‰)	δ^{15}N (‰)	n	THg (μg g^{-1}dw)	δ^{13}C (‰)	δ^{15}N (‰)
2013	8	3.44 ± 0.75 (2.30–4.60)	−20.5 ± 1.5	12.8 ± 1.0	8	3.03 ± 0.87 (1.81–4.13)	−19.7 ± 0.5	13.2 ± 0.6
2014	10	2.07 ± 0.85 (1.09–3.70)	−20.0 ± 0.8	13.1 ± 0.5	8	2.55 ± 1.32 (1.34–4.80)	−20.5 ± 0.4	12.7 ± 0.2
2015	10	1.83 ± 0.45 (1.01–2.74)	−20.5 ± 0.5	13.7 ± 0.4	–	–	–	–
2016	10	3.44 ± 0.86 (2.33–4.46)	−20.2 ± 0.4	13.6 ± 0.3	10	3.02 ± 0.63 (2.19–4.23)	−20.4 ± 0.4	12.9 ± 0.4
2017	10	2.16 ± 0.62 (1.16–3.02)	−21.9 ± 0.3	11.9 ± 0.4	9	2.05 ± 0.56 (1.04–2.81)	−22.1 ± 0.2	11.7 ± 0.3
2018	12	3.02 ± 0.89 (1.78–4.49)	−20.9 ± 0.6	13.1 ± 0.4	12	2.03 ± 0.44 (1.26–2.88)	−20.9 ± 0.4	13.2 ± 0.3
2019	11	2.20 ± 0.71 (1.47–3.59)	−20.9 ± 0.4	12.6 ± 0.4	12	1.87 ± 0.80 (0.80–3.08)	−21.1 ± 0.5	12.4 ± 0.2
2020	11	1.90 ± 0.38 (1.43–2.64)	−20.7 ± 0.4	12.9 ± 0.2	11	2.17 ± 0.58 (1.27–3.10)	−20.8 ± 0.5	12.6 ± 0.2
Overall	**82**	**2.49 ± 0.92 (1.01 to 4.60)**	**−20.7 ± 0.8**	**13.0 ± 0.7**	**70**	**2.34 ± 0.85 (0.80 to 4.80)**	**−20.8 ± 0.8**	**12.7 ± 0.6**

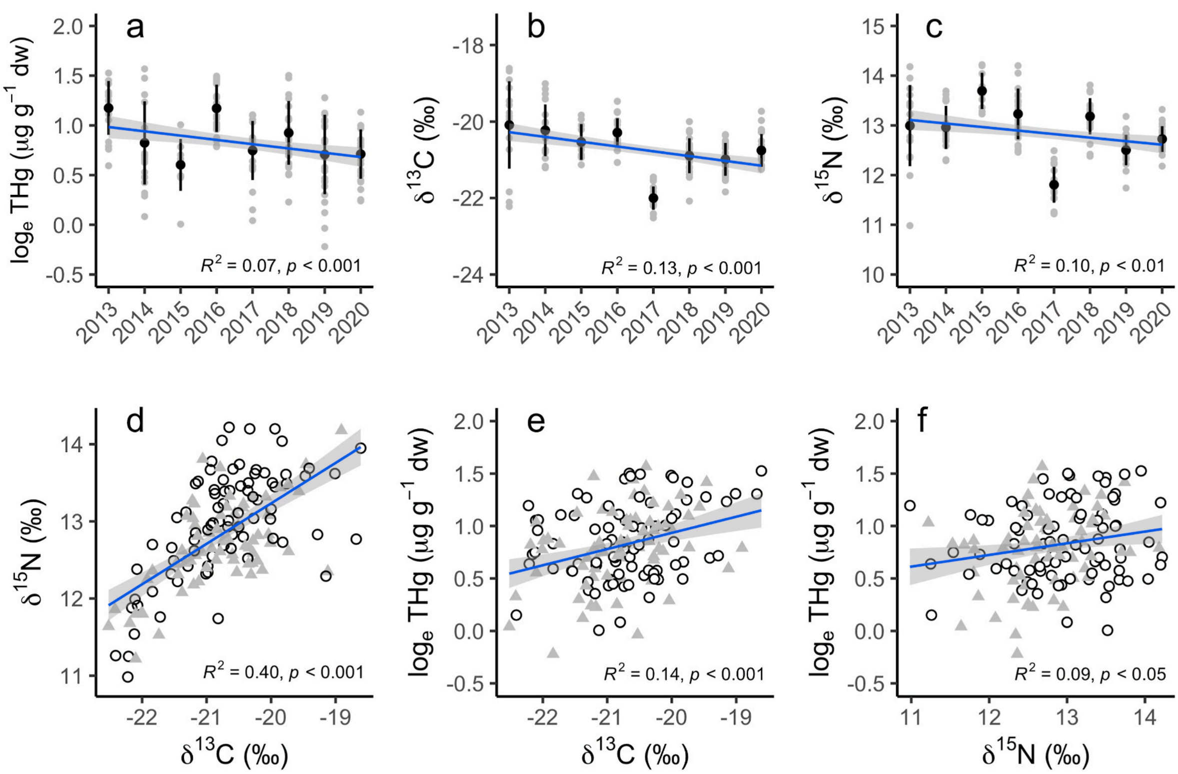

Fig. 1. Annual variation in (**a**) total mercury (THg) concentrations (μg g^{-1} dw) and stable isotope values (‰) of (**b**) carbon (δ^{13}C) and (**c**) nitrogen (δ^{15}N) of northern *Macronectes halli* and southern giant petrel *M. giganteus* chick feathers from Bird Island, South Georgia (southwest Atlantic Ocean) (2013–2020). Individual and mean (±SD) data are presented in the top row. Relationships between (**d**) δ^{15}N and δ^{13}C values; (**e**) THg concentrations and δ^{13}C; and (**f**) THg concentrations and δ^{15}N values are shown on the bottom row, with northern giant petrels being represented by circles and southern giant petrels by triangles. Solid lines are fitted linear regressions (see text for further details). THg concentrations were ln-transformed in all cases.

trophic positions in subantarctic food webs (Hunter, 1985), and so are susceptible to accumulating high Hg concentrations in their tissues. After model simplification, the species term was not retained in the GLM explaining variation in THg concentrations in chick feathers in this study. Hence, levels of Hg contamination were similar between the two species at Bird Island during the 2010s, which is likely due to their comparable trophic ecology. Chick feather δ^{13}C values, which are typically used to infer dietary carbon sources, were not significantly different between the two giant petrel species. This is perhaps unsurprising as during chick-rearing there is considerable overlap in their foraging areas (Granroth-Wilding and Phillips, 2019); however, due to allochrony, breeding commences approximately 6 weeks earlier in northern giant petrels. Moreover, diet composition based on stomach contents analyses collected during chick-rearing in the mid-2010s at Bird Island (2015–2017) was similar between species in terms of the proportion by mass of the main components (Mills et al., 2021). Although δ^{15}N values were significantly higher in northern giant petrel chicks (mean ± SD, 13.0 ± 0.7 ‰ and 12.7 ± 0.6 ‰, respectively), implying that their diet included a greater proportion of higher trophic level prey resources, the difference was small and there was a great deal of overlap (Fig. 1a). That differences in diet composition were not found in the analyses of stomach contents may reflect methodological biases (e.g., different digestion rates of prey).

Mean chick feather THg concentrations of northern giant petrels in this study were much lower than those of the same species at the Kerguelen (5.31 ± 1.12 μg g^{-1} dw, n = 12) and Crozet (5.76 ± 1.77 μg g^{-1} dw, n = 10) archipelagos (Blévin et al., 2013; Carravieri et al., 2014; Renedo et al., 2017). Similarly, mean chick feather THg concentrations of southern giant petrels in this study were lower than at Crozet (5.77 ± 0.82 μg g^{-1} dw, n = 11) (Renedo et al., 2017). In addition to potential

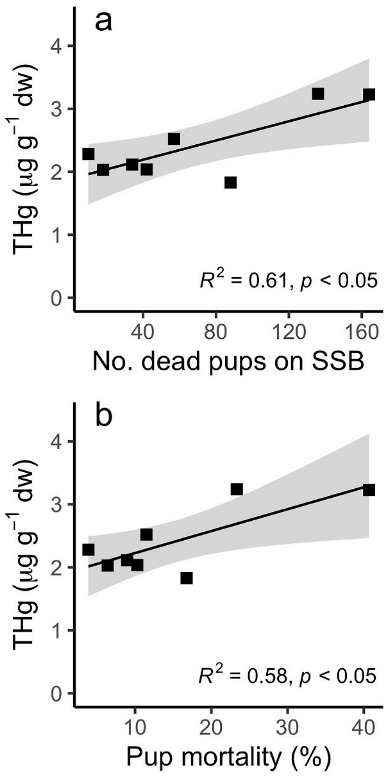

Fig. 2. Annual mean (±SD) total mercury (THg) concentrations (μg g^{-1} dw) of northern giant petrel *Macronectes halli* and southern giant petrel *M. giganteus* chick feathers from Bird Island, South Georgia (2013–2020), in relation to the (**a**) number of dead Antarctic fur seal pups *Arctocephalus gazella* and (**b**) percentage (%) mortality of pups at the designated Special Study Beach (SSB) on Bird Island (Forcada et al., 2023).

differences in diet composition among sites, these geographical differences are in agreement with the well-documented pattern that seabirds feeding in higher latitude waters (i.e., Antarctic) in the Southern Ocean show lower levels of contamination than those feeding at lower latitudes, such as Kerguelen and Crozet (Carravieri et al., 2016, 2017; Renedo et al., 2020; Mills et al., 2022).

4.2. Changes in Hg contamination among years

Feather THg concentrations declined significantly over the study period (2013–2020) (Fig. 1a). Given that the interaction term was not significant (i.e., not retained after model simplification), the slope of the relationship with year did not differ between species. One explanation for the decrease could be a decline in the bioavailability of Hg within giant petrel foraging areas. Indeed, similar decreases in Hg concentrations were found in some cephalopods and myctophids collected in the waters around South Georgia and in the Scotia Sea (Seco et al., 2020a, 2020b). However, an alternative explanation is that the declining THg concentrations are due to concurrent changes in giant petrel diets over time. This is supported by the significant decreases in $\delta^{13}C$ and $\delta^{15}N$ values over the study period, and the significant correlations between THg concentrations and stable isotope values (Fig. 1e and f).

Stable isotope data from the main prey items (based on previous analyses of stomach contents) suggest that higher $\delta^{13}C$ and $\delta^{15}N$ values of giant petrel chicks are characteristic of land-based foraging on Antarctic fur seal carrion and penguins, particularly macaroni penguins, rather than marine resources (e.g., Antarctic krill) (Table 2). Hence, the declining $\delta^{13}C$ and $\delta^{15}N$ values over time imply gradual shifts in trophic niches, corresponding to a likely reduction in carrion consumption. The relationship between THg concentrations and $\delta^{13}C$ could also reflect an influence of feeding latitude, as female Antarctic fur seals from South Georgia usually feed in waters to the north of the islands (Boyd et al., 2002). Seabird feather $\delta^{13}C$ values primarily indicate foraging latitude in the southwest Atlantic sector of the Southern Ocean (Phillips et al., 2009; Mills et al., 2024b). Increasing consumption of prey from lower latitudes should lead to higher Hg contamination, as birds feeding in Antarctic waters (with more negative $\delta^{13}C$ values) tend to show lower Hg contamination than those that feed on prey from subantarctic waters (Carravieri et al., 2016, 2017; Renedo et al., 2020; Mills et al., 2022).

In agreement with the significant correlations between THg concentrations and stable isotope values, chick feather THg concentrations of giant petrels were also positively correlated with the number of dead Antarctic fur seal pups and their mortality rate at Bird Island. There were no relationships between these annual indices and stable isotope values of the giant petrel chicks, but this was likely due to the large overlap in isotopic signatures of the main dietary items (Table 2). Antarctic fur seals have higher THg concentrations than alternative prey at South Georgia (Bengston-Nash et al., 2021). Hence, this study shows that changes in the availability of key prey within the food webs at South Georgia and the Scotia Sea have repercussions for giant petrel diets and therefore Hg exposure.

Among giant petrel prey, the Antarctic fur seal population in particular has undergone considerable changes at South Georgia (Forcada et al., 2023). Sealing began soon after South Georgia was discovered in the 1770s, and ≥1.2 million furs were estimated to have been collected by the 1820s, driving the species close to extinction (Bonner, 1968; Forcada et al., 2023). Pups were rediscovered on Bird Island in the 1930s and the population increased rapidly, stabilised (albeit with high annual variation), and then declined after 2009 such that numbers are now comparable to the 1970s (Bonner, 1968; Forcada et al., 2023). Hence the abundance of carrion for giant petrels has reduced during the timescale of this study. Giant petrels feed on dead adult fur seals (mainly males), pups and placentae, but are also active predators, primarily attacking the small and weak pups in areas with fewer adults (Hunter, 1983; Mills et al., 2021; Nagel et al., 2022). It is unknown whether such predation has population-level impacts on the seals. Though our study suggests that Hg contamination is reduced when less fur seal carrion is consumed, the benefits of lower contaminant levels may be offset by the reduction of an energy-dense resource. Indeed, at South Georgia, dietary shifts have been shown to negatively

Table 2
Mean (± SD) stable isotope values of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of potential prey of northern giant petrels *Macronectes halli* and southern giant petrels *M. giganteus* at South Georgia (southwest Atlantic Ocean). Prey were identified based on previous analyses of stomach contents (Hunter, 1983; Mills et al., 2021). Blood samples were collected from adult birds and seals (females only) at Bird Island. Antarctic krill *Euphausia superba* were collected on research cruises near South Georgia. Lipids were not extracted from blood (C:N ratios, all ≤ 3.5) (Stowasser et al., 2012), or Antarctic krill; however, data from the latter were normalised mathematically (Seco et al., 2021).

Species	Sampling year	Tissue	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Citation
Antarctic krill *Euphausia superba*	2017	Whole organism	30	−25.0 ± 0.7	3.4 ± 0.4	Seco et al. (2021)
Antarctic prion *Pachyptila desolata*	2008	Whole blood	5	−22.4 ± 1.2	8.6 ± 0.3	Stowasser et al. (2012)
South Georgia diving petrel *Pelecanoides georgicus*	2008	Whole blood	5	−22.6 ± 0.2	9.3 ± 0.4	Stowasser et al. (2012)
Macaroni penguin *Eudyptes chrysolophus*	2008	Whole blood	6	−21.9 ± 0.7	9.8 ± 0.2	Stowasser et al. (2012)
Antarctic fur seal *Arctocephalus gazella* (females)	2008	Whole blood	10	−22.2 ± 0.8	9.4 ± 1.1	Stowasser et al. (2012)

impact the breeding success of other procellariiform seabirds (Mills et al., 2020b).

Penguins comprised approximately 50% of giant petrel diets at Bird Island in the most recent diet analysis (Mills et al., 2021). Although the species could not be identified from stomach contents, macaroni penguins are much more numerous than other penguins at Bird Island, and top-down predation by giant petrels is considered to have a greater impact on survival than bottom-up processes (Horswill et al., 2014, 2016). The macaroni penguin population at Bird Island declined steeply from the mid-1980s to the early 2000s; however, it has since stabilised, and there were no clear trends in the numbers of pairs and chicks over the study period. Nor was there were a clear trend in numbers of breeding pairs or chicks of gentoo penguins. The non-significant relationships between Hg concentrations in the giant petrels and these variables may be explained by the lack of consistent directional trends over time in population sizes or productivity of the two penguin species, or because Hg concentrations in penguins are lower than in fur seal carrion (Bengston-Nash et al., 2021), and so it is abundance of the latter that is the primary driver of Hg exposure.

5. Conclusion

In summary, this study demonstrates decreasing Hg contamination of giant petrels during the 2010s at South Georgia, which corresponded with changes in their trophic niches (i.e., a likely reduction in carrion consumption) and was related to annual indices of fur seal carrion availability (dead pups). Hence, annual changes in prey abundance appear to have influenced pollutant exposure to these top predators. The two giant petrel species are categorised as Least Concern (i.e., not threatened) according to the IUCN Red List, which contrasts with the more threatened classifications of other albatrosses and petrels at South Georgia (e.g., white-chinned petrel *Procellaria aequinoctialis*, wandering *Diomedea exulans*, black-browed *Thalassarche melanophris* and grey-headed albatrosses *T. chrysostoma*) (Phillips et al., 2016; Poncet et al., 2017, 2020). However, despite being associated with reduced pollutant burdens, the ongoing decline of Antarctic fur seals (and subsequent reduction in carrion availability) may well have negative long-term repercussions for giant petrel populations at South Georgia. Future work could investigate how changing prey availability (e.g., annual variation in Antarctic krill abundance) affects the diets and pollutant exposure of other marine predators at South Georgia.

CRediT authorship contribution statement

William F. Mills: Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Danielle L. Buss:** Writing – review & editing, Visualization, Formal analysis. **Paco Bustamante:** Writing – review & editing, Investigation. **Francisco Ramírez:** Writing – review & editing, Investigation. **Jaume Forcada:** Writing – review & editing, Resources. **Manuela G. Forero:** Writing – review & editing, Investigation. **Richard A. Phillips:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization.

Declaration of competing interest

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

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Data availability

Data will be made available on request.

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