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Accumulate or eliminate? Seasonal mercury dynamics in albatrosses, the most contaminated family of birds

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An adult light-mantled sooty albatross at rest in a cliff on Possession Island, Crozet Archipelago, southern Indian Ocean

ABSTRACT: Albatrosses (Diomedeidae) are iconic pelagic seabirds whose life-history traits (longevity, high trophic position) put them at risk of high levels of exposure to methylmercury (MeHg), a powerful neurotoxin that threatens humans and wildlife. Here, we report total Hg (THg) concentrations in body feathers from 516 individual albatrosses from 35 populations, including all 20 taxa breeding in the Southern Ocean. Our key finding is that albatrosses constitute the family of birds with the highest levels of contamination by Hg, with mean feather THg concentrations in different populations ranging from moderate (3.8 µg/g) to exceptionally high (34.6 µg/g). Phylogeny had a significant effect on feather THg concentrations, with the mean decreasing in the order Diomedea > Phoebetria > Thalassarche. Unexpectedly, moulting habitats (reflected in feather $\delta^{13}C$ values) was the main driver of feather THg concentrations, indicating increasing MeHg exposure with decreasing latitude, from Antarctic to subtropical waters. The role of moulting habitat suggests that the majority of MeHg eliminated into feathers by albatrosses is from recent food intake (income strategy). They thus differ from species that depurate MeHg into feathers that has been accumulated in internal tissues between two successive moults (capital strategy). Since albatrosses are amongst the most threatened families of birds, it is noteworthy that two albatrosses listed as Critical by the World Conservation Union (IUCN) that moult and breed in temperate waters are the most Hg contaminated species (the Amsterdam and Tristan albatrosses). These data emphasize the urgent need for robust assessment of the impact of Hg contamination on the biology of albatrosses and they document the high MeHg level exposure of wildlife living in the most remote marine areas on Earth.

KEYWORDS: Antarctica; Feathers; Foraging; Methylmercury; Moult; Seabirds; Southern Ocean; Stable isotopes

INTRODUCTION

Mercury (Hg) is a persistent and non-essential trace element that ranks third on the priority list of hazardous substances, based on toxicity and prevalence at contaminated sites (ATSDR; https://www.atsdr.cdc.gov/spl/). Hg is mobilized from geological deposits through both natural and anthropogenic processes and travels long distances within the atmosphere to reach even the most remote regions on Earth located far from emission sources. After atmospheric deposition, microorganisms methylate inorganic Hg (iHg) into methylmercury (MeHg), a powerful neurotoxin that bioaccumulates in organisms and biomagnifies in food webs to levels that pose major health risks to humans and wildlife (Driscoll et al., 2013). Among consumers, birds exhibit varying levels of trophic, spatial and temporal integration of contaminants and so are effective sentinels of MeHg bioavailability (Furness, 1993; Evers et al., 2005). Since MeHg contamination increases from terrestrial to aquatic ecosystems, consumption of freshwater and marine foods constitutes the major sources of MeHg exposure in humans and animals (Evers et al., 2005; Driscoll et al., 2013). Hence, seabirds have been frequently used as indicators of MeHg contamination in the marine environment (Monteiro and Furness, 1995; Burger and Gochfeld, 2004).

Albatrosses are iconic pelagic seabirds with life-history traits that make them potentially at high risk of MeHg exposure. They are extremely long-lived animals with some individuals living >50 years (Wasser and Sherman, 2010), and they are at the top of the food web, typically preying on, or scavenging large carnivorous nekton (Cherel and Klages, 1998; Cherel et al., 2017). The liver is the principal tissue for long-term Hg storage (Thompson, 1990), and pioneering studies have shown that some albatross livers contained amongst the highest total Hg (THg) levels documented for apparently healthy free-living vertebrates, albeit lower than those recorded in some marine mammals (Muirhead and Furness, 1988; Honda et al., 1989;

Stewart et al., 1999). Subsequent measurements generally confirmed substantial Hg contamination of albatrosses, but with large variation depending on tissue type, individual, population and species (Thompson et al., 1993; Kim et al., 1996; Hindell et al., 1999; Stewart et al., 1999). Comparison between contemporary and historical specimens showed slight or no increase in albatross THg levels over time, thus suggesting that contamination results primarily from natural - not anthropogenic - processes (Thompson et al., 1993, but see Vo et al., 2011). The inference is that albatrosses are amongst the organisms most contaminated by Hg (Thompson et al., 1993), but the available data set remained largely incomplete and suffered from several limitations: (i) many taxa and populations have not been sampled, (ii) sample sizes were often low ($n < 5$), and (iii) relating published data to a species under the current taxonomy can be difficult because of splitting of species in the last decade (Phillips et al., 2016). This, together with the remoteness of most colonies, has resulted in a critical lack of comprehensive knowledge on Hg contamination in albatrosses.

Here, we report THg concentrations in 516 individual albatrosses from35 populations, including all 20 species and subspecies that breed in the Southern Ocean, thus providing new information on THg levels in 11 taxa and 22 populations (Table 1). THg concentration was measured in body feathers for practical, ethical and scientific reasons: (i) body feathers can be collected easily and noninvasively from live birds and they allow comparisons of metal exposure over time using museum specimens (Thompson et al., 1993; Vo et al., 2011; Carravieri et al., 2016), (ii) body feathers present less THg variation than do wing and tail feathers, and their collection does not impair flying ability (Furness et al., 1986; Thompson et al., 1993), (iii) most THg in feathers is organic, thus providing a mean of measuring MeHg exposure of birds (Thompson and Furness,1989b; Renedo et al., 2017), and (iv) plumage is a major pathway for MeHg elimination in avian species (Burger, 1993; Monteiro and Furness, 1995). We tested for the importance of several potential factors that might drive Hg exposure,

including breeding frequency, geographical location of the breeding colonies and isotopic proxies of the foraging habitats and trophic levels during moult (feather d13C and d15N, respectively). In addition, we examined a potential latitudinal effect on Hg exposure in the Southern Ocean, because recent investigations indicate that birds foraging in colder, southerly waters present lower tissue Hg concentrations than those feeding further north in temperate waters (Carravieri et al., 2014a, 2016, 2017).

MATERIALS AND METHODS

Study sites, birds and sampling

Body feathers were collected at each breeding site from 7 to 33 randomly chosen adult albatrosses over the period 2004-2013. Fieldwork was carried out on 14 islands and archipelagos that are scattered within the Southern Ocean (south of the Subtropical Front, STF) or in warmer fringing waters (Table S1). Two, five and seven islands were located in the Atlantic, Indian and Pacific oceans, respectively. The Subtropical (STZ), Subantarctic (SAZ) and Antarctic (AZ) Zones are here defined as the zones north of the STF, between the STF and the Polar Front (PF), and south of the PF, respectively (Fig. 1). The 14 sampling sites are located within the STZ (Amsterdam, Tasmanian and Chatham islands), the SAZ (Gough, Prince Edward, Crozet, Kerguelen, Auckland, Snares, Campbell, Antipodes and Bounty islands), and the AZ (South Georgia and Heard Island) (Table S1). Based on feather $\delta^{13}C$ isoscapes (Jaeger

et al., 2010), values of > -18.3‰, -21.2 to -18.3‰, and < -21.2‰ were considered to correspond to STZ, SAZ and AZ, respectively.

Moult in albatrosses and feather sampling

To test for the potential effects of foraging habitat and trophic position on feather THg concentrations, THg and isotopic values were measured on the same body feather taken from each individual albatross. In the Southern Ocean, d13C values of seabirds can be used to infer their foraging habitats (Cherel and Hobson, 2007; Phillips et al., 2009; Quillfeldt et al., 2010) and $\delta^{15}N$ values increase with trophic level (Cherel et al., 2010). Because keratin is a metabolically inactive molecule that is inert following synthesis, isotope values reflect the diet at the time of feather growth (Hobson and Clark, 1992; Bearhop et al., 2002). Hence, stable isotope analysis of feathers documents the feeding ecology of albatrosses during moult (Cherel et al., 2000; Phillips et al., 2009). Three potential limitations of the method are notable. (i) The exact timing of growth of body feathers in albatrosses is unknown as they are replaced gradually over the long inter-breeding period, with only ~7% of body feathers being moulted and regrown at any one time (Battam et al., 2010). The temporal window represented in the composition of body feathers depends on albatross breeding frequency and duration of the breeding cycle. Consequently, the interbreeding (moulting) period spans a full year plus a winter (~16 months) in small biennial breeders (the grey-headed, sooty and light-mantled albatrosses), a full year (~12 months) in large biennial breeders of the genus Diomedea (seven taxa), and one winter (~4 months) in annual breeders (10 taxa) (Table S1). (ii) Moult of body feathers in albatrosses rarely occurs during the breeding period (Catry et al., 2013). In the present study, most feather $\delta^{13}C$ and $\delta^{15}N$ values were different from the values that characterize feeding near the breeding sites (Cherel et al., 2013), thus verifying that feather moult took place during the inter-breeding

period. (iii) More importantly, there is a temporal mismatch between isotopic values and THg concentrations in feathers of adult birds. The latter is considered to represent Hg accumulated between two consecutive moulting cycles, i.e. a much longer integration period than that corresponding to feather growth (Bond, 2010). However, a preliminary analysis of our data indicated a more complex picture; feather THg concentrations were correlated with $\delta^{13}C$ in feathers, which represents the carbon source in moulting habitat (see Results). The very low THg concentrations in feathers that were grown in Antarctic waters (but not further north) prompted further investigations using three albatross populations that partly moult in Antarctic waters; grey-headed, sooty and light-mantled albatrosses from the Prince Edward, Gough, and Kerguelen Islands, respectively (Jaeger et al., 2013; Cherel et al., 2013). In those birds, THg concentrations and $\delta^{13}C$ and $\delta^{15}N$ values were measured on three additional body feathers from each individual (for a total of four feathers per bird) to better investigate potential relationships between Hg exposure and the foraging ecology of albatrosses during the inter-breeding period.

Mercury and stable isotope analyses

THg concentrations, $\delta^{13}C$ and $\delta^{15}N$ values were measured on the same individual body feathers. Feathers were first cleaned to remove surface contaminants using a 2:1 chloroform:methanol solution followed by two methanol rinses. They were then oven dried for 48 h at 50 °C. Feather samples (1-5mg dry weight, dw) were analyzed for THg with an Advanced Mercury Analyzer spectrophotometer (Altec AMA 254) (Bustamante et al., 2006). The analyses were repeated in duplicate or triplicate until the relative standard deviation was <10% for multiple aliquots. Tort-2 Lobster Hepatopancreas, NRC, Canada (THg concentration: 0.27 ± 0.06 µg/g dw) was used as Certified Reference Material (CRM) to check the accuracy of the method. After adjusting the CRM mass to represent the same amount of THg in reference samples as in those from

feathers, our measured values for CRM averaged 0.273 ± 0.008 µg/g dw (n = 53), thus corresponding to a recovery rate of 101 ± 3%. Blanks were analyzed at the beginning of each set of samples, and the detection limit of the method was 0.005 µg/g dw. Feather THg concentrations are presented relative to the dry weight.

For isotopic analyses, ~0.4 mg subsamples of the feather homogenates were weighed in tin cups. A continuous flow mass spectrometer (Thermo Scientific Delta V Advantage) was coupled to an elemental analyzer (Thermo Scientific Flash EA 1112) to measure feather $\delta^{13}C$ and $\delta^{15}N$ values, and feather carbon and nitrogen contents, respectively. Stable isotope ratios are expressed using standard d notation relative to carbonate Vienna PeeDee Belemnite and atmospheric nitrogen. The internal laboratory standards were acetanilide. Observed analytical errors were <0.10‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. The data on feather THg concentrations of albatrosses from the Kerguelen Islands, and most of the data presented here on feather $\delta^{13}C$ and $\delta^{15}N$ values are already published, but in distinct scientific contexts (Cherel et al., 2013; Carravieri et al., 2014b). Values are means ± SD.

Statistical analyses

The effects of species, phylogeny (*Diomedea*, large *Thalassarche*, small *Thalassarche*, *Phoebetria*), breeding frequency, breeding location, oceanographic zone (Table S1), ocean basin (Indian, Pacific, Atlantic), and foraging habitat and trophic level during moult ($\delta^{13}C$ and $\delta^{15}N$, respectively) on feather THg concentrations (516 feathers from 516 individuals from 35 populations) were investigated using non-parametric smoothing regression techniques. While

body condition is a main driving factor of avian THg concentrations (Fort et al., 2015), its effect was not tested because moult occurs at sea, thus precluding handling albatrosses at that time.

We used Generalised Additive Mixed Models (GAMM) in order to model potential non-linear relationships between THg concentrations and covariates, and to account for pseudo-replication. Indeed, our sampling unit was the population (n = 35, Table S1), represented by several individuals (mean of 15 ± 6, range 7-33). Population was thus modelled as a random effect in the GAMM. Data exploration was first carried out following Zuur et al. (2009). We then used variance inflation factors to assess which explanatory variables were collinear and should be dropped, based on a cut-off value of 4 (Zuur et al., 2009). The following was then considered as a starting model:

THg ~ s(δ^{13}C) + s(δ^{15}N) + species + phylogeny + breeding frequency + breeding location + oceanographic zone + ocean basin + two by two interactions between all categorical variables + random(population).

We then searched for the optimal model in terms of the explanatory variables and their interactions using a top-down strategy removing terms with non-significant p-values (significance level of $\alpha < 0.01$). The GAMM models ('gamm4' library, version 0.2-4) were specified with a Gaussian family and a penalized thin plate regression spline, the optimal span for smoothing was determined by AIC, and the smoothing parameters estimated using restricted maximum likelihood (Wood, 2003; Zuur et al., 2009). The adjusted R-squared for the model was defined as the proportion of variance explained, where original variance and residual variance were both estimated using unbiased estimators. Model validation was performed by inspecting the relationship between residuals and fitted values (Zuur et al., 2009). GAMM

analyses were performed using R 3.3.2 (R Development Core Team, 2016) and other statistical analyses using SYSTAT 13 for WINDOWS (Systat Software, Chicago).

RESULTS

THg concentrations varied 49-fold within the whole data set (618 body feathers), with the lowest value in a light-mantled albatross from the Kerguelen Islands and the highest in an Amsterdam albatross from Amsterdam Island (1.4 and 70.6 µg/g dw, respectively). All measurements of feather THg were >1 µg/g, of which 74.1% and 1.1% were >5 µg/g and >40 µg/g, respectively, which are the two most widely used toxicity thresholds for feather THg (Burger and Gochfeld, 1997; Evers et al., 2008). Notably, all of the seven most THg-contaminated feathers (>40 mg/g) were from *Diomedea* albatrosses, including four Amsterdam albatrosses. At the population level (n = 35), THg concentrations varied nine-fold, with mean values ranging from 3.8 µg/g in Atlantic yellow-nosed albatross to 34.6 µg/g in Amsterdam albatross (Fig. 2, Table S1). Accordingly, feather THg concentrations differed significantly between populations (Kruskal-Wallis, $H = 353.3$, $p < 0.0001$).

Results from the optimal GAMM model are presented in Table 2. Of the fixed factors, species, breeding frequency, breeding location, oceanographic zone and ocean basin were not retained, but phylogeny and feather $\delta^{13}C$ and $\delta^{15}N$ values had significant effects on feather THg concentrations. THg concentrations differed between albatross taxa, from 6.4 ± 4.4 µg/g in small *Thalassarche* species to 21.9 ± 11.0 µg/g in *Diomedea* spp. (Fig. 3). Feather THg concentrations were positively related to feather $\delta^{13}C$ values (Fig. 4) and the estimated degree of freedom of the smooth term (2.74) indicated a near-linear effect. In contrast, the relationship between feather $\delta^{15}N$ and THg concentrations was clearly non-linear (Fig. 4). The overall deviance explained by the optimal model was 49.5%. The population random effect explained

48.9% of the total variance of the residuals. There was no pattern between the residuals and the fitted values.

As expected, feather $\delta^{13}C$ values ranged widely in the three populations for which isotopic values and THg concentrations were determined on four body feathers per bird. Grey-headed, sooty and light-mantled albatrosses moulted over a large latitudinal gradient from Antarctica to the subtropics, with considerable variation both within and between individuals (Table 3, Fig. 5). Two features are notable: (i) all feathers that were grown in the AZ contained less THg than those moulted and regrown further north, and (ii) THg population concentrations of feathers grown in the AZ remained low over a wide range of $\delta^{15}N$ values. For example, feathers of light-mantled albatrosses contained 8.8 times more THg if they were grown in the STZ than in the AZ, with no overlap in feather THg concentrations between the two groups. There was no change in THg concentration in feathers grown in the AZ, while their $\delta^{15}N$ values ranged from 7.3 to 11.7‰ (a 4.4‰ difference). When feathers grew in warmer waters, THg concentrations were high, ranged widely and were associated with higher $\delta^{15}N$ values (Fig. 5). Conversely, feathers of grey-headed albatrosses that were grown south and north of the PF showed no significant difference in mean $\delta^{15}N$ values ($n = 8$ and 36, 11.0 ± 1.1 and 11.8 ± 1.5‰, respectively, Mann-Whitney test, $U = 86.0$, $p = 0.078$), but those grown in the AZ contained 2.4 times less THg than those grown further north (4.5 ± 1.2 and 10.9 ± 6.4 µg/g; $U = 22.0$, $p < 0.0001$).

DISCUSSION

Our key finding is that albatrosses are the most contaminated by Hg of all families of birds. The present work provides extensive new data on MeHg exposure in albatrosses from the Southern Ocean, where most species breed, thus allowing a comprehensive synthesis of the available

information on albatrosses worldwide (Table 1). Two features are notable: (i) THg measurements are urgently needed from two Pacific *Phoebastria* species, waved albatross and short-tailed albatross (but see Shinsuke et al., 2003), and (ii) seven (32%) of the albatross species and subspecies present mean body feather THg concentrations > 20 mg/g, including all five taxa of the wandering albatross species complex (wandering, Antipodean, Gibson's, Amsterdam and Tristan albatrosses), sooty albatross, and black-footed albatross. A review of THg body feathers emphasizes the exceptionally high contamination levels of albatrosses when compared to adult seabirds from the more investigated Northern Atlantic and Northern Pacific (>35°N; from 0.6 to 22.6 µg/g, and from 0.9 to 10.3 µg/g, respectively) (Kim et al., 1996; Monteiro et al., 1999; Bond and Diamond, 2008; Eagles-Smith et al., 2009). Only four populations of Procellariidae (closely-related to Diomedeidae) showed THg levels > 20 µg/g, northern giant petrel *Macronectes halli* and great-winged petrel *Pterodroma macroptera* from Prince Edward Islands, Atlantic petrel *P. incerta* from Gough, and Bulwer's petrel *Bulweria bulwerii* from the Azores, Madeira and Salvages (Monteiro et al., 1999; Becker et al., 2016). In contrast, average THg body feather levels >20 µg/g are very rare in other avian species, occurring only in a few diurnal and nocturnal raptors from the more contaminated Northern Hemisphere (Burger, 1993; Bowerman et al., 1994), and in tern chicks in two highly polluted areas (Furness et al., 1995; Herring et al., 2012).

Phylogeny explained much of the variation in feather THg concentrations in albatrosses; *Diomedea* species ranked first, and their body feathers contained on average 3.4 more THg than smaller *Thalassarche* species (Fig. 3). The wandering albatross species complex were the most Hg contaminated taxa, whereas northern and southern royal albatrosses showed moderate THg levels. These two groups of *Diomedea* albatrosses have essentially the same life history traits, differing ecologically only in their main feeding grounds. Royal albatrosses forage primarily in neritic waters, whereas the wandering albatross and related taxa are essentially oceanic

(Nicholls et al., 2002; Waugh and Weimerskirch, 2003), which fits well with a pattern of increasing feather THg values from coastal to oceanic seabirds (Ochoa-acuña et al., 2002). *Phoebetria* albatrosses ranked second, with the differences between the two species in feather THg concentrations likely explained by contrasting distributions; light-mantled albatrosses partly moult in the AZ, whereas sooty albatrosses do so further north (see below). Finally, the lowest feather THg concentrations were found in *Thalassarche* albatrosses; these are small to medium-sized albatrosses that are mostly annual breeders and, because they tend to eat more crustaceans, do not feed at as high trophic levels as the *Diomedea* albatrosses (Prince et al., 1993; Cherel and Klages, 1998; Jaeger et al., 2013). They thus differ from *Diomedea* and *Phoebetria* albatrosses in several life-history traits, which likely explain the lower THg concentrations in their feathers (this study), and also in internal tissues (Stewart et al., 1999).

Feather $\delta^{15}N$ was also related to THg concentrations, which was to some extent expected given $\delta^{15}N$ values is a proxy of trophic level and hence linked to biomagnification processes within ecosystems (the higher the trophic position, the higher the MeHg exposure). However, the relationship was nonlinear (Fig. 4), indicating a more complex relationship involving other confounding factors, including varying $\delta^{15}N$ baselines at moulting grounds. The large range of feather $\delta^{13}C$ values showed that plumage replacement took place in habitats that varied from Antarctic oceanic waters to northern coastal upwelling zones, depending on species, population and individual (Cherel et al., 2013). The different moulting habitats are likely marked by contrasting $\delta^{15}N$ baselines that propagate up the food webs and thus raw $\delta^{15}N$ values do not directly indicate relative trophic level. For example, the $\delta^{15}N$ baseline varies little within the Southern Ocean but increases sharply at the STF, remaining elevated further north (Altabet and

François, 1994), and the $\delta^{15}N$ baseline varies significantly within the Humboldt Current where many albatrosses moult (Mollier-Vogel et al., 2012; Cherel et al., 2013).

Another key finding of the present study was the major influence of feather $\delta^{13}C$ values, which reflect moulting habitat, on feather THg concentration in albatrosses. Conversely, breeding locality, oceanographic zone and ocean basin during breeding did not show significant relationships with feather THg concentration. This is presumably related largely to the timing of body feather moult, which takes place during the inter-breeding period. Importantly, our results indicate that in albatrosses, body feather THg concentration integrates predominantly very short-term MeHg intake at the temporal scale of a single growing body feather (Fig. 5). Consequently, there is no temporal mismatch between feather stable isotopic values and THg concentrations, all three parameters reflecting the feeding habits of albatrosses during feather growth. Hence, unlike feathers from most birds (Furness et al., 1986; Braune and Gaskin, 1987; Bond, 2010), body feathers of albatrosses carry information about MeHg availability on the moulting grounds, with differences in the carbon source reflected in $\delta^{13}C$ values.

Furthermore, it follows that because albatross body feather THg concentrations reflect MeHg intake over the time of feather growth, feather THg concentrations do not fully reflect MeHg accumulation over the long-term. Thus, plumage renewal in albatrosses does not appear to be a mechanism by which much of MeHg accumulated during the inter-moult period can be eliminated, unlike many other bird species that excrete most ingested and stored MeHg into newly grown feathers (Burger, 1993; Monteiro & Furness, 1995). Consequently, a critical issue for albatrosses is the fate of ingested MeHg, specifically in order to cope with potentially toxic effects. Since albatrosses are known to efficiently demethylate MeHg, we propose that they use two complementary detoxification mechanisms: (i) during moult, dietary MeHg is primarily eliminated directly into the keratin of growing feathers, and (ii) outside the moulting period, MeHg is continuously converted to iHg in the liver where it accumulates. These two

mechanisms explain: (i) why feather THg does not increase with age in albatrosses (Thompson et al., 1993; Tavares et al., 2013; Bustamante et al., 2016), (ii) the records of exceptionally high liver THg concentrations, with a large predominance of iHg over MeHg, in some (presumably old) individual albatrosses (Honda et al., 1989; Thompson and Furness, 1989a; Kim et al., 1996; Stewart et al., 1999), and (iii) the much lower THg burden in feathers (<10%) than in the whole body, indicating that THg excretion during the moult is negligible in albatrosses (Honda et al., 1989; Kim et al., 1996).

We conclude that two strategies to deal with ingested MeHg operate in birds and we propose to call them the income and capital strategies in reference to the previous definition of those terms in the management of energy for breeding (Jonsson, 1997). Birds adopting the income strategy (e.g. albatrosses) convert ingested MeHg to iHg in the liver outside the moulting period and only eliminate MeHg ingested during feather growth into newly growing feathers. In species using the capital strategy (e.g. gulls; Braune and Gaskin, 1987), most feather MeHg comes from the accumulation of dietary MeHg into the body reservoir during the period between successive moults. A consequence of the capital strategy is that, unlike in albatrosses, feathers grown by these other species contain a major part (56-94%) of the THg burden of the whole body, indicating that they are the endpoint in a primary pathway for THg elimination (Burger, 1993; Monteiro and Furness, 1995). The concept of income and capital strategies requires further investigation, especially because some birds probably fall somewhere along an income-capital continuum. Albatrosses stands at the income end of the spectrum, and the income strategy is likely to be the prominent strategy in seabirds for which the moulting habitat affects feather THg concentrations (Fort et al., 2014; Watanuki et al., 2016).

Overall, feather d13C values were near-linearly and positively related to feather THg concentrations (Fig. 4). Hence, Hg exposure is higher for albatrosses moulting in warmer, more northerly, than colder, more southerly waters, because both baseline and consumer d13C values

vary with latitude; the higher the latitude, the lower the $\delta^{13}C$ values (Cherel and Hobson, 2007; Phillips et al., 2009; Jaeger et al., 2010; Quillfeldt et al., 2010). This relationship held both between and within individual birds. While all body feathers of grey headed, sooty and light-mantled albatrosses grown in the STZ and the SAZ had elevated THg levels, feathers grown in the AZ showed consistently low THg concentrations (Fig. 5). Surprisingly, feather THg concentrations remained low whatever their corresponding $\delta^{15}N$ values, indicating that habitat is much more important than trophic level when moulting in the AZ. The large feather $\delta^{15}N$ range suggests that albatrosses fed on prey from low trophic levels (probably including Antarctic krill *Euphausia superba*) in southern Antarctic waters to high trophic levels (fish and squid) south of the PF, but with no concomitant feather THg increase. The primary importance of feeding latitude on Hg levels is highlighted by intra and inter-individual variation in moulting grounds. Some individuals (e.g. light-mantled albatrosses shown in green and pink on Fig. 5) replaced their plumage in various oceanic zones, resulting in contrasting THg concentrations. Other individuals moulted over a more restricted latitudinal range, and consequently, levels of Hg contamination of birds moulting in the AZ were approximately ten times lower than in those moulting further north (e.g. the cyan vs. red individuals, 2.1 vs. 19.9 µg/g; Fig. 5).

Our data confirm that exposure to MeHg of top predators decreased with increasing latitude in the Southern Ocean (Carravieri et al., 2014a, 2016, 2017). Moreover, they show a stepwise drop in MeHg availability at the PF, thus suggesting that the PF acts as an oceanographic barrier (Guynn and Peterson, 2008). Lower Hg contamination in predators feeding in the AZ in our study contrasts with earlier work on Hg in the Southern Ocean, which showed higher MeHg concentrations available at shallower depths in waters to the south, compared to the north, of the PF (Cossa et al., 2011). Two non-exclusive explanations for this apparent mismatch between the base and the top of the trophic web merit further investigations: (i) a more complex oceanic food web involving more trophic levels and thus higher MeHg biomagnification processes in

warmer (northern) than colder (southern) waters, and (ii) a higher MeHg enrichment within the trophic web due to higher production of MeHg by pelagic organisms (Pucko et al., 2014) to the north of the PF.

Conclusions

Overall, albatrosses clearly illustrate how elevated THg levels in avian species are governed by a combination of several factors, specifically (i) foraging grounds marked by high MeHg bioavailability (temperate waters) and (ii) feeding at the top of trophic webs (maximal biomagnification). The Diomedeidae is among the world's most threatened families of birds, will all the 22 species classified from Near Threatened to Critically Endangered in the IUCN Red List (Table S1). They face a number of direct and indirect threats that are causes of population declines, including climate change, fishery-related mortality, infectious diseases, introduced predators, and pollutants (Phillips et al., 2016). In this context, it is noteworthy that two of the three Critically Endangered species were also the most contaminated by Hg (Amsterdam and Tristan albatrosses), and that information is lacking on the third species (waved albatross). It is especially relevant that most individuals with THg levels above the upper feather toxicity threshold (40 µg/g; Burger and Gochfeld, 1997; Evers et al., 2008) were breeding Amsterdam albatrosses, the rarest albatross on Earth with a single population of approximately 165 adults (C. Barbraud et al., unpublished data). The whole population of Amsterdam albatrosses is at risk, because chicks are also heavily contaminated, with body feather concentrations averaging 7.8 µg/g (Y. Cherel et al., unpublished data).

One of the main problems in environmental toxicology is to interpret the impact of observed contaminant concentrations on wildlife. Most adult albatrosses have THg levels above the lower feather toxicity threshold (5 µg/g; Fig. 2), but seabirds are expected to have higher toxicity

resistance than other avian taxa since they cope with relatively high MeHg ingestion through efficient hepatic demethylation processes (Thompson and Furness, 1989a; Ikemoto et al., 2004). However, pioneering investigations on the biological consequences of Hg contamination pointed out (i) negative effects of blood THg on the immune function of black-footed albatrosses (Finkelstein et al., 2007), and (ii) negative effects of blood THg on demographic parameters of wandering albatrosses (Goutte et al., 2014). These data emphasize the urgent need for robust assessment of the impact of Hg exposure on the physiology and demography of albatrosses at a species, population and individual level, because Hg loading to the World Ocean is likely to continue rising (Lamborg et al., 2014), thus driving an increase accumulation of Hg in the biota, including albatrosses (Vo et al., 2011; Becker et al., 2016).

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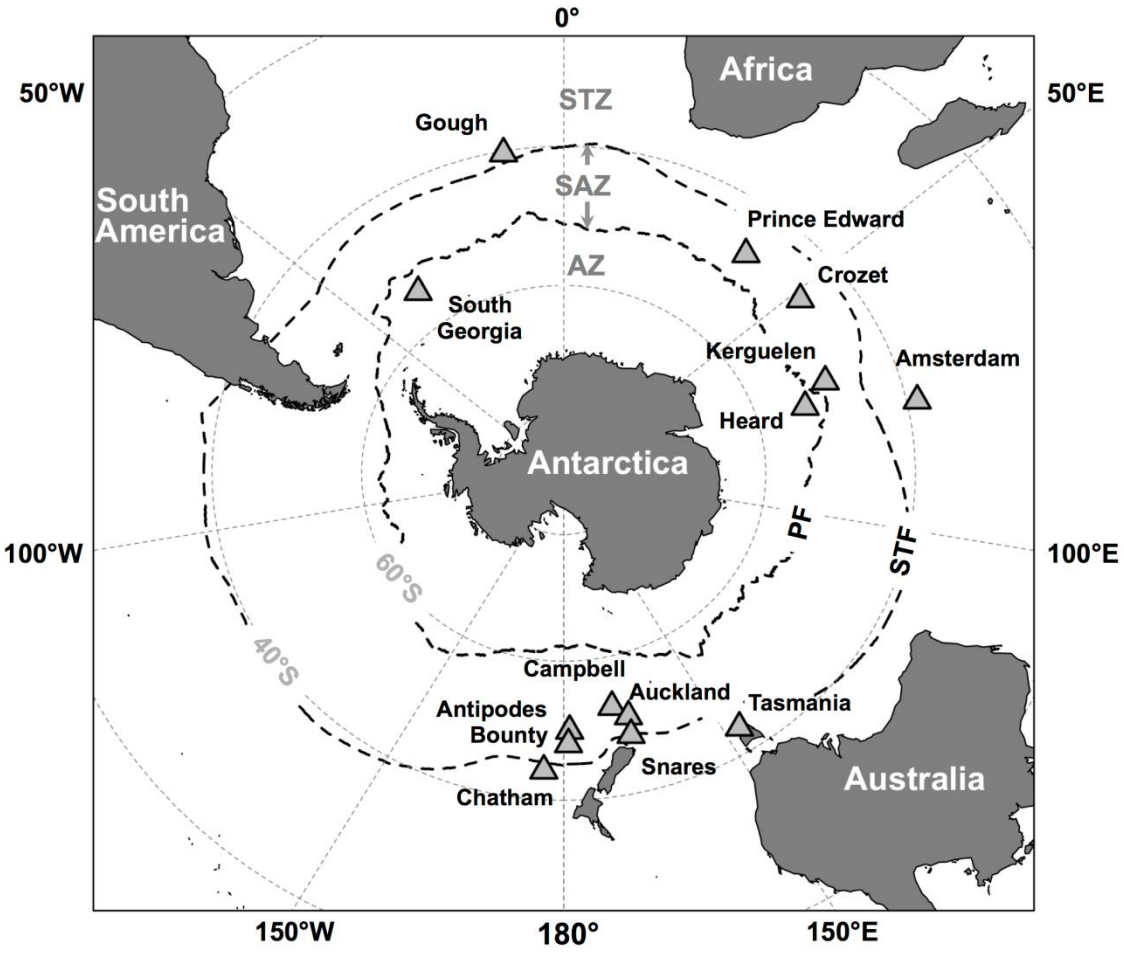

Figure 1. Location of albatross breeding localities and of the main oceanic fronts and zones of the Southern Ocean and fringing waters. Abbreviations: AZ, Antarctic Zone; PF, Polar Front; SAZ, Subantarctic Zone; STF, Subtropical Front; STZ, Subtropical Zone.

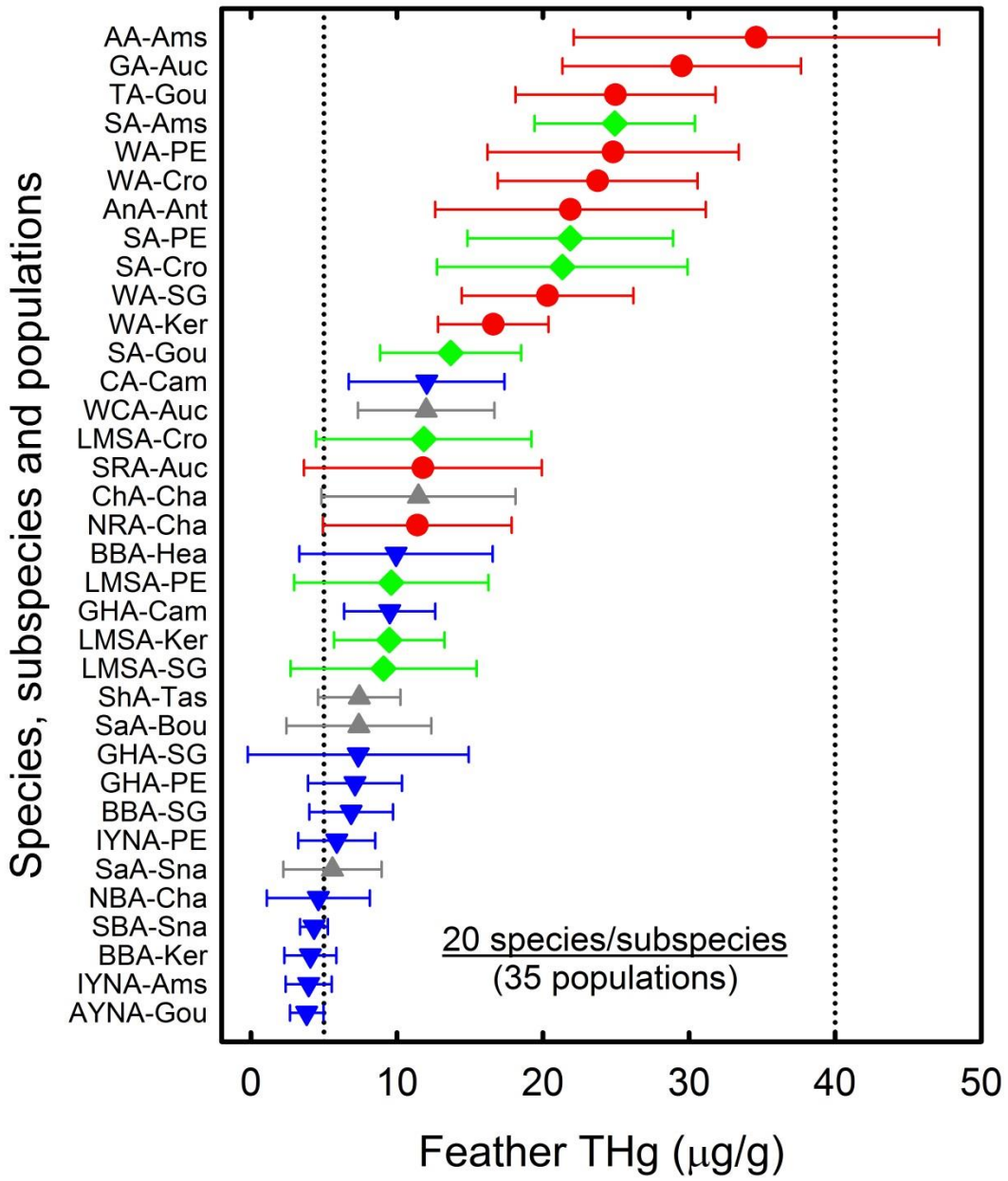

Figure 2. Concentrations of total mercury (THg) in body feathers of albatrosses from the Southern Ocean and fringing subtropical waters. Albatross taxa were deliberately placed in a sequence of increasing feather THg concentrations. Limited data for THg concentrations in feathers indicate a range of 5 to 40 µg/g (dotted lines) as being associated with adverse effects in birds (Burger & Gochfeld 1997, Evers et al. 2008). Colour and symbols: red circles (*Diomedea* albatrosses), grey triangles up (large *Thalassarche* spp.), blue triangles down (small *Thalassarche* spp.), green diamonds (*Phoebetria* spp.). Abbreviations are detailed in Table S1. Values are means ± SD. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.).

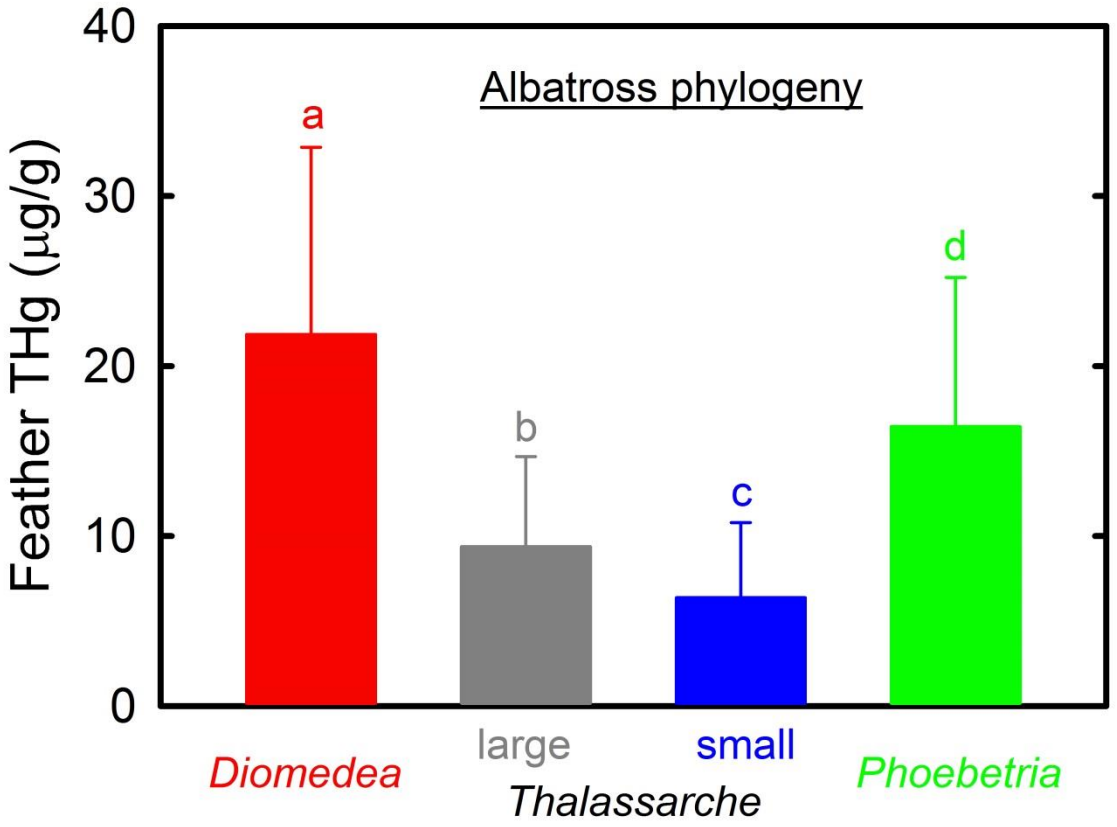

Figure 3. Histograms of feather THg concentrations in relation to albatross phylogeny. Kruskal-Wallis, H = 219.89, p <0.001; superscript letters indicate results from Conover-Inman tests for pairwise comparisons, all p <0.0001; see also text and Table 2 for GAMM statistics. Values are means ± SD.

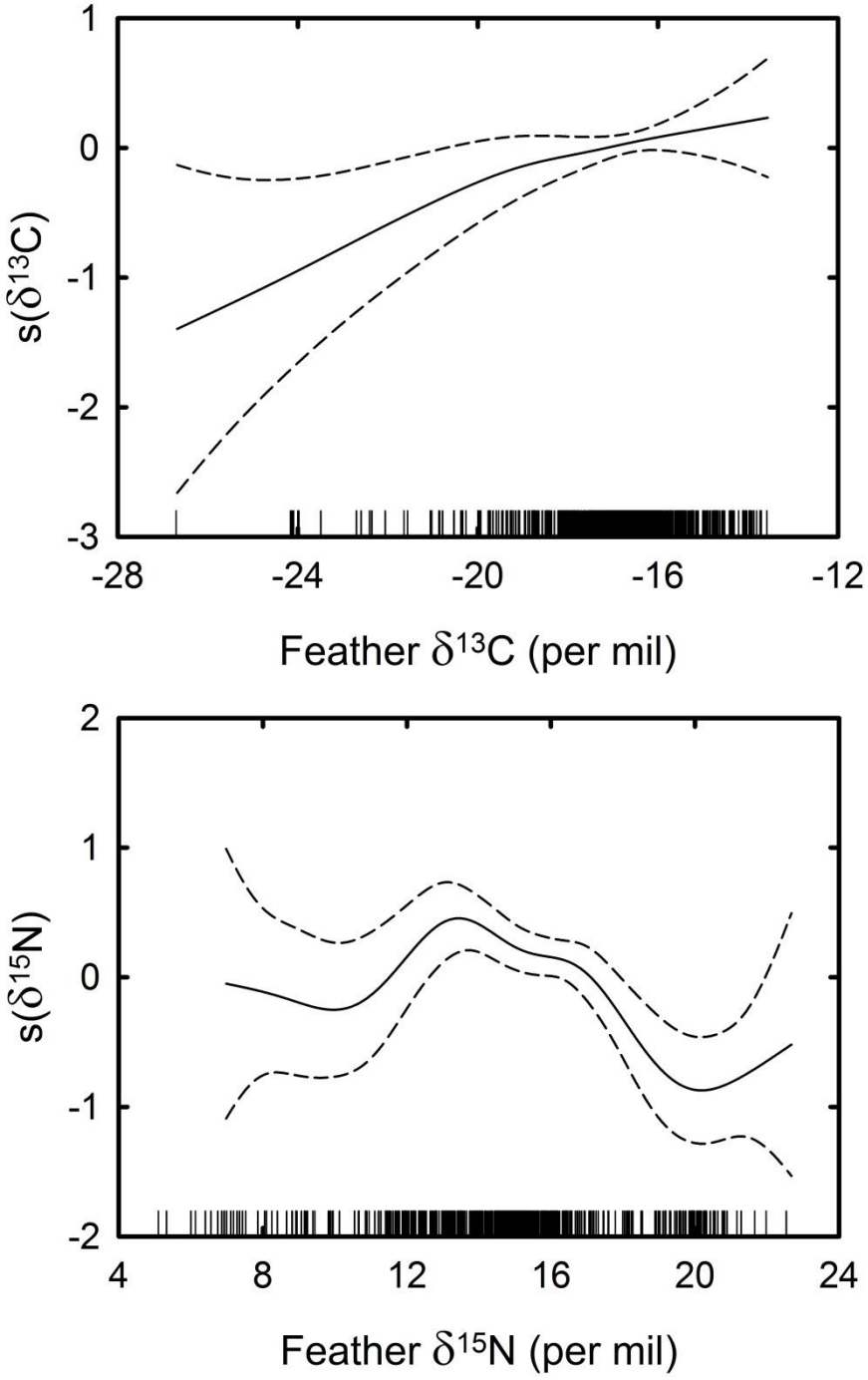

Figure 4. Fitted GAMM results showing the relationship between feather THg concentration and feather $\delta^{13}C$ and $\delta^{15}N$ values for the 516 sampled albatrosses. The y-axis gives the smooth transformed value, and the little vertical lines along the x-axis indicate the feather THg values of the observations. Dashed lines indicate the 95% confidence intervals.

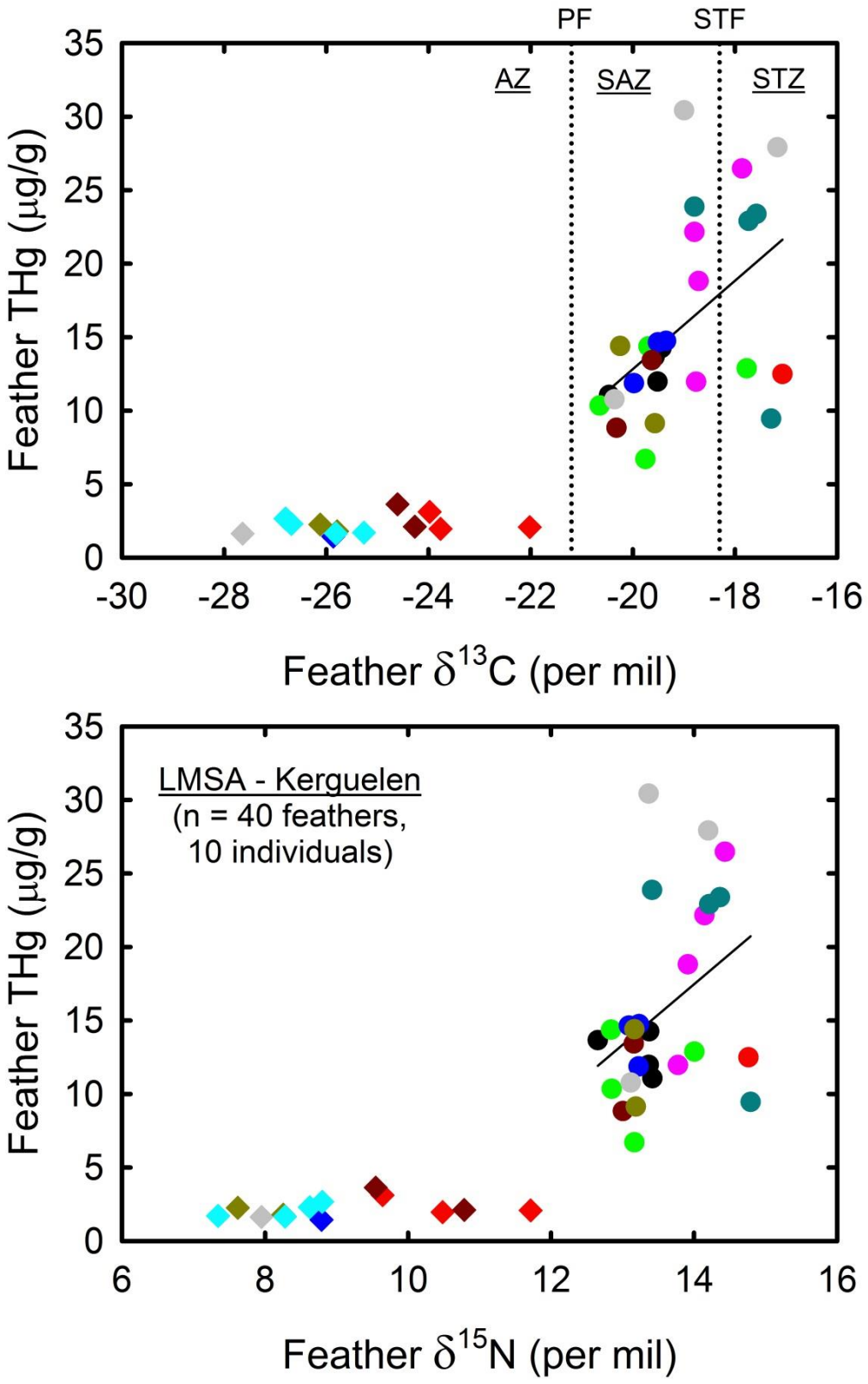

Fig. 5. Total mercury (THg) versus $\delta^{13}C$ (a proxy of moulting habitat) and $\delta^{15}N$ (a proxy of trophic position) in feathers of light-mantled sooty albatrosses from Kerguelen Islands. THg concentrations and $\delta^{13}C$ and $\delta^{15}N$ values were measured in four different body feathers per individual (one different colour per bird). Following Jaeger et al. (2010), dashed lines correspond to the isotopic estimation of the Polar Front (PF) and of the Subtropical Front (STF), which delimit the Antarctic (AZ), Subantarctic (SAZ) and Subtropical (STZ) Zones; LMSA, light-mantled albatross. Diamonds and circles indicate feathers that grew in the Antarctic Zone and further north, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1. Review of total mercury (THg) concentrations in body feathers of adult albatrosses. All the existing literature was reviewed up to date (December 2017). A few data were deleted due to various problems, including (i) too small sample sizes (n <5; Ochoa-acuña et al. 2002, Shinsuke et al. 2003), (ii) taxonomic uncertainties (*e.g.* the *Diomedea exulans* species complex; Thompson & Furness (1989b), Thompson et al. 1993), and (iii) geographical uncertainties together with other feather types than body feathers (*e.g.* North Pacific and flight feathers; Honda et al. 1989, Kim et al. 1996). Values are means ± SD with ranges in parentheses.

Taxa	Location	Individuals (n)	THg (µg/g)	References
***Diomedea* spp.**				
Wandering albatross	South Georgia	66	19.59 ± 10.12 (5.44 - 73.42)	Thompson et al. (1993)
		14	27.43 ± 8.14 (15.40 – 45.36)	Anderson et al. (2009)
		34	20.14 ± 7.64 (8.09 – 39.82)	Tavares et al. (2013)
		10	20.31 ± 5.88 (14.69 – 29.97)	This study
	Prince Edward	29	24.83 ± 12.35 (11.84 - 58.58)	Thompson et al. (1993)
		12	24.80 ± 8.61 (11.87-41.95)	This study
	Crozet	201	23.87 ± 11.83. (5.86 - 94.72)	Bustamante et al. (2016)
		12	23.75 ± 6.84 (13.79-38.30)	This study
	Kerguelen	12	16.59 ± 3.78 (9.84 - 24.13)	Carravieri et al. (2014b), this study
Antipodean albatross	Antipodes	15	21.87 ± 9.27 (9.22 - 41.93)	This study
Gibson's albatross	Auckland	15	29.50 ± 8.17 (16.85 - 50.09)	This study
Amsterdam albatross	Amsterdam	18	34.60 ± 12.50 (18.57-70.63)	This study
Tristan albatross	Gough	59	30.2 ± 15.6	Thompson et al. (1990)
		27	28.00 ± 14.31 (10.80 - 65.50)	Thompson et al. (1993)
		12	24.96 ± 6.85 (15.74-35.74)	This study
Southern royal albatross	Campbell	22	11.52 ± 13.86 (1.95 - 45.46)	Thompson et al. (1993)
	Auckland	15	11.78 ± 8.14 (2.33 - 27.57)	This study
Northern royal albatross	Chatham	20	11.40 ± 6.46 (3.50 - 26.27)	This study
***Phoebastria* spp.**				
Black-footed albatross	Midway	17	19.60 ± 1.75	Burger & Gochfeld (2000a,b)
Laysan albatross	Midway	13	3.46 ± 0.39	Burger & Gochfeld (2000a,b)
		10	1.86 ± 0.35	Burger & Gochfeld (2000c)
Large *Thalassarche* spp.				
Shy albatross	Tasmania	8	7.42 ± 2.82 (5.26-13.12)	This study
White-capped albatross	Auckland	31	11.99 ± 4.67 (3.87 - 20.80)	This study
Salvin's albatross	Snares	15	5.59 ± 3.36 (2.04-15.60)	This study
	Bounty	16	7.39 ± 4.96 (2.68-22.16)	This study
Chatham albatross	Chatham	11	11.46 ± 6.65 (2.32 - 23.10)	This study
Small *Thalassarche* spp.				
Black-browed albatross	Falklands	30	2.68 ± 1.22 (1.00 – 6.64)	Thompson et al. (1993)
	South Georgia	20	4.57 ± 1.98 (1.41 – 9.14)	Thompson et al. (1993)
		16	5.39 ± 2.05	Becker et al. (2002)
		16	8.35 ± 2.63 (4.24 – 12.97)	Anderson et al. (2009)
		10	6.86 ± 2.87 (4.31 – 12.76)	This study
	Kerguelen	33	4.07 ± 1.78 (1.71 - 7.75)	Carravieri et al. (2014b), this study
	Heard	8	9.93 ± 6.61 (2.60-19.63)	This study
Campbell albatross	Campbell	35	10.06 ± 4.40 (3.52 - 19.54)	Thompson et al. (1993)
		20	12.03 ± 5.33 (3.59 - 22.31)	This study

Southern Buller's albatross	Snares	15	4.32 ± 0.96 (2.69 - 6.31)	This study
Northern Buller's albatross	Chatham	20	4.62 ± 3.53 (2.18 - 16.11)	This study
Atlantic yellow-nosed albatross	Gough	10	4.22 ± 1.68 (2.27-7.97)	Becker et al. (2016)
		12	3.82 ± 1.14 (2.12-5.40)	This study
Indian yellow-nosed albatross	Prince Edward	10	5.88 ± 2.63 (2.43-11.84)	This study
	Amsterdam	20	3.96 ± 1.57 (1.93-8.69)	This study
Grey-headed albatross	South Georgia	34	4.20 ± 2.27 (1.22 - 11.00)	Thompson et al. (1993)
		19	8.93 ± 2.85	Becker et al. (2002)
		15	9.50 ± 2.84 (4.34 – 13.24)	Anderson et al. (2009)
		10	7.35 ± 7.57 (2.12 – 28.25)	This study
	Prince Edward	11	7.12 ± 3.21 (3.00-14.07)	This study
	Campbell	30	6.91 ± 2.40 (3.10 - 13.63)	Thompson et al. (1993)
		20	9.50 ± 3.11 (3.79-15.53)	This study
***Phoebetria* spp.**				
Sooty albatross	Gough	7	9.4 ± 3.9	Thompson & Furness (1989b)
		40	6.7 ± 4.2	Thompson et al. (1990)
		32	6.16 ± 4.23 (1.42 - 16.13)	Thompson et al. (1993)
		5	17.69 ± 3.64 (13.72 - 23.00)	Becker et al. (2016)
		13	13.67 ± 4.84 (1.76 - 20.09)	This study
	Prince Edward	14	21.86 ± 7.04 (8.78-32.97)	This study
	Crozet	12	21.32 ± 8.58 (7.41-35.36)	This study
	Amsterdam	22	24.92 ± 5.49 (14.37-36.37)	This study
Light-mantled sooty albatross	South Georgia	11	9.08 ± 6.36 (1.90 - 19.18)	This study
	Prince Edward	7	9.61 ± 6.65 (2.55-19.84)	This study
	Crozet	10	11.84 ± 7.38 (2.02-20.59)	This study
	Kerguelen	16	9.47 ± 3.78 (2.31 - 14.22)	Carraviéri et al. (2014b), this study

Table 2. GAMM results for feather THg concentrations as a function of covariates for the optimal model (516 sampled individuals from 35 populations). Variance components plus their SD are shown for random effects; edf indicates the estimated degrees of freedom for the smooth terms.

Effect	Estimate	SD	t-test	edf	F-test	p
Fixed effects						
Intercept	3.177	0.168	18.902			<0.001
Genus	-0.341	0.058	-5.842			<0.001
$s(\delta^{13}C)$				2.738	10.26	<0.001
$s(\delta^{15}N)$				7.385	14.15	<0.001
Random effects						
Population	0.159	0.399				
Residual	0.167	0.408				

Table 3. Feather $\delta^{13}C$ and $\delta^{15}N$ values and total mercury (THg) concentrations in relation to albatross moulting zones (according to the estimated isotopic positions of oceanic fronts in Jaeger et al. 2010). Stables isotopes and THg were measured on four different body feathers per individual bird. Kruskal-Wallis H tests were performed to compare moulting zones and species. Significant statistics ($p < 0.05$) are highlighted in bold. Values are means ± SD.

	Grey-headed albatross Prince Edward (n = 11)	Sooty albatross Gough (n = 13)	Light-mantled sooty albatross, Kerguelen (n = 10)	Kruskal-Wallis H tests
Antarctic Zone				
Feathers (n)	8	9	13	
Feather $\delta^{13}C$ (‰)	-22.2 ± 0.6	-22.5 ± 0.4	-25.3 ± 1.5	**H = 17.3, p <0.0001**
Feather $\delta^{15}N$ (‰)	11.0 ± 1.1	8.7 ± 0.7	9.1 ± 1.3	**H = 12.2, p = 0.002**
Feather THg (µg/g dry mass)	4.5 ± 1.2	4.6 ± 2.8	2.2 ± 0.6	**H = 14.8, p = 0.001**
Subantarctic Zone				
Feathers (n)	25	34	20	
Feather $\delta^{13}C$ (‰)	-19.7 ± 0.7	-19.0 ± 0.4	-19.6 ± 0.6	**H = 21.6, p <0.0001**
Feather $\delta^{15}N$ (‰)	11.6 ± 1.6	13.4 ± 0.7	13.3 ± 0.4	**H = 21.6, p <0.0001**
Feather THg (µg/g dry mass)	11.9 ± 7.3	14.7 ± 3.9	14.4 ± 5.6	**H = 7.0, p = 0.031**
Subtropical Zone				
Feathers (n)	11	9	7	
Feather $\delta^{13}C$ (‰)	-17.2 ± 0.5	-17.8 ± 0.3	-17.5 ± 0.3	**H = 7.4, p = 0.025**
Feather $\delta^{15}N$ (‰)	12.3 ± 1.1	14.2 ± 0.5	14.4 ± 0.3	**H = 12.9, p = 0.002**
Feather THg (µg/g dry mass)	8.8 ± 2.7	14.0 ± 4.2	19.4 ± 7.5	**H = 11.7, p = 0.003**
Kruskal-Wallis H tests				
Feather $\delta^{13}C$ (‰)	**H = 34.2, p <0.0001**	**H = 36.2, p <0.0001**	**H = 32.6, p <0.0001**	
Feather $\delta^{15}N$ (‰)	H = 4.3, p = 0.116	**H = 29.9, p <0.0001**	**H = 32.4, p <0.0001**	
Feather THg (µg/g dry mass)	**H = 14.01, p = 0.001**	**H = 19.5, p <0.0001**	**H = 26.6, p <0.0001**	
All three oceanic zones				
Feathers (n)	44	52	40	
Feather $\delta^{13}C$ (‰)	-19.5 ± 1.8	-19.4 ± 1.6	-21.1 ± 3.2	**H = 8.2, p = 0.016**
Feather $\delta^{15}N$ (‰)	11.7 ± 1.4	12.7 ± 2.0	12.1 ± 2.3	**H = 14.2, p = 0.001**
Feather THg (µg/g dry mass)	9.8 ± 6.3	12.8 ± 5.3	11.3 ± 8.3	**H = 8.9, p = 0.012**

Supplementary material

Table S1. Conservation status, breeding frequency, sampling sites, stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) and total mercury (THg) concentrations in body feathers of breeding albatrosses from the Southern Ocean and fringing subtropical waters. Values are means ± SD.

Taxa	Populations (Fig. 2)	IUCN Red List (2017)	Breeding frequency	Breeding location	Oceanographic zone	Individuals (n)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	THg (µg/g dry mass)
***Diomedea* spp.**									
Wandering albatross *D. exulans*	WA-SG	vulnerable	biennal	South Georgia	Antarctic	10	-17.4 ± 1.1	15.4 ± 0.6	20.3 ± 5.9 (14.7 – 30.0)
	WA-PE			Prince Edward	Subantarctic	12	-17.5 ± 1.0	15.4 ± 0.7	24.8 ± 8.6 (11.9-42.0)
	WA-Cro			Crozet	Subantarctic	12	-17.1 ± 0.7	15.7 ± 0.7	23.7 ± 6.8 (13.8-38.3)
	WA-Ker			Kerguelen	Subantarctic	12	-16.8 ± 0.6	15.8 ± 0.8	16.6 ± 3.8 (9.8-24.1)
Antipodean albatross *D. antipodensis antipodensis*	AnA-Ant	vulnerable	biennal	Antipodes	Subantarctic	15	-16.8 ± 0.6	15.3 ± 1.3	21.9 ± 9.3 (9.2 - 41.9)
Gibson's albatross *D. antipodensis gibsoni*	GA-Auc	vulnerable	biennal	Auckland	Subantarctic	15	-16.0 ± 0.6	16.4 ± 0.7	29.5 ± 8.2 (16.9 - 50.1)
Amsterdam albatross *D. amsterdamensis*	AA-Ams	critically endangered	biennal	Amsterdam	Subtropical	18	-16.2 ± 0.4	16.7 ± 0.6	34.6 ± 12.5 (18.6-70.6)
Tristan albatross *D. dabbenena*	TA-Gou	critically endangered	biennal	Gough	Subantarctic	12	-16.4 ± 0.5	16.5 ± 0.7	25.0 ± 6.9 (15.7-35.7)
Southern royal albatross *D. epomophora*	SRA-Auc	vulnerable	biennal	Auckland	Subantarctic	15	-16.0 ± 1.1	17.1 ± 1.5	11.8 ± 8.1 (2.3 - 27.6)
Northern royal albatross *D. sanfordi*	NRA-Cha	endangered	biennal	Chatham	Subtropical	20	-14.7 ± 1.0	19.6 ± 1.7	11.4 ± 6.5 (3.5 - 26.3)
Large *Thalassarche* spp.									
Shy albatross *T. cauta*	ShA-Tas	near threatened	annual	Tasmania	Subtropical	8	-17.4 ± 0.3	16.9 ± 0.4	7.4 ± 2.8 (5.3-13.1)
White-capped albatross *T. steadi*	WCA-Auc	near threatened	annual	Auckland	Subantarctic	31	-15.8 ± 1.3	16.6 ± 1.1	12.0 ± 4.7 (3.9 - 20.8)
Salvin's albatross *T. salvini*	SaA-Sna	vulnerable	annual	Snares	Subantarctic	15	-15.0 ± 0.9	19.3 ± 2.4	5.6 ± 3.4 (2.0-15.6)
	SaA-Bou			Bounty	Subantarctic	16	-15.1 ± 0.4	19.8 ± 1.1	7.4 ± 5.0 (2.7-22.2)
Chatham albatross *T. eremita*	ChA-Cha	vulnerable	annual	Chatham	Subtropical	11	-16.0 ± 0.5	17.5 ± 3.5	11.5 ± 6.6 (2.3 - 23.1)
Small *Thalassarche* spp.									
Black-browed albatross *T. melanophrys*	BBA-SG	near threatened	annual	South Georgia	Antarctic	10	-15.3 ± 1.7	15.4 ± 1.8	6.9 ± 2.9 (4.3 – 12.8)
	BBA-Ker			Kerguelen	Subantarctic	33	-17.1 ± 0.7	15.5 ± 0.6	4.1 ± 1.8 (1.7-7.7)
	BBA-Hea			Heard	Antarctic	8	-17.7 ± 0.3	14.9 ± 0.9	9.9 ± 6.6 (2.6-19.6)
Campbell albatross *T. impavida*	CA-Cam	vulnerable	annual	Campbell	Subantarctic	20	-16.8 ± 0.9	15.7 ± 2.0	12.0 ± 5.3 (3.6 - 22.3)
Southern Buller's albatross *T. bulleri bulleri*	SBA-Sna	near threatened	annual	Snares	Subantarctic	15	-16.3 ± 0.2	20.1 ± 0.5	4.3 ± 1.0 (2.7 - 6.3)
Northern Buller's albatross *T. bulleri platei*	NBA-Cha	near threatened	annual	Chatham	Subtropical	20	-15.9 ± 0.3	20.1 ± 0.6	4.6 ± 3.5 (2.2 - 16.1)
Atlantic yellow-nosed albatross *T. chlororhynchos*	AYNA-Gou	endangered	annual	Gough	Subantarctic	12	-15.6 ± 0.4	15.8 ± 0.5	3.8 ± 1.1 (2.1-5.4)

Indian yellow-nosed albatross *T. carteri*	IYNA-PE	endangered	annual	Prince Edward	Subantarctic	10	-15.5 ± 0.5	15.1 ± 0.7	5.9 ± 2.6 (2.4-11.8)
	IYNA-Ams			Amsterdam	Subtropical	20	-16.9 ± 0.5	15.5 ± 0.8	4.0 ± 1.6 (1.9-8.7)
Grey-headed albatross *T. chrysostoma*	GHA-SG	endangered	biennal	South Georgia	Antarctic	10	-19.2 ± 1.8	10.7 ± 0.8	7.3 ± 7.6 (2.1 – 28.3)
	GHA-PE			Prince Edward	Subantarctic	11	-19.5 ± 1.9	11.7 ± 1.5	7.1 ± 3.2 (3.0-14.1)
	GHA-Cam			Campbell	Subantarctic	20	-17.7 ± 1.3	11.6 ± 3.1	9.5 ± 3.1 (3.8-15.5)
***Phoebetria* spp.**									
Sooty albatross *P. fusca*	SA-Gou	endangered	biennal	Gough	Subantarctic	13	-19.2 ± 1.4	12.8 ± 2.0	13.7 ± 4.8 (1.8 - 20.1)
	SA-PE			Prince Edward	Subantarctic	14	-17.2 ± 0.8	14.4 ± 0.9	21.9 ± 7.0 (8.8-33.0)
	SA-Cro			Crozet	Subantarctic	12	-17.3 ± 1.0	14.0 ± 1.2	21.3 ± 8.6 (7.4-35.4)
	SA-Ams			Amsterdam	Subtropical	22	-16.6 ± 0.5	15.4 ± 0.8	24.9 ± 5.5 (14.4-36.4)
Light-mantled sooty albatross *P. palpebrata*	LMSA-SG	near threatened	biennal	South Georgia	Antarctic	11	-20.6 ± 2.3	11.8 ± 2.0	9.1 ± 6.4 (1.9 - 19.2)
	LMSA-PE			Prince Edward	Subantarctic	7	-19.9 ± 2.5	12.1 ± 2.0	9.6 ± 6.6 (2.6-19.8)
	LMSA-Cro			Crozet	Subantarctic	10	-20.5 ± 2.1	11.9 ± 2.1	11.8 ± 7.4 (2.0-20.6)
	LMSA-Ker			Kerguelen	Subantarctic	16	-19.8 ± 2.4	12.9 ± 1.6	9.5 ± 3.8 (2.3-14.2)