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

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A B S T R A C T

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.

1. 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

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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 from 35 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 non-invasively 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 $\delta^{13}C$ and $\delta^{15}N$, 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).

2. Materials and methods

2.1. 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.

2.2. 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, $\delta^{13}C$ 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 inter-breeding (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