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Alice Carravieri[1]*, Jérôme Fort[2], Arnaud Tarroux[3], Yves Cherel[1], Oliver Love[4], Solène Prieur[2], Maud Brault-Favrou[2], Paco Bustamante[2], Sébastien Descamps[3]

[1] Centre d'Etudes Biologiques de Chizé (CEBC) UMR 7372 CNRS-University of La Rochelle, 79360 Villiers-en-Bois, France

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

[3] Norwegian Polar Institute, Fram Centre, 9296 Tromsø, Norway

[4] The Great Lake Institute for Environmental Research (GLIER), University of Windsor, 401 Sunset Avenue, Windsor, Ontario, Canada, N9B 3P4

Corresponding author: alice.carravieri@gmail.com

Abstract: Mercury (Hg) is a pervasive contaminant reaching Antarctic environments through atmospheric transport and deposition. Seabirds as meso to top predators can accumulate high quantities of Hg through diet. Reproduction is one of the most sensitive endpoints of Hg toxicity in marine birds. Yet, few studies have explored Hg exposure and effects in Antarctic seabirds, where increasing environmental perturbations challenge animal populations. This study focuses on the Antarctic petrel *Thalassoica antarctica* from Svarthamaren, Antarctica, where the world's largest breeding population is thought to be in decline. Hg and the stable isotopes of carbon ($\delta^{13}C$, proxy of feeding habitat) and nitrogen ($\delta^{15}N$, trophic position/diet) were measured in red blood cells from 266 individuals over two breeding years (2012-13, 2013-14). Our aims were to 1) quantify the influence of individual traits (size and sex) and feeding ecology (foraging location, $\delta^{13}C$ and $\delta^{15}N$ values) on Hg exposure, and 2) test the relationship between Hg concentrations with body condition and breeding output (hatching success and chick survival). Hg concentrations in Antarctic petrels (mean ± SD, 0.84 ± 0.25, min-max, 0.42-2.71 µg g^{-1} dw) were relatively low when compared to other Antarctic seabirds. Hg concentrations increased significantly with $\delta^{15}N$ values, indicating that individuals with a higher trophic level (i.e. feeding more on fish) had higher Hg exposure. By contrast, Hg exposure was not driven by feeding habitat (inferred from both foraging location and $\delta^{13}C$ values), suggesting that Hg transfer to predators in Antarctic waters is relatively homogeneous over a large geographical scale. Hg concentrations were not related to body condition, hatching date and short-term breeding output. At present, Hg exposure is likely not of concern for this population. Nevertheless, further studies on other fitness parameters and long-term breeding output are warranted because Hg can have long-term population-level effects without consequences on current breeding success.

Keywords: Antarctica; Bioaccumulation; Body condition; Breeding success; Stable isotopes; Trophic position

1. Introduction

Increasing evidence shows that Antarctica is exposed to pervasive contaminants of natural and anthropogenic origins (Kallenborn et al., 2013; Mastromonaco et al., 2016). For instance, mercury (Hg), a non-essential metal, can travel long distances under its gaseous, elemental form (Fitzgerald et al., 2007) from its emission areas in industrialized countries through atmospheric transport, and reach Antarctica (Mastromonaco et al., 2016). There, Hg enters marine and terrestrial environments through wet and dry deposition processes, especially, but not exclusively, during springtime atmospheric Hg depletion events (Ebinghaus et al., 2002; Mastromonaco et al., 2016). Although Hg is partly re-emitted into the air, a fraction of waterborne Hg is assimilated by phyto- and zooplankton, in particular when Hg is under its methylated form (Morel et al., 1998). Once assimilated, methyl-Hg biomagnifies up the food web, with increasing Hg concentrations in tissues of organisms at higher trophic levels (Atwell et al., 1998; Bargagli et al., 1998). Upper predators such as seabirds can thus be exposed to large quantities of Hg via food intake (Bargagli et al., 1998). Consequently, seabirds are increasingly used as bioindicators of Hg distribution in the marine environment, including the polar regions (Carravieri et al., 2016; Fort et al., 2014; Polito et al., 2016), and are susceptible to Hg toxicity both at the individual and population levels (Goutte et al., 2014a,b; Tartu et al., 2013, 2016). In contrast to the Arctic, where spatio-temporal trends and negative effects of seabird exposure to Hg are relatively well known (e.g., Bond et al., 2015; Braune et al., 2014a; Dietz et al., 2013; Fort et al., 2016, 2014; Goutte et al., 2015; Scheuhammer et al., 2015; Tartu et al., 2013), Hg occurrence and toxicity in Antarctic species are poorly studied. Hg exposure has mainly been assessed in penguins in a variety of tissues (Brasso et al., 2015; Carravieri et al., 2016) especially in West Antarctica (e.g., Ancora et al., 2002; Brasso et al., 2012; dos Santos et al., 2006; Jerez et

al., 2011). By contrast, Antarctic flying seabirds have received much less attention (Tartu et al., 2014, 2015); most studies have reported Hg concentrations in eggs or tissues within a limited number of individuals, revealing similar levels to Arctic species, despite lower Hg concentrations in abiotic matrices (Bargagli et al., 1998; Calle et al., 2015; Cipro et al., 2017a; Nygård et al., 2001). Flying seabirds usually have larger foraging ranges than penguins during the breeding and/or wintering periods (BirdLife International, 2004), and thus visit a larger range of sites with potentially contrasting Hg bioavailability. As such, flying seabirds may be more at risk of exposure to high quantities of Hg.

Hg is a potent neurotoxin and an endocrine disruptor (Tan et al., 2009; Wolfe et al., 1998), and it has also been associated with decreased body condition and immune responses (Scheuhammer et al., 2007; Wayland et al., 2002). In aquatic and marine birds, reproduction is one of the most sensitive endpoints of toxicity (Evers et al., 2008; Wolfe et al., 1998). Specifically, Hg can reduce egg hatchability and embryo survival (Scheuhammer et al., 2007), but it can also impact parents' breeding decisions, behaviour and investment (Evers et al., 2008; Goutte et al., 2015; Tartu et al., 2013, 2015), with negative fitness consequences such as decreased breeding success over the short- and long-term (Evers et al., 2008; Goutte et al., 2014a,b). Antarctic species may be particularly sensitive to the toxic effects of contaminants as they have to cope with multiple additional environmental stressors in this rapidly changing, extreme environment (Barbraud and Weimerskirch, 2001; Descamps et al., 2015; Goutte et al., 2014a). Therefore, more studies are required to determine Hg concentrations and effects in Antarctic flying bird species and thereby fully grasp exposure, toxic effects and ultimately population-level consequences of Hg in this region.

In this context, the present study focuses on the Antarctic petrel *Thalassoica antarctica*, from Svarthamaren, Dronning Maud Land, Antarctica. The Antarctic petrel is a long-lived, middle-sized seabird and one of the least-studied Antarctic species. Svarthamaren hosts the largest known colony of this seabird, totalling 200 000 breeding pairs historically (Mehlum et al., 1988; van Franeker et al., 1999). However, lower numbers have been reported recently (<100 000 breeding pairs, Descamps et al., 2016a and unpublished data), and the population is thought to be in overall decline. Evaluating exposure and potential negative effects of Hg in this population is thus a pressing priority. The present study has two main aims: first, to quantify Hg exposure and disentangle the influence of individual traits (body size and sex) and feeding ecology on Hg concentrations, and second, to relate individual Hg exposure to fitness components. To this end, Hg burdens were quantified in blood in a large number of individuals across two consecutive breeding years. Blood is considered to be an excellent tool to evaluate Hg exposure in seabirds: circulating quantities are representative of recent dietary intake and are in equilibrium with internal tissue burdens (Bearhop et al., 2000; Fort et al., 2015; Fromant et al., 2016). Feeding ecology was evaluated by measuring blood values of the stables isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), which are chemical proxies of feeding habitat and trophic position, respectively (Newsome et al., 2007), and by equipping birds with Global Positioning System (GPS) loggers. During the breeding period, Antarctic petrels forage in high Antarctic waters over a large spatial scale, travelling up to 2000 km from the colony (Descamps et al., 2016b). Latitude dependentHg exposure has been previously shown in subantarctic (Carravieri et al., 2014a) and Antarctic (Tartu et al., 2014) seabirds. We thus predicted a geographical variation in exposure in individuals feeding at distant oceanic sites. Antarctic petrels are mainly krill-eaters, but their diet at Svarthamaren also includes a variable proportion of fish and squid (Descamps et al., 2016b).

Given the biomagnifying properties of Hg, we predicted individuals with higher $\delta^{15}N$ values (i.e. feeding at higher trophic positions) to bear higher Hg concentrations. Considering previous evidence of Hg effects on polar seabirds, we predicted individuals with high Hg concentrations to have a low body condition index and decreased breeding output (later hatching date, lower hatching success and chick survival) (Tartu et al., 2014, 2015).

2. Material and methods

2.1. Study site and sampling procedure

Fieldwork was carried out at the Svarthamaren Antarctic petrel colony (71°53'S, 5°10'E) where Antarctic petrels lay a single egg at the end of November/early December. Chicks hatch around mid-January and fledge early March. Both parents contribute to incubation and chick rearing, with the chick being continuously guarded for the first 7-15 days following hatching (Lorentsen and Røv, 1995). A total of 266 breeding individuals were captured during incubation or chick brooding over two breeding years (2012-13 and 2013-14). After taking morphometric measures (see section 2.2.), a small amount of blood (<2 ml) was sampled from the brachial vein, and temporarily preserved unfrozen in heparinized microtubes until being centrifuged. Red blood cells and plasma were then kept frozen in separate microtubes until subsequent analyses (see section 2.3). Some individuals (N = 91) were equipped with GPS loggers, which were attached to tail feathers using Tesa® tape (Descamps et al., 2016b; Tarroux et al., 2016; see also section 2.4.). Birds were immediately released onto their nests after handling, which typically lasted 10-20 min. Upon retrieval, GPS birds were sampled for blood again and weighed following the same procedures. In addition, all nests were monitored every other day on average from incubation to chick-rearing as presented in Descamps et al. (2015), to estimate hatching date,

hatching success and chick survival. For logistical reasons, nests could not be monitored until fledging and chick survival was therefore estimated 15 days after hatching.

2.2. Morphological measurements and body condition index

Birds were weighed with a 1000-g Pesola balance (precision ± 5 g), their bill height and culmen measured with a calliper (±0.1 mm), and their wing length measured with a ruler (±1.0 mm). In order to define body condition, the "scaled mass index" (Peig and Green, 2010, 2009), hereafter SMI, was calculated following Meillère et al. (2015). This body condition index adjusts the mass of all individuals to that expected if they had the same body size (Peig and Green, 2009).

2.3. Hg, stable isotope analyses and molecular sexing

Total Hg (hereafter "Hg") was quantified at the laboratory Littoral, Environment and Societies (LIENSs) from lyophilized and homogenised red blood cells with an Altec AMA 254 spectrophotometer (aliquots mass: ~5 mg dry weight, dw) as described in Bustamante et al. (2006). All analyses were carried out in duplicate, and the relative standard deviation (SD) for each individual was <10%. Accuracy was checked using a certified reference material (CRM, TORT-2 Lobster Hepatopancreas, NRC, Canada; certified Hg concentration: 0.27 ± 0.06 µg g^{-1} dw) every five samples. Measured values were 0.26 ± 0.01 µg g^{-1} dw, N = 103. Mass of the CRM was adjusted to represent an amount of Hg similar to that in red blood cell samples. Blanks were analysed at the beginning of each set of samples and the limit of detection was 0.005 µg g^{-1} dw.

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios were determined in red blood cells and delipidated plasma at the laboratory LIENSs with a continuous flow mass spectrometer (Thermo

Scientific Delta V Advantage) coupled to an elemental analyser (Thermo Scientific Flash EA 1112) (aliquots mass: ~0.3 mg dw). Results are in δ notation relative to Vienna PeeDee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively. Accuracy of the mass spectrometer was checked using internal laboratory standards (acetanilide) which showed measurement errors < 0.15‰for both $\delta^{13}C$ and $\delta^{15}N$. We evaluated the overall precision of measurement by duplicating a random subset of 22 samples (Jardine and Cunjak, 2005). The mean absolute difference between duplicates was 0.05‰ (range = [0; 0.14]), and 0.05‰ (range = [0.02; 0.10]), respectively for $\delta^{13}C$ and $\delta^{15}N$.

Gender was determined in a subsample of individuals (N = 139) after DNA extraction and polymerase chain reaction (PCR) amplification of CHD genes using primers from Fridolfsson and Griffiths. Genes were separated in 2% agarose gel by electrophoresis. Briefly, copies of CHD genes are present in both Z and W bird sexual chromosomes. CHD-Z and CHD-W genes differ in the base pair length of their non-coding regions. Because females are heterogametic (ZW) and males homogametic (ZZ), separation of gene amplification products by size results in a single band for males and two bands for females. DNA extraction negative controls were included for every runs.

2.4. GPS tracking

GPS (CatTrack 1, Catnip Technologies Ltd., Anderson, USA; 25 X 45 X 9 mm, ca. 20 g with a shrink tube used for water proofing) were used to estimate the location of birds' foraging grounds during one or two consecutive trips (Descamps et al., 2016b; Tarroux et al., 2016). GPS units were programmed to record bird position every 5-90 min (median = 10 min) and were deployed for an average of 11 days (min = 2 d, max = 28 d). From GPS recordings, latitude and longitude

of the furthest location from the breeding colony were extracted and used as a proxy for an individual's foraging ground. Only complete foraging trips (i.e. trips with data recorded until birds returned to the colony) were considered. To validate the consistency of foraging grounds used over time by individual birds, we investigated the relationship between $\delta^{13}C$ values in plasma and red blood cells. $\delta^{13}C$ values indeed have contrasted turn-over rates in plasma (a few days, thus corresponding well to the period of GPS tracking) and in red blood cells (several weeks) (Hobson and Clark, 1993) meaning that $\delta^{13}C$ values measured in both plasma and red blood cells are indicators of the short- and medium-term feeding habitats, respectively. We found a strong positive relationship between $\delta^{13}C$ values measured in these two tissues ($R^2 = 0.59$, $F_{1,20} = 30.79$, $p < 0.001$), indicating that birds show consistent feeding habitats over the medium term (Xavier et al., 2017). All analyses were thus carried out on red blood cell sample data (hereafter "blood").

2.5. Statistical analyses

Statistical analyses were carried out using R 3.3.2 (R Core Team, 2016). as summarised in Table S1. In a first step, the relationship between feeding ecology (inferred from blood $\delta^{13}C$ and $\delta^{15}N$ values), foraging ground (inferred from the latitude and longitude of the furthest location from the breeding colony), sampling date and breeding years and blood Hg concentrations was assessed through a generalized linear model (GLM) with a gamma distribution and a log link function. This model specification is appropriate for continuous, positive dependent variables with a positive skew (i.e. non-normal, with a long tail on the right, Crawley, 2007), a pattern that was present here and that is overall common in the distribution of contaminant concentrations. Only Hg and stable isotope data at GPS retrieval were considered, so that GPS tracking, blood

Hg and stable isotope values were representative of a similar time window. The variable "sampling date" was included in models as the number of days from the 1st of December of the respective breeding year. The maximal model was set as Hg ~ $\delta^{13}C$ + $\delta^{15}N$ + date + latitude + longitude + sex + year. All potential biological models without interactions were compared using the Bayesian Information Criterion (BIC), and a relative weight of evidence (w_i normalized model likelihood given the set of models) was calculated for each model (Burnham and Anderson, 2002). The explanatory power of a given model was judged by the explained deviance adjusted for sample size and number of parameters. The effect of explanatory variables was interpreted by their parameter estimates (slope ± standard error, SE) in the selected model.

In a second step, relationships between blood Hg concentrations and physiological (SMI) and fitness parameters (hatching date and success, chick survival) were examined on a larger sample size including also birds that were not equipped with GPS loggers (Table S1). Mixed-effect models (function lme from the nlme package, Pinheiro et al., 2017) were fitted using maximum likelihood (ML) as follows: physiological/fitness parameter ~ Hg + $\delta^{15}N$ + sampling date + year (+breeding status for SMI and chick survival data). These covariates were included in order to adjust for potential confounding effects. In particular, $\delta^{15}N$ was included as results from the first step indicated a significant association between $\delta^{15}N$ and Hg (see Results). The significance of the relationship between Hg and the physiological/fitness parameters was examined using log-likelihood ratio tests (LRT) between models including or removing the term "Hg". Hatching date was analysed as the number of days from the 1st of December of the respective breeding year. Model assumptions were checked through visual inspection of the residuals. For binomial models, model fit was checked through the overdispersion term value. All results are mean ± SD.

3. Results

3.1. Explanatory factors of Hg concentrations

We detected quantifiable concentrations of Hg in all individuals: 0.84 ± 0.25 (range 0.42-2.71) µg g^{-1} dw (Table 1). Blood Hg concentrations in males and females, as well as during the 2012-13 and 2013-14 breeding years are presented in Table 1 and Table S2. Blood $\delta^{13}C$ values in individuals equipped with GPS units ranged from -26.4 to -25.0‰ (Table 1), while blood $\delta^{15}N$ values ranged from 8.3 to 10.2‰ (Table 1). The most parsimonious model for explaining blood Hg concentrations (Table 2) included the effect of $\delta^{15}N$ values (estimate ± SE, 0.228 ± 0.065, $p < 0.001$, Fig. 1), sex (males: -0.141 ± 0.046, $p = 0.003$) and sampling date, although the effect size was very small (0.004 ± 0.001, $p = 0.008$, Table 2).

Models including maximum latitude or longitude of foraging trips, or $\delta^{13}C$ values, had less support ($\Delta BIC > 2$, Table 2).

3.2. Hg relationships with SMI and reproductive parameters

SMI values were not significantly related to blood Hg, when taking into account $\delta^{15}N$, sampling date, year, status (-17.12 ± 18.01, LRT: LR = 0.92, $p = 0.338$, N = 258, Table S1), and sex (18.01 ± 22.49, LR = 0.66, $p = 0.418$, N = 163, Table S1). The relationship between blood Hg concentrations and hatching date and success was tested in incubating individuals. The mean hatching date was January 15th (±2 days) in 2012-13 and January 16th (±3 days) in 2013-14, and was not related to blood Hg concentrations in incubating individuals (2.38 ± 1.66, LR = 2.23, $p = 0.136$, N = 52, Table S1), even when an individual's sex was accounted for (2.68 ± 1.98, LR = 2.14, $p = 0.144$, N = 36, Table S1).

Hatching success in the sampled population was higher in 2012-13 than in 2013-14 (54% and 33%, respectively), but it was not related to blood Hg concentrations in incubating individuals (0.01 ± 0.75, LR < 0.001, p = 0.980, N = 175, Table S1) also when taking sex into account (0.40 ± 0.82, LR = 0.22, p = 0.639, N = 115, Table S1). Survival of chicks 15 days after hatching was higher in 2012-13 than in 2013-14 (58% and 36%, respectively), but again it was not related to their parent blood Hg concentrations (0.47 ± 0.56, LR = 0.635, p = 0.426, N = 106, Table S1), even when an individual's sex was accounted for (0.28 ± 0.78, LR = 0.14, p = 0.713, N = 70, Table S1).

4. Discussion

This study is a comprehensive evaluation of the causes and consequences of Hg exposure in an Antarctic flying seabird, focusing on one of the least known seabird species in this region, the Antarctic petrel. Overall, our results demonstrate low blood Hg concentrations in breeding birds with no apparent link to reproductive output. Results also provide new important information regarding the role played by avian trophic ecology on exposure to Hg at a time when rapidly-changing environmental conditions in polar regions (and in Antarctica in particular) might modify ecosystem functioning, food web structure, and Hg bioavailability to top predators.

4.1. Hg exposure: trophic ecology and other explanatory factors

When compared to other flying seabirds from Antarctica, Antarctic petrels generally had low Hg concentrations. Specifically, the fish-eating snow petrel *Pagodroma nivea* and the penguin-eating Antarctic skua *Catharacta maccormicki* from Adélie Land had approximately two-three times higher blood (Goutte et al., 2014a,b; Tartu et al., 2014, 2015) and tissue burdens (Nygård

et al., 2001). By contrast, Antarctic petrels had higher blood Hg concentrations than krill-eating Antarctic penguins (Polito et al., 2016; authors' unpublished data). Interestingly, Hg blood burdens in Antarctic petrels were very similar to those of chinstrap penguins *Pygoscelis antarctica*, which feed mainly on Antarctic krill *Euphasia superba* and to a lesser extent on mesopelagic fish (Polito et al., 2016). Antarctic petrels also feed mainly on krill, although they feed on fish and squid as well (Descamps et al., 2016b; Lorentsen et al., 1998). The similar burdens between chinstrap penguins and Antarctic petrels are therefore not surprising. Feeding ecology is indeed considered to be the main driver of Hg exposure in seabirds, in contrast to intrinsic factors such as phylogeny (Carravieri et al., 2014b). In particular, trophic position plays a pivotal role, because of Hg biomagnifying properties (Atwell et al., 1998; Bargagli et al., 1998). Accordingly, blood $\delta^{15}N$ values were the main driver of blood Hg concentrations in Antarctic petrels: individuals with higher blood $\delta^{15}N$ values (i.e. with likely higher proportions of fish in their diet (Cherel et al., 2014) had significantly higher blood Hg concentrations than those with lower $\delta^{15}N$ values (i.e. feeding more largely on krill (Fig. 1). Inter-specific differences in seabird Hg concentrations are usually explained by d15N values, especially in blood, where the time integrations of Hg and $\delta^{15}N$ match (Anderson et al., 2009; Bearhop et al., 2000; Bond and Diamond, 2009). However, such a clear effect within one single seabird population is rarely observed (Tartu et al., 2014), specifically when variation in $\delta^{15}N$ values is relatively small (~2‰, i.e. less than one trophic level, Newsome et al., 2007). This result thus suggests that the mesopelagic fish prey of Antarctic petrels has disproportionately higher Hg content than krill, as has been reported from other sites in the Southern Ocean (Anderson et al., 2009; Cipro et al., 2017b; Polito et al., 2016). Consequently, even a small proportion of fish in the diet of some individuals likely critically increased their Hg exposure. This also highlights that Hg

measurements in the prey of Antarctic petrels prey are urgently needed to validate our results and further help determining potential risks of Hg exposure for Antarctic seabirds and other marine top predators.

Very negative blood $\delta^{13}C$ values indicate that Antarctic petrels fed strictly in high Antarctic waters (Cherel, 2008, Cherel et al., 2011) across a very wide longitudinal range, as shown by GPS tracking (Descamps et al., 2016b). Contrary to our prediction though, feeding habitat showed no significant relationship with Hg exposure, as shown by the poor support of models including $\delta^{13}C$ values and the location of the most distant foraging grounds (Table 2). Hg exposure thus appeared to be homogeneous over the vast oceanic region exploited by Antarctic petrels. This is consistent with previous results in Antarctic penguins; different populations from all around the Antarctic Peninsula had very similar Hg concentrations, thus suggesting homogeneity of Hg bioavailability in high Antarctic waters over large geographical scales (Brasso et al., 2012). This assertion is also supported by results in Antarctic prions *Pachyptila desolata* at South Georgia, which also feed primarily on Antarctic krill and secondarily on mesopelagic fish (Reid et al., 1997), and which have a similar blood Hg concentration to Antarctic petrels (Anderson et al., 2009). The homogeneity of Hg transfer to predators in high Antarctic waters contrasts with results in subantarctic and subtropical waters of the Southern Ocean, where Hg transfer to predators shows a latitudinal gradient increasing northward (Carravieri et al., 2014a, 2017). The sharp differences in physico-chemical properties between the water masses of the Southern Ocean could drive different rates of Hg deposition, re-emission to the air, and methylation in the water column (Fitzgerald et al., 2007), ultimately explaining the contrasting Hg transfer to predators at different latitudes. Hg exposure has been shown to differ depending on latitude also in Arctic seabirds (higher concentrations in the high Arctic, Braune et

al., 2014b), likely as a consequence of dietary differences or of atmospheric Hg sources at low and high latitudes. The homogeneity of Hg exposure highlighted here thus appears to be specific to Antarctica.

Male and female Antarctic petrels had similar blood Hg concentrations (Table 1). Yet, when considering individuals equipped with GPS loggers, sex significantly predicted Hg exposure while accounting for feeding strategies (Table 2), with females having slightly higher Hg concentrations than males (Fig. 1). This result was unexpected, first because females partly excrete accumulated Hg to their eggs (Agusa et al., 2005), and second because sex related differences in Hg burdens in seabirds are often the result of sexual segregation in feeding ecology (Carravieri et al., 2014a; Robinson et al., 2012). In Antarctic petrels though blood $\delta^{13}C$ and $\delta^{15}N$ values, and feeding tactics (Descamps, unpublished data) were similar between sexes. Hence, despite statistical significance, this result does not seem biologically meaningful. Alternatively, the higher concentrations in females could stem from: i) sex-related physiological differences in Hg kinetics in the organism (absorption, internal organ storage, and excretion), ii) sex-related differences in diet, during the breeding or wintering periods, that are not mirrored in blood d13C and d15N values, or iii) other direct or indirect unknown factors (Provencher et al., 2016). Further studies, and in particular a detailed description of sex-specific prey choice, could help to verify the sex-related difference in Hg accumulation depicted here.

Antarctic petrels blood Hg concentrations increased slightly during the breeding season (i.e. effect of the date of capture), although the effect was very weak. Temporal variation in blood Hg concentrations could be the result of intrinsic factors, such as Hg accumulation in internal tissues before moult, when a large proportion of Hg can be excreted into feathers (Monteiro and Furness, 2001), or due to physiological changes related to breeding status. Nonetheless, extrinsic

factors could also be involved, such as a diet change over time, for example as a result of an increase of food intake to counterbalance higher energy expenditure along with the increasing nutritional needs of growing chicks. In addition, there could be a temporal variability in Hg bioavailability in food webs (Braune et al., 2014a). Nevertheless, disentangling the influence of such complex intrinsic and extrinsic factors is beyond the scope of the present study. In addition, longitudinal investigations on temporal changes in Hg concentrations in wild seabirds' tissues are still dramatically lacking. On the other hand, blood Hg concentrations were not significantly related to the year of sampling, highlighting low inter-annual variability in exposure over the short-term, as usually observed at oceanic sites far from Hg point sources (Brasso et al., 2014; Carravieri et al., 2016).

In conclusion, even though feeding ecology, sex, and capture date were significant predictors of Hg exposure in breeding Antarctic petrels, a large component of individual variation in blood Hg concentrations (~70%) remained unexplained. In the current study the age of the birds was unknown, and even though age-related changes in blood Hg concentrations in adult seabirds are usually not significant or weak (Carravieri et al., 2014a; Tartu et al., 2014; Tavares et al., 2013), taking age into account may have explained some of the remaining variation in Hg burdens. Other factors, such as individual-specific excretion capacities in the feathers (Bearhop et al., 2000), demethylation capacity in the liver, or rate of absorption in the gut, in addition to extrinsic factors such as individual-specialisation on particular prey species (Anderson et al., 2009; Polito et al., 2016), could all have played a role and merit further investigation.

4.4. Effects of Hg on physiology and fitness components

Very few studies have established threshold levels of Hg deleterious effects in wild bird populations, because of the need to quantify several endpoints of toxicity (physiological, behavioural, and reproductive), to follow populations over the long-term, and because of the difficulty, for ethical reasons, of experimentally manipulating exposure in protected species (Evers et al., 2008; Goutte et al., 2015). However, studies on the common loon *Gavia immer*, an obligate piscivorous bird, showed that blood concentrations >3.0 µg g^{-1} ww (~12.0 µg g^{-1} dw) were associated with reproductive impairment (Evers et al., 2008). Similarly, the most contaminated male snow petrels (~2 µg g^{-1} dw) were more prone to neglect their egg during incubation, likely as a result of hormonal disruption (Tartu et al., 2015). Blood Hg concentrations in snow petrels were lower than the common loon threshold, stressing the fact that Hg sensitivity can be species-specific (Heinz et al., 2009), and that toxic effects may appear at lower concentrations in polar environments (Goutte et al., 2014a). Here, the hatching date and success, as well as the chick survival of Antarctic petrels were not related to Hg exposure. This result highlights that the current levels of exposure to Hg might not be of concern to Antarctic petrels. Yet, further studies should confirm this trend, by focusing on other fitness traits and other phases of the birds' annual cycle (Tartu et al., 2013; Fort et al., 2014). Pre-laying Hg exposure is governed by feeding intake on early breeding grounds, but also on burdens previously accumulated in wintering habitats. During the long polar winter, Antarctic petrels remain in Antarctic waters, but they increase their foraging range (Descamps et al., 2016b), potentially increasing exposure to food webs with contrasting Hg concentrations. Measuring Hg concentrations in feathers, or in blood upon arrival at the colony, will be necessary to better evaluate long-term and pre-breeding Hg exposure in Antarctic petrels. Hg contamination in birds

has the potential to modify physiological functions, such as energy metabolism, which is associated with detoxification mechanisms (Lucia et al., 2012). Although such modifications might not have immediate consequences on fitness, they might alter an individual's body condition. Body-condition can be an important determinant of fitness-related traits including breeding success and survival (Labocha and Hayes, 2012). In our study, body condition was not related to blood Hg concentrations, further highlighting that current Hg concentrations are not of concern to Antarctic petrels. However, Goutte et al. (2014a,b) reported that blood Hg concentrations were negatively related to long-term breeding success in wandering albatrosses *Diomedea exulans* and brown skuas *Stercorarius antarcticus*, without a link to current reproduction. Furthermore, species living in high Antarctic regions were shown to be more sensitive to the negative reproductive effects of Hg (Goutte et al., 2014a,b). This is likely because these species are exposed to increasing environmental stress factors, such as changes in large- and small-scale climatic events, and could thus be affected by Hg burdens even when no "acute" toxicity is observed. Demographic parameters of the Antarctic petrel population at Svarthamaren are explained by large-scale climatic oscillations and by the occurrence of extreme events such as snow storms (Descamps et al., 2015, 2016a). Yet, even when accounting for these environmental factors, chick production and adult survival have significantly declined in the last three decades (Descamps et al., 2016a). There is therefore an important need to determine whether exposure to Hg or other environmental contaminants could contribute to this decline through long-term effects.

5. Conclusions

This study confirms that feeding ecology plays a key role in Hg exposure in seabirds, even at the population level. Yet, the large unexplained part of total variation in blood Hg concentrations warrants more studies on physiological parameters that could influence individual differences. The level of exposure to Hg in Antarctic petrels is low at present, and with non-detectable effects on current reproduction and body condition. Nonetheless, and despite a recent decrease in Hg emissions on a global scale (Zhang et al., 2016), the temporal lag between emissions of Hg and its integration in marine food webs (Driscoll et al., 2013; Fitzgerald et al., 2007) might enhance exposure of Antarctic petrels and Antarctic biota in the future. Importantly, a reorganisation of food web structure and/or a modification in food availability following largescale environmental change might also modify Hg intake by Antarctic petrels (Braune et al., 2014a), in particular if krill abundance decreases (Kawaguchi et al., 2013). Furthermore, Antarctic biota is exposed to a complex mixture of environmental contaminants that could have synergistic or antagonistic effects on physiology and reproduction. For all these reasons, future monitoring actions of Hg and other contaminants in this vulnerable Antarctic seabird population are needed.

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Table 1. Hg concentrations and stable isotope values in red blood cells of Antarctic petrels from Svarthamaren, Antarctica, with 2012-13 and 2013-14 breeding years combined. Values are mean ± SD with range in parenthesis.

		N	Hg (μg g^{-1} dw)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
All sampled individuals	All	266	0.84 ± 0.25 (0.42–2.71)	−25.2 ± 0.5 (−26.4–24.1)	9.7 ± 0.5 (8.2–10.9)
	F	88	0.83 ± 0.24 (0.44–2.04)	−25.2 ± 0.4 (−26.3–24.4)	9.6 ± 0.5 (8.2–10.6)
	M	79	0.83 ± 0.23 (0.48–1.81)	−25.3 ± 0.6 (−26.3–24.1)	9.7 ± 0.4 (8.8–10.7)
GPS individuals	All	91	0.80 ± 0.20 (0.45–1.62)	−25.7 ± 0.3 (−26.4–25.0)	9.2 ± 0.4 (8.3–10.2)
	F	48	0.83 ± 0.22 (0.56–1.62)	−25.6 ± 0.3 (−26.4–25.1)	9.2 ± 0.4 (8.3–10.2)
	M	43	0.75 ± 0.18 (0.45–1.17)	−25.7 ± 0.4 (−26.4–25.0)	9.2 ± 0.3 (8.5–10.1)

Table 2. Model selection for blood Hg concentrations at GPS retrieval in breeding Antarctic petrels from Svarthamaren, Dronning Maud Land, Antarctica. Models are ranked by increasing ΔBIC (i.e., decreasing model fit). Only the null, maximal and the first 10 best models are presented. Abbreviations: BIC, Bayesian Information Criteria; wi, weight of evidence interpreted as a proportion; Exp. Dev., explained deviance; Lat and Lon, latitude and longitude, respectively, of the furthest GPS location from the breeding colony.

Models	k[a]	BIC	ΔBIC	w_i[b]	Exp. Dev. (%)[c]
Maximal model: Hg ~ $\delta^{13}C + \delta^{15}N$ + Lat + Lon + Year + Sex + Date					
Hg ~ $\delta^{15}N$ + Date + Sex	4	−52.97	0	0.62	27.5
Hg ~ $\delta^{15}N$ + Date + Year + Sex	5	−48.88	4.10	0.08	27.8
Hg ~ $\delta^{15}N$ + Date + Lat + Sex	5	−48.80	4.17	0.08	27.8
Hg ~ $\delta^{13}C + \delta^{15}N$ + Date + Sex	5	−48.48	4.50	0.07	27.5
Hg ~ $\delta^{15}N$ + Date + Lon + Sex	5	−48.47	4.50	0.07	27.5
Hg ~ $\delta^{15}N$ + Date	3	−47.69	5.28	0.04	19.3
Hg ~ $\delta^{15}N$ + Date + Lat	4	−45.31	7.66	0.01	21.2
Hg ~ $\delta^{15}N$ + Date + Lat + Year + Sex	6	−44.89	8.09	0.01	28.2
Hg ~ $\delta^{13}C + \delta^{15}N$ + Date + Year + Sex	6	−44.51	8.47	0.01	28.0
Hg ~ $\delta^{15}N$ + Date + Lon + Year + Sex	6	−44.39	8.58	0.01	27.9
Null model	1	−36.98	15.99	0.00	0.00
Maximal model	8	−36.31	16.66	0.00	0.29

[a] Number of parameters.
[b] Weights across all models (not all shown) sum to 1.00.
[c] Explained deviance adjusted by k and N.

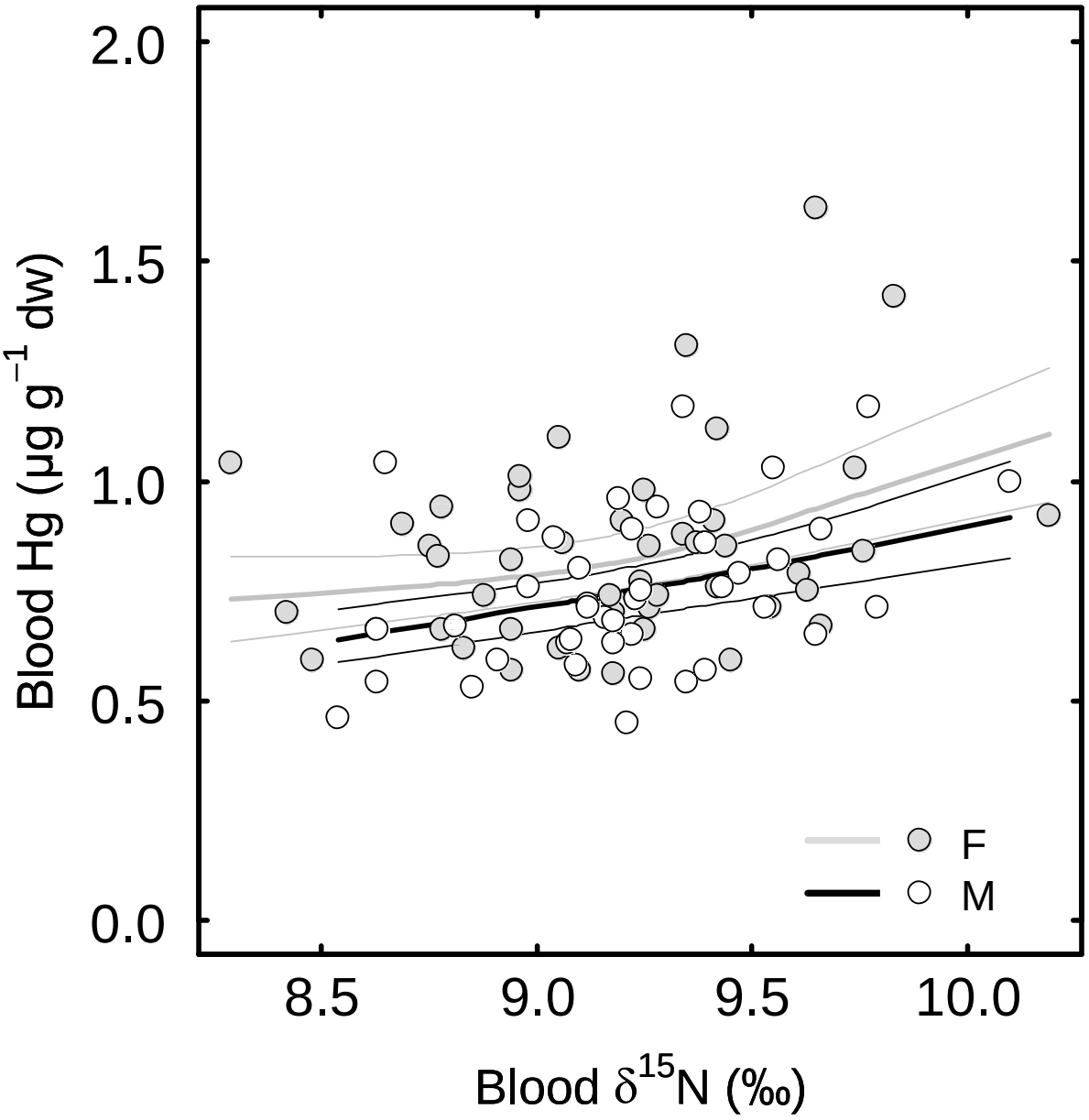

Figure 1. Blood Hg concentrations increase with increasing δ^{15}N values in breeding Antarctic petrels from Svarthamaren, Dronning Maud Land, Antarctica. The represented model corresponds to the first ranked model from **Table 1**.

Supplementary Material

Table S1. Models' specification and sample size (N) details.

Dependent variable	Type	N	Model specification	Explanatory variables	Random effects
Hg	Continuous, positive	91	GLM, Gamma family, log link function (function glm)	$\delta^{13}C$, $\delta^{15}N$, Date, Latitude, Longitude, Year	-
Body condition (SMI)	Continuous, positive	All: 258	Mixed-effects linear model (function lme)	Hg, $\delta^{15}N$, Date, Year, Status	Individual
		Known sex F: 86 M: 77	Mixed-effects linear model (function lme)	Hg, $\delta^{15}N$, Date, Year, Status, Sex	Individual
Hatching date	Continuous, positive	Incubating individuals All: 52	Mixed-effects linear model (function lme)	Hg, $\delta^{15}N$, Date, Year, Sex	Individual
		Known sex F: 19 M: 17	Mixed-effects linear model (function lme)	Hg, $\delta^{15}N$, Date, Year, Sex	Individual
Hatching success	Binary	Incubating individuals All: 175	Mixed-effects generalized linear model (function lmer), Binomial family, logit link function	Hg, $\delta^{15}N$, Date, Year	Individual
		Known sex F: 61 M: 54	Mixed-effects generalized linear model (function lmer), Binomial family, logit link function	Hg, , $\delta^{15}N$, Date, Year, Sex	Individual
Chick survival	Binary	Incubating individuals All: 106	Mixed-effects generalized linear model (function lmer), Binomial family, logit link function	Hg, $\delta^{15}N$, Date, Year	Individual
		Known sex F: 35 M: 35	Mixed-effects generalized linear model (function lmer), Binomial family, logit link function	Hg, , $\delta^{15}N$, Date, Year, Sex	Individual

Table S2. Hg concentrations and stable isotope values in red blood cells of Antarctic petrels from Svarthamaren, Antarctica, with the 2012-13 and 2013-14 breeding years separated. Values are means ± SD with range in parenthesis.

		N	Hg (μg g^{-1} dw)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
All sampled individuals	All	266	0.84 ± 0.25 (0.42-2.71)	-25.2 ± 0.5 (-26.4–-24.1)	9.7 ± 0.5 (8.2-10.9)
	F	88	0.83 ± 0.24 (0.44-2.04)	-25.2 ± 0.4 (-26.3–-24.4)	9.6 ± 0.5 (8.2-10.6)
	M	79	0.83 ± 0.23 (0.48-1.81)	-25.3 ± 0.6 (-26.3–-24.1)	9.7 ± 0.4 (8.8-10.7)
2012-13	All	184	0.86 ± 0.24 (0.42-2.04)	-25.0 ± 0.4 (-25.9–-24.1)	9.7 ± 0.5 (8.2-10.9)
	F	53	0.88 ± 0.26 (0.55-2.04)	-25.1 ± 0.4 (-25.8–-24.4)	9.6 ± 0.5 (8.2-10.6)
	M	49	0.85 ± 0.24 (0.50-1.81)	-25.0 ± 0.5 (-25.9–-24.1)	9.8 ± 0.4 (8.8-10.5)
2013-14	All	82	0.80 ± 0.28 (0.42-2.71)	-25.7 ± 0.4 (-26.4–-24.9)	9.5 ± 0.4 (8.4-10.7)
	F	35	0.75 ± 0.17 (0.44-1.13)	-25.5 ± 0.4 (-26.3–-24.9)	9.5 ± 0.4 (8.6-10.1)
	M	30	0.81 ± 0.21 (0.48-1.37)	-25.7 ± 0.4 (-26.3–-24.9)	9.6 ± 0.4 (8.8-10.7)
GPS individuals	All	91	0.80 ± 0.20 (0.45-1.62)	-25.7 ± 0.3 (-26.4–-25.0)	9.2 ± 0.4 (8.3-10.2)
	F	48	0.83 ± 0.22 (0.56-1.62)	-25.6 ± 0.3 (-26.4–-25.1)	9.2 ± 0.4 (8.3-10.2)
	M	43	0.75 ± 0.18 (0.45-1.17)	-25.7 ± 0.4 (-26.4–-25.0)	9.2 ± 0.3 (8.5-10.1)
2012-13	All	34	0.88 ± 0.25 (0.46-1.62)	-25.4 ± 0.2 (-26.0–-25.0)	9.3 ± 0.4 (8.3-10.2)
	F	19	0.96 ± 0.27 (0.56-1.62)	-25.4 ± 0.2 (-25.9–-25.1)	9.3 ± 0.5 (8.3-10.2)
	M	15	0.79 ± 0.18 (0.46-1.17)	-25.4 ± 0.3 (-26.0–-25.0)	9.3 ± 0.4 (8.5-10.1)
2013-14	All	57	0.74 ± 0.15 (0.45-1.17)	-25.8 ± 0.3 (-26.4–-25.3)	9.1 ± 0.3 (8.4-9.8)
	F	29	0.75 ± 0.12 (0.57-0.98)	-25.8 ± 0.3 (-26.4–-25.3)	9.1 ± 0.3 (8.4-9.6)
	M	28	0.73 ± 0.17 (0.45-1.17)	-25.9 ± 0.2 (-26.4–-25.5)	9.2 ± 0.3 (8.6-9.8)