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High feather mercury concentrations in the wandering albatross are related to sex, breeding status and trophic ecology with no demographic consequences

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ABSTRACT

Hg can affect physiology of seabirds and ultimately their demography, particularly if they are top consumers. In the present study, body feathers of >200 wandering albatrosses from Possession Island in the Crozet archipelago were used to explore the potential demographic effects of the long-term exposure to Hg on an apex predator. Variations of Hg with sex, age class, foraging habitat (inferred from $\delta^{13}C$ values), and feeding habits (inferred from $\delta^{15}N$ values) were examined as well as the influence of Hg on current breeding output, long-term fecundity and survival. Wandering albatrosses displayed among the highest Hg feather concentrations reported for seabirds, ranging from 5.9 to 95 $\mu g\ g^{-1}$, as a consequence of their high trophic position ($\delta^{15}N$ values). These concentrations fall within the same range of those of other wandering albatross populations from subantarctic sites, suggesting that this species has similar exposure to Hg all around the Southern Ocean. In both immature and adult albatrosses, females had higher Hg concentrations than males (28 vs. 20 $\mu g\ g^{-1}$ dw on average, respectively), probably as a consequence of females foraging at lower latitudes than males ($\delta^{13}C$ values). Hg concentrations were higher in immature than in adult birds, and they remained fairly constant across a wide range of ages in adults. Such high levels in immature individuals question (i) the frequency of moult in young birds, (ii) the efficiency of Hg detoxification processes in immatures compared to adults, and (iii) importantly the potential detrimental effects of Hg in early life. Despite very high Hg concentrations in their feathers, neither effects on adults' breeding probability, hatching failure and fledgling failure, nor on adults' survival rate were detected, suggesting that long-term bioaccumulated Hg was not under a chemical form leading to deleterious effects on reproductive parameters in adult individuals.

1. Introduction

Mercury (Hg) is a non-essential element that bioaccumulates in organisms and biomagnifies through food webs. Both processes are due to the conversion of inorganic Hg into organic forms (mainly methylmercury, MeHg) in aquatic ecosystems, MeHg being highly bioavailable and toxic. As such, MeHg is harmful to biota, being associated with adverse effects such as neurological, immunological, physiological and reproductive impacts in both humans and wildlife (e.g., Evans et al., 1982; Thompson and Furness, 1989a; Burger and Gochfeld, 1997; Tan et al., 2009). Nonetheless, the natural occurrence of Hg (Nriagu, 1996) has involved adaptations of predators to the presence of this toxic metal in their environment. This is particularly obvious for many top predators whose high trophic position and long life span lead to important levels of exposure. Most marine top predators feed on fish and cephalopods, which concentrate Hg mainly under MeHg (Bloom 1992; Bustamante et al., 2006). Marine apex predators have thus developed efficient detoxification capacities to support elevated exposure to MeHg (reviews in Cuvin-Aralar and Furness, 1991; Das et al., 2000). In marine mammals, demethylation of MeHg in the liver leads to the production of non-toxic granules of tiemannite (Koeman et al., 1973; Martoja and Berry, 1980). The accumulation of tiemannite granules makes the liver the ultimate organ of retention of Hg (Wagemann et al., 1998, 2000). Since

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these granules are not excreted (Nigro and Leonzio, 1996), inorganic Hg is basically stored through the whole life, thus inducing particularly elevated and increasing liver Hg concentrations throughout life, without any apparent toxic effect (Cuvin-Aralar and Furness, 1991).

In aquatic birds, efficiency of Hg detoxification processes is critical to prevent the toxic effects of Hg, which can affect their breeding, hatching and fledging successes (Tan et al., 2009; Frederick and Jayasena, 2010; Tartu et al., 2013; Goutte et al., 2014a, 2014b). As in mammals, demethylation of Hg in the liver appears to be a significant detoxification mechanism in seabirds (Thompson and Furness, 1989b; Thompson et al., 1993). However, birds present another complementary and efficient way to detoxify and excrete Hg on a regular basis, namely moult. Hg binds to keratin in the form of MeHg, hence, most feather Hg is MeHg (Thompson and Furness, 1989a), thus leading to a direct elimination of the toxic organic form during feather growth and subsequent loss. Feathers are considered as the main route for Hg excretion in seabirds (Monteiro and Furness, 1995), with feather growth contributing to the elimination of $>90\%$ of the Hg accumulated since the previous moult (Braune and Gaskin, 1987). In some cases, moult of all feathers is synchronous, as in penguins that renew their whole plumage in a few weeks (Brasso et al., 2013; Carravieri et al., 2013, 2014a), but generally moult is sequential and takes many weeks to months to be completed. For example, the wandering albatross *Diomedea exulans* replaces its feathers slowly and infrequently over several consecutive interbreeding periods (Weimerskirch, 1991) and this extreme moulting pattern is believed to contribute significantly to high feather Hg concentrations in the species (Anderson et al., 2009; Becker et al., 2002).

The present study adds new information on Hg exposure, the factors explaining its variations, and its demographic consequences on the wandering albatross breeding at Possession Island in the Crozet archipelago (southern Indian Ocean). There, an exceptional long-term demographic capture-mark-recapture survey (1965-present) allows a robust knowledge of the life history of each individual (Weimerskirch et al., 1997). The wandering albatross was chosen as a model animal because (i) it is an apex predator that occupies the highest trophic position within the diverse community of subantarctic seabirds, being thus submitted to contaminant biomagnification processes (Blévin et al., 2013), (ii) it is a very long-lived species (>50 years) making it a species of particular interest to investigate Hg bioaccumulation patterns over the long term (Tavares et al., 2013; Carravieri et al., 2014b), and (iii) consequently the species presents consistently high Hg levels in various tissues, including liver, blood and feathers (Hindell et al., 1999; Stewart et al., 1999; Anderson et al., 2009; Carravieri et al., 2014b, 2014c). The study is a companion work to a broader investigation using the same birds and data set that focused on (i) the complex foraging pattern of wandering albatrosses according to age, sex and breeding status using stable isotopes (Jaeger et al., 2014), (ii) the effect of all these factors and foraging ecology as explanatory variables of blood contaminants (Hg and persistent organic pollutants) (Carravieri et al., 2014b), and (iii) the corresponding consequences of blood contamination levels on birds' demography (Goutte et al., 2014b).

We focused here on Hg in body feathers to complement the previous investigations on blood, because the two tissues represent short- and long-term exposure to Hg, respectively. Blood Hg is directly influenced by recent dietary intake, while feathers are representative of Hg bioaccumulation over the inter-moult period (at least two years for body feathers in the wandering albatross). Our goal was three fold, by increasing order of importance (i) to describe body feather Hg concentrations in a larger data set of sampled birds ($n>200$) than in most previous investigations on marine predators, (ii) to quantify the main intrinsic (sex, age and breeding status) and extrinsic (foraging habitat and trophic position) factors contributing to Hg variation, and (iii) the demographic consequences of feather Hg levels in terms of current probabilities of breeding success, and of long-term apparent probabilities of adult survival, return to the breeding colony, and breeding, hatching and fledgling successes. We also further investigated the surprising recent finding on a few birds showing that feather Hg concentrations were higher in young immature wandering albatrosses than in older immatures and adults (Tavares et al., 2013).

2. Materials and methods

2.1. Study area, species and fieldwork

Wandering albatrosses nest on subantarctic islands throughout the Southern Ocean. The study was conducted at Possession Island in the Crozet Archipelago (46°S, 52°E), Southern Indian Ocean, where 300–400 pairs nest each year (Delord et al., 2008). Although the minimal age at first reproduction is five years old, ten years is the mean age of first breeding in this population (Weimerskirch et al., 1997). Wandering albatrosses return to their breeding grounds each year in December and females lay a single egg in late December–early January. Both parents incubate alternatively until hatching in March. Chicks are reared for ≈ 280 days and most young are fledged in November. It was recently demonstrated that up to 6% of the birds that fledged a chick still breed 2 years in a row, and the species is now considered as a quasi-biennial breeding species (Barbraud and Weimerskirch, 2012). Approximately 80% of birds that failed the previous year engage in another breeding attempt the following year. All wandering albatrosses had been ringed and sexed as part of a long-term mark recapture programme (Weimerskirch et al., 1997), with nestlings being ringed since 1965. In December, prebreeding adults are counted over the whole island. From mid-January to mid-February, nest contents were checked every ten days to determine the identity of the breeding pairs and breeding status (egg laid/egg hatched) of each individual. In mid-April, June and August, all nests are checked to monitor the survival of chicks.

In the present work, sampled wandering albatrosses were grouped per sex according to their breeding history and age: (i) immatures refer to young birds (3–11 years) that never bred, and (ii) adult albatrosses were those that bred at least once. From 21 December 2007 to 04 March 2008, body feathers were collected on 201 immature and adult wandering albatrosses. Since Hg is mostly excreted in growing feathers, Hg level in feathers is considered to be a reliable measure of Hg bioaccumulation since the last moult (Furness et al., 1986). In wandering albatrosses, feather replacement takes place exclusively during the non-breeding period (Weimerskirch, 1991). Once collected, body feathers were stored dry in individual plastic bags.

2.2. Hg and stable isotope analyses

Four body feathers per individual were pooled to obtain a mean isotopic value and an average of Hg level for body feathers (Bond and Diamond, 2008; Jaeger et al., 2014; Carravieri et al., 2014a). Prior to chemical analysis, feathers were cleaned to remove surface contaminants using a 2:1 chloroform:methanol solution followed by two successive methanol rinses. After cleaning, body feathers were oven dried for 48 h at 50 °C. Total Hg was measured at the laboratory Littoral Environnement et Sociétés (LIENSs) with an Advanced Mercury Analyzer spectrophotometer (Altec AMA 254). At least two aliquots ranging from 5 to 10 mg dry weight (dw) were analysed for each individual and measurement quality was certified by reference material, as described by Bustamante et al., (2006). 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} dry mass. Mass of the CRM was adjusted to represent the same amount of Hg introduced in the AMA compared to the one in the feathers. Recovery was 98 ± 4% proving good repeatability and reliability of the method. Blanks were analysed at the beginning of each set of samples and the detection limit of the method was 0.005 µg g^{-1} dry mass. Hg concentrations are presented in µg g^{-1} dry mass.

To test potential effect of foraging habitat and trophic position on feather Hg levels, the isotopic niche was used as a proxy of the trophic niche (Newsome et al., 2007). The isotopic method was validated in the southern Indian Ocean, with $\delta^{13}C$ values of seabirds indicating their foraging habitats (Cherel and Hobson, 2007; Jaeger et al., 2010) and their $\delta^{15}N$ values increasing with trophic level (Cherel et al., 2010). Feather is a metabolically inactive tissue that reflects the diet at the time it was grown, because keratin is inert after synthesis (Hobson and Clark, 1992; Bearhop et al., 2002). Cleaned pooled feathers (see above) were finely grounded with steel scissors and 0.30 ± 0.05 mg subsamples of the resulting powder were weighed in tin cups. Isotopic analyses were performed at the laboratory LIENSs with a Thermo Scientific Delta V Advantage mass spectrometer coupled to a Thermo Scientific Flash EA1112 elemental analyser. Results are presented in the usual δ notation relative to the deviation from international standards (Vienna PeeDee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively). Replicate measurements of internal laboratory standards (acetanilide) indicate measurements errors < 0.10‰ for both $\delta^{13}C$ and $\delta^{15}N$ values.

2.3. Statistical analyses

Statistical tests were performed using R 2.15.1 (R Core Team, 2012). A significance level of $\alpha < 0.05$ was used for all tests, both in unifactorial and multifactorial analyses. Values are means ± SD. The effects of intrinsic (age, sex, reproductive status the previous year, 2007) and extrinsic (feeding ecology) factors on Hg concentrations in feathers were tested using Generalised Linear Models (GLM). Data exploration was carried out following Zuur et al., (2009). Multifactorial analyses were used to test multiple alternative hypotheses on the influence of age, sex, reproductive status, foraging habitat ($\delta^{13}C$) and trophic level ($\delta^{15}N$) on feather Hg concentrations. Continuous variables that were significantly correlated were not included in multifactorial models. Notably, feather $\delta^{13}C$ and $\delta^{15}N$ values were strongly correlated (Pearson correlation, $r = 0.80$, $p < 0.0001$, $N = 201$) due to the slight baseline latitudinal enrichment in $\delta^{15}N$ values from cold to warm waters of the southern Indian Ocean (Jaeger et al., 2010). GLM with a gamma distribution and an inverse-link function were constructed as follows: Hg concentrations as the response variable, sex and reproductive status as a categorical explanatory variables and age and feather $\delta^{13}C$ values as continuous explanatory variables. The models were restricted to primary effects and two-way interactions. Immature birds were considered separately from the adults as they showed a different age-related variation in feather Hg concentrations. In both cases (immatures and adults), model selection was based on Akaïke's Information Criteria adjusted for small sample sizes (AIC_c). The model with the lowest AIC_c value was considered to be the most accurate. Models with AICc values differing by less than two have a similar level of support in the data. Since our aim was to make inference on the variables affecting contaminant burdens, the effect of variables was inferred through Akaike's weights (w_i), and without using model averaging (Burnham and Anderson, 2002). Model fit was checked by residual analysis.

The effects of Hg (log-transformed) on breeding probability at the year of sampling (thereafter 2008) and during the last breeding attempt preceding the year of sampling (thereafter in 2005, 2006 or 2007) were tested on sexually-mature albatrosses, using GLM binomial error distribution and a logit link function. Breeding probability was coded as 1 if a bird was observed as a breeder (*i.e.,* incubating an egg or raising a chick) and as 0 if a bird was observed as a non-breeder at the colony. Finally, we tested whether breeding success during the year of sampling (2008) or during the last breeding attempt preceding the year of sampling (2005, 2006 or 2007) were linked to feather Hg levels in individuals sampled as breeders (incubating or chick-rearing), by using GLMs with binomial error distribution and a logit link function. Breeding success was coded as 1 for birds that successfully fledged a chick, and as 0 for those that failed at the egg or chick stage. Models were then checked for assumptions that are constancy of variance and residual normality.

The effects of Hg on long-term demographic parameters were evaluated using the capture-recapture data of sampled sexually-mature albatrosses from, 2008 to 2012. A multi-stage mark-recapture (MSMR) model as developed by Pardo et al., (2013a, 2013b) was built. This model includes eight states: dead, failed breeder on egg (FBE, defined as an individual that was observed with one egg that failed to hatch), failed breeder on chick (FBC, defined as an individual that was observed with one chick but that failed to fledge the chick), successful breeder (SB, defined as an individual that fledged one chick), observable non-breeder (ONB, defined as an individual that was observed at the colony but that was not observed with an egg or a chick), and three unobservable states (UNB) consisting of non-breeders that were observed at the colony during the previous breeding attempt (PONB), non-breeders whose previous breeding attempt failed (PFB) and non-breeders whose previous breeding attempt was successful (PSB). The state dead (†) was an absorbing state representing death or permanent emigration from the study area. The unobservable states account for temporary absence corresponding to birds that skip breeding after breeding unsuccessfully or successfully. States occupied are not directly observed; rather at each occasion t, an event happens and is recorded leading to an observed encounter history. In our case, we thus considered five events; 0 = "not observed", 1 = "seen as a failed breeder on egg", 2 = "seen as a failed breeder on chick", 3 = "seen as a successful breeder", 4 = "seen as a non-breeder", which were used to build capture histories. Events and states are considered as random variables, and it is assumed that an event at occasion t depends only on an underlying state (which is not observed) of the individual at the moment, and that successive states follow a Markov chain. Models were parameterised in terms of the probability of survival (s), the probability to return at the colony given survival (r), the probability of breeding given return at the colony (β), the probability of successful hatching given breeding (ω), the probability of successful fledgling given hatching (γ), and the detection probability (p). Transition probabilities between states were thus modelled with a five-step procedure where s, r, β, ω and γ were considered as five successive steps in transition matrices. Parameters of the model are defined in Table 1. We chose a MSMR approach since this allows taking into account the probability of detecting individuals given their return to the study site. It also allows taking into account the previous breeding state of individuals which might be important to obtain unbiased estimates of demographic parameters (Lebreton and Pradel, 2002).

Table 1
Definition of parameters used in the multistate mark-recapture model.

Parameter	Definition
s_s^t	Probability that an individual in state *s* at time *t* survives to time *t*+1 and does not permanently emigrate from the study area
r_s^t	Probability that an individual in state *s* at time *t* returns at the colony to time *t*+1 given that it survives to *t*+1
β_s^t	Probability that an individual in state *s* at time *t* breeds at time *t*+1 given that it survives to and returns at the colony at time *t*+1
γ_s^t	Probability that an individual in state *s* at time *t* incubates successfully at time *t*+1 given that it survives to, returns at the colony and breeds at time *t*+1
δ_s^t	Probability that an individual in state *s* at time *t* raises successfully one chick at time *t*+1 given that it survives to, returns at the colony and incubates successfully at time *t*+1
p_s^t	Probability that an individual in state *s* at time *t* is encountered at time *t*+1

Table 2
Hg concentrations (μg g^{-1} dw) and stable isotope values in body feathers of the wandering albatross from Possession Island (F: females; M: males).

	N	Hg		δ^{13}C		δ^{15}N	
		Mean ± SD	Min–Max	Mean ± SD	Min–Max	Mean ± SD	Min–Max
All	201	23.87 ± 11.83	5.86–94.72	− 17.32 ± 1.12	− 20.99–15.32	15.79 ± 0.99	12.21–17.91
F	91	28.00 ± 11.33	10.85–74.72	− 16.94 ± 1.03	− 20.02–15.32	15.87 ± 1.04	12.65–17.51
M	110	20.44 ± 11.17	5.86–94.72	− 17.64 ± 1.09	− 20.99–15.64	15.73 ± 0.94	12.21–17.91
Immatures	36	31.80 ± 14.96	10.4–74.72	− 16.77 ± 0.84	− 18.65–15.32	16.13 ± 0.71	14.65–17.48
F	18	37.06 ± 14.60	20.76–74.72	− 16.54 ± 0.90	− 18.65–15.32	16.17 ± 0.82	14.65–17.48
M	18	26.53 ± 13.74	10.4–59.69	− 16.99 ± 0.76	− 18.13–15.64	16.08 ± 0.61	15.13–17.17
Adults	165	22.14 ± 10.30	5.86–94.72	− 17.44 ± 1.13	− 20.99–15.59	15.72 ± 1.02	12.21–17.91
F	73	25.77 ± 9.20	10.85–53.11	− 17.04 ± 1.04	− 20.02–15.59	15.79 ± 1.08	12.65–17.51
M	92	19.25 ± 10.26	5.86–94.72	− 17.76 ± 1.10	− 20.99–15.87	15.66 ± 0.98	12.21–17.91
Age classes							
3–12	67	28.67 ± 12.96	10.40–74.72	− 16.85 ± 0.86	− 19.54–15.32	16.04 ± 0.83	13.71–17.48
13–25	53	23.40 ± 12.83	7.39–94.72	− 17.13 ± 0.91	− 19.20–15.59	15.94 ± 0.94	12.98–17.70
26–35	43	19.54 ± 7.90	5.86–48.15	− 17.54 ± 1.10	− 20.77–15.62	15.67 ± 1.03	12.21–17.51
> 35	38	20.95 ± 9.08	6.08–53.11	− 18.18 ± 1.28	− 20.99–15.87	15.31 ± 1.09	12.65–17.91

This MSMR model was parameterised by the survival–transition probabilities matrix:

$$\begin{array}{cc}
 & \begin{array}{cccccccc} \mathrm{FBE} & \mathrm{FBC} & \mathrm{SB} & \mathrm{ONB} & \mathrm{PFB} & \mathrm{PSB} & \mathrm{PONB} & \dagger \end{array} \\
\begin{array}{c} \mathrm{FBE} \\ \mathrm{FBC} \\ \mathrm{SB} \\ \mathrm{ONB} \\ \mathrm{PFB} \\ \mathrm{PSB} \\ \mathrm{PON} \\ \mathrm{B} \\ \dagger \end{array} &
\begin{bmatrix}
\mathrm{sr}\beta(1-\omega) & \mathrm{sr}\beta\omega(1-\gamma) & \mathrm{sr}\beta\omega\gamma & \mathrm{sr}(1-\beta) & \mathrm{s}(1-\mathrm{r}) & - & - & * \\
\mathrm{sr}\beta(1-\omega) & \mathrm{sr}\beta\omega(1-\gamma) & \mathrm{sr}\beta\omega\gamma & \mathrm{sr}(1-\beta) & \mathrm{s}(1-\mathrm{r}) & - & - & * \\
\mathrm{sr}\beta(1-\omega) & \mathrm{sr}\beta\omega(1-\gamma) & \mathrm{sr}\beta\omega\gamma & \mathrm{sr}(1-\beta) & - & \mathrm{s}(1-\mathrm{r}) & - & * \\
\mathrm{sr}\beta(1-\omega) & \mathrm{sr}\beta\omega(1-\gamma) & \mathrm{sr}\beta\omega\gamma & \mathrm{sr}(1-\beta) & - & - & \mathrm{s}(1-\mathrm{r}) & * \\
\mathrm{sr}\beta(1-\omega) & \mathrm{sr}\beta\omega(1-\gamma) & \mathrm{sr}\beta\omega\gamma & \mathrm{sr}(1-\beta) & - & - & - & * \\
\mathrm{sr}\beta(1-\omega) & \mathrm{sr}\beta\omega(1-\gamma) & \mathrm{sr}\beta\omega\gamma & \mathrm{sr}(1-\beta) & - & - & - & * \\
\mathrm{sr}\beta(1-\omega) & \mathrm{sr}\beta\omega(1-\gamma) & \mathrm{sr}\beta\omega\gamma & \mathrm{sr}(1-\beta) & - & - & - & * \\
\mathrm{sr}\beta(1-\omega) & \mathrm{sr}\beta\omega(1-\gamma) & \mathrm{sr}\beta\omega\gamma & \mathrm{sr}(1-\beta) & - & - & - & * \\
- & - & - & - & - & - & - & *
\end{bmatrix}
\end{array}$$

Asterisks (*) in the column for dead birds (†) represent the complementary parameter (complement of the sum of positive row entries).

Models' construction and constraints on parameters were exactly the same than those previously detailed in a paper about the demographic consequences of blood Hg levels in the wandering albatross (Goutte et al., 2014b). We tested for an effect of Hg on demographic parameters to test the hypothesis that feather Hg levels in one breeding season may influence the long-term survival and breeding outputs of an individual over the following years. The 95% confidence interval of the slope parameters and AICc was used for inference. The goodness-of-fit (GOF) of the time-dependent MSMR model was tested using U-CARE (Choquet et al., 2009a). Model selection was based on AIC$_c$ and all models were run under programme E-SURGE 1.8.5 allowing splitting transition probabilities between states (Choquet et al., 2009b). To avoid estimating parameters at a local minimum of the likelihood function, each model was run five times with random initial values.

3. Results

3.1. Influence of biological and environmental factors on Hg bioaccumulation

Overall, feather Hg concentrations of wandering albatrosses averaged 24 ± 12 μg g^{-1} and showed a wide range of values, from 6 to 95 μg g^{-1} (Table 2), with the latter value being considered an outlier. Univariate multifactorial analyses were performed to estimate the influence of sex, age, reproductive status, and feeding habitat (δ^{13}C) on Hg concentrations in feathers of immature and adult birds separately, because feather Hg concentration was higher in immatures than in adults (32 ± 15 vs. 22 ± 10 μg g^{-1}; Table 2). For immature and adult albatrosses, multiple models had a similar support, and explained at best 17% and 23% of the total variation, respectively (Table 3). In immatures, age was clearly the most influential variable, with sex having also a relatively high explanatory power as shown by the sum of Akaike's weights across all models (Table 3). Feather Hg concentrations decreased with age in immature birds (Fig. 1a) and were overall lower in males than females (26 ± 14 and 37 ± 15 μg g^{-1}, respectively; Table 2).

Table 3
Model selection for Hg concentrations in feathers of immature and adult wandering albatrosses from Possession Island. Models are sorted by increasing ΔAICc (*i.e.*, decreasing model fit). Abbreviations: AICc: Akaike's Information Criteria adjusted for small sample-sizes; Exp. var.: explained variation of the model; *wi*: Akaike's weights; Σw_i Sum of Akaike's weights across all models of each tested explanatory variable.

Models	*k*	AIC_c	ΔAIC_c	*Exp. var.* (%)	w_i	*Variable*	Σw_i
Immatures – GLM (gamma distribution, inverse link function), n=36 (M: 18, F: 18)							
Age	2	288	0.00	15	0.324	Age	0.80
Age+Sex	3	289	0.45	17	0.258	Sex	0.58
Sex	2	290	1.66	11	0.142	$\delta^{13}C$	0.17
$\delta^{13}C$+Age+Sex	4	291	2.56	16	0.090		
Age+Sex+Age:Sex	4	291	3.05	15	0.070		
$\delta^{13}C$+Age+$\delta^{13}C$:Age	4	292	3.57	14	0.054		
Null	1	293	4.62	0	0.032		
$\delta^{13}C$+Sex+$\delta^{13}C$:Sex	4	294	5.96	8	0.016		
$\delta^{13}C$	2	295	6.50	0	0.013		
Adults – GLM (gamma distribution, inverse link function), n=165 (M: 92, F: 73)							
$\delta^{13}C$+Age+Sex+Status+Age:Status	8	1002	0.00	23	0.350	Age	0.61
$\delta^{13}C$+Sex	3	1003	1.10	20	0.201	Sex	0.99
$\delta^{13}C$+Age+Sex+Status+$\delta^{13}C$:Sex+Age:Status	9	1004	2.29	23	0.111	Status	0.62
$\delta^{13}C$+Sex+Status	5	1005	2.54	20	0.098	$\delta^{13}C$	0.87
Sex	2	1005	3.05	18	0.076		
$\delta^{13}C$+Age+Sex	4	1005	3.23	19	0.070		
$\delta^{13}C$+Age+Sex+Status+$\delta^{13}C$:Age+$\delta^{13}C$:Sex+Age:Status	10	1007	4.61	22	0.035		
Age+Sex	3	1007	4.96	18	0.029		
Sex+Status	4	1008	5.88	18	0.018		
Age+Sex+Status	5	1010	7.77	17	0.007		
$\delta^{13}C$+Age+Sex+Status+$\delta^{13}C$:Age+$\delta^{13}C$:Sex+$\delta^{13}C$:Status+Age:Status	12	1011	9.01	21	0.004		
$\delta^{13}C$	2	1023	21.19	8	0.00		
$\delta^{13}C$+Status	4	1023	21.35	9	0.00		
$\delta^{13}C$+Age	3	1025	22.99	7	0.00		
$\delta^{13}C$+Age+Status	5	1025	23.03	9	0.00		
Age	2	1033	30.92	2	0.00		
Age+Status	4	1034	32.26	2	0.00		
Null	1	1034	32.26	0	0.00		
Status	3	1036	34.28	0	0.00		

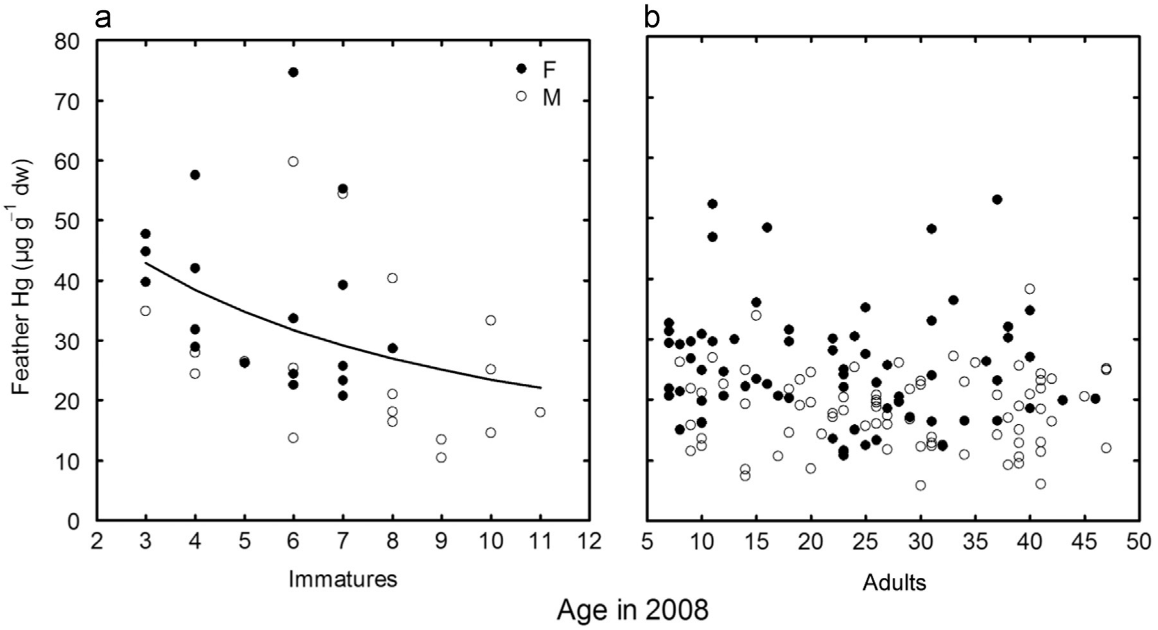

Fig. 1. Hg concentrations (μg g^{-1} dw) in body feathers of immature and adult wandering albatrosses from Possession Island as a function of age. F: females; M: males; continuous line: GLM (gamma distribution, inverse link function: immature feather Hg=age).

The effect of sex on feather Hg concentrations was much stronger in adults than immature wandering albatrosses. In contrast to immature birds, age had no significant influence on feather Hg concentrations of adult albatrosses (Fig. 1b). Instead, the sum of Akaike's weights across all models showed that feather $\delta^{13}C$ values and sex were the most influential variables on adult feather Hg concentrations (Table 3). Specifically, Hg concentrations were positively related to $\delta^{13}C$ values (Fig. 2a) and were significantly lower in males than in females (19 ± 10 vs. 26 ± 9 μg g^{-1}, respectively; Table 2, Fig. 2). Hg concentrations were also positively related to $\delta^{15}N$ values (Fig. 2b), given the strong correlation between feather $\delta^{13}C$ and $\delta^{15}N$ values (see Materials and methods).

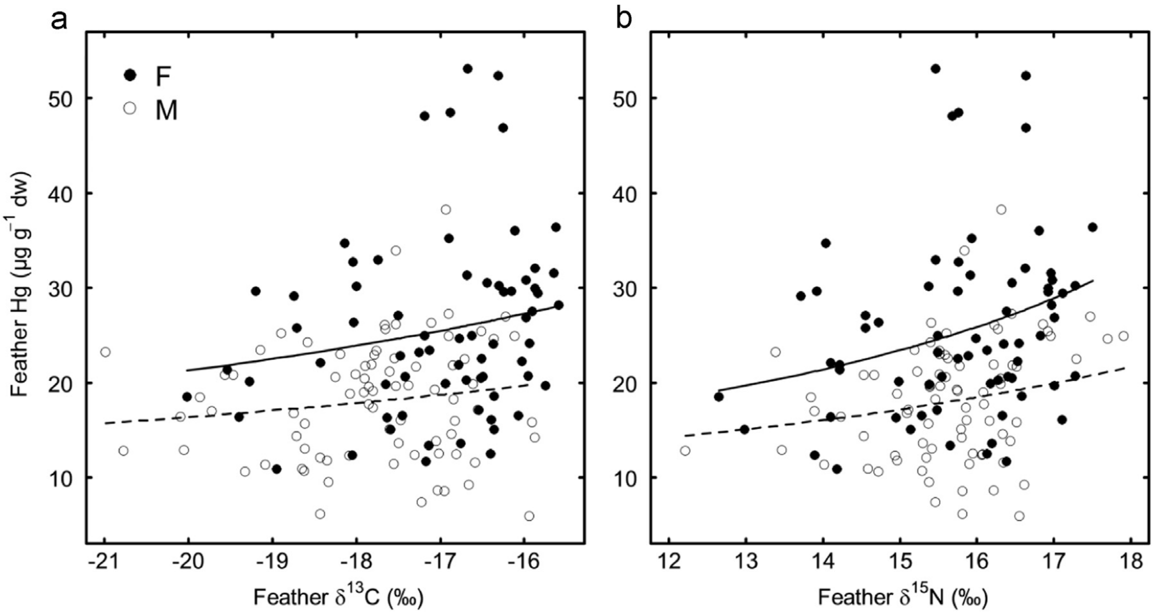

Fig. 2. Hg concentrations (µg g^{-1} dw) in body feathers of adult wandering albatrosses from Possession Island as a function of (a) feather δ^{13}C and (b) feather δ^{15}N. F: females; M: males; continuous and dotted lines for females and males, respectively: GLM (gamma distribution, inverse link function: feather Hg=δ^{13}C+sex and feather Hg=δ^{15}N+sex).

3.2. *Effects of Hg on current breeding output*

The probability of breeding during the last breeding attempt (between 2005 and 2007) and during the 2008 season was not linked to Hg concentrations in feathers (last breeding attempt: df=1159, χ^2=1.742, p=0.189; 2008: df=1165, χ^2=0.288, p=0.592). When considering only breeders, current breeding success was not related to Hg levels in feathers (last breeding attempt: df=1118, χ^2=2.105, p=0.147; 2008: df=1129, χ^2=1.849, p=0.174).

3.3. *Long-term fitness consequences of Hg exposure*

The GOF of the MSMR model was overall not significant (males: χ^2=25.186, d.f.=25, p=0.452 and females: χ^2=7.094, d.f.=25, p=1.000). Model 5 and model 14 had lower AICc than the intercept model (Table 4) suggesting that Hg in feathers were negatively related to return rate of individuals previously in state SB and positively related to breeding probability of males previously in states FBE or FBC. However, ΔAICc values with the intercept model were less than 2 (1.61 and 0.5) and the confidence intervals of estimated slope included 0 (Table 4). Therefore it must be considered that there was no effect of feather Hg levels on any demographic parameters.

4. Discussion

The present study benefits from the long-term demographic investigation (from 1965 onward) on wandering albatrosses from Possession Island, resulting in the unique sampling of >200 birds of known sex, age and breeding status during the same summer season. Together with previous investigations on blood Hg using the same individual birds (Carravieri et al., 2014b; Goutte et al., 2014b), this study is one of the most comprehensive evaluations of

Table 4

Modelling the effects of standardized Hg levels in feathers on demographic parameters (N=167 individuals). The estimated slope and 95% confidence intervals (CI) for models with a lower AICc than the intercept model (0) are given.

Hypothesis	Model	Rank	Deviance	ΔAICc	Slope	[CI-; CI+]
Effect of Hg on return rate of individuals previously in state SB	14	24	1632.73	0	−0.38	[−0.76; 0.01]
Effect of Hg on breeding probability of males previously in states FBE or FBC	5	24	1633.84	1.11	1.31	[−0.37; 2.99]
Intercept model: no effect of Hg on demographic parameters	0	23	1636.55	1.61		
Effect of Hg on breeding probability of females previously in state ONB	10	24	1634.66	1.93		
Effect of Hg on breeding probability of females previously in state SB	8	24	1634.67	1.95		
Effect of Hg on fledgling success of individuals previously in states ONB or UNB	2	24	1635.45	2.72		
Effect of Hg on breeding probability of males previously in state ONB	9	24	1635.76	3.04		
Effect of Hg on breeding probability of females previously in states PFB, PSB or PONB	12	24	1635.88	3.15		
Effect of Hg on fledgling success of individuals previously in states FB and SB	1	24	1636.03	3.30		
Effect of Hg on survival rate of males	16	24	1636.17	3.44		
Effect of Hg on breeding probability of males previously in states PFB, PSB or PONB	11	24	1636.31	3.58		
Effect of Hg on survival rate of females	17	24	1636.52	3.79		
Effect of Hg on breeding probability of females previously in states FBE or FBC	6	24	1636.54	3.89		
Effect of Hg on hatching success of individuals previously in states FB and SB	3	24	1636.55	3.90		
Effect of Hg on breeding probability of males previously in state SB	7	24	1636.55	3.82		
Effect of Hg on hatching success of individuals previously in states ONB or UNB	4	24	1636.55	3.82		
Effect of Hg on return rate of individuals previously in states ONB, PFB, PSB or PONB	15	24	1636.55	3.82		
Effect of Hg on return rate of individuals previously in states FBE or FBC	13	24	1636.55	3.82		

Hg levels, with its explanatory factors and demographic consequences, in free-living animals of known life-history traits. The previous studies considered blood Hg that represents the short-term exposure of the birds, while the present work focused on feather Hg that represents the long-term exposure. Accumulated Hg since the last moult is excreted into the feathers, which represent more than one year exposure in the case of the wandering albatross.

4.1. Comparison to other populations and species

Average feather Hg concentration of wandering albatrosses from Possession Island (24 $\mu g\ g^{-1}$) is within the range of values obtained in other localities from the southern Indian Ocean (Marion: 25 $\mu g\ g^{-1}$, Kerguelen: 17 $\mu g\ g^{-1}$; Thompson et al., 1993; Carravieri et al., 2014c) and southern Atlantic Ocean (South Georgia: 20–27 $\mu g\ g^{-1}$; Thompson et al., 1993; Anderson et al., 2009; Tavares et al., 2013). This suggests that Hg has a fairly similar bioavailability within these different sectors of the Southern Ocean, which is in agreement with its circumpolar annular (latitudinal) oceanographic structure (Sokolov and Rintoul, 2007). The observed feather Hg levels in the wandering albatross confirm that large albatrosses (Family Diomedeidae; Thompson et al., 1993), together with some other Procellariiformes (Procellariidae and Hydrobatidae; Monteiro et al., 1999; Carravieri et al., 2014c) are amongst the most Hg-contaminated seabird species overall (mean values $>10\ \mu g\ g^{-1}$) (authors' unpublished review).

Body feather Hg concentrations of wandering albatrosses from Possession Island varied with a 16 magnification factor among individuals, with one 23 years-old male showing the remarkably high feather concentration of 95 $\mu g\ g^{-1}$ (Table 2). To the best of our knowledge, this value is the highest ever recorded in body feathers for any bird in the current open scientific literature, followed by the levels of one common loon *Gavia immer* (76 $\mu g\ g^{-1}$; Evers et al., 2008), two other wandering albatrosses (75 and 73 $\mu g\ g^{-1}$; this study and Thompson et al., 1993, respectively) and one common tern chick *Sterna hirundo* from a highly-polluted area (70 $\mu g\ g^{-1}$; Furness et al., 1995). Noticeably, these values are well above the commonest used toxicity threshold (5 $\mu g\ g^{-1}$; Burger and Gochfeld, 1997) and above the adverse effect threshold for adult loons (40 $\mu g\ g^{-1}$), the best studied species in the wild up to date (Evers et al., 2008). Together with the highest Hg concentration reported in the liver of any bird species (1800 $\mu g\ g^{-1}$ dw; Hindell et al., 1999), the wandering albatross and probably related species of the Genus *Diomedea*, appear to be thus good model animals to investigate the detoxification mechanisms allowing to cope with such high Hg body burdens.

4.2. Explanatory factors

Interestingly, feather Hg concentrations of wandering albatrosses were only influenced by age in immature birds (pre-breeders) and no effect of this factor was detected in individuals over 12 years-old. The lack of age-dependent variation in Hg concentrations has already been reported for known-age seabirds both in blood of e.g., wandering albatrosses (Tavares et al., 2013; Carravieri et al., 2014b), and in feathers of e.g., red-billed gulls *Larus novaehollandiae* and great skuas *Catharacta skua* (Furness et al., 1990; Thompson et al., 1991), with also some possible decreasing trends being observed as in adult snow petrels (Tartu et al., 2014). Our finding for immature wandering albatrosses is consistent with the results of Tavares et al., (2013) who reported an increase of Hg concentrations between chicks and immature albatrosses returning for the first time to the colony (age ranging from 4 to 6 years) and then a decline to a lower constant average value in breeding adults. Although no chicks were sampled in the present study, it is noteworthy that wandering albatross chicks from South Georgia and Kerguelen Islands had similar Hg levels, ranging between 2 and 10 $\mu g\ g^{-1}$ (Becker et al., 2002; Blévin et al., 2013; Tavares et al., 2013). These Hg levels represent the assimilated metal accumulated during chick growth over months that was ultimately excreted in newly grown feathers at the end of the period (Lewis and Furness, 1991). The subsequent Hg bioaccumulation in fledged young albatrosses up to their first reproduction would therefore reflect elevated exposure to the metal. The higher feather Hg concentrations in immatures than in adults would firstly be due to a difference in the foraging areas exploited by the two age classes. Indeed, taking into account latitudinal changes in $\delta^{13}C$ in the southern Indian Ocean (Jaeger et al., 2010), lower $\delta^{13}C$ values in the feathers of adult individuals show that they forage in more southern waters compared to immatures during the inter-breeding period (Table 2). Because of the temporal uncoupling of Hg (representing exposure during the whole inter-moult period) and stable isotopes (representing food assimilated during feather synthesis) in feathers, the use of stable isotopes to interpret Hg concentrations in this tissue has to be done cautiously (Bond, 2010). Nevertheless, adult individuals foraging at higher latitudes (subantarctic waters) had lower Hg concentrations compared to those foraging in the northern subtropics (Fig. 2). As immatures feed all year round in subtropical waters (Jaeger et al., 2014; Weimerskirch et al., 2014), they should be exposed to higher quantity of Hg compared to adults that forage at higher latitudes at least during the reproduction period.

Higher Hg concentrations in the feathers of immature rather than adult wandering albatrosses were attributed to differences in moulting patterns (Tavares et al., 2013). Indeed, immatures show greater difficulties in replacing their feathers because they are less experienced to find and catch their prey compared to breeders (Weimerskirch, 1991). If a nutritional deficit occurs, it might reduce the capacity of immature albatrosses to synthetise new feathers. The decreasing Hg levels with increasing age in immature birds corroborate this hypothesis, likely reflecting (i) the change in foraging behaviour (shift to more southern habitats) and (ii) the progressive establishment of a regular moult. Feather Hg concentrations reflect blood Hg concentrations at the time of moult (Bearhop et al., 2000; Evers et al., 2008). Feather Hg concentrations are therefore dependent of both (i) the exposure at the time of their synthesis (dietary Hg), and (ii) the release of Hg accumulated since the last moulting event (Furness et al., 1986; Thompson et al., 1998). Therefore, moult appears as a crucial mechanism of Hg detoxification in birds. If moult occurs at a lower frequency in immatures compared to adults, feather Hg concentrations should be higher in immatures. On the other hand, demethylation of Hg and its subsequent co-precipitation with Se in the liver of Procellariiforms appears to constitute a significant detoxification strategy (Nigro and Leonzio, 1996; Thompson and Furness, 1989b; Thompson et al., 1993), which leads to extremely high concentrations of accumulated Hg in this organ (e.g., Muirhead and Furness, 1988; Stewart et al., 1999; Hindell et al., 1999). It is possible that such a detoxification process is not yet fully efficient in young albatrosses, making feathers the major pathway of detoxification for this age class, whereas it may allow at maintaining almost constant the quantity of Hg subsequently excreted in feathers of adults.

In adult albatrosses, Hg concentrations were higher in females than in males showing that maternal transfer of Hg to the egg seems limited in the wandering albatross. Data for stable isotopes in both feathers (present study) and blood (Carravieri et al., 2014b) rather suggest that such a gender difference is related to sexual segregation in foraging areas and hence diets. Male wandering albatrosses mainly forage in subantarctic waters during the breeding period, whereas they moult in subtropical waters outside the breeding period (Weimerskirch et al., 2014; Jaeger et al., 2014). On the other hand, females rely essentially on subtropical waters throughout their life, visiting also subantarctic waters during incubation (Weimerskirch et al., 2014). On average, females thus forage at more northern latitudes than males (Jaeger et al., 2014). Wandering albatrosses prey predominantly upon large squids, both at northern and southern latitudes (Cherel and Weimerskirch, 1999). Cephalopods mainly bioaccumulate Hg under its methylated form (MeHg), which is thus highly bioavailable for their consumers (Bustamante et al., 2006). Even if information on Hg concentrations in the prey of the wandering albatross is missing over its wide-range foraging area, it is likely that cephalopods from subtropical waters had higher Hg concentrations than those from the subantarctic area as it is the case in Kerguelen Island waters (Bustamante et al., 2003; unpublished data). This would reduce the Hg bioaccumulation of adult males when compared to females, at least during the breeding period, as shown by blood Hg analyses (Carravieri et al., 2014b). This pattern has already been reported for other seabird species from the Kerguelen Islands, with species foraging predominantly within the limits of the Southern Ocean year-round (e.g., the light-mantled albatross *Phoebetria palpebrata*) having lower Hg concentrations than those foraging in northern subtropical and neritic waters (Carravieri et al., 2014c). In this context, the wandering albatross appears as a valuable species to document latitudinal variations in Hg transfer in their food web.

4.3. Demographic consequences of long-term Hg exposure

Few studies have explored the demographic consequences of Hg on wild aquatic birds, with a main focus on short-term exposure using blood Hg (e.g., Evers et al., 2008; Burgess and Meyers, 2008; Goutte et al., 2014a, 2014b, 2015). Using a long-term data set and MSMR models, the present study is among the first to explore the effects of feather Hg on current breeding output, long-term fecundity and survival in seabirds. Even if Hg concentrations in body feathers were extremely high, no effect on neither breeding probability, hatching and fledgling successes, nor adult survival was detected. This finding contrasts strongly with results obtained with blood that highlighted a negative impact of Hg on long-term breeding, hatching and fledging probabilities in the wandering albatross (Goutte et al., 2014b). Contrary to previous studies on blood Hg (e.g., Brasso and Cristol, 2008; Frederick and Jayasena, 2010; Tartu et al., 2013, 2014, 2015a, 2015b), no negative effect of feathers Hg was detected on the breeding probability and the breeding success at the year of sampling. These results deserve further investigations as one can expect that the integrated Hg would have stronger effect on reproduction than blood Hg concentrations during the reproductive period.

Although Hg in feathers is considered to be an integrative measure of total Hg body burden (Furness et al., 1986), our analyses did not detect any strong correlation between Hg in feathers and long-term reproductive outputs. As commented previously, feathers replacement in wandering albatross takes more than a year (Weimerskirch, 1991), leading to Hg bioaccumulation in the liver (see above). Hence, Hg in feathers would reflect different exposure periods of wandering albatrosses according to the analysed feathers. In contrast, blood reflects dietary contaminants exposure during the energetically challenging breeding period, and Hg in blood appears to be more critical for long-term reproductive responses (Goutte et al., 2014a, 2014b).

Estimated demographic parameters were similar to those previously estimated in the same population of wandering albatrosses, using all ringed individuals (Pardo et al., 2013a; Barbraud and Weimerskirch, 2012). Despite high Hg concentrations in the feathers which revealed an elevated exposure to Hg since the previous moult (Carravieri et al., 2014a), the survival rate of wandering albatrosses was not jeopardised by Hg. This is consistent with previous studies that did not detect an effect of Hg on adult mortality in free-living birds (Mitro et al., 2008; Wayland et al., 2008; Hallinger et al., 2011; Goutte et al., 2014a, 2014b, 2015). However, our study did not exclude that Hg could jeopardise the survival rate of immature wandering albatrosses, since they had higher Hg concentrations (Tavares et al., 2013), and lower survival rate (Weimerskirch et al., 1997) than sexually-mature adults.

5. Conclusion

The wandering albatrosses from Possession Island displayed remarkably elevated Hg concentrations in their feathers as a consequence of their high trophic position. Hg concentrations are the highest in immatures and, after birds start reproduction, they remained stable in adults. Both a different moulting frequency and detoxification processes could be responsible for such differences between maturity stages. In both immatures and adults, females had higher Hg concentrations as they forage at lower latitude on prey that are likely enriched in Hg compared to higher latitude prey. Despite elevated Hg concentrations in their feathers reflecting long-term exposure to the metal, no effect on the demographic parameters were evidenced suggesting that long-term bioaccumulated Hg was not under a form leading to deleterious effects.

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References

Anderson, O.R.J., Phillips, R.A., McDonald, R.A., Shore, R.F., McGill, R.A.R., Bearhop, S., 2009. Influence of trophic position and foraging range on mercury levels within a seabird community. Mar. Ecol. Prog. Ser. 375, 277–288.

Barbraud, C., Weimerskirch, H., 2012. Estimating survival and reproduction in a quasi-biennially breeding seabird with uncertain and unobservable states. J. Ornithol. 152, 605–615.

Bearhop, S., Ruxton, G.D., Furness, R.W., 2000. Dynamics of mercury in blood and feathers of great skuas. Environ. Toxicol. Chem. 19, 1638–1643.

Bearhop, S., Waldron, S., Votier, S.C., Furness, R.W., 2002. Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. Physiol. Biochem. Zool. 75, 451–458.

Becker, P.H., González-Solís, J., Behrends, B., Croxall, J., 2002. Feather mercury levels in seabirds at South Georgia: influence of trophic position, sex and age. Mar. Ecol. Prog. Ser. 243, 261–269.

Blévin, P., Carravieri, A., Jaeger, A., Chastel, O., Bustamante, P., Cherel, Y., 2013. Wide range of mercury contamination in chicks of Southern Ocean seabirds. Plos One 8 (1), e54508.

Bloom, N.S., 1992. On the chemical form of mercury in edible fish and marine invertebrate tissue. Can. J. Fish. Aquat. Sci. 49, 1010–1016.

Bond, A.L., Diamond, A.W., 2008. High within-individual variation in total mercury concentration in seabird feathers. Environ. Toxicol. Chem. 27, 2375–2377.

Bond, A.L., 2010. Relationships between stable isotopes and metal contaminants in feathers are spurious and biologically uninformative. Environ. Pollut. 158, 1182–1184.

Brasso, R.L., Cristol, D.A., 2008. Effects of mercury exposure on reproductive success of tree swallows (*Tachycineta bicolor*). Ecotoxicology 17, 133–141.

Brasso, R.L., Drummond, B.E., Borrett, S.R., Chiaradia, A., Polito, M.J., Rey, A.R., 2013. Unique pattern of molt leads to low intraindividual variation in feather mercury concentrations in penguins. Environ. Toxicol. Chem. 32, 2331–2334.

Braune, B.M., Gaskin, D.E., 1987. Mercury levels in Bonaparte's gulls (*Larus philadelphia*) during autumn moult in the Quoddy region. New. Brunsw., Can. Arch. Env. Contam. Toxicol. 16, 539–549.

Burger, J., Gochfeld, M., 1997. Risk, mercury levels, and birds: relating adverse laboratory effects to field biomonitoring. Environ. Res. 75, 160–172.

Burgess, N.M., Meyer, M.W., 2008. Methylmercury exposure associated with reduced productivity in common loons. Ecotoxicology 17. http://dx.doi.org/10.1007/s10646-007-0167-8.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multi-model Inference: A Practical Information Theoretic Approach, Second Edition Springer, New York.

Bustamante, P., Bocher, P., Cherel, Y., Miramand, P., Caurant, F., 2003. Distribution of trace elements in the tissues of benthic and pelagic fish from the Kerguelen Islands. Sci. Total Environ. 313, 25–39.

Bustamante, P., Lahaye, V., Durnez, C., Churlaud, C., Caurant, F., 2006. Total and organic Hg concentrations in cephalopods from the North East Atlantic waters: influence of geographical origin and feeding ecology. Sci. Total Environ. 368, 585–596.

Carravieri, A., Bustamante, P., Churlaud, C., Cherel, Y., 2013. Penguins as bioindicators of mercury contamination in the Southern Ocean: Birds from the Kerguelen Islands as a case study. Sci. Total Environ. 454–455, 141–148.

Carravieri, A., Bustamante, P., Churlaud, C., Fromant, A., Cherel, Y., 2014a. Moulting patterns drive within-individual variations of stable isotopes and mercury in seabird body feathers: implications for monitoring of the marine environment. Mar. Biol. 161 (4), 963–968.

Carravieri, A., Bustamante, P., Tartu, S., Meillère, A., Labadie, P., Budzinski, H., Peluhet, L., Barbraud, C., Weimerskirch, H., Chastel, O., Cherel, Y., 2014b. Wandering albatrosses document latitudinal variations in the transfer of persistent organic pollutants and mercury to Southern Ocean predators. Environ. Sci. Technol. 48, 14746–14755.

Carravieri, A., Cherel, Y., Blévin, P., Brault-Favrou, M., Chastel, O., Bustamante, P., 2014c. Mercury exposure in a large subantarctic avian community. Environ. Pollut. 190C, 51–57.

Cherel, Y., Fontaine, C., Richard, P., Labat, J.P., 2010. Isotopic niches and trophic levels of myctophid fishes and their predators in the Southern Ocean. Limnol. Ocean. 55, 324–332.

Cherel, Y., Hobson, K.A., 2007. Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Mar. Ecol. Prog. Ser. 329, 281–287.

Cherel, Y., Weimerskirch, H., 1999. Spawning cycle of onychoteuthid squids in the southern Indian Ocean: new information from seabird predators. Mar. Ecol. Prog. Ser. 188, 93–104.

Choquet, R., Lebreton, J.D., Gimenez, O., Reboulet, A.M., Pradel, R., 2009a. U-CARE: Utilities for performing goodness of fit tests and manipulating CApture-REcapture data. Ecography 32, 1071–1074.

Choquet, R., Rouan, L., Pradel, R., 2009b. Program E-SURGE: a software application for fitting multievent models. In: Thomson, D.L., Cooch, E.G., Conroy, M.J. (Eds.), Modeling Demographic Processes in Marked Populations. Springer, New York, pp. 845–865.

Cuvin-Aralar, A., Furness, R.W., 1991. Mercury and selenium interaction: a review. Ecotox. Env. Saf. 21, 348–364.

Core Team, R., 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, URL.

Das, K., Debacker, V., Bouquegneau, J.M., 2000. Metallothioneins in marine mammals. Cell. Mol. Biol. 46, 283–294.

Delord, K., Besson, D., Barbraud, C., Weimerskirch, H., 2008. Population trends in a community of large Procellariiforms of Indian Ocean: potential effects of environment and fisheries interactions. Biol. Cons. 141, 1840–1856.

Evans, H.L., Garman, R.H., Laties, V.G., 1982. Neurotoxicity of methylmercury in the pigeon. Neurotoxicology 3, 21–36.

Evers, D.C., Savoy, L.J., DeSorbo, C.R., Yates, D.E., Hanson, W., Taylor, K.M., Siegel, L.S., Cooley, J.H., Bank, M.S., Major, A., 2008. Adverse effects from environmental mercury loads on breeding common loons. Ecotoxicology 17, 69–81.

Frederick, P., Jayasena, N., 2010. Altered pairing behaviour and reproductive success in white ibises exposed to environmentally relevant concentrations of methylmercury. Proc. R. Soc. B 278, 1851–1857.

Furness, R.W., Muirhead, S.J., Woodburn, M., 1986. Using bird feathers to measure mercury in the environment: relationship between mercury content and moult. Mar. Pollut. Bull. 17, 27–37.

Furness, R.W., Lewis, S.A., Mills, J.A., 1990. Mercury levels in the plumage of red-billed gulls *Larus novaehollandiae scopulinus* of known sex and age. Environ. Pollut. 63, 33–39.

Furness, R.W., Thompson, D.R., Becker, P.H., 1995. Spatial and temporal variation in mercury contamination of seabirds in the North Sea. Helgölander Meeres 49, 605–615.

Goutte, A., Bustamante, P., Barbraud, C., Delord, K., Weimerskirch, H., Chastel, O., 2014a. Demographic responses to mercury exposure in two closely related Antarctic top predators. Ecology 95, 1075–1086.

Goutte, A., Barbraud, C., Meillère, A., Carravieri, A., Bustamante, P., Labadie, P., Budzinski, H., Delord, K., Cherel, Y., Weimeskirch, H., Chastel, O., 2014b. Demographic consequences of heavy metals and persistent organic pollutants in a vulnerable long-lived bird, the wandering albatross. Proc. R. Soc. B 281, 20133313.

Goutte, A., Barbraud, C., Herzke, D., Bustamante, P., Angelier, F., Tartu, S., Clément-Chastel, C., Moe, B., Bech, C., Gabrielsen, G.W., Bustnes, J.O., Chastel, O., 2015. Survival rate and breeding outputs in a high Arctic seabird exposed to legacy persistent organic pollutants and mercury. Environ. Pollut. 200C, 1–9.

Hallinger, K.K., Cornell, K.L., Brasso, R.L., Cristol, D.A., 2011. Mercury exposure and survival in free-living tree swallows (*Tachycineta bicolor*). Ecotoxicology 20, 39–46.

Hindell, M.A., Brothers, N., Gales, R., 1999. Mercury and cadmium concentrations in the tissues of three species of southern albatrosses. Polar Biol. 22, 102–108.

Hobson, K.A., Clark, R.G., 1992. Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. Condor 94, 181–188.

Jaeger, A., Lecomte, V.J., Weimerskirch, H., Richard, P., Cherel, Y., 2010. Seabird satellite tracking validates the use of latitudinal isoscapes to depict predators' foraging areas in the Southern Ocean. Rapid Comm. Mass. Spectr. 24, 3456–3460.

Jaeger, A., Goutte, A., Lecomte, V.J., Richard, P., Chastel, O., Barbraud, C., Weimerskirch, H., Cherel, Y., 2014. Age, sex, and breeding status shape a complex foraging pattern in an extremely long-lived seabird. Ecology 95, 2324–2333.

Koeman, J.H., Peeters, W.H.M., Koudstaal-Hol, C.H.M., Tjioe, P.S., De Goeij, J.J.M., 1973. Mercury-selenium correlations in marine mammals. Nature 245, 385–386.

Lebreton, J.-D., Pradel, R., 2002. Multistate recapture models: modelling incomplete individual histories. J. Appl. Stat. 29, 353–369.

Lewis, S.A., Furness, R.W., 1991. Mercury accumulation and excretion in laboratory reared black-headed gull *Larus ridibundus* chicks. Arch. Env. Contam. Toxicol. 21, 316–320.

Martoja, R., Berry, J.P., 1980. Identification of tiemannite as a probable product of demethylation of mercury by selenium in cetaceans. A complement to the scheme of the biological cycle of mercury. Vie Milieu 30, 7–10.

Mitro, M.G., Evers, D.C., Meyer, M.W., Piper, W.H., 2008. Common loon survival rates and mercury in New England and Wisconsin. J. Wildl. Manag. 72, 665–673.

Monteiro, L.R., Furness, R.W., 1995. Seabirds as monitors of mercury in the marine environment. Water Air Soil Pollut. 80 (1–4), 851–870.

Monteiro, L.R., Granadeiro, J.P., Furness, R.W., Oliveira, P., 1999. Contemporary patterns of mercury contamination in the Portuguese Atlantic inferred from mercury concentrations in seabird tissues. Mar. Env. Res. 47, 137–156.

Muirhead, S.J., Furness, R.W., 1988. Heavy metal concentrations in the tissues of seabirds from Gough Island. South Atl. Ocean. Mar. Pollut. Bull. 19, 278–283.

Newsome, S.D., Martinez del Rio, C., Bearhop, S., Phillips, D.L., 2007. A niche for isotopic ecology. Front. Ecol. Env. 5, 429–436.

Nigro, M., Leonzio, C., 1996. Intracellular storage of mercury and selenium in different marine vertebrates. Mar. Ecol. Prog. Ser. 135, 137–143.

Nriagu, J.O., 1996. A history of global metal pollution. Science 272, 223–224.

Pardo, D., Weimerskirch, H., Barbraud, C., 2013a. When celibacy matters: incorporating non-breeders improves demographic parameter estimates. Plos One 8, e60389.

Pardo, D., Weimerskirch, H., Barbraud, C., 2013b. Females better face senescence in the wandering albatross. Oecologia 173, 1283–1294.

Sokolov, S., Rintoul, S.R., 2007. On the relationship between fronts of the Antarctic circumpolar current and surface chlorophyll concentrations in the Southern Ocean. J. Geophys. Res. 112, C07030.

Stewart, F.M., Phillips, R.A., Bartle, J.A., Craig, J., Shooter, D., 1999. Influence of phylogeny, diet, moult schedule and sex on heavy metal concentrations in New Zealand Procellariiformes. Mar. Ecol. Prog. Ser. 178, 295–305.

Tan, S.W., Meiller, J.C., Mahaffey, K.R., 2009. The endocrine effects of mercury in humans and wildlife. Crit. Rev. Toxicol. 39, 228–269.

Tartu, S., Goutte, A., Bustamante, P., Angelier, F., Moe, B., Clément-Chastel, C., Bech, C., Gabrielsen, G.W., Bustness, J.O., Chastel, O., 2013. To breed or not to breed: endocrine response to mercury contamination by an arctic seabird. Biol. Lett. 9 (4), 20130317.

Tartu, S., Bustamante, P., Goutte, A., Cherel, Y., Weimeskirch, H., Bustness, J.O., Chastel, O., 2014. Age-related mercury contamination and relationship with luteinizing hormone in a long-lived Antarctic bird. Plos One 9 (7), e103642.

Tartu, S., Angelier, F., Wingfield, J.C., Bustamante, P., Labadie, P., Budzinski, H., Weimerskirch, H., Bustnes, J.O., Chastel, O., 2015a. Corticosterone, prolactin and egg neglect behaviour in relation to mercury and legacy POPs in a long-lived Antarctic bird. Sci. Tot. Env. 505C, 180–188.

Tartu, S., Bustamante, P., Angelier, F., Lendvai, A.Z., Moe, B., Blévin, P., Bech, C., Gabrielsen, G.W., Bustnes, J.O., Chastel, O., 2015b. Mercury exposure, stress and prolactin secretion in an Arctic seabird: an experimental study. Funct. Ecol. . http://dx.doi.org/10.1111/1365-2435.12534

Tavares, S., Xavier, J.C., Phillips, R.A., Pereira, M.E., Pardal, M.A., 2013. Influence of age, sex and breeding status on mercury accumulation patterns in the wandering albatross *Diomedea exulans*. Environ. Pollut. 181, 315–320.

Thompson, D.R., Furness, R.W., 1989a. Comparison of the levels of total and organic mercury in seabird feathers. Mar. Pollut. Bull. 20, 557–579.

Thompson, D.R., Furness, R.W., 1989b. The chemical form of mercury stored in South Atlantic seabirds. Environ. Pollut. 60, 305–317.

Thompson, D.R., Hamer, K.C., Furness, R.W., 1991. Mercury accumulation in great skuas *Catharacta skua* of known age and sex, and its effects upon breeding and survival. J. Appl. Ecol. 28, 672–684.

Thompson, D.R., Furness, R.W., Lewis, S.A., 1993. Temporal and spatial variation in mercury concentrations in some albatrosses and petrels from the sub-Antarctic. Polar Biol. 13, 239–244.

Thompson, D.R., Furness, R.W., Monteiro, L.R., 1998. Seabirds as biomonitors of mercury inputs to epipelagic and mesopelagic marine food chains. Sci. Total Environ. 213, 299–305.

Wagemann, R., Trebacz, E., Boila, G., Lockhart, W.L., 1998. Methylmercury and total mercury in tissues of arctic marine mammals. Sci. Total Environ. 218, 19–31.

Wagemann, R., Trebacz, E., Boila, G., Lockhart, W.L., 2000. Mercury species in the liver of ringed seals. Sci. Total Environ. 261, 21–32.

Wayland, M., Drake, K.L., Alisauskas, R.T., Kellett, D.K., Traylor, J., Swoboda, C., Mehl, K., 2008. Survival rates and blood metal concentrations in two species of free-ranging North American sea ducks. Environ. Toxicol. Chem. 27, 698–704.

Weimerskirch, H., 1991. Sex-specific differences in molt strategy in relation to breeding in the Wandering albatross. Condor 93, 731–737.

Weimerskirch, H., Brothers, N., Jouventin, P., 1997. Population dynamics of wandering albatross *Diomedea exulans* and Amsterdam albatross *D. amsterdamensis* in the Indian Ocean and their relationships with long-line fisheries: conservation implications. Biol. Conserv. 79, 257–270.

Weimerskirch, H., Cherel, Y., Delord, K., Jaeger, A., Patrick, S.C., Riotte-Lambert, L., 2014. Lifetime foraging patterns of the wandering albatross: life on the move. J. Exp. Mar. Biol. Ecol. 450, 68–78.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, p. 529. http://dx.doi.org/10.1007/978-0-387-87458-6.