Environmental Pollution 190 (2014) 51–57

Contents lists available at ScienceDirect

Environmental Pollution

journal homepage: www.elsevier.com/locate/envpol

Mercury exposure in a large subantarctic avian community

Alice Carravieri [a,b,*], Yves Cherel [b], Pierre Blévin [b], Maud Brault-Favrou [a], Olivier Chastel [b], Paco Bustamante [a]

[a] Littoral Environnement et Sociétés (LIENSs), UMRi 7266 CNRS-Université de La Rochelle, 2 rue Olympe de Gouges, 17000 La Rochelle, France
[b] Centre d'Etudes Biologiques de Chizé, UMR 7372 CNRS-Université de La Rochelle, BP 14, 79360 Villiers-en-Bois, France

ARTICLE INFO

Article history:
Received 31 December 2013
Received in revised form
17 March 2014
Accepted 19 March 2014
Available online xxx

Keywords:
Feeding ecology
Kerguelen
Procellariiformes
Seabirds
Southern Ocean

ABSTRACT

Mercury (Hg) contamination poses potential threats to ecosystems worldwide. In order to study Hg bioavailability in the poorly documented southern Indian Ocean, Hg exposure was investigated in the large avian community of Kerguelen Islands. Adults of 27 species (480 individuals) showed a wide range of feather Hg concentrations, from 0.4 ± 0.1 to 16.6 ± 3.8 μg g^{-1} dry weight in Wilson's storm petrels and wandering albatrosses, respectively. Hg concentrations increased roughly in the order crustacean- < fish- ≤ squid- ≤ carrion-consumers, confirming that diet, rather than taxonomy, is an important driver of avian Hg exposure. Adults presented higher Hg concentrations than chicks, due to a longer duration of exposure, with the only exception being the subantarctic skua, likely because of feeding habits' differences of the two age-classes in this species. High Hg concentrations were reported for three species of the poorly known gadfly petrels, which merit further investigation.

1. Introduction

Mercury (Hg) is a pervasive non-essential metal affecting ecosystem health. Despite its natural origin, Hg has been mobilized by human activities such as mining and fossil-fuel combustion (UNEP, 2013), thus resulting in a significant increase in Hg available for cycling among land, air and the ocean since pre-industrial times (Selin, 2009). Hg emissions are transported through the atmosphere on a hemispheric-to-global scale, allowing for transport to remote locations such as sub-polar and polar regions (Fitzgerald et al., 1998). After atmospheric deposition and through biotic and abiotic mechanisms, Hg is readily transformed in methyl-Hg, the highly toxic form that bioaccumulates in the tissues of living organisms and biomagnifies up food webs, especially in aquatic environments (Fitzgerald et al., 2007). Top predators are thus exposed to significant quantities of Hg *via* their diet, providing information on Hg bioavailability within their food webs (Morel et al., 1998). Among consumers, birds have varied levels of ecological, spatial and temporal integration of contaminants depending on species, and they have been identified as effective indicators of Hg bioavailability in both terrestrial and marine environments (Burger and Gochfeld, 2004; Solonen and Lodenius, 1990).

The Kerguelen Islands are a remote subantarctic archipelago in the southern Indian Ocean, where the level of Hg bioavailability is poorly documented (Bocher et al., 2003; Bustamante et al., 2003; Cipro et al., 2014; Cossa et al., 2011). This archipelago hosts a large and highly diverse avian assemblage (35 different breeding species). The community includes a few terrestrial species and many seabirds, with Sphenisciformes (penguins) and Procellariiformes (albatrosses and petrels) dominating by mass and numbers, respectively (Guinet et al., 1996; Weimerskirch et al., 1989). Overall Kerguelen seabirds feed on a few key species of marine organisms, including some crustaceans (euphausiids, hyperiids), fish (myctophids, notothenioids) and cephalopods (oceanic squids) (Bocher et al., 2001; Cherel et al., 2010; Cherel and Hobson, 2005; Guinet et al., 1996), with some seabirds relying extensively on carrion. This biological richness can be related to the large and productive shelf surrounding the archipelago (Blain et al., 2001). Kerguelen seabirds show a wide range of contrasted feeding strategies, with species foraging in the benthic and pelagic environments and ranging from neritic to oceanic waters. Noticeably, the oceanic species forage over a large latitudinal gradient, from subtropical to Antarctic waters (Supplementary Table S1). Kerguelen seabirds therefore offer a unique opportunity to study Hg bioavailability over diverse water masses of the Southern Ocean.

The present study aims to assess Hg bioavailability in the southern Indian Ocean by using birds from the Kerguelen Islands as bioindicators. Hg exposure was evaluated by using body feathers,

* Corresponding author.
E-mail address: alice.carravieri@cebc.cnrs.fr (A. Carravieri).

http://dx.doi.org/10.1016/j.envpol.2014.03.017
0269-7491/

because feathers are the main route of Hg excretion in birds (Braune and Gaskin, 1987). Importantly, this work complements a recent investigation on Hg in chicks (Blévin et al., 2013) by focussing on breeding adults and by including more species. While Hg concentrations in chick feathers are representative of a well-defined, relatively short period of exposure (the chick-rearing period), adult feathers provide a wider perspective on Hg exposure of the species over their whole life cycles (Evers et al., 2005). Thus adult feather Hg concentrations were determined in 27 representative species, including the only two terrestrial birds of the assemblage, in order to: (i) describe Hg exposure in a large number of sympatric bird species from the poorly documented southern Indian Ocean; (ii) compare the exposure pattern to that of avian communities from other subantarctic and oceanic remote locations worldwide; (iii) test the effect of age-class on feather Hg concentrations by using the recently published Hg data on chicks (Blévin et al., 2013), and (iv) investigate the influence of various factors (taxonomy, diet, feeding habitats, moulting patterns) on Hg exposure. Taxonomy, which was not tested in Blévin et al. (2013), was expected to play a minor role in explaining feather Hg concentrations when compared to feeding strategies, since diet is considered to be the main factor driving Hg variation in birds (Becker et al., 2002; Blévin et al., 2013; Bocher et al., 2003; Monteiro et al., 1998; Stewart et al., 1999). In addition, adult birds were expected to show higher feather Hg concentrations than chicks, as they are exposed over a longer period to Hg *via* their diet (Catry et al., 2008; Stewart et al., 1997).

2. Materials and methods

Fieldwork was carried out from 2003 to 2011 on the Kerguelen Islands (49°21′ S, 70°18′ E, Fig. 1), which are located in the southern part of the Polar Frontal Zone, in the immediate vicinity of the Polar Front (Orsi et al., 1995; Park and Gamberoni, 1997). Breeding adults from 27 bird species belonging to 5 orders and 10 families were sampled ($n = 5$ to 33 individuals per species, Supplementary Table S2). Sampling was conducted at different locations of the archipelago, depending on the species breeding sites. Resident neritic seabird species (Kerguelen shag and gentoo penguin) were sampled at colonies close to the open sea, while terrestrial species (lesser sheathbill and Kerguelen pintail) were sampled on islands of the large Morbihan Bay (closed sea). Birds were non-destructively captured by mist net or by hand, depending on species, and released immediately after sampling. A few whole body feathers (6–10) were pulled out from the lower back of the birds and then stored dry in sealed plastic bags until analysis at the University of La Rochelle, France.

Depending on bird and hence feather size, 1 to 5 whole feathers per individual were cleaned, oven-dried to a constant mass and homogenised as described in Blévin et al. (2013). An Advanced Mercury Analyzer spectrophotometer (Alted AMA 254) was used to measure total Hg, which approximates the amount of methyl-Hg in feathers (Bond and Diamond, 2009; Thompson and Furness, 1989a). For each individual, analyses were run in duplicate-triplicate by taking sub-samples of the homogenised feathers (relative standard deviation <10% for each individual). Accuracy was checked using certified reference material (Tort-2 Lobster Hepatopancreas, NRC, Canada; certified Hg concentration: 0.27 ± 0.06 μg g^{-1} dry weight). Our measured values were 0.24 ± 0.01 μg g^{-1} dry weight, $n = 22$. 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 weight. Hg concentrations are presented μg g^{-1} dry weight (dw).

Statistical analyses were performed using R 2.15.1 (R Core Team, 2012). Data exploration was performed mainly following Zuur et al. (2010). The influence of taxa (species, genus, family and order) on adult feather Hg concentrations was tested by using generalized linear models (GLM) with a gamma distribution and an inverse link function. Model selection was based on Akaïke's Information Criteria adjusted for small sample sizes (AICc) (Burnham and Anderson, 2002). The sampling year was not included in the models because most species were sampled in only one year (Supplementary Table S2) and thus the year effect would be confounded by the species effect. Nonetheless, no inter-annual differences in feather Hg concentrations were found on the six species that were sampled in two different years (light-mantled sooty albatross, soft-plumaged and Kerguelen petrels, black-bellied storm petrel, South Georgia diving petrel and lesser sheathbill, data not shown). As biometric measurements were not performed on individual birds during the sampling procedure, the effect of size and mass on feather Hg concentrations could not be incorporated in the models. However, mean values of size and mass were obtained for each species from the literature (Supplementary Table S1) and their correlations with mean feather Hg concentrations were tested. Finally, the effect of age-class on feather Hg concentrations was investigated on 21 out of the 27 species by comparing adult data from the present study with chick data from the same Kerguelen locations (Blévin et al., 2013). A significance level of $\alpha < 0.05$ was used for all statistical tests. Results are means ± SD.

General information on the feeding ecology of Kerguelen birds was based on published and unpublished data obtained using various methods (stomach content and stable isotope analyses and tracking devices), and is summarized in Supplementary Table S1. Importantly, dietary information was restricted to the chick food, collected during the chick-rearing period, because parent birds carry significant amounts of food in their stomach at that time only. By contrast, adult diet is poorly known both during and outside the breeding period. The relationship between Hg exposure and trophic ecology was not studied here using stable isotopes, because of the uncoupled temporal integration of Hg and stable isotopes in feathers of adult birds (Bond, 2010; Thompson et al., 1998).

3. Results

Feather Hg concentrations were measured in a total of 480 adult birds from the Kerguelen Islands (details in Supplementary Table S2). Feather Hg concentrations varied widely within the avian community, with means ranging from 0.42 ± 0.13 to 16.6 ± 3.8 μg g^{-1} dw in Wilson's storm petrels and wandering albatrosses, respectively (Fig. 2). The lowest feather Hg concentration occurred in a South-Georgian diving petrel and the highest in a northern giant petrel (0.10 and 32.1 μg g^{-1}, respectively). Model selection showed that species was the most important factor explaining feather Hg concentrations when compared to other taxonomic levels (Table 1). Coefficients of variations (CV) also varied considerably between species, ranging from 13 to 109% (Supplementary Table S2). Mean feather Hg concentration was significantly related to species size (Pearson correlation, $r = 0.50$, $p = 0.008$, $n = 27$), but not to species mass ($r = 0.23$, $p = 0.256$, $n = 27$).

By combining feather Hg data of adults from this study with those of chicks from Blévin et al. (2013), a total of 654 individuals from 21 seabird species were analysed. The model including

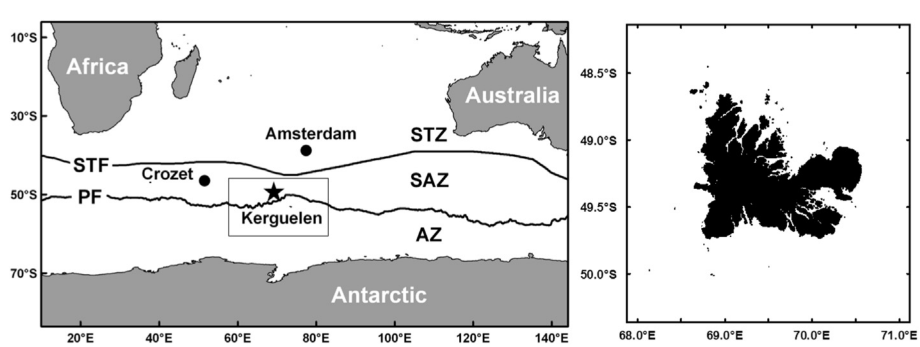

Fig. 1. Map and location of the Kerguelen Islands and of the main oceanic fronts and zones within the southern Indian Ocean. Abbreviations: STF, Subtropical Front; PF, Polar Front; STZ, Subtropical Zone; SAZ, Subantarctic Zone; AZ, Antarctic Zone.

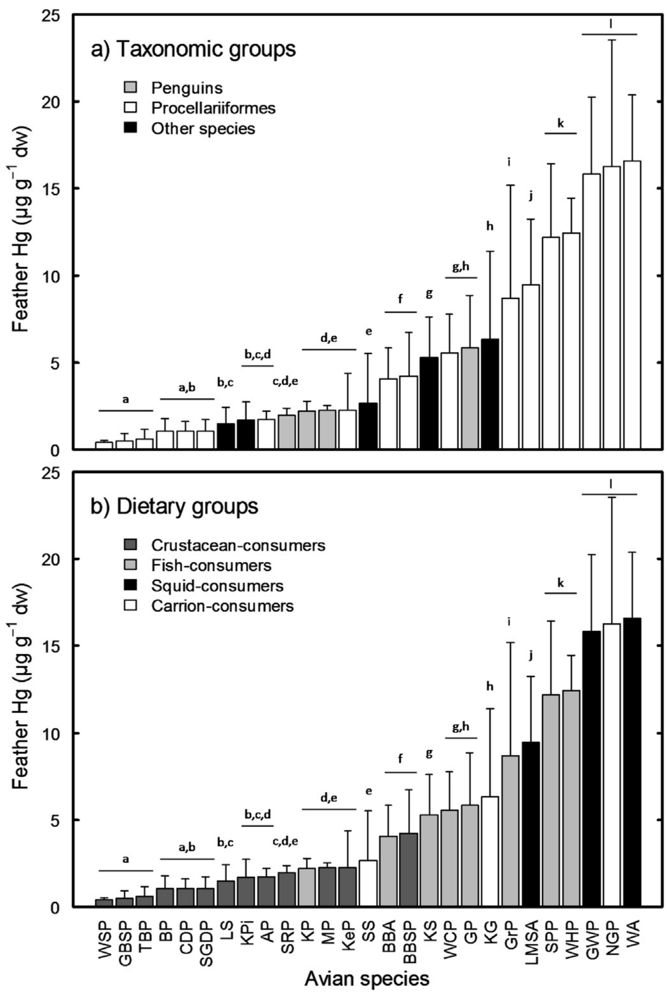

Fig. 2. Inter-specific differences in adult feather Hg concentrations within the Kerguelen avian community. Species are presented according to a) taxonomic groups: penguins (grey), procellariiform seabirds (white) and other species (black); and b) dietary groups: terrestrial species and crustacean- (dark grey), fish- (grey), squid- (black) and carrion- (white) consumers. Species sharing the same letter are not statistically different (Tukey HSD, $p < 0.05$). Values are means ± SD. Species abbreviations: WSP, Wilson's storm petrel; GBSP, grey-backed storm petrel; TBP, thin-billed prion; BP, blue petrel; CDP, common diving petrel; SGDP, South Georgian diving petrel; LS, lesser sheathbill; KPi, Kerguelen pintail; AP, Antarctic prion; SRP, southern rockhopper penguin; KP, king penguin; MP, macaroni penguin; KeP, Kerguelen petrel; SS, subantarctic skua; BBA, black-browed albatross; BBSP, black-bellied storm petrel; KS, Kerguelen shag; WCP, white-chinned petrel; GP, gentoo penguin; KG, kelp gull; GrP, grey petrel; LMSA, light-mantled sooty albatross; SPP, soft-plumaged petrel; WHP, white-headed petrel; GWP, great-winged-petrel; NGP, northern giant petrel; WA, wandering albatross.

species, age-class and their interaction as explaining factors of feather Hg concentrations showed the best fit to the data (Table 1). Feather Hg concentrations were significantly higher in adults than in chicks in all but two species: the blue petrel (no statistical difference) and subantarctic skua (higher chick level) (Fig. 3). The ratio of adult to chick feather Hg concentrations varied between species, ranging from 0.5 to 20.7 in the subantarctic skua and South-Georgian diving petrel, respectively (Supplementary Table S2).

4. Discussion

To the best of our knowledge, this study is the first to report feather Hg concentrations for such a large number of adult sympatric birds, including representative species of all the four families of the order Procellariiformes, namely albatrosses, petrels, storm

Table 1
AIC_c model ranking for adult feather Hg concentrations within the Kerguelen avian community. Models are GLM with a gamma distribution and an inverse link function. Abbreviations: AIC_c, Akaike's Information Criteria adjusted for small sample-sizes values; w_i, AIC_c weights.

Models	N° parameters	AIC_c	ΔAIC_c[a]	w_i[b]
Adults (*N* = 480)				
Species	28	1698	0	1
Genus	22	1719	20	0
Family	11	2226	528	0
Order	6	2422	723	0
Null	2	2459	760	0
Adults and chicks (*N* = 654)				
Species * Age-class	43	1684	0	1
Species + Age-class	23	2276	592	0
Species	22	2471	787	0
Age-class	3	2915	1231	0
Null	2	3037	1353	0

[a] Scaled ΔAIC_c; $\Delta AIC_c = 0.00$ is interpreted as the best fit to the data among the models.
[b] Weight of evidence interpreted as a proportion. Weights across all models sum to 1.00.

petrels and diving petrels. Hg exposure varied widely within the community, showing a remarkable 40-fold difference between the species with the lowest and highest Hg concentrations. The community exposure pattern agrees with results on chicks (Blévin et al., 2013): small petrels, penguins and terrestrial species generally showed low levels of exposure (<2.5 µg g^{-1} dw), coastal seabirds, *Procellaria* petrels and small albatrosses had intermediate concentrations (<10 µg g^{-1} dw), while *Pterodroma* petrels, northern giant petrels and wandering albatrosses were the species having the highest concentrations (>10 µg g^{-1} dw).

4.1. Comparisons with other avian communities

The pattern of Hg concentrations among members of the Kerguelen avian community fits well with that of other subantarctic

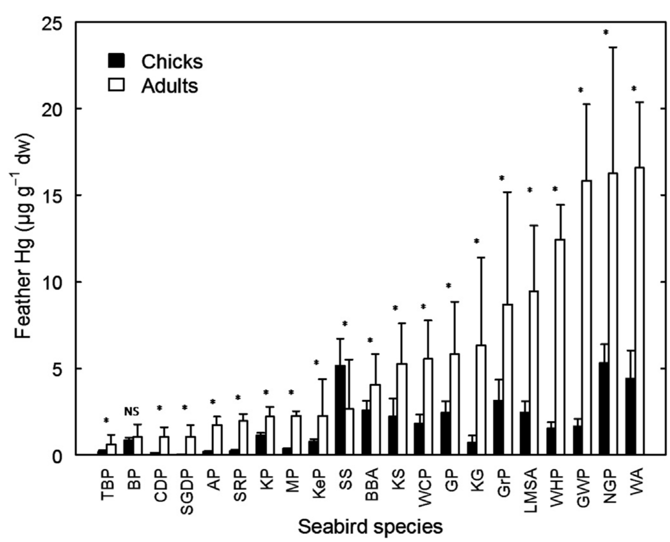

Fig. 3. Age-class differences in feather Hg concentrations within the Kerguelen seabird community. * Statistically different (Wilcoxon, $p < 0.05$); NS: not significant. Values are means ± SD. Species abbreviations: TBP, thin-billed prion; BP, blue petrel; CDP, common diving petrel; SGDP, South Georgian diving petrel; AP, Antarctic prion; SRP, southern rockhopper penguin; KP, king penguin; MP, macaroni penguin; KeP, Kerguelen petrel; SS, subantarctic skua; BBA, black-browed albatross; KS, Kerguelen shag; WCP, white-chinned petrel; GP, gentoo penguin; KG, kelp gull; GrP, grey petrel; LMSA, light-mantled sooty albatross; WHP, white-headed petrel; GWP, great-winged-petrel; NGP, northern giant petrel; WA, wandering albatross.

sites, such as South Georgia, southern Atlantic Ocean (Fig. 4). Feather Hg concentrations were comparable in seabirds from the two localities, with the exception of the northern giant petrel and wandering albatross (Anderson et al., 2009; Becker et al., 2002). This could be related to inter-site dietary differences of these two top predators. Moreover, similar feather Hg concentrations were reported for some species of albatrosses and petrels from the southern Pacific Ocean (Thompson et al., 1990, 1993). Hg bioavailability thus seems to be similar within the three sectors of the Southern Ocean, which agrees well with its circumpolar annular oceanographic structure (Sokolov and Rintoul, 2007). At lower latitudes of the Southern Hemisphere, only the tropical seabird communities from the western Indian Ocean have been investigated, revealing much lower feather Hg concentrations (~0.05–1.5 μg g^{-1}; Catry et al., 2008; Kojadinovic et al., 2007) than in Kerguelen birds. This trend could result from differences in the physical and biological factors driving methyl-Hg production and food web transfer in the two regions (i.e., the atmospheric deposition of inorganic Hg, the rate of primary productivity, the abundance of sinking organic matter and the structure of the microbial community, Mason et al., 2012). The wide range of Hg exposure of Kerguelen birds compares well with avian communities of remote archipelagos of the Northern Hemisphere, namely the tropical Midway Atoll, North Pacific Ocean and the subtropical Azores Islands, North Atlantic Ocean (both ~ 1–20 μg g^{-1}; Burger and Gochfeld, 2000a; Gochfeld et al., 1999; Monteiro et al., 1998). These wide ranges of contamination are related to the presence of highly contaminated species of albatrosses and gadfly petrels within the communities (see below). Indeed, the avian assemblage of the temperate Machias Seal Island, North Atlantic Ocean, which includes neither albatrosses nor gadfly petrels, had lower feather Hg concentrations (0.7–7 μg g^{-1}; Bond and Diamond, 2009). Therefore, the specific composition of the avian communities rather than the proximity to highly industrialized countries seems to be a key factor driving the level of Hg exposure within avian assemblages from open sea regions. In this context, the range of Hg exposure within the Kerguelen avian community is remarkable, as it encompasses the concentrations reported worldwide in remote oceanic locations (Blévin et al., 2013).

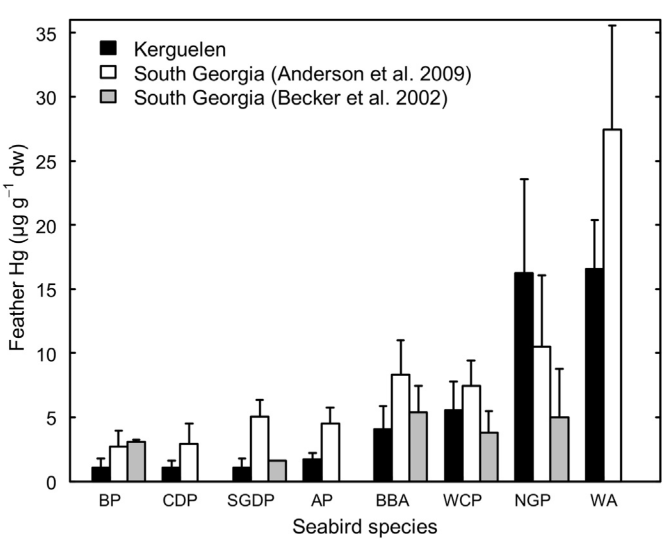

Fig. 4. Comparison of feather Hg concentrations between the same seabird species breeding in the southern Indian Ocean (Kerguelen Islands, present study) and in the southern Atlantic Ocean (South Georgia, Anderson et al., 2009, Becker et al., 2002). Species abbreviations: BP, blue petrel; CDP, common diving petrel; SGDP, South Georgian diving petrel; AP, Antarctic prion; BBA, black-browed albatross; WCP, white-chinned petrel; NGP, northern giant petrel; WA, wandering albatross.

4.2. Influence of taxonomy

The best taxonomic explanatory variable of feather Hg concentrations in the Kerguelen community was species, as it integrates a large range of ecological, behavioural, physiological and life-history traits that are susceptible to drive variation in feather Hg concentrations (Anderson et al., 2009; Bond and Diamond, 2009). Although inter-specific differences in avian Hg exposure have often been investigated, taxonomic-related variations were rarely tested in a large number of species (Anderson et al., 2009; Ochoa-Acuna et al., 2002). Here, statistical models including genus, family or order as explanatory variables had a poor fit to feather Hg data. Indeed, closely-related species at Kerguelen often showed very different levels of exposure. For example, black-bellied storm petrels displayed higher Hg concentrations than the other two Hydrobatidae species, despite similar size and life-history traits. The same pattern was highlighted for Sphenisciformes, with the gentoo penguins having higher feather Hg concentrations than the other three penguin species (Carravieri et al., 2013). Therefore, the effect of taxonomy seems to play a minor role in avian Hg exposure when compared to other ecological factors (Becker et al., 2002; Lock et al., 1992; Stewart et al., 1999). Nevertheless, the present study provides new and interesting results regarding a particular taxonomic group: the gadfly petrels (genus *Pterodoma*, Warham, 1990), which were amongst the species with the highest Hg concentrations (Fig. 2). Our data together with a review of the scientific literature (Table 2) point out the high Hg exposure of almost all the *Pterodroma* petrels so far investigated, including species living in different marine ecosystems. Nevertheless, the Barau's Petrel *P. baraui* from La Réunion Island, western Indian Ocean, showed surprisingly low feather Hg concentrations (1.0 μg g^{-1}), suggesting again a regional trend of low Hg bioavailability at tropical latitudes of the Indian Ocean (see Subsection 4.1).

4.3. Influence of diet and feeding habitat

Inter-specific variability in Hg exposure is typically attributed to diet (Arcos et al., 2002; Monteiro et al., 1998; Stewart et al., 1999). Since Hg is efficiently biomagnified up food webs (Atwell et al., 1998; Campbell et al., 2005; Jarman et al., 1996), high trophic level prey, such as fish and cephalopods show higher Hg concentrations than crustaceans and other planktonic organisms (Bustamante et al., 2006; Kojadinovic et al., 2006; Stewart et al., 1997). This is consistent with feather Hg concentrations of Kerguelen birds increasing roughly in the order crustacean- $<$ fish- $\leq$ squid- $\leq$ carrion-consumers (Fig. 2b), as previously shown in chicks (Blévin et al., 2013). This confirms that Hg is efficiently biomagnified and that diet plays a key role in explaining Hg exposure. Accordingly, the positive correlation highlighted between bird size and feather Hg concentrations is likely explained by a trophic effect, as larger avian species tend to occupy higher trophic positions and/or to consume larger prey items (Burger and Gochfeld, 2000a).

Differences in dietary exposure over diverse habitats within and outside the breeding period can also account for important variability in feather Hg concentrations (Anderson et al., 2009; Blévin et al., 2013). Here, inshore non-migratory species (Kerguelen shag, kelp gull, gentoo penguin), which feed on benthic organisms, showed intermediate to high Hg concentrations. This agrees with high Hg bioavailability in benthic environments due to methyl-Hg production in coastal marine sediments (Bustamante et al., 2006; Fitzgerald et al., 2007). In the oceanic domain, methyl-Hg concentration reaches a maximum in mesopelagic waters (Driscoll et al., 2013; Fitzgerald et al., 2007), resulting in enhanced contamination of mesopelagic prey (Chouvelon et al., 2012, Choy et al., 2009).

Table 2
An overall synthesis of Hg concentrations in body feathers of adult gadfly petrels. Values are means ± SD with ranges in parentheses.

Species	Site	Ocean	Breeding region	n	Hg (μg g^{-1} dw)	Reference
Atlantic petrel (*Pterodroma incerta*)	Gough Island	South Atlantic	Subantarctic	23	13.9 ± 3.6[a]	Thompson et al. (1990)
	Gough Island	South Atlantic	Subantarctic	15	13.5 ± 4.1 (3.9– 20.1)[a]	Thompson et al. (1993)
Barau's petrel (*Pterodroma baraui*)	La Réunion Island	Indian	Tropical	20	1.0 ± 0.3	Kojadinovic et al. (2007)
Bonin petrel (*Pterodroma hypoleuca*)	Midway Atoll	North Pacific	Subtropical	27	19.7 ± 1.1[b]	Gochfeld et al. (1999), Burger and Gochfeld (2000a)
Great-winged petrel (*Pterodroma macroptera*)	Kerguelen Archipelago	South Indian	Subantarctic	14	15.8 ± 4.4 (9.8–27.1)	This study
Juan Fernandez petrel (*Pterodroma externa*)	Juan Fernandez Archipelago	South Pacific	Subtropical	5 (M)	4.2 ± 0.3	Ochoa-Acuna et al. (2002)
				11 (F)	3.9 ± 0.2	
Soft-plumaged petrel (*Pterodroma mollis*)	Gough Island	South Atlantic	Subantarctic	21	10.3 ± 2.3[a]	Thompson et al. (1990)
	Gough Island	South Atlantic	Subantarctic	17	9.8 ± 2.3 (5.4–13.4)[a]	Thompson et al. (1993)
	Kerguelen Archipelago	South Indian	Subantarctic	19	12.2 ± 4.2 (4.7–25.5)	This study
White-headed petrel (*Pterodroma lessonii*)	Kerguelen Archipelago	South Indian	Subantarctic	10	12.4 ± 2.0 (9.2–17.1)	This study

Studies with too low numbers of sampled individuals ($n < 4$) were excluded.
[a] Values are in μg g^{-1} wet weight.
[b] Values are means ± SE.

This could explain the high feather Hg concentrations of oceanic species relying extensively on mesopelagic fish and cephalopods (e.g. gadfly petrels, Ochoa-Acuna et al., 2002, Ridoux, 1994). On the other hand, migratory seabirds can travel thousands of kilometres away from their breeding sites after reproduction (e.g., Warham, 1990), being potentially exposed to different quantities of Hg. Here, species visiting northern subtropical and neritic waters during the non-breeding period (e.g. the wandering albatross) tended to have higher feather Hg concentrations than those that forage predominantly within the limits of the Southern Ocean year-round (e.g. the light-mantled sooty albatross) (Cherel et al., 2013). However, further investigations on i) the poorly known feeding strategies outside the breeding season and ii) Hg distribution and speciation in the Southern Ocean could elucidate the rationale of this latitudinal trend (see Blévin et al., 2013).

4.4. Influence of moulting patterns

Feather Hg concentrations reflect blood Hg levels at the time of moult (Bearhop et al., 2000; Evers et al., 2008). This means dietary Hg but also Hg accumulated over the inter-moult period and remobilized during feather synthesis (Furness et al., 1986; Thompson et al., 1998). Another important intrinsic driver of Hg concentrations in feathers is therefore the timing, duration and frequency of moult. For instance, the irregular and infrequent moulting patterns of large albatrosses are believed to contribute significantly to high Hg concentrations in their feathers (Anderson et al., 2009; Becker et al., 2002). However, enhanced feather Hg concentrations were also reported in Kerguelen species with annual moult cycles, like great-winged and white-chinned petrels. This indicates that moulting patterns alone cannot explain all the inter-specific variation in Hg concentrations. In Procellariiformes, demethylation of Hg in the liver appears to be a significant detoxification strategy (Thompson and Furness, 1989b; Thompson et al., 1993). The efficiency of demethylation mechanisms is species-dependent and could contribute to explain the inter-specific differences in feather Hg concentrations among members of the Kerguelen avian community.

4.5. Adults and chicks

As previously shown by several other studies (e.g., Burger and Gochfeld, 2000b; Catry et al., 2008), feather Hg concentrations were higher in adults than in chicks in almost all Kerguelen species (Fig. 3). Indeed, adults have more time to bioaccumulate Hg in their tissues during the long inter-moult period (≈one year) before excreting it in feathers (Monteiro et al., 1995; Thompson et al., 1991). By contrast, chick feather Hg concentrations represent the dietary exposure over the chick-rearing period (Ackerman et al., 2011; Becker et al., 1993), which ranges from several weeks to several months in Kerguelen species. Assuming a similar rate of Hg intake of adults and chicks, species with short and long chick-rearing periods should show high and low adult-to-chick ratios in feather Hg concentrations, respectively. The hypothesis was verified in the two diving petrels (high ratios, ≥9) and in the wandering albatross and northern giant petrel (low ratios, ∼ 2–4), respectively. Exceptions to this pattern are likely indicative of differential relative Hg exposures in the two age-classes, as observed in blue petrels and subantarctic skuas (ratios: 1.3 and 0.5, respectively). Adult blue petrels from the Kerguelen Islands feed at the same low trophic level in cold Antarctic waters both during the breeding and moulting periods (Cherel et al., 2002, 2006). By contrast, chick food includes a significant proportion of mesopelagic fish (Cherel et al., 2002; Connan et al., 2008), which is consistent with their enhanced Hg exposure over adults. At Kerguelen, subantarctic skua chicks are mainly fed with blue petrels (Mougeot et al., 1998), thus explaining their high feather Hg concentrations. The chick data are in accordance with previous results on chicks of the closely-related great skua that feeds on bird meat (Stewart et al., 1997). The low Hg concentrations of adult subantarctic skuas are puzzling and strongly suggest that moulting adults do not rely on small petrels for feeding. Indeed, previous findings on subantarctic skuas from South Georgia suggest that they have a mixed diet of zooplankton and low trophic-level prey over the wintering grounds (Phillips et al., 2007). Therefore, both the duration of Hg exposure and feeding habits are key factors explaining differences in feather Hg concentrations between seabird chicks and adults.

5. Conclusions

Results from this study reinforce previous findings showing that taxonomy plays a minor role in determining avian Hg exposure when compared to feeding strategies (Stewart et al., 1999). Our results confirm that Hg concentrations are very high in some subantarctic birds, with many species showing levels of potential concern. The most common used toxic threshold of feather Hg concentration in birds is 5 μg g^{-1} (e.g., Evers et al., 2008). Here, this level was exceeded by some individuals of 11 seabird species and by all individuals of wandering albatross, northern giant petrel, and white-headed and great-winged petrels. Although subantarctic species may have evolved to cope with high Hg exposure in their environment (Blévin et al., 2013; Thompson et al., 1993), there is an urgent need to investigate the inter- and intra-specific physiological differences of Hg metabolism, excretion and toxicity, in order to establish whether some species, or some particular individuals, could be at risk. Evidence of Hg consequences on breeding, hatchling and fledging success has indeed been reported in polar birds (Goutte et al. in press; Tartu et al., 2013). Such investigations on risk related to Hg exposure are particularly relevant in the context of global warming that would favour the methylation rate of Hg in the Ocean (Cossa, 2013). Finally, the present study enables selecting the white-headed petrel as a good bioindicator species of Hg bioavailability in the Southern Ocean, considering its high level of exposure and low intra-specific variation. The white-headed petrel adds to the list of Kerguelen bioindicator species recently identified according to their foraging ecology and exposure patterns, i.e. the gentoo and king penguins, the black-browed, light-mantled sooty and wandering albatrosses (Blévin et al., 2013; Carravieri et al., 2013). The periodic examination of feather Hg concentrations in species from these remote regions over the long-term will make it possible to monitor temporal trends of Hg bioavailability to predators in the open ocean in relation to global trends of Hg emissions.

Conflict of interest

The authors declare that there are no conflicts of interest.

Acknowledgements

The authors thank the numerous fieldworkers who helped with collecting feathers, F. Capoulun and A. Jaeger for preparing some of the samples and L. Thiers for helpful suggestions on R coding. The present work was supported financially and logistically by the Poitou-Charentes Region through a PhD grant to A. Carravieri, the Agence Nationale de la Recherche (program POLARTOP, O. Chastel), the Institut Polaire Français Paul Emile Victor (IPEV, program no. 109, H. Weimerskirch) and the Terres Australes et Antarctiques Françaises (TAAF). The Contrat de Projet Etat Région (CPER 13) is also acknowledged for funding the AMA.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.envpol.2014.03.017.

References

Ackerman, J.T., Eagles-Smith, C.A., Herzog, M.P., 2011. Bird mercury concentrations change rapidly as chicks age: toxicological risk is highest at hatching and fledging. Environ. Sci. Technol. 45, 5418–5425.
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.
Arcos, J.M., Ruiz, X., Bearhop, S., Furness, R.W., 2002. Mercury levels in seabirds and their fish prey at the Ebro Delta, NW Mediterranean: the role of trawler discards as a source of contamination. Mar. Ecol. Prog. Ser. 232, 281–290.
Atwell, L., Hobson, K.A., Welch, H.E., 1998. Biomagnification and bioaccumulation of mercury in an arctic marine food web: insights from stable nitrogen isotope analysis. Can. J. Fish. Aquat. Sci. 55, 1114–1121.
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.
Becker, P.H., Furness, R.W., Henning, D., 1993. The value of chick feathers to assess spatial and interspecific variation in the mercury contamination of seabirds. Environ. Monit. Assess. 28, 255–262.
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.
Blain, S., Tréguer, P., Belviso, S., Bucciarelli, E., Denis, M., Desabre, S., Fiala, M., Martin Jézéquel, V., Le Fèvre, J., Mayzaud, P., 2001. A biogeochemical study of the island mass effect in the context of the iron hypothesis: Kerguelen Islands, Southern Ocean. Deep Sea Res. Part I: Oceanogr. Res. Pap. 48, 163–187.
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, e54508. http://dx.doi.org/10.1371/journal.pone.0054508.
Bocher, P., Caurant, F., Miramand, P., Cherel, Y., Bustamante, P., 2003. Influence of the diet on the bioaccumulation of heavy metals in zooplankton-eating petrels at Kerguelen archipelago, Southern Indian Ocean. Polar Biol. 26, 759–767.
Bocher, P., Cherel, Y., Labat, J.-P., Mayzaud, P., Razouls, S., Jouventin, P., 2001. Amphipod-based food web: *Themisto gaudichaudii* caught in nets and by seabirds in Kerguelen waters, Southern Indian Ocean. Mar. Ecol. Prog. Ser. 223, 251–260.
Bond, A.L., 2010. Relationships between stable isotopes and metal contaminants in feathers are spurious and biologically uninformative. Environ. Pollut. 158, 1182–1184.
Bond, A.L., Diamond, A.W., 2009. Mercury concentrations in seabird tissues from Machias Seal Island, New Brunswick, Canada. Sci. Total Environ. 407, 4340–4347.
Braune, B.M., Gaskin, D.E., 1987. Mercury levels in Bonaparte's gulls, *Larus philadelphia*. during autumn molt in the Quoddy region, New Brunswick, Canada. Arch. Environ. Contam. Toxicol. 16, 539–549.
Burger, J., Gochfeld, M., 2000a. Metal levels in feathers of 12 species of seabirds from Midway Atoll in the Northern Pacific Ocean. Sci. Total Environ. 257, 37–52.
Burger, J., Gochfeld, M., 2000b. Metals in albatross feathers from Midway Atoll: influence of species, age, and nest location. Environ. Res. 82, 207–221.
Burger, J., Gochfeld, M., 2004. Marine birds as sentinels of environmental pollution. EcoHealth 1, 263–274.
Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multi-model Inference: a Practical Information-Theoretic Approach, second ed. 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 Eastern Atlantic waters: influence of geographical origin and feeding ecology. Sci. Total Environ. 368, 585–596.
Campbell, L.M., Norstrom, R.J., Hobson, K.A., Muir, D.C.G., Backus, S., Fisk, A., 2005. Mercury and other trace elements in a pelagic Arctic marine food web, Northwater Polynya, Baffin Bay. Sci. Total Environ. 351, 247–263.
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. http://dx.doi.org/10.1016/j.scitotenv.2013.02.060.
Catry, T., Ramos, J.A., Le Corre, M., Kojadinovic, J., Bustamante, P., 2008. The role of stable isotopes and mercury concentrations to describe seabird foraging ecology in tropical environments. Mar. Biol. 155, 637–647.
Cherel, Y., Bocher, P., Trouvé, C., Weimerskirch, H., 2002. Diet and feeding ecology of blue petrels *Halobaena caerulea* at lies Kerguelen, Southern Indian Ocean. Mar. Ecol. Prog. Ser. 228, 283–299.
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. Oceanogr. 55, 324.
Cherel, Y., Hobson, K.A., 2005. Stable isotopes, beaks and predators: a new tool to study the trophic ecology of cephalopods, including giant and colossal squids. Proc. R. Soc. B: Biol. Sci. 272, 1601–1607.
Cherel, Y., Jaeger, A., Alderman, R., Jaquemet, S., Richard, P., Wanless, R.M., Phillips, R.A., Thompson, D.R., 2013. A comprehensive isotopic investigation of habitat preferences in nonbreeding albatrosses from the Southern Ocean. Ecography 36, 277–286.
Cherel, Y., Phillips, R.A., Hobson, K.A., McGill, R., 2006. Stable isotope evidence of diverse species-specific and individual wintering strategies in seabirds. Biol. Lett. 2, 301–303.
Chouvelon, T., Spitz, J., Caurant, F., Méndez-Fernandez, P., Autier, J., Lassus-Débat, A., Chappuis, A., Bustamante, P., 2012. Enhanced bioaccumulation of mercury in deep-sea fauna from the Bay of Biscay (North-East Atlantic) revealed by stable isotope analysis. Deep-Sea Res. Part I 65, 113–124.
Choy, C.A., Popp, B.N., Kaneko, J.J., Drazen, J.C., 2009. The influence of depth on mercury levels in pelagic fishes and their prey. Proc. Natl. Acad. Sci. 106, 13865–13869.
Cipro, C.V.Z., Cherel, Y., Miramand, P., Caurant, F., Méndez-Fernandez, P., Bustamante, P., 2014. Trace elements in the white-chinned-petrel (*Procellaria aequinoctialis*) from the Kerguelen Islands, Southern Indian Ocean. Polar Biol.. http://dx.doi.org/10.1007/s00300-014-1476-z.
Connan, M., Mayzaud, P., Trouvé, C., Barbraud, C., Cherel, Y., 2008. Interannual dietary changes and demographic consequences in breeding blue petrels from Kerguelen Islands. Mar. Ecol. Prog. Ser. 373, 123–135.
Cossa, D., 2013. Marine biogeochemistry: methylmercury manufacture. Nat. Geosci. 6, 810–811. http://dx.doi.org/10.1038/ngeo1967.
Cossa, D., Heimbürger, L.E., Lannuzel, D., Rintoul, S.R., Butler, E.C.V., Bowie, A.R., Averty, B., Watson, R.J., Remenyi, T., 2011. Mercury in the Southern Ocean. Geochim. Cosmochim. Acta 75, 4037–4052.
Driscoll, C.T., Mason, R.P., Chan, H.M., Jacob, D.J., Pirrone, N., 2013. Mercury as a global pollutant: sources, pathways, and effects. Environ. Sci. Technol. 47, 4967–4983.
Evers, D.C., Burgess, N.M., Champoux, L., Hoskins, B., Major, A., Goodale, W.M., Taylor, R., Poppenga, R., Daigle, T., 2005. Patterns and interpretation of mercury

exposure in freshwater avian communities in northeastern North America. Ecotoxicology 14, 193–221.
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.
Fitzgerald, W.F., Engstrom, D.R., Mason, R.P., Nater, E.A., 1998. The case for atmospheric mercury contamination in remote areas. Environ. Sci. Technol. 32, 1–7.
Fitzgerald, W.F., Lamborg, C.H., Hammerschmidt, C.R., 2007. Marine biogeochemical cycling of mercury. Chem. Rev. Columb. 107, 641–662.
Furness, R.W., Muirhead, S.J., Woodburn, M., 1986. Using bird feathers to measure mercury in the environment: relationships between mercury content and moult. Mar. Pollut. Bull. 17, 27–30.
Gochfeld, M., Gochfeld, D.J., Minton, D., Murray, B.G., Pyle, P., Seto, N., Smith, D., Burger, J., 1999. Metals in feathers of bonin petrel, Christmas shearwater, wedge-tailed shearwater, and red-tailed tropicbird in the Hawaiian Islands, northern Pacific. Environ. Monit. Assess. 59, 343–358.
Goutte, A., Bustamante, P., Barbraud, C., Delord, K., Weimerskirch, H., Chastel, O., 2014. Demographic responses to mercury exposure in two closely-related Antarctic top predators (in press). Ecology. http://dx.doi.org/10.1890/13-1229.1.
Guinet, C., Cherel, Y., Ridoux, V., Jouventin, P., 1996. Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters: changes in relation to consumer biomass 1962–85. Antarct. Sci. 8, 23–30.
Jarman, W.M., Hobson, K.A., Sydeman, W.J., Bacon, C.E., McLaren, E.B., 1996. Influence of trophic position and feeding location on contaminant levels in the Gulf of the Farallones food web revealed by stable isotope analysis. Environ. Sci. Technol. 30, 654–660.
Kojadinovic, J., Bustamante, P., Churlaud, C., Cosson, R.P., Le Corre, M., 2007. Mercury in seabird feathers: insight on dietary habits and evidence for exposure levels in the western Indian Ocean. Sci. Total Environ. 384, 194–204.
Kojadinovic, J., Potier, M., Le Corre, M., Cosson, R.P., Bustamante, P., 2006. Mercury content in commercial pelagic fish and its risk assessment in the Western Indian Ocean. Sci. Total Environ. 366, 688–700.
Lock, J.W., Thompson, D.R., Furness, R.W., Bartle, J.A., 1992. Metal concentrations in seabirds of the New Zealand region. Environ. Pollut. 75, 289–300. http://dx.doi.org/10.1016/0269-7491, 92.90129-X.
Mason, R.P., Choi, A.L., Fitzgerald, W.F., Hammerschmidt, C.R., Lamborg, C.H., Soerensen, A.L., Sunderland, E.M., 2012. Mercury biogeochemical cycling in the ocean and policy implications. Environ. Res. 119, 101–117.
Monteiro, L.R., Furness, R.W., Del Nevo, A.J., 1995. Mercury levels in seabirds from the Azores, mid-north Atlantic Ocean. Arch. Environ. Contam. Toxicol. 28, 304–309.
Monteiro, L.R., Granadeiro, J.P., Furness, R.W., 1998. Relationship between mercury levels and diet in Azores seabirds. Mar. Ecol. Prog. Ser. 166, 259–265.
Morel, F.M.M., Kraepiel, A.M.L., Amyot, M., 1998. The chemical cycle and bioaccumulation of mercury. Annu. Rev. Ecol. Syst., 543–566.
Mougeot, F., Genevois, F., Bretagnolle, V., 1998. Predation on burrowing petrels by the brown skua, *Catharacta skua lönnbergi*. at Mayes Island, Kerguelen. J. Zool. 244, 429–438.
Ochoa-Acuna, H., Sepúlveda, M.S., Gross, T.S., 2002. Mercury in feathers from Chilean birds: influence of location, feeding strategy, and taxonomic affiliation. Mar. Pollut. Bull. 44, 340–345.
Orsi, A.H., Whitworth, T., Nowlin, W.D., 1995. On the meridional extent and fronts of the Antarctic circumpolar current. Deep Sea Res. Part I: Oceanogr. Res. Pap. 42, 641–673.
Park, Y.H., Gamberoni, L., 1997. Cross-frontal exchange of Antarctic intermediate water and Antarctic bottom water in the Crozet Basin. Deep Sea Res. Part II: Top. Stud. Oceanogr. 44, 963–986.
Phillips, R.A., Catry, P., Silk, J.R., Bearhop, S., McGill, R., Afanasyev, V., Strange, I.J., 2007. Movements, winter distribution and activity patterns of Falkland and brown skuas: insights from loggers and isotopes. Mar. Ecol. Prog. Ser. 345, 281–291.
R Core Team, 2012. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Ridoux, V., 1994. The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. Mar. Ornithol. 22, 1–192.
Selin, N.E., 2009. Global biogeochemical cycling of mercury: a review. Annu. Rev. Environ. Resour. 34, 43–63.
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.
Solonen, T., Lodenius, M., 1990. Feathers of birds of prey as indicators of mercury contamination in southern Finland. Ecography 13, 229–237.
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.
Stewart, F.M., Phillips, R.A., Catry, P., Furness, R.W., 1997. Influence of species, age and diet on mercury concentrations in Shetland seabirds. Mar. Ecol. Prog. Ser. 151, 237–244.
Tartu, S., Goutte, A., Bustamante, P., Angelier, F., Moe, B., Clément-Chastel, C., Bech, C., Gabrielsen, G.W., Bustnes, J.O., Chastel, O., 2013. To breed or not to breed: endocrine response to mercury contamination by an Arctic seabird. Biol. Lett. 9, 20130317. http://dx.doi.org/10.1098/rsbl.2013.0317.
Thompson, D.R., Bearhop, S., Speakman, J.R., Furness, R.W., 1998. Feathers as a means of monitoring mercury in seabirds: insights from stable isotope analysis. Environ. Pollut. 101, 193–200.
Thompson, D.R., Furness, R.W., 1989a. Comparison of the levels of total and organic mercury in seabird feathers. Mar. Pollut. Bull. 20, 577–579.
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., 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., 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., 672–684.
Thompson, D.R., Stewart, F.M., Furness, R.W., 1990. Using seabirds to monitor mercury in marine environments: the validity of conversion ratios for tissue comparisons. Mar. Pollut. Bull. 21, 339–342.
UNEP, 2013. Global Mercury Assessment 2013: Sources, Emissions, Releases and Environmental Transport. UNEP Chemicals Branch, Geneva, Switzerland.
Warham, J., 1990. The Petrels: Their Ecology & Breeding Systems. Academic Press, London.
Weimerskirch, H., Zotier, R., Jouventin, P., 1989. The avifauna of the Kerguelen Islands. Emu 89, 15–29.
Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. http://dx.doi.org/10.1111/j.2041-210X.2009.00001.x.