Environmental Pollution 216 (2016) 253–263

Contents lists available at ScienceDirect

Environmental Pollution

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

Feather mercury concentrations in Southern Ocean seabirds: Variation by species, site and time[☆]

Peter H. Becker [a, *], Vassilis Goutner [b], Peter G. Ryan [c], Jacob González-Solís [d]

[a] Institute of Avian Research “Vogelwarte Helgoland”, An der Vogelwarte 21, D 26386, Wilhelmshaven, Germany
[b] Department of Zoology, School of Biology, Aristotle University of Thessaloniki, GR-541 24, Thessaloniki, Greece
[c] Percy FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town, Rondebosch, 7701, South Africa
[d] Departament de Biologia Animal, Av Diagonal 643, 08028, Barcelona, Spain

ARTICLE INFO

Article history:
Received 21 January 2016
Received in revised form
19 May 2016
Accepted 23 May 2016

Keywords:
Polar front
Trophic level
Diet
25 marine bird species
Hg monitoring

ABSTRACT

We studied mercury contamination in 25 seabird species breeding along a latitudinal gradient across the Southern Ocean, from Gough Island (40°S) through Marion Island (47°S) to Byers Peninsula (63°S). Total mercury concentrations in body feather samples of adults caught at breeding colonies from 2008 to 2011 were determined. Krill (*Euphausia* spp.) and other zooplankton consumers had low mercury concentrations (gentoo penguin *Pygoscelis papua*, chinstrap penguin *Pseudomonas Antarctica*, common diving petrel *Pelecanoides urinatrix*, broad-billed prion *Pachyptila vittata*; mean levels 308–753 ng g^{-1}), whereas seabirds consuming squid or carrion had high mercury concentrations (ascending order: Kerguelen petrel *Aphrodroma brevirostris*, southern giant petrel *Macronectes giganteus*, soft-plumaged petrel *Pterodroma mollis*, sooty albatross *Phoebetria fusca*, Atlantic petrel *Pterodroma incerta*, northern giant petrel *Macronectes halli*, great-winged petrel *Pterodroma macroptera*; 10,720–28038 ng g^{-1}). The two species with the highest mercury concentrations, northern giant petrels and great-winged petrels, bred at Marion Island. Among species investigated at multiple sites, southern giant petrels had higher mercury levels at Marion than at Gough Island and Byers Peninsula. Mercury levels among Byers Peninsula seabirds were low, in two species even lower than levels measured 10 years before at Bird Island, South Georgia. Replicate measurements after about 25 years at Gough Island showed much higher mercury levels in feathers of sooty albatrosses (by 187%), soft-plumaged petrels (53%) and Atlantic petrels (49%). Concentrations similar to the past were detected in southern giant petrels at Gough and Marion islands, and in northern giant petrels at Marion. There were no clear indications that timing of moult or migratory behavior affected mercury contamination patterns among species. Causes of inter-site or temporal differences in mercury contamination could not be verified due to a lack of long-term data related to species' diet and trophic levels, which should be collected in future together with data on mercury contamination.

1. Introduction

In our changing world where human activities expand to the most remote places of the earth, environmental pollution is an increasing hazard. Within the wide spectrum of toxic substances both natural and artificial, mercury (Hg), a non-essential metal, is of particular concern (UNEP, 2013). Some Hg derives from natural sources, linked to volcanic and geothermal activities, and it is widely distributed due to its ability to remain in a gaseous form and be carried with air masses (Ebinghaus et al., 2002; Fitzgerald and Lamborg, 2003). Human activities, such as coal burning, have increased the amount of mercury cycling among land, atmosphere and ocean by a factor of three to five, despite some areas of uncertainty in the global biogeochemical cycle of mercury still remain (Selin, 2009). Global emissions of mercury decreased from 1990 to 2007 in Europe and North America but increased in Asia to 56% of all anthropogenic emissions (Fitzgerald and Lamborg, 2003; Driscoll et al., 2013). Mercury dynamics involve transport and

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[☆] This paper has been recommended for acceptance by W. Wen-Xiong.

[*] Corresponding author.

E-mail addresses: peter.becker@ifv-vogelwarte.de (P.H. Becker), vgoutner@bio.auth.gr (V. Goutner), pryan31@gmail.com (P.G. Ryan), jgsolis@ub.edu (J. González-Solís).

http://dx.doi.org/10.1016/j.envpol.2016.05.061

deposition as principal pathways for Hg to oceanic surface waters. This highly dynamic process through air-sea exchange plays a role in the redistribution of Hg across the Earth's surface (Lamborg et al., 1999). In this respect, emitted Hg may be deposited anywhere in its hemisphere of origin, but also transported between hemispheres, although in a less efficient manner (Driscoll et al., 2013). Though inputs in the Northern Hemisphere have declined in recent decades (Mason et al., 2012; Burgess et al., 2013; Driscoll et al., 2013), most industrial activity still occurs in northern regions (UNEP, 2013), and therefore concentrations are generally lower in the Southern Hemisphere (by 30% in the air, Driscoll et al., 2013). Anyway, the high summer concentrations of Hg in South Polar air and biota raises the concern that Antarctica may become an important sink in the global Hg cycle, especially in view of possible changes in sea ice coverage and increasing anthropogenic emissions of Hg in the Southern Hemisphere (Bargagli, 2008). Further, once in water, Hg is both methylated leading to methylmercury (CH_3Hg) which is highly toxic to biota (Driscoll et al., 2013; UNEP, 2013) or demethylated by UV light (in the euphotic area; Blum et al., 2014). Methylated Hg is ubiquitous in the open ocean (Mason and Sullivan, 1999; Lamborg et al., 2014); concentrations are biomagnified through the food web, reaching levels in marine top predators several orders of magnitude higher than those in the water.

In this regard, seabirds are excellent bioindicators to monitor Hg in marine ecosystems because their high trophic positions in marine food webs reflect the hazards of Hg to marine ecosystems and humans better than abiotic samples (e.g. Burger, 1993; Furness, 1993; ICES, 1999; Becker and Dittmann, 2009; Dittmann et al., 2012; Helgason et al., 2008; Braune et al., 2014). Hg is toxic, influencing endocrine-related mechanisms including accumulation and specific cytotoxicity in endocrine tissues, and interactions with sex hormones affecting enzymes within the steroidogenesis pathway (Tan et al., 2009). Sublethal effects of Hg on birds include adverse impacts on blood and tissue chemistry, metabolism, growth, development, reproduction and behavior (Eisler, 1987; Boening, 2000). To correctly interpret their levels, however, we need to understand both the main uptake and excretion pathways of Hg in birds. As a decontamination procedure, Hg from prey is either inactivated in the liver or is excreted into feathers during moult (Muirhead and Furness, 1988; Kim et al., 1996) or into eggs (e.g. Lewis et al., 1993). The chemical form of Hg in seabird feathers is almost entirely methylmercury (Braune and Gaskin, 1987; Thompson and Furness, 1989). Given their non-destructive collection, feathers have been widely used as an effective index of seabird contamination with Hg (e.g. Lock et al., 1992; Thompson et al., 1992, 1993; Burger and Gochfeld, 2000a, 2000b; Becker et al., 2002; Kojadinovic et al., 2007; Elliott and Elliott, 2013; Carravieri et al., 2014b).

The uptake of Hg in seabirds is dependent on a variety of factors, including diet (Monteiro et al., 1998; Burger and Gochfeld, 2000a,b; Becker et al., 2002; Bocher et al., 2003; Kojadinovic et al., 2007; Anderson et al., 2009), prey size (Croxall and Prince, 1980; Xavier and Croxall, 2007), habitat use and seasonal movements (Kojadinovic et al., 2007; Anderson et al., 2009; Hipfner et al., 2011; Tavares et al., 2013; Carravieri et al., 2014a), species-specific life-history traits such as longevity and gender (Becker et al., 2002; Tavares et al., 2013; Carravieri et al., 2014a), behavioural and physiological traits such as constraints on the elimination of mercury from the body due to slow moult patterns and duration (Muirhead and Furness, 1988; Stewart et al., 1999; Tavares et al., 2013), and differences in Hg detoxification (Muirhead and Furness, 1988; Bocher et al., 2003). Furthermore, Hg levels in feathers formed during the non-breeding season appear to be more strongly governed by species effects (such as moult schedule) than by trophic relationships across taxa (Anderson et al., 2009).

Although atmospheric deposition, the main source of inorganic mercury to open ocean systems, occurs in all ocean basins, inputs of anthropogenic mercury into the ocean are spatially variable (Mason et al., 2012), leading to the need to understand spatial variability of Hg in marine biota. In the Southern Ocean, feathers or blood have been used to monitor Hg levels in seabird communities such as those at South Georgia (Becker et al., 2002; Anderson et al., 2009; Tavares et al., 2013) and other areas (Blévin et al., 2013; Carravieri et al., 2014b; Goutte et al., 2014a,b), but spatial coverage of Southern Ocean and surrounding marine areas' Hg contamination in seabirds is generally poor. Moreover, we need to assess temporal trends in Hg, since biological exposure in the upper ocean may respond slowly to atmospheric deposition, and bioaccumulation into oceanic food chains may take years to decades (Mason et al., 2012). In the 1980s, high Hg concentrations recorded in some Southern Ocean albatrosses and petrels were attributed to their scavenging behavior and physiological peculiarities related to Hg excretion, but it was suggested to ultimately derive from naturally high "background" Hg concentrations within Southern Ocean food chains (Thompson et al., 1993; Anderson et al., 2009). In the 1990s, Becker et al. (2002) reported elevated Hg concentrations in a seabird community breeding at South Georgia. They hypothesised that this could result from on-going Hg pollution by industrial and agricultural emissions originating mainly from the Northern Hemisphere. However, no consistent results on temporal changes have been produced for Antarctic seabirds, so these hypotheses need further evaluation.

In this paper we provide comprehensive recent data and review existing literature on Hg concentrations in feathers of 25 seabird species sampled across a large-scale (5900 km) longitudinal gradient in three very different marine regions, the Southern Ocean, the temperate South Atlantic Ocean and the sub-Antarctic Indian Ocean. Our main purpose is to (1) interpret Hg contamination patterns among the species in relation to trophic position and diets, (2) expand current geographic coverage to understand spatial differences in Hg levels in seabirds, and (3) investigate temporal changes after 25 years in Hg concentrations in some of these seabird species.

2. Materials and methods

2.1. Study areas

Byers Peninsula (62°38′S, 61°50′W) is an Antarctic Specially Protected Area (ASPA No. 126) situated on Livingston Island in South Shetlands, about 500 km south of the Antarctic Convergence (Fig. 1). Byers Peninsula has been one of the largest ice-free areas in the Antarctic Peninsula over at least the last 3000 years (Björck et al., 1991), which allows a relatively large number of seabirds to breed there compared to other Antarctic localities. Gil-Delgado et al. (2013) estimated populations of 2793 southern giant petrels *Macronectes giganteus*, 3746 Antarctic terns *Sterna vittata*, 1884 kelp gulls *Larus dominicanus*, 60–91 sub-Antarctic skuas *Stercorarius antarcticus*, 4200 pairs of gentoo penguin *Pygoscelis papua* and 50 pairs of chinstrap penguin *Pseudomonas antarctica*.

Sub-Antarctic Marion Island (46°54′S, 37°44′E), the larger of the two Prince Edward Islands (Fig. 1), lies between the Subtropical Convergence and the Antarctic Convergence (300 km north). It is downstream from the Indian Ocean Ridge, which creates a diverse range of oceanographic habitats resulting in some of the most productive marine regions of Earth. The Prince Edward Islands are home to 28 breeding species of seabirds, several of which are listed as threatened (Ryan et al., 2009; Taylor et al., 2011). Marion Island alone supports some 0.8–1.0 million pairs of seabirds (Ryan and

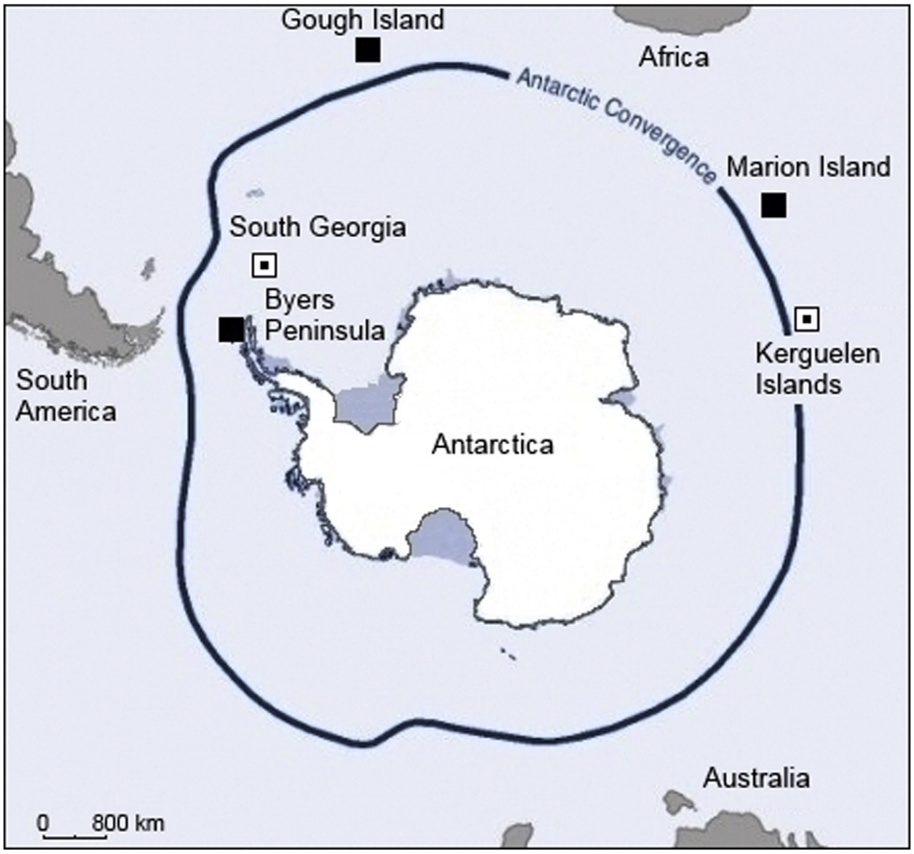

Fig. 1. Locations of the three breeding islands where seabirds were sampled (black squares): Byers Peninsula (2008–2009), Gough Island (2009) and Marion Island (2011). Data from Antarctic Peninsula (Brasso et al., 2014), Bird Island, South Georgia (Becker et al., 2002; Anderson et al., 2009), and from Kerguelen Islands (Carravieri et al., 2014b) are available for comparison (white squares; Table 1).

Bester, 2008). Considerable scientific research has been carried out in this region (Woehler et al., 2001; Chown and Froneman, 2008).

Gough Island (40°20′S, 9°55′W) lies 380 km SSW of the Tristan da Cunha archipelago in the central South Atlantic Ocean. It is located 670 km north of the Antarctic Convergence (= Polar Front) and close to the Sub-Antarctic Convergence (Fig. 1). It is a nature reserve and a UNESCO World Heritage Site of international importance for breeding seabirds. It holds many endemic plants, invertebrates and a rich avifauna including 22 species of seabirds with a total population probably in the order of 4–6 million pairs (Richardson, 1984; Muirhead and Furness, 1988; Cuthbert and Sommer, 2004; Ryan, 2007; Ryan et al., 2014, 2015; Robertson et al., 2016).

For convenience “Southern Ocean” is used as superordinate term of the oceans in focus, the Southern Ocean, the temperate South Atlantic Ocean and the sub-Antarctic Indian Ocean.

2.2. Feather sampling

Mercury concentrations were investigated in breast feathers of 25 species of seabirds collected during field visits to these three Southern Oceanic islands. Adults were caught at their breeding colonies: at Byers Island from 22 December 2008 to 6 January in 2009; at Gough Island from 12 September to 1 October 2009, and at Marion Island from 15 April to 5 May in 2011, during the pre-breeding, breeding and post-breeding period, respectively. The species sampled (Table 1, with sample size per species and site) included penguins (Sphenisciformes), albatrosses, shearwaters, prions, petrels (Procellariiformes) and skuas (Stercorariidae). A range of 5–15 breast feathers per individual were taken, stored in Hg-free polyethylene bags at room temperature. Averaging the Hg content of several body feathers has been used to integrate Hg concentrations over the year (Furness et al., 1986; Becker et al., 2002), which is important in species with asynchronous moult and representative of the individual bird (Carravieri et al., 2014c).

2.3. Feather Hg analysis

Feather samples were analysed by the Institute of Avian Research in the laboratory of ICBM-Terramare in Wilhelmshaven, Germany. Prior to analysis all samples were washed for 15 min in ultrasonic baths of bi-distilled water and then for 15 min in acetone (pro-analysis grade), repeated three times, and then were dried in a fume cupboard. Hg measurements were made with a DMA-80 Direct Mercury Analyser by MLS GmbH. This allows rapid sample analysis without chemical preparation and no waste disposal. Each sample of 2–3 feathers was weighed, wrapped in Hg-free aluminium foil and introduced into the analyser's sample boat. The sample is dried and burned at 750 °C in oxygen, which decomposes Hg compounds, releasing elementary Hg. Hg vapours are collected on a gold amalgamation trap and subsequently desorbed for quantification. Hg content is determined using atomic absorption spectrometry at 254 nm.

All samples were analysed in duplicate. For each series of 20 samples, a reference measurement was made. The certified reference material (CRM) was bought at NRC-CNRC, Canada, and was DORM2 (dog fish muscle CRM for trace metals, 4640 ng g^{-1}) and DORM3 (fish protein CRM for trace metals, 409 ng g^{-1}). Blanks with empty sample boats and empty packets of foil were used in every batch of 20 samples, and a batch was assessed only if blanks with

Table 1

Mercury concentrations (ng g^{-1} dw; mean ± SD, (n), range) in feathers of seabird species from this (in bold) and other studies in the Southern Ocean. Species' names according to birdlife.org. Historical data or studies from other sites are shown for comparison, 1) Becker et al. (2002); 2) Anderson et al. (2009); 3) Thompson et al. (1993); 4) Carravieri et al. (2014a,b,c); 5) − 7) Brasso et al. (2014), King George Island, 2006–2011: 5) 420 ± 410 (89); 6) 340 ± 130 (98); 7) 630 ± 240 (89); *) Species not included in statistical comparisons because of sample size < 4.

Scientific name	Common name	Abbrev.	South Georgia		Byers Peninsula	Gough Island		Marion Island		Kerguelen
			1998 1)	2001/02 2)	2008/09	1985 3)	2009	1986 3)	2011	2003 − 2011 4)
Aptenodytes patagonicus	King penguin	KP							**2998** ± **707** (**10**) 2229–4647	2220 ± 590 (12) 1450–3210
Pygoscelis papua	Gentoo penguin	GP	948 ± 848 (14) 169–3061		**308** ± **143** (**10**) 5) 110–634					5850 ± 3000 (12) 1280–9430
Pygoscelis adeliae *)	Adélie penguin	ADP			**278** ± **252** (**2**) 6) 100–456					
Pygoscelis antarcticus	Chinstrap penguin	CP			**402** ± **227** (**10**) 7) 196–846					
Eudyptes chrysocome	Southern rockhopper penguin	SRP							**1804** ± **676** (**10**) 929–2574	1960 ± 410 (12) 1220–2620
Eudyptes moseleyi	Northern rockhopper penguin	NRP					**2339** ± **472** (**20**) 1412–3369			
Eudyptes chrysolophus	Macaroni penguin	MP	3420 ± 732 (20) 2084–4940						**3251** ± **640** (**10**) 2386–4597	2240 ± 290 (12) 1870–2750
Phoebetria fusca	Sooty albatross	SA				6160 ± 4230 (32) 1420–16,130	**17,687** ± **3637** (**5**) 13,716–22,997			
Thalassarche chlororhynchos	Atlantic yellow-nosed-albatross	AYA					**4224** ± **1681** (**10**) 2270–7971			
Macronectes giganteus	Southern giant petrel	SGP	7774 ± 3571 (29) 2389–16,626	8250 ± 3980 (16) 2150–14,080	**4801** ± **1885** (**20**) 2063–9058	11,900 ± 6150 (8) 3740–23,440	**7290** ± **3444** (**9**) 2640–13,492	11,380 ± 6400 (30) 1830–27,610	**13,145** ± **7153** (**14**) 4890–33,195	
Macronectes halli	Northern giant petrel	NGP	4988 ± 3762 (37) 406–17,416	10,520 ± 5540 (15) 4500–23,540				19,620 ± 13,270 (30) 7560–56,530	**27147** ± **16,103** (**16**) ((**16**) 4644–54,578	16,260 ± 7270 (18) 7990–32,110
Pterodroma incerta	Atlantic petrel	AP				13,520 ± 4140 (15) 3920–20,090	**20,118** ± **5006** (**10**) 12,658–27,757			
Halobaena caerulea	Blue petrel	BP	3098 ± 143 (3) 2958–3244	2690 ± 1290 (5) 1940–4990					**4619** ± **4108** (**9**) 895–11,050	1050 ± 720 (25) 430–33,320
Pachyptila vittata	Broad-billed prion	BBP					**753** ± **624** (**10**) 305–2258			
Aphrodroma brevirostris *)	Kerguelen petrel	KPT							**10,720** ± **7198** (**3**) 2444–15,526	2270 ± 2110 (24) 620–10,890
Pterodroma mollis	Soft-plumaged petrel	SPP				9820 ± 2320 (17) 5360–13,400	**15,063** ± **3512** (**10**) 9180–19,983		**7202** ± **4977** (**5**) 1715–11,546	12,210 ± 4230 (19) 4670–25,480
Pterodroma macroptera	Great-winged petrel	GWP							**28,038** ± **9984** (**5**) 16,617–39,150	15,820 ± 4440 (14) 9760–27,130
Procellaria aequinoctialis *)	White-chinned petrel	WCP	3790 ± 1717 (10)	7430 ± 1970 (16)					**1963** (**1**)	5540 ± 2240 (14)

			2053–8070	4350–11,390				2820–9380
Ardenna gravis	Great shearwater	GS				**3119 ± 947 (20)**		
						1428–5093		
Puffinus elegans$^{*)}$	Sub-Antarctic shearwater	LS				**1619 (1)**		
Oceanites oceanicus	Wilson's storm petrel	WSP			**2875 ± 827 (8)**			420 ± 130 (12)
					1772–4344			270–680
Garrodia nereis$^{*)}$	Grey-backed Storm petrel	GBSP				**1975 ± 2066 (2)**	**543 (1)**	510 ± 440 (23)
						514–3436		220–2390
Pelagodroma marina	White-faced storm petrel	WFP				**1409 ± 438 (10)**		
						1009–2166		
Pelecanoides urinatrix	Common diving petrel	CDP	594 ± 150 (2)	2900 ± 1630 (15)		**580 ± 188 (10)**		1060 ± 540 (29)
			488–700	620–5460		340–874		350–2430
Stercorarius antarctica	Sub-Antarctic skua	BS			**2179 ± 1125 (11)**	**4488 ± 1914 (10)**	**6475 ± 5870 (14)**	2650 ± 2870 (26)
					785–3933	2454–8553	607–17,738	390–13,380

empty sample boats and empty packets of foil were in the range of detection limit (see below). The analytical performance of this method has also been evaluated by analysis of CRM (measured values and analytical variance for DORM2 were 4385 ± 567 ng g^{-1} ($N = 10$ replicates), coefficient of variance (CV) = 10.5%, recovery rate 94.5%, and for DORM3 414 ± 43 ng g^{-1}, $CV = 12.9\%$, recovery rate = 101.2%), and has been proposed as a ready-to-use analytical method to rapidly analyse a large number of samples (Roy and Bose, 2008; Maggi et al., 2009). The detection limit was 0.003 ng total Hg and concentrations are given in ng g^{-1} dry mass.

The correlation of Hg concentrations in the two sample series analysed was high ($r = 0.949$, $n = 245$, $p < 0.001$), as was the repeatability (0.949 ± 0.100 SD), and therefore the average of the duplicate measurement was used for further analysis.

2.4. *Information on species' diet, migration and moult*

We related mercury residues in seabirds to their diets, migration and moulting patterns (Table S2). The information was generalized per species (Fig. 2), based on the relevant literature (listed in the Supplementary Material).

2.5. *Statistical procedures*

Results are presented as mean Hg values ± 1 standard deviation, minimum and maximum per species and site, in ng Hg g^{-1} dw, if not otherwise mentioned; in the Figures Hg values are presented in µg Hg g^{-1} dw. For statistical analyses Hg values were log transformed, and only species with $N \geq 4$ individuals per site were included in statistical tests (cf. Table 1). Significance of effects of species, site and their interaction on Hg concentrations were tested by GLM, supplemented by post-hoc comparisons and derived homogenous sub-groups ($p > 0.05$) using the conservative, robust Scheffé test suitable for groups with unequal sample sizes. For species lacking homogeneity of variance the Tamhane T_2 test was used in addition (see Supplementary Material, Table S1). Southern rockhopper penguins *Eudyptes chrysocome* and northern rockhopper penguins *Eudyptes moseleyi* were included as one species in the GLM. Student t-tests were used to compare between two groups (year, sites). All tests were performed with SPSS 22, IBM, were two-tailed, and the level of significance was set at $p < 0.05$.

3. Results

3.1. *Interspecific and inter-site variation of feather mercury levels*

Hg feather concentrations of 25 seabird species studied from 2008 to 2011 (Table 1) differed strongly among species and the three sampling sites (19 species included in the GLM-model based on log10 Hg values, $n = 275$, corrected R^2 model = 0.827; species, $F = 57.6$, $df = 18$, $p < 0.001$; site, $F = 16.9$, $df = 2$, $p < 0.001$). Interaction between species and site was significant ($F = 5.1$, $df = 4$, $p < 0.001$; see 3.3.). The three sites represented distinct and homogenous subgroups, respectively (Scheffé-test). Overall, seabirds sampled at Marion Island had the highest Hg concentrations in their feathers, Gough Island birds were intermediate, and those at Byers Peninsula had the lowest Hg levels (Table 1, Fig. 2). However, these patterns were influenced by the composition of the species' group sampled at each site.

Three distinct species groups emerged from the analysis of homogenous subgroups (cf. Fig. 2; Scheffé-test, confirmed by Tamhane T_2 test, Table S1), corresponding to low (L), intermediate (I) and high (H) Hg concentrations. The group L with the lowest feather concentrations (Hg ranging from 278 to 753 ng g^{-1}) included Adélie *Pygoscelis adeliae* (not in test), gentoo and

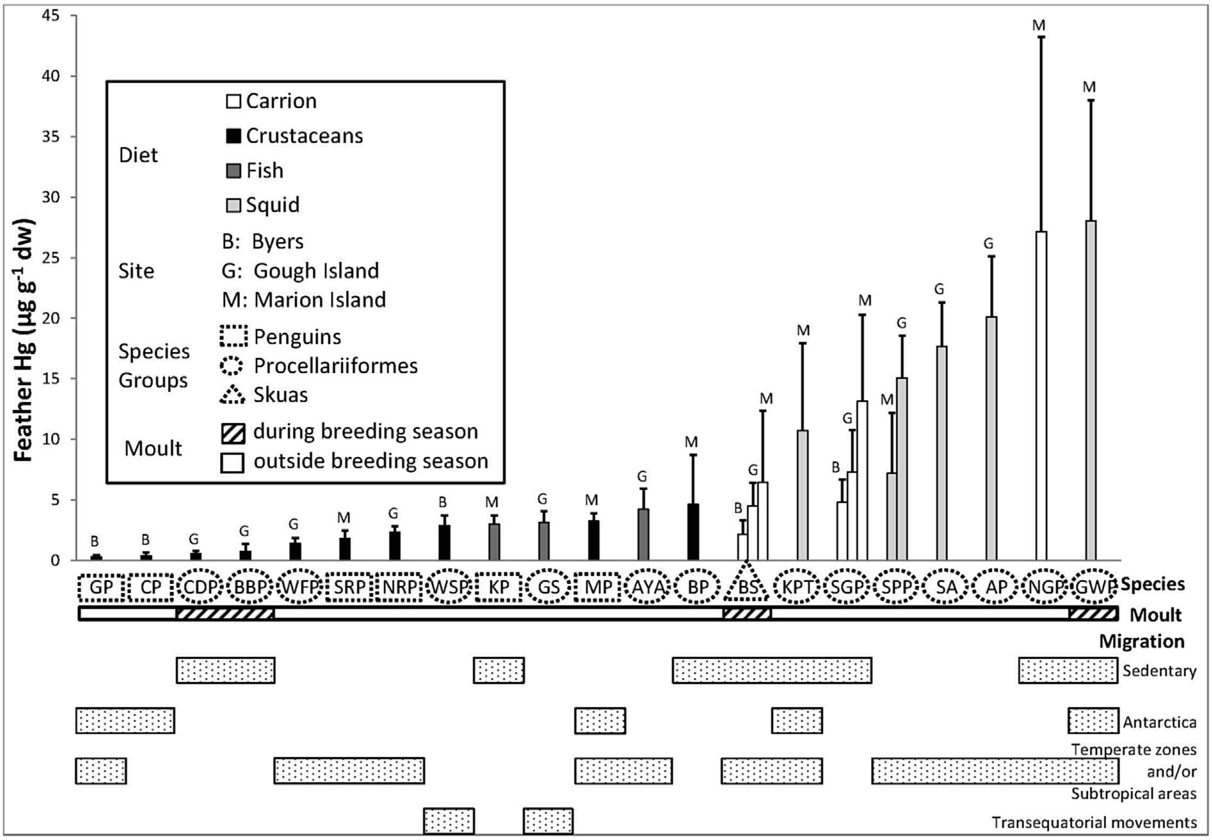

Fig. 2. Body feather mercury concentrations (mean ± 1 SD, n ≥ 3 per site, µg g^{-1} dw) in 21 species from Byers Peninsula (B), Gough Island (G) and Marion Island (M) (cf. Fig. 1). See Table 1 for scientific names, sample size and further species with n < 3. The species are ranked according to their mercury level. Species groups are indicated by different frame forms. Species abbreviations: gentoo penguin (GP), chinstrap penguin (CP), common diving petrel (CDP), broad-billed prion (BBP), white-faced storm petrel (WFP), southern rockhopper penguin (SRP), northern rockhopper penguin (NRP), Wilson's storm petrel (WSP), king penguin (KP), great shearwater (GS), macaroni penguin (MP), Atlantic yellow-nosed albatross (AYA), blue petrel (BP), sub-Antarctic skua (BS), Kerguelen petrel (KPT), southern giant petrel (SGP), soft-plumaged petrel (SPP), sooty albatross (SA), Atlantic petrel (AP), northern giant petrel (NGP), great-winged petrel (GWP). Further, generalized information is given to diet (cf. Table S2), moulting season as well as migration habits and areas (references see Supplementary Material).

chinstrap penguins from Byers Peninsula, and common diving-petrels *Pelecanoides urinatrix* and broad-billed prions *Pachyptila vittata* from Gough Island (listed with increasing Hg means).

Species in group I with intermediate Hg concentrations (1409–4557 ng g^{-1}) included white-faced storm-petrels *Pelagodroma marina* (Gough Island), southern rockhopper penguins (Marion Island), northern rockhopper penguins (Gough Island), Wilson's storm-petrels *Oceanites oceanicus* (Byers Peninsula), king penguins *Aptenodytes patagonicus* (Marion), great shearwaters *Ardenna gravis* (Gough Island), blue petrels *Halobaena caerulea* (Marion Island), macaroni penguins *Eudyptes chrysolophus* (Marion Island), Atlantic yellow-nosed albatrosses *Thalassarche chlororhynchos* (Gough Island) and sub-Antarctic skuas *Stercorarius antarcticus* (Byers Peninsula, Marion Island and Gough Island). Also sub-Antarctic shearwaters *Puffinus elegans* (not in test) belong to group I, and grey-backed storm petrels *Garrodia nereis* (not in test) fell between group L and I.

Southern giant petrels link the groups I and H, varying according to sampling site (Byers Peninsula 4801 ng g^{-1}, Gough Island 7290 ng g^{-1}, Marion Island 13,145 ng g^{-1}; mean 8039 ng g^{-1}; Fig. 2, Table S1). The group H with the highest Hg overall mean concentrations (10,720–28,038 ng g^{-1}) includes Kerguelen petrels *Aphrodroma brevirostris* (Marion island, not in test), soft-plumaged petrels *Pterodroma mollis* (Gough Island, Marion Island), sooty albatrosses *Phoebetria fusca* (Gough Island), Atlantic petrels *Pterodroma incerta* (Gough island), northern giant petrels *Macronectes halli* (Marion Island), and great-winged petrels *Pterodroma macroptera* (Marion Island).

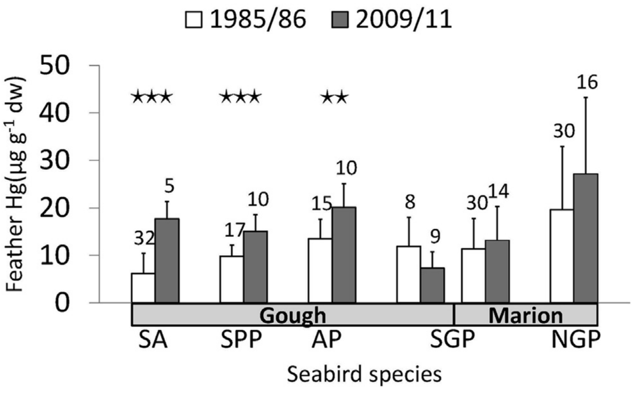

Fig. 3. Mercury levels (mean ± SD, µg g^{-1} dw) in body feathers of seabird species sampled at Gough Island and Marion Island in 2009/2011 (this paper, cf. Table 1) compared with 1985/1986 (Thompson et al., 1993); sooty albatross (SA), soft-plumaged petrel (SPP), Atlantic petrel (AP), southern giant petrel (SGP, sampled at both sites) and northern giant petrel (NGP). Sample size is given above the columns. Significance of temporal differences is indicated by $^{**}p < 0.01$; $^{***}p < 0.001$; *t*-test (see text for details).

The three species' groups showed associations with their generalized diet composition (Fig. 2, Table S2). Crustaceans dominate the diet in the species with low Hg feather levels. Crustaceans or fish are the main food of species with intermediate Hg levels, and squid or carrion characterize the diet of species with the highest Hg feather levels. Moulting periods within or outside the breeding season or migration patterns, however, showed no obvious relationships to the seabirds' Hg contamination patterns.

3.2. *Temporal differences at Gough Island and Marion Island*

Compared to the mid-1980s (Thompson et al., 1993), Atlantic petrels, soft-plumaged petrels and sooty albatrosses from Gough Island all had significantly higher feather Hg concentrations in 2009. The increases were by a factor 1.15 to 2.87 (Fig. 3, Table 1). No significant differences were detected in either southern or northern giant petrels on Marion Island compared to 1986 (Thompson et al., 1993) nor in southern giant petrels on Gough Island between 1985 and 2009.

3.3. *Inter-site variation within species*

In southern giant petrels, which were sampled at all three locations, Hg feather concentrations were greatest on Marion Island, intermediate on Gough Island and lowest on Byers Peninsula ($F = 19.9$, $df = 2$, $p < 0.001$; Byers/Gough $p < 0.106$, Byers/Marion $p < 0.001$, Gough/Marion $p < 0.013$; Fig. 2, Table 1). Sub-Antarctic skua Hg concentrations did not differ significantly among the three areas ($F = 2.9$, $df = 2$, $p = 0.069$). Among the species pair of rockhopper penguins, Hg concentrations were significantly greater in northern rockhopper penguins from Gough Island than in southern rockhopper penguins from Marion Island, although the difference was small ($t = 2.264$, $df = 11.3$, $p = 0.044$). Among soft-plumaged petrels, Hg concentrations were similar between Gough Island and Marion Island ($t = 2.281$, $df = 4.26$, $p = 0.081$).

Material was not available for all species for inter-site comparisons but high Hg concentrations in most petrel species investigated were detected on Marion Island (Table 1, Fig. 2): In six of eight petrel species, Hg concentrations exceeded 4500 ng g^{-1} (peaking in great-winged petrel and northern giant petrel). On Gough Island, Hg concentrations in soft-plumaged petrels, Atlantic petrels and southern giant petrels were >7200 ng g^{-1}, whereas the remaining six petrel species sampled had Hg concentrations <3200 ng g^{-1}.

4. Discussion

Our investigation sampled 25 seabird species, measured and reviewed their Hg contamination across a 2500 km latitudinal gradient and a 5900 km longitudinal gradient (Fig. 1, from Byers Peninsula to Kerguelen Island) and identified differences in mercury contamination among species, sites (Marion > Gough > Byers Peninsula; most obvious for southern giant petrels) and decades. Comparisons with the findings of other large-scale studies (Thompson et al., 1993; Becker et al., 2002; Anderson et al., 2009; Carravieri et al., 2014b; Brasso et al., 2015) generally indicate greater Hg levels in feathers from the same island than found in previous years. Although the lack of continuous monitoring prevents a small-scale assessment of temporal trends in Hg contamination, all pairwise comparisons between samplings about two decades apart available for several species and localities either showed no significant differences or rather substantial increases in Hg levels in Southern Ocean seabirds (3.3.). Increasing Hg levels could just be caused by a rise of seabirds' trophic level (Burgess et al., 2013; Braune et al., 2014). However, several studies in the Southern Ocean are generally showing that seabirds' trophic level did not change or even declined over the last decades, possibly due to the removal of fur seal and whales, the depletion of fish by industrial fishing or the decrease in productivity linked to increasing temperatures (e.g. Emslie and Patterson, 2007; Ainley and Blight, 2009; Jaeger and Cherel, 2011; Emslie et al., 2013; Huang et al., 2013; Bond and Lavers, 2014). Therefore, an increase in the environmental contamination with mercury is the most likely explanation for the increase in Hg levels in Southern Ocean seabirds.

In all species investigated there was a striking inter-individual variability in feather Hg levels: even within populations sampled at a specific site and breeding season, Hg concentrations typically span an order of magnitude or more (Table 1). Extreme examples are gentoo penguin (South Georgia, 1998; Becker et al., 2002), broad-billed prion (Gough Island), blue petrel (Marion Island), Kerguelen petrel, grey-backed storm petrel (Kerguelen, Carravieri et al., 2014b) and sub-Antarctic skua (Marion Island, Kerguelen, Carravieri et al., 2014b, Table 1), with coefficients of variation of up to 100%. Such huge variation in Hg levels among individuals also

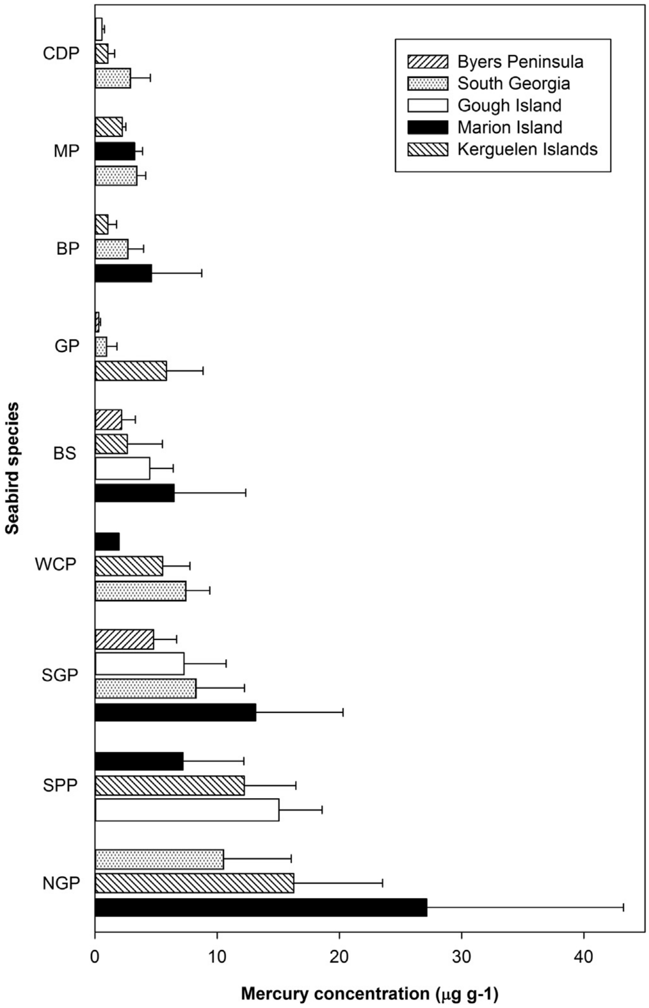

Fig. 4. Inter-site variation of Hg feather levels (mean ± SD, µg g^{-1} dw) in nine seabird species studied at multiple sites (3–4) in Southern Ocean Islands (Fig. 1). This paper: Byers Peninsula, Gough Island, Marion Island; published information: Bird Island, South Georgia, Becker et al., 2002, Anderson et al., 2009; Kerguelen Islands, Carravieri et al., 2014b); see Table 1 for sample size and range. The species and the nested sites are ranked according to their mercury level (from top with low to bottom with high mercury level, respectively), and the sites are marked by different hatching. Most data originate from the decade 2001–2011 (cf. Table 1). Species abbreviations: Common diving petrel (CDP), macaroni penguin (MP), blue petrel (BP), gentoo penguin (GP), sub-Antarctic skua (BS), white-chinned petrel (WCP), southern giant petrel (SGP), soft-plumaged petrel (SPP), northern giant petrel (NGP).

reflects the high variety of dietary specializations, moulting strategies, migration patterns and geographical range of the seabirds included in this study.

4.1. Hg content in seabird feathers in relation to diet

The most important factor determining mercury levels in Southern Ocean seabirds is their diet and trophic position, regardless of locality or period (Fig. 2, Table S2). Seabird species ranked with the lowest feather Hg concentrations all feed predominantly on crustaceans (Table S2; for penguins see also Croxall and Lishman, 1987; Brasso et al., 2014, 2015), which show low levels of mercury concentrations (Anderson et al., 2009). Thus, we expected low Hg concentrations in feathers of seabirds feeding mainly on crustaceans compared to those feeding at higher trophic levels by taking higher proportions of fish and/or squid, birds and mammals, as previously reported in several studies (Stewart et al., 1999; Becker et al., 2002; Bocher et al., 2003). Some species display more variability in their dietary composition than others, such as gentoo penguins (Carravieri et al., 2013), which is reflected in higher variation of Hg levels among populations (see below, and Fig. 4).

The diets of species with intermediate feather Hg concentrations are more varied (Fig. 2, Table S2). Blue petrels, Wilson's storm petrels, macaroni and both rockhopper penguin species feed extensively on crustaceans, but also take some fish and squid. White-faced storm petrels and Atlantic yellow-nosed albatross are primarily piscivorous, although they also take some squid and crustaceans, whereas king penguins and great shearwaters have a mixed diet of fish and cephalopods. Sub-Antarctic skuas are important predators on birds while breeding, feeding mainly on burrowing petrels or penguins. However, during the non-breeding period when their feathers are moulted they disperse widely at sea where they eat a diverse diet (Mougeot et al., 1998; Reinhardt et al., 2000). The lowest Hg concentrations in skuas breeding at Byers Peninsula probably reflect the short food chain in the Antarctic ecosystem and the resultant high proportion of crustacean-feeding birds on which the skuas prey (Becker et al., 2002). The lack of a statistically significant difference among skuas from different areas probably is due to the small sample sizes and the wide range of concentrations measured within each area (Table 1).

Among seabirds with the highest feather Hg concentrations, Kerguelen petrels (Marion Island), Atlantic petrels and sooty albatrosses (both Gough Island) are primarily squid feeders, whereas the albatrosses also eat small seabirds and carrion. Breeding wandering albatrosses *Diomedea exulans* also exhibited high feather Hg concentrations at Possession Island in the Crozet Archipelago (22,140 ng g^{-1}, Bustamante et al., 2016) and at South Georgia (27,430 ng^{-1}, Anderson et al., 2009), where young pre-breeders even had levels of 48,130 ng g^{-1} (Tavares et al., 2013).

In this study, the highest Hg concentrations were reported in great-winged petrels and northern giant petrels (NGP) on Marion Island (Table 1). Northern giant petrels, like southern giant petrels (SGP), are primarily scavengers and predators, feeding on penguins and seals (Hunter and Brooke, 1992; De Bruyn et al., 2007; González-Solís et al., 2008; Cooper and Klages, 2009; Copello et al., 2011). They tend to be more predatory on seabirds and seals at Marion Island (Woehler et al., 2001; Dilley et al., 2013) than SGPs (as also reported by Thompson et al., 1993), which might in part account for their Hg concentrations being significantly higher than in SGPs at the same site, or in NGPs at other breeding sites, although they also have a higher proportion of cephalopods and fish in their diet (Table S2). Stable isotopes (d15N) indicate that cephalopods in the southern oceans generally feed at a similar trophic level as fish, but contain higher levels of Hg (Anderson et al., 2009). Consequently, Hg levels in seabirds cannot be explained solely by trophic level, but also the type of prey consumed must be considered.

Although relationships between Hg feather concentrations and the relative proportions of prey types are obvious, in some species similarities in Hg feather concentrations cannot be attributed exclusively to diet. Hg uptake in the seabirds may be affected by changes in the availability and composition of prey species due to the dependence of the dynamic links within the food web (Bargagli et al., 1998; Barrera-Oro, 2002; Bocher et al., 2003) or to population or even individual diet specialization (e.g. Nisbet et al., 2002; Brasso et al., 2015). At a small geographical scale, two colonies of gentoo penguins in the Kerguelen archipelago exhibited very different levels of Hg contamination due to differences in their trophic ecology and dietary preferences (Carravieri et al., 2013; cf. Fig. 4). In one colony, the pattern of Hg contamination showed inter-individual variability due to individual feeding specialization. At a larger geographical scale, Hg contamination in wandering albatrosses was influenced by latitudinal foraging habitats, with individuals feeding in warmer subtropical waters (mainly females) having higher concentrations of mercury than those feeding in colder sub-Antarctic waters (mainly males; Carravieri et al., 2014a). Imbalances in basic links of the food chain, such as those already reported or expected for Antarctic krill *Euphausia superba* (Croxall et al., 1999; Reid and Croxall, 2001; Atkinson et al., 2004; Forcada et al., 2012), could drive such changes. Also, the dependence of some seabirds on fishery discards (Copello et al., 2008) or overlap with fisheries ranges (Reid et al., 2004; Copello and Quintana, 2009) might lead to changes in prey composition. The combination of recent harvest changes and those caused by global warming (see below) may produce rapid shifts rather than gradual changes (Croxall et al., 2002), with consequences for Hg contamination of seabirds.

4.2. Detoxification processes, moult and migration

Another important factor affecting the levels of Hg in feathers is the detoxification procedure. Seabirds tend to accumulate toxic metals in their bodies and use storage of bound metals as a detoxification mechanism, thus the high levels in some species are a function of their uptake, storage and elimination properties (Muirhead and Furness, 1988). In birds, methylmercury is mainly excreted through feathers, whereas the inorganic metal is bound and immobilized in the liver (Thompson and Furness, 1989). Hg concentrations in feathers depend on the dietary uptake of Hg during their formation and the release of Hg accumulated in the body since the last moult (e.g. Braune and Gaskin, 1987; Thompson and Furness, 1989; Bustamante et al., 2016). The importance of feathers as excreting route can be seen in albatrosses which show particularly high Hg accumulation in feathers and liver due to slow moult patterns (Muirhead and Furness, 1988; Thompson and Furness, 1989). The very high concentrations in immature wandering albatrosses (even higher than adults; Tavares et al., 2013; Bustamante et al., 2016) may be caused by less efficient detoxification process due to reduced moult frequency and function of feathers as the major pathway of Hg elimination for this age class.

Since feathers are usually moulted during the non-breeding period, their Hg concentrations are also inextricably linked to migration patterns and wintering areas, and may also be influenced by the uptake during this period (Nisbet et al., 2002; Lavoie et al., 2014; Watanuki et al., 2016). However, in our study, associations of Hg with timing of moult and migration patterns were less obvious (Fig. 2). Despite the large variation in migrating and moulting patterns among species, no general patterns emerged, suggesting a limited influence of these factors compared to diet

(Fig. 2). Indeed, differences among breeding localities were in some cases more evident than among migratory and moulting strategies. For example, most sub-Antarctic skuas from Marion Island and Gough Island winter in the Benguela upwelling region (JG-S and PR, unpublished data) where they also moult. However, skuas on Marion Island showed greater mercury levels than those on Gough Island, in line with general mercury levels between these two localities (see below), suggesting that most mercury uptake occurs during the breeding season (Ramos et al., 2008). Indeed, mercury in feathers reflects not only the intake when the feather was grown, but also the Hg accumulated in body reservoirs over a protracted period until it can be eliminated through moulting feathers (Braune and Gaskin, 1987; Thompson and Furness, 1989; Bond, 2010). In addition, in most species considered here, non-breeding periods are short compared to breeding periods and therefore the potential to accumulate mercury in body reservoirs is greater during the breeding period.

4.3. Spatial differences

Sampling species at two or more sites showed that patterns of inter-site differences in Hg levels were not uniform among species (Table 1, Fig. 2). Inclusion of published Hg feather levels from seabirds studied during the same decade at two further sites, South Georgia (Anderson et al., 2009) and Kerguelen Islands (Carravieri et al., 2014b) offers the possibility of larger-scale longitudinal inter-site comparisons (Table 1, Fig. 4) and confirms that the highest Hg contamination of most seabirds occurred at Marion Island. Among seven species of disparate trophic levels with data from three or four sites, Marion showed the highest Hg levels in four species (both species of giant petrels, blue petrel and sub-Antarctic skua). Adding comparisons between two sites (Table 1), king penguins and great-winged petrels had higher Hg levels at Marion than at Kerguelen or the Crozet Islands (Scheifler et al., 2005). Soft-plumaged petrels had their highest concentrations at Gough Island, and gentoo penguins at Kerguelen (Fig. 4). In three species from three or four sites including Byers Peninsula, birds from this locality had the lowest Hg levels. Consequently, in general, species with the highest Hg feather levels bred at Marion Island, those with intermediate levels at South Georgia, Gough Island or Crozet/Kerguelen, and breeders at Byers Peninsula were least contaminated.

This spatial trend shows no clear correspondence with distance from the Antarctic Convergence: South Georgia and Byers Peninsula are located about 500 km south of the Polar Front, whereas Kerguelen is located on the Antarctic Convergence, or north of it (Marion Island 300 km, Gough Island 670 km north). This result is consistent with the hypothesis of a homogeneous Hg concentration across the Southern Ocean due to the Antarctic Circumpolar Current (e.g. Sokolov and Rintoul, 2007; for surface chlorophyll). Differences in Hg contamination of seabird species among localities may change according to the local bioavailability of Hg, which probably results from local oceanographic conditions, and with differences in food preferences at different breeding sites (see above, Carravieri et al., 2013). Among penguins, differences in trophic level or foraging habitat provide the most explanatory power for intra-specific differences in mercury exposure (Brasso et al., 2015), although in some cases local environmental factors impacting the bioavailability of mercury were the most important drivers of mercury levels rather than trophic level alone (Brasso and Polito, 2013; Brasso et al., 2015).

4.4. Concluding remarks

In line with previous studies, we found marked differences in feather mercury concentrations among seabird species, varying over a 90-fold range from the lowest concentration in Adélie and gentoo penguins in the Antarctic Peninsula to the highest concentration in great-winged petrels breeding on Marion Island. These differences were mainly due to differences in diet, not only related to trophic level but also to the type of prey. Thus, in general, species feeding at lower trophic levels (e.g. on crustaceans) exhibited lower mercury values than those feeding at medium trophic levels (e.g. on fish and squid), and species feeding on seal carrion and penguins contained the highest levels. However, although squid occupy a similar trophic level as fish, their greater mercury concentrations resulted in raised Hg levels in seabirds specializing squid prey, such as gadfly petrels (soft-plumaged and Atlantic petrels) and sooty albatrosses.

In some seabird species breeding on Gough Island in the South Atlantic considerably higher Hg concentrations were detected compared to the mid-1980s. These comparisons were based on two temporal points only and not on continuous monitoring of mercury levels or of potential changes in diet and trophic levels – information necessary to explain Hg pollution trends and their sources (Brasso and Polito, 2013; Brasso et al., 2014; Burgess et al., 2013; Braune et al., 2014). Nevertheless, most studies in the Southern Ocean seabirds found trophic level remained constant or decreased over the last decades, implying the increase in Hg cannot solely be explained by changes in diet but on a concomitant increase in Hg contamination.

Indeed, Hg in surface reservoirs probably will continue to increase even if future anthropogenic emissions remain constant (Driscoll et al., 2013), and rapid physical-chemical change takes place (Lamborg et al., 2014) including acidification with the potential to enhance biological processes such as increased Hg methylation (Scheuhammer, 1991). The wide range of environmental perturbations in Antarctic regions (including climate change, fisheries and complex mixtures of pollutants) could exacerbate seabirds' demographic responses to Hg levels (Goutte et al., 2014b). The combination of environmental change with potential increase in Hg and some persistent organic pollutants may affect seabird biology in various ways towards impaired breeding probability and success, leading to critical demographic declines of these long-lived and often endangered species (Goutte et al., 2014a,b; 2015). As a consequence, monitoring of demography, ecology and pollutants in seabirds should be intensified in the Southern Ocean and adjacent oceanic areas, to use them as an early warning system for the marine environment and its top predators including man.

Acknowledgements

We thank U. Pijanowska, H. Mühlichen for assistance during the chemical analyses, and R. Ramos Garcia, Katharina Weißenfels for collating information on species diets and migration, and Olav Geiter, Benita Gottschlich, Frank Mattig, Rieke Schäfer, Marie-Theres Stiegler and Götz Wagenknecht for preparing tables and figures. The valuable comments of three anonymous referees helped to improve the paper. V. Goutner was supported with a sabbatical from the University of Thessaloniki.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.envpol.2016.05.061.

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Supplementary Material

Feather mercury concentrations in Southern Ocean seabirds: Variation by species, site and time

Peter H. Becker, Vassilis Goutner, Peter G. Ryan, Jacob González-Solís

Supplementary REFERENCES

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ENVPOL Supplementary material, “**Feather mercury concentrations in Southern Ocean seabirds: Variation by species, site and time**”,
by *Peter H. Becker, Vassilis Goutner, Peter G. Ryan, Jacob González-Solís*

Table S1: Results of the interspecific differences in mercury levels based on Tamhane T_2 test. See Table 1 for mercury levels, scientific names, sample size and further species with n<4. The species are ranked according to their mercury level, and three species-groups of different mercury contamination (see 3.1) are indicated by different shading. Species abbreviations: gentoo penguin (GP), chinstrap penguin (CP), common diving petrel (CDP), broad-billed prion (BBP), white-faced storm petrel (WFP), rockhopper penguin (RP), Wilson’s storm petrel (WSP), king penguin (KP), great shearwater (GS), macaroni penguin (MP), Atlantic yellow-nosed albatross (AYA), blue petrel (BP), sub-Antarctic skua (BS), southern giant petrel (SGP), soft-plumaged petrel (SPP), sooty albatross (SA), Atlantic petrel (AP), northern giant petrel (NGP), great-winged petrel (GWP). Blue petrel (high SD) is linking all three groups, southern giant petrel the group of medium and highly contaminated species.

CP	CDP	BBP	WFP	RP	WSP	KP	GS	MP	AYA	BP	BS	SGP	SPP	SA	AP	NGP	GWP	**Species**
░	░	░	□	□	□	□	□	□	□	□	□	□	□	□	□	□	□	GP
	░	░	□	□	□	□	□	□	□	□	□	□	□	□	□	□	□	CP
		░	□	□	□	□	□	□	□	▒	□	□	□	□	□	□	□	CDP
			▒	□	▒	□	□	□	□	▒	□	□	□	□	□	□	□	BBP
				▒	▒	□	□	□	□	▒	□	□	□	□	□	□	□	WFP
					▒	▒	▒	□	□	▒	▒	□	□	□	□	□	□	RP
						▒	▒	▒	▒	▒	▒	□	□	□	□	□	□	WSP
							▒	▒	▒	▒	▒	□	□	□	□	□	□	KP
								▒	▒	▒	▒	□	□	□	□	□	□	GS
									▒	▒	▒	□	□	□	□	□	□	MP
										▒	▒	▒	▒	□	□	□	□	AYA
											▒	▒	▒	▒	▒	□	□	BP
												▒	□	□	□	□	□	BS
													▒	□	□	□	□	SGP
														▓	▓	▓	▓	SPP
															▓	▓	▓	SA
																▓	▓	AP
																	▓	NGP

Hg level

░ low

▒ intermediate

▓ high

░▒▓ **Interspecific difference n.s.**

□ **Interspecific difference p ≤ 0.05**

ENVPOL Supplementary Material "Feather mercury concentrations in Southern Ocean seabirds: Variation by species, site and time" - Table S2.

Peter H. Becker, Vassilis Goutner, Peter G. Ryan, Jacob González-Solís

Table S2: Prey composition of seabirds investigated in this study. Main prey categories presented as reconstituted fresh mass unless other wise mentioned (under comments). X: unspecified quantities

Species	Crustaceans	Cephalopods	Fish	Other	Area	Reference	Comments
King penguin (KP)	–	90	10	–	South Georgia	Croxall and Prince (1980a)	
	trace	31,3	68,7	–	Marion Island	Adams and Klages (1987)	trace: < 0.1 % or < 1% depending on the data accuracy presentation
	?	?	90	?	Posession Island, Crozet Arch.	Bost et al. (1997)	?: Not stated
	–	0,2	99,8	–	Posession Island, Crozet Arch.	Cherel and Ridoux (1992)	
	–	7,6	92,4	–	Crozet Islands	Ridoux (1994)	
	–	2,2	97,8	–	Macquarie Island	Hindel (1987)	
	–	3	97	–	South Georgia	Olsson and North (1997)	
	trace	28,4	71,6	trace	Heard Island	Moore et al. (1998)	
Gentoo penguin (GP)	68	–	32	–	South Georgia	Croxall and Prince (1980a)	
	trace	8,3	91,6	–	Macquarie Island	Robinson and Hindell (1996)	
	36	11	53	–	Falkland Islands	Clausen and Pütz (2002); Pütz et al. (2001)	
	54	1,8	43,9	trace	Crozet Islands	Ridoux (1994)	
	46,2	0,6	53,2	–	Marion Island	Adams and Wilson (1987)	
	44,4	2,1	53,5		Marion Island	Adams and Klages (1989)	
	84,6	–	15,4	–	King George Island, S. Shetland Islands	Volkman et al. (1980)	
Adélie penguin (AP)	81-63	–	19-37	–	Petrel Island	Wienecke et al. (2000)	breeding
	74-70	–	26-30	–	Shirley Island	Wienecke et al. (2000)	breeding
	98,6	–	1,4	–	Signy Island, South Orkney Islands	Lishman (1985)	breeding 1980/81
	99,6	–	0,4	–	Signy Island, South Orkney Islands	Lishman (1985)	breeding 1981/82
	99,9	trace	0,1	–	Signy Island, South Orkney Islands	Lynnes et al. (2004)	breeding 1997-2001
	99,9	–	0,1	–	King George Island, S. Shetland Islands	Volkman et al. (1980)	
Chinstrap penguin (CP)	96	–	4	–	Elephant Island, South Shetland Islands	Croxall and Furse (1980)	breeding
	97,1	–	2,9	–	Signy Island, South Orkney Islands	Lishman (1985)	breeding 1980/81
	99,9	–	0,1	–	Signy Island, South Orkney Islands	Lishman (1985)	breeding 1981/82
	99,9	trace	0,1	–	Signy Island, South Orkney Islands	Lynnes et al. (2004)	breeding 1997-2001
	96,7	–	0,3	–	King George Island, S. Shetland Islands	Volkman et al. (1980)	

Species	Crustaceans	Cephalopods	Fish	Other	Area	Reference	Comments
Southern rockhopper penguin (SRP)	91,6	4,6	3,8	–	Marion Island	Brown and Klages (1987)	1983/84
	80,8	5,2	14	–	Marion Island	Brown and Klages (1987)	1984/85
	53	29	18	–	Falkland Islands	Clausen and Pütz (2002); Pütz et al. (2001)	1986/87 to 1999/2000
	73,1	15,1	11,7	–	Crozet Island	Ridoux (1994)	
Northern rockhopper penguin (NRP)	43,7	43,9	12,2	–	Amsterdam Island	Tremblay and Cherel (2003)	breeding females
	92	2	6	–	Gough island	Klages et al. (1988)	moseleyi
	63,8	2,2	24,7	–	Macquarie Island	Hull (1999)	breeding (E. c. filholi)
	99,3	*–*	*0,7*	*–*	Mayes Island, Kerguelen Archipelago	Tremblay and Cherel (2000)	breeding females, *frequencies*
	97,1	–	2,9	–	Mayes Island, Kerguelen Archipelago	Tremblay and Cherel (2003)	breeding females
	95,1	0,6	4,3	–	Possession Island, Crozet Archipelago	Tremblay and Cherel (2003)	breeding females
Macaroni penguin (MP)	87	8,1	4,9	–	Marion Island	Brown and Klages (1987)	1983/84
	62,1	13,2	24,7	–	Marion Island	Brown and Klages (1987)	1984/85
	98	trace	2	–	South Georgia	Croxall and Prince (1980b)	
	75	–	25	–	Elephant Island, South Shetland Islands	Croxall and Furse (1980)	
	60,9	9,8	28,7	0,5	Crozet Island	Ridoux (1994)	
Sooty albatross (SA)	2,7	40,5	5,5	51,3	Crozet Island	Ridoux (1994)	
	11,1	*95,1*	*20,9*	*32.0 carrion*	Crozet Island	Weimerskirch et al. 1986	chick regurgitates, *frequencies*
Atlantic yellow-nosed albatross (AYA)	3,8	38	58,2	–	Crozet Island	Ridoux (1994)	
	55	22	100	0	Crozet Island	Weimerskirch et al. (1986)	chick regurgitates, *frequencies*
	0,6	6,9	92	–	Amsterdam Island	Pinaud et al. (2005)	1996, fresh mass (%) not reconstituted mass, chick and adult regurgitates
	1,4	13,4	80,7	–	Amsterdam Island	Pinaud et al. (2005)	2001, fresh mass (%) not reconstituted mass, chick and adult regurgitates
Southern giant petrel (SGP)	12	2	1	85	Bird Island, South Georgia	Croxall and Prince (1987)	
	1	2	1	96	Bird Island, South Georgia	Hunter (1983)	breeding 1979/80
	21	1	1	77	Bird Island, South Georgia	Hunter (1983)	breeding 1980/81
	trace	–	–	100	Crozet Island	Ridoux (1994)	
	43,7	*65,1*	*19,4*	*90,8*	Patagonia, Argentina	Copello et al. (2008)	2001-2004, *frequencies*
Northern giant petrel (NGP)	15	6	2	77	Bird Island, South Georgia	Croxall and Prince (1987)	
	4	10	1	85	Bird Island, South Georgia	Hunter (1983)	breeding 1979/80
	22	2	3	73	Bird Island, South Georgia	Hunter (1983)	breeding 1980/81
	trace	–	–	100	Crozet Island	Ridoux (1994)	

Species	Crustaceans	Cephalopods	Fish	Other	Area	Reference	Comments
Atlantic petrel (AP)	0,9	86,7	11	1,4	Gough Island	Klages and Cooper (1997)	drained mass (%) not reconstituted fish mass
	13	70	17	–	Gough Island	Imber (1991)	drained mass (%) not reconstituted fish mass
Blue petrel (BP)	91	1	8	–	Bird Island, South Georgia	Croxall and Prince (1987)	
	59,5	15,7	21,2	3,6	Marion Island	Steele and Klages (1986)	
	37,4	2,1	56,8	3,7	Kerguelen Islands	Cherel et al. (2002)	
	60,9	27,2	10,6	1,6	Crozet Island	Ridoux (1994)	
Broad-billed prion (BBP)	100	tr	tr	–	Gough Island	Klages and Cooper (1992)	
Kerguelen petrel (KPT)	24	70	6	–	Marion Island	Schramm (1986)	abstract only found, chick regurgitates
	72,5	6	0,3	21,2	Crozet Island	Ridoux (1994)	21.2% offal
Soft-plumaged petrel (SPP)	10	89	1	–	Marion Island	Schramm (1986)	
	77,8	15,7	tr	6,5	Crozet Island	Ridoux (1994)	
Great-winged petrel (GWP)	6	90	4	–	Marion Island	Schramm (1986)	
	2,5	58,7	38,7	–	Marion Island	Cooper and Klages (2009)	winter diet
	32,1	63,7	4,2	–	Crozet Island	Ridoux (1994)	
White-chinned petrel (WCP)	29	47	24	–	Bird Island, South Georgia	Croxall and Prince (1987)	
	42	19	39	–	Bird Island, South Georgia	Berrow and Croxall (1999)	1996
	46	25	29	–	Bird Island, South Georgia	Berrow and Croxall (1999)	1998
	23,6	17	56,3	3,1	Marion Island	Cooper et al. (1992)	See also Lipinski and Jackson 1989 for cephalopod analysis from Marion
	16,3	24,7	54,7	4,3	Crozet Island	Ridoux (1994)	
	1,6	38,2	54,1	6,1	Posession Island, Crozet Arch.	Connan et al. (2007)	
	14	8,3	71	6,6	Kerguelen Island	Delord et al. (2010)	2005, chick diet
	10,9	25,4	62,3	1,3	Kerguelen Island	Delord et al. (2010)	2006, chick diet
	13,2	11,4	39,7	35.7 fish offal	Southern Benguela Region	Jackson (1988)	1985-86, dry mass, diet at sea
Great shearwater (GS)	26,9	45,5	20,1	7,4	Brier Island, Nova Scotia	Brown et al. (1981)	Proventriculi, 1974
	0,3	89,1	8,3	1,8	Brier Island, Nova Scotia	Brown et al. (1981)	Proventriculi, 1975
	50	22	28	–	Grand Manan archipelago, Canada	Ronconi et al. (2010)	2005-2007 non breeding, potential prey items based on discriminant function analysis of 38 selected fatty acids
	17	*42*	*8*	*58 evertebrates*		Hagen (1952)	*frequencies*, stomach
	–	*96*	*32*	10 insects	Rio Grande do Sul coast, Brazil	Petry et al. (2008)	*frequencies*, 1997, 1998, migration, carcass stomach

Species	**Crustaceans**	**Cephalopods**	**Fish**	**Other**	**Area**	**Reference**	**Comments**
Sub-Antarctic shearwater (LS)	20-50	20-50	< 20	–	South Georgia	Payne and Prince (1979)	
	X	X	X	–		Marchant and Higgins (1990)	cephalopods, krill, small fish, unknown proportions
Wilson's storm petrel (WSP)	68	1,9	28,3	1,8	Bird Island, South Georgia	Croxall et al. (1988)	
	87,5	–	11,9	0,6	Crozet Island	Ridoux (1994)	
	81.0 to 91.0	–	*20.2 to 36.2*	–	King George Island, S. Shetlands	Quillfeldt (2002)	range of *frequencies* between 1996 and 2000
Grey-backed storm petrel (GBSP)	100	–	–	trace	Crozet Island	Ridoux (1994)	
White-faced storm petrel (WFP)	6.4*	0	93,6	–	Eastern tropical Pacific Ocean	Spear et al. (2007)	mass. * More invertebrate taxa included here
Common diving petrel (CDP)	100	–	–	–	Bird Island, South Georgia	Croxall and Prince (1987)	
	100	trace	–	trace	Crozet Island	Ridoux (1994)	
	100	–	trace	–	Kerguelen Island	Bocher et al. (2001)	
Sub-Antarctic skua (BS)	–	–	–	100	Mayes Island, Kerguelen Arc.	Mougeot et al. (1998)	petrels and prions and indetermined
	–	–	–	100	Bird Island, South Georgia	Osborne (1985)	penguins, petrels, seals
	X	X	X	X	Southern Ocean areas (including South Georgia, the Prince Edward,Crozet, Kerguelen and Maquarie islands)	Reinhardt et al. (2000)	mainly penguins and other birds, mammals fish, invertebrates refuse
	–	–	–	100	Cimetiére Island and Verte Island, Kerguelen Arc.	Moncorps et al. (1997)	petrels and rabbits