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Influence of trophic position and foraging range on mercury levels within a seabird community

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ABSTRACT: Seabirds are often advocated as biomonitors for marine contaminants such as mercury (Hg). However, contaminant levels can vary widely depending on among-individual and among-species variation in foraging preferences and physiology, and on tissue types used for analyses. Using stable isotope analysis (SIA), we investigated the effects of trophic position, season, and tissue type on Hg burdens in a group of 10 closely related seabirds (Procellariiformes) from a single colony in the South Atlantic. Analysis of blood (reflecting breeding season diet) showed that among-species Hg concentrations varied as a function of trophic position ($\delta^{15}N$) and were also influenced to a lesser degree by foraging range ($\delta^{13}C$). This pattern did not hold for feathers, which reflect the non-breeding period. Mercury levels in feathers formed during the non-breeding season appear to be more strongly governed by species effects (such as moult schedule), demonstrating the need to carefully consider tissue type when formulating predictions regarding Hg burdens and dynamics. Assessment at a community rather than the species level, and across a number of tissue types, provided a more complete picture of the complex interactions between Hg and foraging ecology in seabirds.

KEY WORDS: Mercury · Procellariiformes · $\delta^{15}N$ · $\delta^{13}C$ · Trophic position · Diet · Seabird

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INTRODUCTION

Mercury (Hg) is a non-essential heavy metal that biomagnifies within food webs (Riisgard & Hansen 1990, Jarman et al. 1996) and can accumulate in toxic concentrations in top predators (Eisler 1987). Although high levels of exposure are often associated with localised sources of pollution (such as chlor-alkali works or lignite burning), elevated concentrations have also been reported in biota from high latitudes (Wagemann et al. 1990, Bocher et al. 2003). This is most likely a result of atmospheric transport and geological seepage (Braune et al. 1991), by which Hg enters the food chain and is then biomagnified.

Seabirds have been identified as potential sentinels for monitoring Hg contamination in the marine environment, partly because many marine bird species are apex predators and thus target the same prey types as some human fisheries (Gilbertson et al. 1987, Walsh 1990, Burger 1993, Monteiro & Furness 1995). The Procellariiformes are the most diverse and abundant group of seabirds in the Southern Ocean, occupying trophic positions ranging from zooplanktivorous grazers to top predators (Croxall & Prince 1980, Reid et al. 1997). Mercury levels in this group are very variable, and in great albatrosses (*Diomedea* spp.) are amongst the highest that occur naturally in any marine taxa (Thompson et al. 1993, Hindell et al. 1999, Stewart et

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al. 1999). Thus, different species within the order have the potential to act as indicators of pollutant exposure for a wide range of Southern Ocean consumers.

Despite the longstanding use of seabirds as indicators of heavy metal contamination, our understanding of the factors driving variation in their Hg burdens remains somewhat limited. Mercury levels vary substantially among tissues, individuals and species, making interpretation of patterns difficult. Moreover, previous work examining the effects of diet and trophic position on Hg concentrations in seabirds has produced contradictory results. Some studies suggest that trophic effects are weak and that foraging location and variation in individual physiology may be more important factors (Thompson et al. 1993, Bearhop et al. 2000a). In contrast, other work has indicated that there are strong trophic effects (Atwell et al. 1998), or that the proportion of particular prey types in the diet (e.g. mesopelagic fish) accessed through fisheries discards may be more important than trophic level per se (Thompson et al. 1998a, Monteiro et al. 1999, Arcos et al. 2002). To date, most studies have either focused on a single or a small number of species (but see Atwell et al. 1998, Becker et al. 2002), or have examined mercury burdens in a wide variety of species, but were unable to compare diet and Hg burden directly, since diets were assessed during the breeding season and the tissues collected (feathers) reflect the non-breeding season (e.g. Stewart et al. 1999, Becker et al. 2002). Moreover, few studies have addressed the issue of temporal variation in mercury burdens resulting from changing foraging patterns over the seasons among Southern Ocean seabirds.

When relating contaminant burdens to diet, conventional analyses (e.g. analyses of regurgitates or pellets) suffer from 2 important problems. First, they can be prone to biases, often under-estimating rapidly digested material (Phillips et al. 1999, Votier et al. 2003, Catry et al. 2004). Second, it is often impossible to assess diet consistently at all times of year, especially during the non-breeding season (Duffy & Jackson 1986, González-Solís et al. 1997). Stable isotope analyses (SIA) address these problems by reflecting assimilated molecules, thus overcoming the issue of relative digestibility of prey (Bearhop et al. 1999). Thus, careful choice of tissue can provide insights into diet at times of year when conventional data cannot be collected. Moreover, this approach provides quantitative foraging data on a continuous scale that facilitate robust statistical analyses and can be particularly powerful when combined with conventional approaches.

SIA provides data on foraging patterns because the isotopic composition of consumer tissue relates predictably to that of prey (DeNiro & Epstein 1978, 1981). $\delta^{15}N$ increases ca. 3 to 5‰ per trophic level (Minagawa & Wada 1984, Wada et al. 1987, Fry 1988), whereas $\delta^{13}C$ increases to a much lesser degree, ca. 1‰ (DeNiro & Epstein 1978, Fry et al. 1984). Stable carbon isotope ratios can act more effectively as spatial markers, because they vary over both large and small spatial scales in marine systems (Rau et al. 1992, Lathja & Marshall 1994, Fry 2006). Stable carbon isotope ratios in seabird tissues can reflect regional foraging, as differences in basal $\delta^{13}C$ are propagated through food webs (Cherel & Hobson 2007).

Moreover, different tissues can reflect different dietary information as isotopic signatures are incorporated over the period of tissue formation (Hobson & Clark 1992, Bearhop et al. 2002). Whole blood or cells incorporate the isotope signatures of a consumer's food over a 3 to 4 wk period (Haramis et al. 2001, Bearhop et al. 2002). Feather isotope ratios reflect diet at the time of their synthesis (Hobson & Clark 1992, Bearhop et al. 2002). Although giant petrels (*Macronectes* spp.) moult some body feathers throughout breeding, in other Procellariiformes, moult starts after adults depart from the colony and proceeds at variable rates during the non-breeding period (Marchant & Higgins 1990). Thus, random sampling of body feathers predominantly provides isotopic information for a period when conventional dietary assessment is extremely difficult. By sampling feathers to reflect the non-breeding period (usually winter), and blood to reflect the breeding period (summer), it is possible to obtain diet information for 2 very distinct parts of the life cycle (Bearhop et al. 2006, Cherel et al. 2006).

Mercury can be found in most body tissues, but feathers provide the main route of excretion in birds (Braune & Gaskin 1987, Bearhop et al. 2000a). Once bound to feather keratin, Hg is effectively inert and cannot be re-incorporated into living tissues (Appelquist et al. 1984). Mercury bound in the plumage may account for as much as 93% of total body burden (Braune & Gaskin 1987), with feathers moulted towards the beginning of the sequence having the highest levels (Furness et al. 1986). These characteristics of Hg excretion mean that the examination of feathers can provide a broad temporal perspective on the fate of Hg in a community of birds (Becker et al. 1993). Conversely, Hg in blood represents that incorporated from food during blood formation and some component of residual Hg residing in other tissues since the cessation of the last feather moult. This residual Hg is thought to equilibrate with levels in the liver, which acts as the main store for Hg between moulting events (Bearhop et al. 2000b). As birds of the Procellariiformes may continue to moult some body feathers until late in the non-breeding period, it is unlikely that residual Hg levels in the blood, at least in the early to mid breeding season, are much higher than that incorporated most

recently from dietary sources, and are therefore providing information on Hg uptake primarily only for this particular stage of the life cycle (Bearhop et al. 2000b).

In the present study we investigated Hg dynamics across a seabird community and across multiple tissue types, seeking generalities in the patterns of Hg accumulation in relation to ecology and phylogeny. We aimed to identify the extent to which trophic level and/or foraging location affect Hg burdens. We also compared results from 2 different tissue types in order to assess the effects of breeding and non-breeding foraging on Hg burdens. We then related this variation to Hg concentrations in known prey items to investigate the relative importance of trophic level over prey type. Previous studies have arrived at different conclusions regarding the relative importances of prey type versus trophic position on resultant Hg burdens in seabirds (e.g. Monteiro et al. 1996, Thompson et al. 1998a, Becker et al. 2002). We recognise the importance of including comprehensive analyses of typical prey items when attempting to understand Hg dynamics within marine food webs and have attempted to address this issue within the present study. Moreover, by examining foraging behaviours and Hg levels within a single speciose order, we hoped to reduce the potential variation attributable to phylogeny that may explain some of the variation found in other multi-species studies where different taxa have much more distinct evolutionary origins (e.g. Atwell et al. 1998). We assumed that species within a family are closely-related and consequently have similar physiology. In this way we aimed to extract more meaningful data on the true impact of foraging behaviour on Hg burdens across a diverse community of biomonitors.

MATERIALS AND METHODS

Sample collection and preparation. Samples were collected on Bird Island, South Georgia (54° 00′ S, 38° 03′ W) between December 2001 and April 2002. We sampled 10 Procellariiform species: Antarctic prion *Pachyptila desolata*, black-browed albatross *Thalassarche melanophrys*, blue petrel *Halobaena caerulea*, common diving petrel *Pelecanoides urinatrix*, South Georgian diving petrel *P. georgicus*, grey-headed albatross *T. chrysostoma*, northern giant petrel *Macronectes halli*, southern giant petrel *M. giganteus*, white-chinned petrel *Procellaria aequinoctialis* and wandering albatross *Diomedea exulans*. Blood and feather samples were taken from surface-nesting species (albatrosses and giant petrels) in the late brood-guard stage and from burrow-nesting petrels (the remaining species) whilst mist-netting adjacent to breeding colonies during early to mid chick-rearing; hence, all species were effectively at a similar stage of breeding. All surface-nesting birds sampled were breeders, while burrowing birds were of unknown status, but most likely to consist predominantly of breeders as many regurgitated prey (presumably intended for chicks) when handled. For each species, the maximum sampling interval between individuals was 1 wk. An equal number of males and females were sampled from each species wherever possible. Whole blood (0.2 to 1.0 ml) was taken from the tarsal vein, stored on ice in the field and centrifuged at 15 000 rpm for 15 min in the laboratory; separated red blood cells and plasma were then frozen within 3 to 4 h of collection. Samples of red blood cells were subsequently freeze-dried to a constant mass, homogenised and again kept frozen until analysis. Feathers (6 to 8) were plucked at random from the mantle region of each bird, stored dry in plastic bags at room temperature and later homogenised in a freezer mill prior to analysis. Feathers were clean, but not washed prior to analysis, which may have introduced some error into Hg results. However, this was unlikely to confound our interpretations for 2 reasons: first, the bulk of each feather was overlaid by more anterior feathers and hence only the tips would have been generally exposed to atmospheric contamination. Second, all feathers were treated in a similar manner and thus any Hg adsorption post-sampling would be standard across all samples and hence simply add a small degree of 'noise' to the dataset. Prey samples were chosen following a review of published literature on diet of the species of Procellariiformes included in the study. Fresh prey samples were collected from regurgitates, or from nets deployed by research vessels in adjacent waters, and immediately stored frozen in plastic bags. Tissue samples were excised from inner muscle with acid-washed tools to minimise the possibility of Hg contamination. These samples were then homogenised in a freezer mill prior to stable isotope and Hg analyses.

Mercury analyses. Each sample was oven-dried for >24 h at 50°C to a constant mass of between 0.05 and 0.1 g dry weight (dry wt), and solubilised in 2 ml of cold nitric acid for 24 h. Samples were then hot-digested for 50 min at 120°C, after which 0.5 ml of hydrogen peroxide was added and left for a final 15 min. Total Hg levels were measured by atomic fluorescence spectrophotometry using a PSA Merlin Fluorescence Detector (PS Analytical). Detection limits were 0.1 µg g^{-1} for blood and feathers, and 1.5 ng g^{-1} for prey samples. Precision and accuracy were measured using replicate samples and certified reference material (TORT-2 lobster hepatopancreas, NRC, Canada; mean ± 95% CI certified value = 0.27 ± 0.06 µg g^{-1} dry wt); our measured values were 0.29 ±

0.02 µg g^{-1} dry wt, n = 15). Mercury concentrations are expressed throughout as µg g^{-1} on a dry weight basis, with ±SD reported throughout using standard notation, unless otherwise specified.

Stable isotope analyses. Homogenised feather, blood cell and prey samples were oven-dried for >24 h at 50°C to a constant mass. For prey samples only, lipids were extracted over a 4 h period by Soxhlet using 1:1 methanol:chloroform, and samples were analysed with and without lipids. Sampled blood cells and feathers were analysed without prior lipid extraction as the proportion of lipid in blood is very low and in feathers is likely to be negligible, and because extraction methods can influence bulk $\delta^{15}N$ signatures (Bearhop et al. 2000c). Carbon and nitrogen isotope ratios were measured by continuous flow isotope ratio mass spectrometry (CF-IRMS) on ~ 0.7 mg subsamples of homogenised dry material loaded into tin cups. These were combusted in a Costech ECS 4010 elemental analyser coupled to a Thermo Finnigan Delta Plus XP mass spectrometer. Each group of 8 to 10 samples was bracketed by 2 laboratory standards, allowing correction for drift. Isotope ratios are expressed in standard δ notation as parts per thousand (‰) against international reference standards: V-PDB (Vienna PeeDee Belemnite) for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$, according to the equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where X is ^{15}N or ^{13}C and R is the corresponding ratio $^{15}N:^{14}N$ or $^{13}C:^{12}C$. Precision for both $\delta^{13}C$ and $\delta^{15}N$ was routinely estimated to be ≥0.3‰.

Statistical analyses. The influences of trophic level and foraging location (inferred from $\delta^{15}N$ and $\delta^{13}C$) upon Hg levels among seabird species were investigated using general linear models (GLMs). Full GLMs were parameterised as follows: $\log_{10}$ transformed Hg concentration (µg g^{-1}) as the dependent variable, species as a factor, $\delta^{15}N$ and $\delta^{13}C$ as covariates, and all 2-way interaction terms. The most parsimonious models were then determined using Akaike Information Criteria (AIC) (Akaike 1973). Prey data were analysed as above, but with each species first assigned to its broader taxonomic grouping (phylum) to allow for easier interpretation of results (Table 1). All data

Table 1. Mean concentrations of $\delta^{15}N$, $\delta^{13}C$ (‰) and mercury (µg g^{-1} dry wt) in muscle tissue of prey species from South Georgia. Values of these variables are means ± SD, with ranges (in parentheses) and coefficients of variation (CV). Species ranked by Hg concentrations within sub-groups

Species	n	$\delta^{15}N$		$\delta^{13}C$		Mercury	
		Ratio	CV	Ratio	CV	Concentration	CV
Crustaceans							
Euphausia superba	10	6.21 ± 0.25 (5.85–6.69)	4	−18.252 ± 0.58 (−19.4 to −17.49)	−3.18	0.01 ± 0.01 (0.00–0.02)	67.08
Themisto gaudichaudii	7	5.58 ± 0.59 (4.63–6.6)	10.62	−18.40 ± 0.49 (−18.97 to −17.69)	−2.66	0.02 ± 0.01 (0.01–0.03)	48.45
Fish							
Champsocephalus gunnari	16	9.28 ± 0.25 (8.93–9.71)	2.66	−20.65 ± 0.49 (−21.27 to −19.68)	−2.36	0.02 ± 0.01 (0.01–0.04)	46.02
Pseudochaenichthys georgianus	5	10.97 ± 0.70 (9.81–11.61)	6.41	−20.11 ± 0.19 (−20.29 to −19.78)	−0.96	0.02 ± 0.01 (0.01–0.04)	49.79
Patagonotothen guntheri	8	8.97 ± 0.31 (8.5–9.48)	3.48	−21.97 ± 0.55 (−22.73 to −21.02)	−2.49	0.03 ± 0.01 (0.02–0.06)	41.72
Geotria australis	11	8.45 ± 0.57 (7.9–9.49)	6.71	−22.27 ± 2.08 (−25.11 to −17.6)	−9.35	0.04 ± 0.04 (0.02–0.14)	87.08
Dissostichus eleginoides	3	11.37 ± 0.11 (11.3–11.5)	0.97	−21.82 ± 0.70 (−22.59 to −21.21)	−3.23	0.05 ± 0.02 (0.04–0.08)	43.3
Parachaenichthys georgianus	1	11.86[a]		−18.25[a]		0.08[a]	
Lepidonotothen larseni	6	14.46 ± 0.22 (14.25–14.8)	1.51	−15.99 ± 0.28 (−16.43 to −15.65)	−1.76	0.27 ± 0.04 (0.22–0.34)	14.81
Cephalopods							
Martialia hyadesi	2	7.30 ± 0.12 (7.21–7.38)	1.65	−20.80 ± 0.09 (−20.86 to −20.73)	−0.44	0.05 ± 0.01 (0.04–0.05)	15.71
Kondakovia longimana	2	7.51 ± 1.08 (6.75–8.27)	14.31	−23.30 ± 0.83 (−23.88 to −22.71)	−3.55	0.10 ± 0.02 (0.08–0.11)	22.33
Moroteuthis knipovitchi	4	10.79 ± 0.48 (10.32–11.41)	4.42	−21.84 ± 0.61 (−22.6 to −21.34)	−2.78	0.16 ± 0.09 (0.07–0.29)	58.18
Psychroteuthis glacialis	2	10.51 ± 0.28 (10.31–10.7)	2.63	−23.22 ± 1.02 (−23.94 to −22.5)	−4.39	0.18 ± 0.11 (0.10–0.25)	60.61
Galiteuthis glacialis	3	9.25 ± 0.29 (8.93–9.47)	3.07	−21.46 ± 0.49 (−21.91 to −20.94)	−2.27	0.23 ± 0.07 (0.18–0.31)	30.43
Gonatus antarcticus	2	11.36 ± 0.78 (10.81–11.91)	6.85	−22.36 ± 0.56 (−22.75 to −21.96)	−2.5	0.60 ± 0.02 (0.58–0.61)	3.57

[a]No SD, Range or CV given due to low n (values excluded throughout from statistical analyses)

were tested for departures from normality and homoscedasicity using Q-Q plots. Where appropriate, data were log transformed to meet requirements for normality and to reduce variance. Data on blood values for 1 species (blue petrel) were omitted from all statistical analyses because of the small sample size (n = 2). All tests were performed using SPSS v. 14.

RESULTS

Hg and stable isotope ratio patterns in seabird tissues

Hg levels varied widely within and among species (Table 2). The highest mean (± SD) Hg concentrations were in wandering albatrosses for both blood cells (11.15. ± 3.38 µg g^{-1} dry wt) and feathers (27.43 ± 8.14 µg g^{-1} dry wt) and the lowest were in common diving petrels for blood (0.31 ± 0.15 µg g^{-1} dry wt) and in blue petrels for feathers (2.69 ± 1.29 µg g^{-1} dry wt). Mercury concentrations were consistently higher in feathers than blood for all species, as might be expected (Fig. 1), but patterns of variation among species remained generally constant between breeding (blood) and non-breeding seasons (feathers).

The most parsimonious model selected by AIC for breeding season data was: $Log_{10}Hg = \delta^{15}N + \delta^{13}C + species + \delta^{13}C \times \delta^{15}N$ (Table 3). Mercury levels in blood differed significantly among species ($F_{8,144}$ = 43.056, p < 0.001) and, at the community level, were significantly related to $\delta^{15}N$ (β = 0.359, $F_{1,144}$ = 4.328, p = 0.039), and marginally to $\delta^{13}C$ (β = −0.177, $F_{1,82}$ = 3.927, p = 0.050), with a significant interaction between $\delta^{13}C$ and $\delta^{15}N$ (β = 0.019, $F_{1,144}$ = 4.568, p = 0.034; Fig. 2). The final model explained a large proportion of the variation in blood Hg levels (r^2 = 0.912). Although the optimal model determined by AIC for non-breeding season data included the same parameters: (Log_{10} Hg = $\delta^{15}N + \delta^{13}C$ + species + $\delta^{13}C \times \delta^{15}N$ interaction), in a detailed break-down the only parameter that proved statistically significant in explaining variation in Hg burdens was species ($F_{8,145}$ = 10.407, p < 0.001). $\delta^{15}N$, $\delta^{13}C$ and the interaction

Table 2. Mean concentrations of $\delta^{15}N$, $\delta^{13}C$ (‰) and mercury (µg g^{-1} dry wt) in blood and feathers of Procellariiformes. Values of these variables are means ± SD, with ranges (in parentheses) and coefficients of variation (CV). Species ranked by feather Hg concentrations

Species		n	$\delta^{15}N$		$\delta^{13}C$		Mercury	
			Ratio	CV	Ratio	CV	Concentration	CV
Blue petrel	Blood	2	7.78 ± 0.49 (7.43–8.13)	6.32	−25.02 ± 0.55 (−25.40 to −24.63)	−2.19	0.56 ± 0.28 (0.36–0.75)	49.67
	Feather	5	7.89 ± 0.45 (7.31–8.53)	5.69	−24.11 ± 0.87 (−25.46 to −23.22)	−3.59	2.69 ± 1.29 (1.94–4.99)	48.01
Common diving petrel	Blood	15	7.95 ± 0.62 (6.74–8.76)	7.78	−21.18 ± 0.67 (−22.41 to −20.07)	−3.15	0.31 ± 0.15 (0.06–0.59)	47.57
	Feather	15	7.99 ± 0.37 (7.38–8.45)	4.65	−20.58 ± 0.76 (−22.58 to −19.66)	−3.71	2.90 ± 1.63 (0.62–5.46)	56.16
Antarctic prion	Blood	16	8.15 ± 0.29 (7.83–8.93)	3.59	−21.50 ± 1.26 (−23.16 to −19.02)	−5.87	0.53 ± 0.21 (0.24–1.19)	40.31
	Feather	15	9.43 ± 1.28 (6.76–11.11)	13.59	−18.43 ± 0.75 (−19.74 to −17.49)	−4.08	4.51 ± 1.26 (2.58–6.82)	27.94
South Georgian diving petrel	Blood	15	8.49 ± 0.63 (7.61–9.54)	7.42	−21.92 ± 0.90 (−22.90 to −20.11)	−4.12	0.41 ± 0.14 (0.12–0.62)	34.91
	Feather	14	8.46 ± 0.52 (7.75–9.98)	6.14	−20.03 ± 0.92 (−22.03 to −18.26)	−4.61	5.07 ± 1.30 (2.18–7.62)	25.67
White-chinned petrel	Blood	16	14.22 ± 0.66 (13.31–15.37)	4.66	−18.13 ± 0.33 (−19.02 to −17.71)	−1.84	5.37 ± 1.18 (3.61–7.34)	21.97
	Feather	16	17.55 ± 1.37 (15.22–20.13)	7.80	−15.53 ± 0.80 (−16.50 to −13.83)	−5.15	7.43 ± 1.97 (4.35–11.39)	26.46
Southern giant petrel	Blood	16	11.86 ± 0.45 (11.11–12.83)	3.82	−21.92 ± 0.97 (−23.18 to −19.74)	−4.41	2.74 ± 1.05 (1.52–4.74)	38.49
	Feather	16	12.89 ± 1.63 (10.73–15.42)	12.71	−21.04 ± 1.37 (−23.20 to −17.98)	−6.50	8.25 ± 3.98 (2.15–14.08)	48.35
Black-browed albatross	Blood	16	10.79 ± 0.89 (9.13–12.86)	8.25	−19.94 ± 0.78 (−22.07 to −18.56)	−3.93	4.38 ± 1.10 (2.49–6.12)	25.09
	Feather	16	15.85 ± 0.97 (12.96–16.87)	6.11	−14.86 ± 0.90 (−17.38 to −13.72)	−6.04	8.35 ± 2.63 (4.24–12.97)	31.54
Grey-headed albatross	Blood	15	10.99 ± 0.42 (10.30–11.70)	3.82	−19.71 ± 0.90 (−21.54 to −18.87)	−4.56	6.57 ± 1.11 (5.35–8.77)	16.86
	Feather	15	10.48 ± 0.89 (9.05–12.06)	8.45	−19.17 ± 1.12 (−21.70 to −17.59)	−5.86	9.50 ± 2.84 (4.34–13.24)	29.86
Northern giant petrel	Blood	16	13.26 ± 0.78 (12.14–14.99)	5.85	−20.59 ± 0.75 (−21.67 to −19.04)	−3.66	3.93 ± 1.37 (2.18–6.38)	34.89
	Feather	15	13.81 ± 1.10 (11.60–15.85)	7.97	−18.76 ± 0.92 (−20.73 to −17.55)	−4.93	10.52 ± 5.54 (4.50–23.54)	52.65
Wandering albatross	Blood	15	13.36 ± 0.46 (12.72–14.14)	3.43	−20.16 ± 0.60 (−21.42 to −19.22)	−2.95	11.15 ± 3.38 (5.66–19.64)	30.29
	Feather	14	15.15 ± 0.78 (13.07–16.72)	5.15	−17.25 ± 0.79 (−18.94 to −15.88)	−4.60	27.43 ± 8.14 (15.40–45.36)	29.55

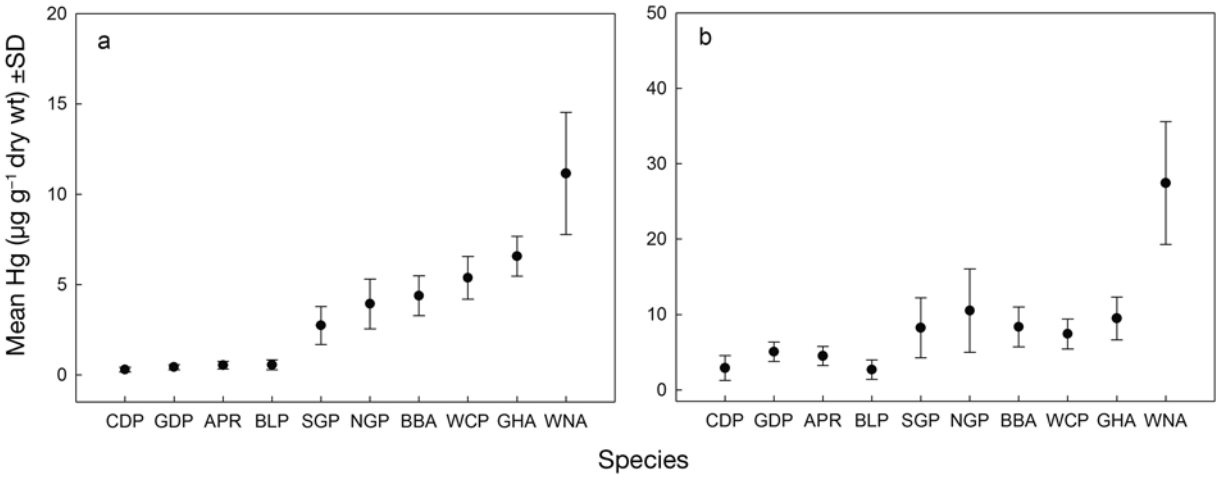

Fig. 1. Mercury levels in (a) blood and (b) feathers in 10 species of Procellariiformes from South Georgia. APR: Antarctic prion (16, 15), BBA: black-browed albatross (16, 16), BLP: blue petrel (2, 5), CDP: common diving petrel (15, 15), GDP: South Georgian diving petrel (15, 14), GHA: grey-headed albatross (15, 15), NGP: northern giant petrel (16, 15), SGP: southern giant petrel (16, 16), WCP: white-chinned petrel (16, 16), WNA: wandering albatross (15, 14). Means ± SD. Sample sizes in parentheses, blood and feathers consecutively

Table 3. Parameter estimates for AIC selected model of blood data (LogHg = $\delta^{15}N + \delta^{13}C$ + species + $\delta^{13}C \times \delta^{15}N$)

Parameter	β	SE	*T*	Significance	95% confidence interval Lower bound	Upper bound
Intercept	−2.292	1.864	−1.229	0.221	−5.980	1.396
APR	−1.479	0.186	−7.969	0.000	−1.846	−1.112
BBA	−0.476	0.118	−4.050	0.000	−0.709	−0.244
CDP	−1.825	0.198	−9.229	0.000	−2.216	−1.434
GDP	−1.626	0.172	−9.471	0.000	−1.966	−1.287
GHA	−0.282	0.115	−2.451	0.016	−0.509	−0.054
NGP	−0.457	0.069	−6.663	0.000	−0.593	−0.322
SGP	−0.590	0.082	−7.191	0.000	−0.752	−0.428
WCP	−0.494	0.106	−4.655	0.000	−0.704	−0.284
WNA	0[a]					
$\delta^{13}C$	−0.177	0.089	−1.982	0.050	−0.353	0.000
$\delta^{15}N$	0.359	0.173	2.080	0.039	0.018	0.701
$\delta^{13}C \times \delta^{15}N$	0.019	0.009	2.137	0.034	0.001	0.036

[a]This parameter is set to zero because it is redundant

between $\delta^{13}C$ and $\delta^{15}N$ were not significant ($F_{1,145}$ = 2.044, p = 0.155, $F_{1,145}$ = 1.387, p = 0.241, and $F_{1,145}$ = 3.172, p = 0.077). Nonetheless, this model explained a substantial proportion of variation in Hg burdens within feathers (r^2 = 0.609).

Patterns in Hg and stable isotope ratios of prey

Generally, the larger mesopelagic prey species had the greatest Hg concentrations. *Lepidonotothen larseni* had the highest Hg concentrations of any fish (0.27 ± 0.04 µg g^{-1} dry wt) and *Gonatus antarcticus* the highest value for any squid (0.60 ± 0.02 µg g^{-1} dry wt). Antarctic krill *Euphausia superba* (0.01 ± 0.01 µg g^{-1} dry wt) and the amphipod *Themisto gaudichaudii* (0.02 ± 0.01 µg g^{-1} dry wt) had the lowest Hg levels. For both fish and squid prey types, the highest Hg concentrations were recorded in predominantly mesopelagic (200 to 1100 m depth) species. This variation was similar in part to that in the isotopic data, with mean (± SD) $\delta^{15}N$ being most enriched in *L. larseni* (14.46 ± 0.22 ‰) and depleted in *T. gaudichaudii* (5.58 ± 0.59 ‰). The highest values for $\delta^{13}C$ were found in *L. larseni* (−15.99 ± 0.28 ‰) and lowest in the squid *Kondakovia longimana* (−23.30 ± 0.83 ‰). However, a number of squid species (e.g. *Gonatus antarcticus*, *Galiteuthis glacialis*, *Moroteuthis knipovitchi*, *Psychroteuthis glacialis*) displayed high Hg levels associated with depleted $\delta^{13}C$ values (Table 1).

At the group level, cephalopods had consistently higher Hg concentrations than either fish or crustacea (Table 1). This was confirmed in statistical analyses, with the most parsimonious model selected by AIC being the fully parameterised model: Log_{10} Hg = $\delta^{15}N + \delta^{13}C$ + group + group × $\delta^{13}C$ + group × $\delta^{15}N$ + $\delta^{13}C \times \delta^{15}N$. Hg levels differed significantly among prey grouping ($F_{2,83}$ = 3.295, p = 0.043), and at the community level were significantly related to $\delta^{13}C$ (β = −0.381, $F_{1,83}$ = 7.222, p = 0.009) and $\delta^{15}N$ (β = 0.824, $F_{1,83}$ = 22.247, p < 0.001), with significant interactions between group and $\delta^{13}C$ ($F_{2,83}$ = 3.198, p = 0.047), group

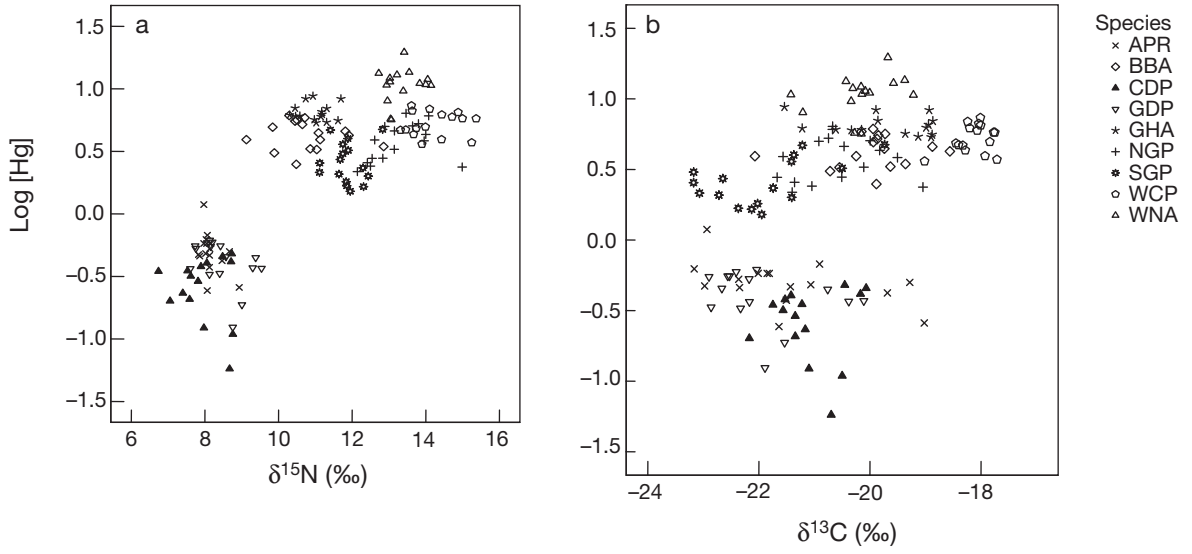

Fig. 2. Relationships between (a) $\delta^{15}N$, and (b) $\delta^{13}C$, and Hg ($\log_{10}$ transformed) in blood of Procellariiformes from South Georgia. BLP not included due to small sample size. For species codes see Fig. 1

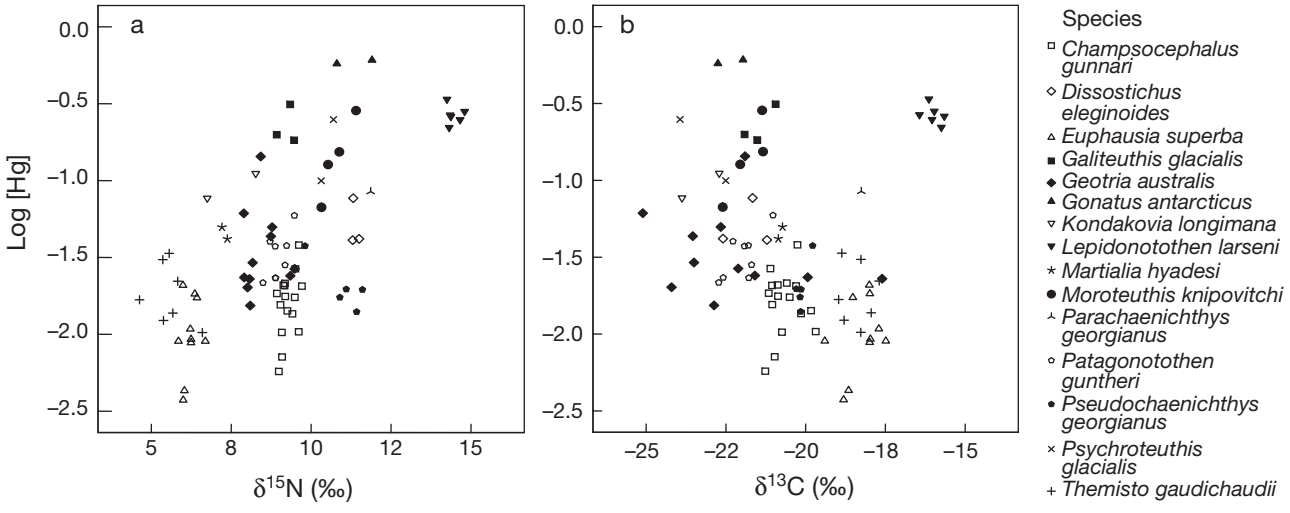

Fig. 3. Relationships between (a) $\delta^{15}N$, and (b) $\delta^{13}C$, and Hg concentration ($\log_{10}$ transformed) in prey of Procellariiformes from South Georgia

and $\delta^{15}N$ ($F_{2,83}$ = 3.679, p = 0.030), and $\delta^{13}C$ and $\delta^{15}N$ (β = 0.036, $F_{1,83}$ = 18.778, p < 0.001) (Fig. 3). The final model explained considerable variation in Hg burdens (r^2 = 0.749) (Table 4).

DISCUSSION

Hg variation in the breeding season

The significant and positive correlation between $\delta^{15}N$ isotope ratios and Hg levels in blood (after accounting for the effect of species) suggests that individual foraging preferences remain relatively constant over extended periods during breeding. The alternative, i.e. that birds change diet over time would, by comparison, result in partial 'uncoupling' of the 2 variables (Thompson et al. 1998b). Blood isotopic ratios represent diet from 3 to 4 wk prior to sampling (Haramis et al. 2001, Bearhop et al. 2002), whereas blood Hg accrues over a somewhat longer timeframe (Bearhop et al. 2000b). The significant relationship between $\delta^{15}N$ and Hg thus indicates a degree of individual adherence to diet and foraging area, as also suggested recently for a number of diving species (Bearhop et al. 2006).

The patterns of variation in blood Hg in relation to foraging location ($\delta^{13}C$) during the breeding season

Table 4. Parameter estimates for AIC selected model of prey group data (LogHg = Group + $\delta^{13}C$ + $\delta^{15}N$ + Group × $\delta^{13}C$ + Group × $\delta^{15}N$ + $\delta^{13}C$ × $\delta^{15}N$)

Parameter	β	SE	*T*	Significance	95% confidence interval Lower bound	Upper bound
Intercept	−10.215	1.768	−5.777	0.000	−13.739	−6.691
Cephalopods	0.340	1.876	0.181	0.857	−3.399	4.080
Crustaceans	8.787	3.427	2.564	0.012	1.957	15.617
Fish	0[a]					
$\delta^{13}C$	−0.381	0.088	−4.309	0.009	−0.557	−0.205
$\delta^{15}N$	0.824	0.153	5.369	0.000	0.518	1.130
Cephalopods × $\delta^{13}C$	0.039	0.079	0.491	0.625	−0.119	0.197
Crustaceans × $\delta^{13}C$	0.388	0.154	2.517	0.014	0.081	0.695
Fish × $\delta^{13}C$	0[a]					
Cephalopods × $\delta^{15}N$	0.134	0.067	2.010	0.048	0.001	0.268
Crustaceans × $\delta^{15}N$	−0.211	0.137	−1.536	0.129	−0.485	0.063
Fish × $\delta^{15}N$	0[a]					
$\delta^{13}C$ × $\delta^{15}N$	0.036	0.008	4.333	0.000	0.020	0.053

[a]This parameter is set to zero because it is redundant

were more difficult to interpret. We might have expected a positive relationship between $\delta^{13}C$ ratios and Hg burdens across a community of wide-ranging foragers such as the Procellariiformes, given the negative relationships between latitude and both $\delta^{13}C$ (Rau et al. 1991a,b, Cherel & Hobson 2007) and Hg (Bergan et al. 1999). However, overall, $\delta^{13}C$ was negatively associated with blood Hg concentrations at the community level, and the relationship was only marginally statistically significant ($p = 0.050$). This could be because we blood-sampled the albatrosses and giant petrels at the end of brood-guard, when foraging ranges are much more tightly constrained than in incubation or the later (post-guard) chick-rearing period (Phillips et al. 2004, 2006, González-Solís et al. 2008, Xavier et al. 2004). Consequently, during this time, $\delta^{13}C$ ratios of blood may be more influenced by the proportion of benthic versus pelagic or inshore versus offshore prey than by latitudinal differences in foraging location. For example, greater reliance on mesopelagic prey, which are accessible to birds foraging at night (depending on their behaviour), and which have greater Hg burdens, could contribute to the negative association between $\delta^{13}C$ ratios and Hg.

Hg variation in the non-breeding season

In the non-breeding season (represented by data from feathers), species-specific effects explained the majority of variation in Hg burdens. It is possible that widening foraging niches, with concurrent changes in diet, could explain this pattern. Equally, changing isotopic baselines as individuals migrate to distant areas (e.g. González-Solís et al. 2002, Phillips et al. 2005, 2006) could also have reduced our ability to detect the influence of dietary/trophic factors on Hg concentrations.

Procellariiformes demethylate organic Hg, accumulating high concentrations of inorganic Hg in sequestering tissues such as feathers (Muirhead & Furness 1988, Wolfe et al. 1998). Thus, inter-specific variability in capacity to demethylate organic Hg and/or sequester Hg may also explain the lack of correlation between $\delta^{15}N$ and feather Hg levels. In addition, differences in moult schedules among species can play a major role in determining feather Hg burdens (Furness 1993, Stewart et al. 1999). Wandering albatrosses moult biennially (Prince et al. 1997) and so have a relatively long period over which to accumulate Hg internally. Therefore, at the onset of moult, they 'offload' more Hg into newly-grown feathers than other Procellariiformes that moult more frequently, hence the greatly elevated feather concentrations. Grey-headed albatrosses also take 2 yr to complete moult (at least of primary feathers), but have a shorter breeding season (Prince et al. 1993) and hence a shorter inter-moult period over which to accumulate Hg before it can be incorporated into newly-grown feathers. Hence, moult schedule may well explain why the differences in feather Hg concentrations between grey-headed and wandering albatrosses are greater than would be expected simply from their trophic separation.

The foraging ranges of breeding birds are restricted by the need to return to the colony to incubate the egg or provision the chick. Outside the breeding season, many species expand their foraging ranges. This is accompanied by an increase in niche width (as reflected by increased coefficients of variation in feather stable isotope ratios relative to blood; Table 2), which reduces inter- and intra-specific competition (Bearhop et al. 2004). Variation in the relationship between feather Hg and stable isotope ratios can also be caused by changes in diet unrelated to trophic level. These may include increased feeding on prey with higher Hg concentrations if birds migrate to more contaminated areas, on offal and discards (including from demersal fisheries), or on mesopelagic prey, a known contributor

to elevated Hg intake by seabirds (Thompson et al. 1998a, Monteiro et al. 1999). Thus, dietary switches between breeding and non-breeding periods can affect Hg burdens in feathers without necessarily engendering a comparable shift in isotopic signatures. Moreover, as individuals move across regions with radically different nutrient regimes (with consequently variable $\delta^{13}C$ and $\delta^{15}N$ baselines), spatial 'uncoupling' of isotope and Hg signatures may occur, obscuring the relationship between the two (Thompson et al. 1998b). We attempted to minimise this effect by analysing a random sample of body feathers assumed to be grown at varying times in the moult cycle. However, a degree of uncoupling probably remains, and may have contributed to the lack of significant correlation between feather isotope and Hg values. Nevertheless, it is perhaps not surprising that an overall 'species' effect contributes most to Hg variation in feathers as this variable essentially integrates a multitude of ecological, behavioural, physiological and life-history differences among taxa. Moreover, among-species differences in Hg burdens were generally reflective of known foraging ranges, with those foraging at markedly lower latitudes on the continental shelf and shelf slope (which are more likely to be exposed to elevated Hg contamination) demonstrating unusually high Hg burdens relative to their trophic position, for example white-chinned petrels (Phillips et al. 2006), and those known to forage at higher latitudes (with less likelihood of contamination) displaying concurrently lower Hg burdens, for example blue petrels (Cherel et al. 2002).

Hg variation in prey

The highest blood and feather Hg concentrations were found in wandering albatrosses, with feather concentrations almost 3 times higher than in any other species (Fig. 1). Such elevated levels are suggestive of foraging at high trophic levels, which is consistent with studies indicating that wandering albatrosses feed predominantly on large squid and to a lesser extent on fish and carrion (Rodhouse et al. 1987, Xavier et al. 2004). Onychoteuthidae is the most important squid family, and *Kondakovia longimana* is the dominant species in the diet of breeding birds, although they also consume *Gonatus antarcticus*, *Martialia hyadesi*, *Moroteuthis knipovitchi* and *M. ingens*. *K. longimana* had high (but not the highest) Hg levels amongst our prey samples (Table 1). However, it should be noted that our sample sizes were relatively low and could include juveniles, whereas birds feed mainly on mature individuals of some species (Rodhouse et al. 1987, Xavier et al. 2004). This agrees with feather isotope signatures, which, after accounting for fractionation, indicate a high trophic level for typical prey items of wandering albatrosses. By comparing isotope ratios and Hg levels in predators and prey in this way, it is possible to begin to understand the routes by which particular individuals and species assimilate high Hg burdens.

Individuals foraging in more contaminated or naturally Hg-rich regions are likely to consume prey with sometimes inconsistent quantities of Hg in their tissues. This seems to be the case for white-chinned petrels, which had the highest blood Hg levels of species other than grey-headed and wandering albatrosses. During the summer, white-chinned petrels travel frequently to the Patagonian shelf to feed (particularly during pre-laying and incubation, Phillips et al. 2006), where it would appear they face greater exposure to Hg contamination. By contrast, although female southern giant petrels also visit the Patagonian Shelf, they tend to forage mainly south of the Polar Front during incubation (González-Solís et al. 2002), which may expose them to less Hg. The reason grey-headed and wandering albatrosses show even higher levels than white-chinned petrels probably has less to do with foraging location than with diet, as both feed heavily on squid (Xavier et al. 2003, 2004), which in turn often have high Hg burdens, most of which (70 to 90%) is in organic form (Bustamante et al. 2006). Hence, these species might reasonably be expected to accumulate more Hg during breeding, irrespective of moult schedule (see earlier discussion), although confirmation of this route of exposure can only come from further analyses of the total body burden of Hg in prey species.

Hg concentrations were found to vary among prey groups (Table 4), and biomagnification clearly plays an important role, as indicated by the positive association between trophic position ($\delta^{15}N$) and Hg within and among groups (Fig. 3a). Foraging location ($\delta^{13}C$) was also found to be an important determinant of Hg burdens in prey, but displayed more complex patterns (Fig. 3b). For prey, $\delta^{13}C$ is not a particularly useful proxy for latitudinal distribution, given the confounding effect of differences in distribution both in the water column (benthic versus pelagic) and in distance from shore. Indeed, the negative correlation at the community level confirms that Hg in prey species was more influenced by these factors than by larger scale changes across latitudes.

Conclusions

During the breeding season we found that species was the predominant factor affecting the assimilation of Hg levels by Procellariiformes, but that trophic position was also significant. The relationship between

trophic position and Hg has been shown to hold across a community comprised of species foraging at different trophic levels and spatial scales. However, within species patterns were not always consistent with those observed at the community level. Moreover, during the non-breeding season, we found that species was the only factor that significantly explained Hg accumulation in feathers, and no significant effect of trophic position could be detected. This is probably because of the influence of numerous other behavioural, ecological, physiological and life-history factors.

While feathers appear less useful in determining trophic/Hg relationships across taxa, future work might examine disparities in Hg burdens of individuals of the same species with different moult strategies. For example, there is the potential to examine the Hg in feathers from individuals that are successful breeders compared to those that are not. Moreover, it is not clear to what extent our findings for Hg can be extrapolated to other toxic heavy metals or organic pollutants, and further research is clearly warranted.

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