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Variability in mercury concentrations of great skuas *Catharacta skua*: the influence of colony, diet and trophic status inferred from stable isotope signatures

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ABSTRACT: A range of parameters thought to contribute to intra-specific variation in mercury levels were investigated using the feathers and blood of adult great skuas *Catharacta skua* from 2 northeast Atlantic colonies as sampling units. Different feather types and blood were taken to represent intake over different temporal scales. Mercury concentrations and stable isotope signatures of these tissues were determined. General linear models demonstrated that trophic status, as indicated by $\delta^{15}N$, had an influence on tissue mercury concentrations. However this effect was relatively minor compared to that of foraging area. Samples of the same feather types from the same individuals in consecutive years suggest that a factor other than dietary specialisation and foraging area is of major importance in determining intra-specific variability in mercury levels. It was concluded that there are a number of interacting factors contributing to intra-specific variability in mercury levels and the relative importance of these factors varies both spatially and temporally.

KEY WORDS: Mercury dynamics · Ttrophic status Intra-specific variation · Carbon-13 · Nitrogen-15 · Stable isotopes

INTRODUCTION

The oceans act as a sink for mercury, both natural and anthropogenic. The use of seabird tissues as monitors of mercury contamination in the marine environment and the advantages they offer has become well established in recent years (Burger 1993, Furness 1993). Many tissues can be used as monitoring units, but it has become commonplace to use those that can be sampled non-destructively, such as feathers and now blood. Aside from the ethical and possible conservation issues, non-destructive methods allow re-sampling of the same tissue from the same individual in following years.

Feathers are particularly attractive as monitoring units as they are the main route by which birds void mercury from the body (Braune & Gaskin 1987). During moult, levels in body tissues fall as mercury accumulated during the intermoult period is excreted into the growing feathers (Braune & Gaskin 1987), where it is chemically and physically stable (Appelquist et al. 1984). Feathers grown at the beginning of moult tend to have the highest mercury concentrations, with those grown later showing a gradual decline according to moult sequence. The implication is that the lower levels are a result of the body pool of mercury becoming de-

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pleted (Furness et al. 1986, Honda et al. 1986, Braune & Gaskin 1987).

Mercury levels in blood have not been studied in as much detail, but it is thought that they reflect short-term exposure (Furness 1993, Monteiro & Furness 1995, Evers et al. 1998, Thompson & Dowding in press). However the half times of mercury in the blood of Cory's shearwater *Calonectris diomedea* range from 40 to 65 d (Monteiro 1996), so it seems likely that these concentrations reflect exposure over months rather than weeks.

There are a number of factors thought to contribute to variation in mercury levels between seabird species such as foraging area, dietary preferences, migratory habits, age, moult and physiology (Walsh 1990). Perhaps surprisingly, there are often high levels of variation in mercury concentrations between individuals within a local population. Causes of intra-specific variation are not well understood. Whereas foraging area, moult, age, sex and season have been argued as potential sources (e.g. Walsh 1990), only recently has dietary specialisation within a species been considered (Stewart et al. 1997), and the possible influences of differences in migratory habits and physiology within a species have been somewhat neglected. Since mercury is the only heavy metal in which there is good evidence for biomagnification up food chains (Bryan 1979, Atwell et al. 1998, Monteiro et al. 1998), it seems likely that within a species individuals feeding at higher trophic levels would have higher mercury levels in their tissues (Thompson et al. 1998).

Surprisingly, there has been very little success in linking intra-specific variation in tissue mercury levels with diet. This is possibly because assessing diet by conventional means is subject to a number of biases (Duffy & Jackson 1986), although Stewart et al. (1997) found that the amount of mercury in great skua *Catharacta skua* body feathers was correlated with the proportion of bird meat in their diet. Diet studies tend to sample only during the breeding season whereas tissues sampled may not reflect mercury intake over the same period. However analysing stable isotope ratios and mercury concentrations in the same tissue could help overcome this problem. The use of stable isotopes as indicators of diet and their advantages over conventional approaches are now well established (Michener & Schell 1994). In the case of nitrogen the ratio of $^{15}N:^{14}N$ ($\delta^{15}N$) exhibits a stepwise enrichment of between 3 and 5‰ at each trophic level (e.g. DeNiro & Epstein 1981, Hobson & Welch 1992, Bearhop et al. 1999). Carbon isotope ratios ($^{13}C:^{12}C$, expressed as $\delta^{13}C$) can also increase with trophic level (Hobson & Welch 1992), but more importantly, because of differences in the $\delta^{13}C$ value of source carbon used in different photosynthetic pathways this ratio can be used to assess the relative importance of different carbon sources to a consumer such as inshore versus pelagic feeding habits (e.g. Hobson et al. 1994). Isotopic signatures of feathers reflect diet at the time of growth (Hobson & Clark 1992) and blood isotope signatures reflect diet over the preceding 2 to 3 wk (Hobson & Clark 1992).

In this study we use tissues from great skuas to investigate the influence of a wide range of parameters that contribute to intra-specific variation in mercury levels such as colony (foraging area), season, trophic status and food sources (as determined by stable isotope signatures). Three different feather types and blood were sampled to represent mercury accumulation over several temporal and spatial scales. The great skua is an ideal species for this type of study as individuals are known to specialise on particular prey types (Furness 1987). Further, great skua moult is reasonably well known, and age and sex have been shown to have no significant influence on mercury levels (Thompson et al. 1991). We provide the first quantitative assessment of the proportions of variation in mercury concentrations between individuals that can be attributed to particular factors.

METHODS

Sample collection and preparation. Samples were collected from great skua adults at Foula, Shetland (60° 08' N, 02° 05' W) during the 1996 (n = 58) breeding season and at St Kilda archipelago, Western Isles (57° 49' N, 08° 05' W), during the 1996 (n = 21) and 1997 (n = 57) breeding seasons. The 21 individuals trapped on St Kilda in 1996 had been colour ringed and the same 21 individuals were re-trapped as part of the 1997 sample. Body feather samples comprised 8 to 10 randomly sampled feathers. These should reflect mercury intake over an extended period, possibly over the whole year (inter-moult period accumulation, March to August, and intake during moult August to March). Distal portions of the 8th secondary (secondary 8) were clipped from each wing. Thompson et al. (1998) demonstrated that this feather is grown late in the great skua moult cycle when the body pool of mercury is depleted and therefore should reflect intake during winter. Distal portions of both 1st primaries (primary 1) (St Kilda only) were also taken. Primary 1 is grown at the onset of moult (immediately after breeding) and therefore should reflect mercury accumulation during the breeding season. Feather samples were stored in sealed plastic bags until preparation for analysis.

Blood samples were drawn from skuas via venepuncture of the tarsal vein using a 23 gauge × 1" (~2.54 cm) needle. These were transferred to glass

vials and stored frozen until preparation for analysis. Blood samples were taken to represent mercury intake over the breeding season prior to sampling as half times in avian blood are several weeks.

Adults often freely regurgitate their stomach contents during handling, and such samples were collected in sealed plastic bags and stored frozen. Regurgitates were divided into 6 categories reflecting the most common dietary items at the 2 colonies in these years: auk (Alcidae), herring *Clupea harengus*, sandeel *Ammodytes* spp., whitefish (Gadidae), mackerel *Scomber scombrus* and storm petrel (Hydrobatidae).

Blood and diet samples were subsequently freeze-dried to constant mass. Feather samples were briefly washed in 0.25 M sodium hydroxide to remove surface contamination and rinsed thoroughly in distilled water before being dried at 50°C to constant mass. All samples were then ground to a fine powder using an impactor mill (Spex 6700, Glen Creston, UK) operating under liquid nitrogen.

Mercury analysis. Between 50 and 100 mg of sample was placed in a 50 ml PTFE beaker with 10 ml of concentrated nitric acid. The beaker was covered with a watch glass and the digest was gently boiled for 2 h. Samples were then left to cool for half an hour after which 0.3 ml of hydrogen peroxide was added and the beaker was returned to the hotplate for a further hour. The digest was made up to 50 ml with distilled water in a volumetric flask and reduced using 2% tin (II) chloride in 10% hydrochloric acid. Total mercury concentrations were measured by atomic fluorescence spectrophotometry using a PSA 10.004 Vapour Generator coupled to a PSA 10.023 Merlin Fluorescence Detector (PS Analytical, Orpington, UK). Detection limits on a typical run (10 ppb calibration) were less than 0.1 ng g^{-1}, which is 1 order of magnitude lower than lowest concentrations measured in this study. Precision and accuracy of the method were tested using standard reference materials (TORT-2 lobster hepatopancreas ± 95% CI = 0.26 ± 0.03, n = 17, certified value = 0.27 ± 0.06) and replicate samples. Mercury levels are expressed in µg g^{-1} on a dry weight basis.

Isotope analysis. Isotopic analyses were carried out by continuous flow isotope ratio mass spectrometry (CF-IRMS) using a Europa Anca 20-20 C/N/S analyser. Samples were loaded into miniature tin cups (4 mm × 6 mm) for combustion. Runs comprised a reference sample, followed by duplicate analyses of 2 standards, and then 8 to 10 samples. This sequence was repeated throughout the batch, allowing a correction to be made for drift, if necessary. Isotope ratios are expressed in parts per thousand (‰), according to the following equation:

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

where X is ^{15}N or ^{13}C and R is the corresponding ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$. $R_{standard}$ for ^{13}C is PDB (Pee Dee belemnite) and for ^{15}N is atmospheric nitrogen (AIR). Precision and accuracy for $\delta^{13}C$ measurements was ≤0.2‰, and ≤0.4‰ for $\delta^{15}N$.

Statistical analyses. To compare mercury levels between colonies, general linear models (GLM) (general factorial) were run for each tissue type with mercury levels as the dependent variable, colony and sex as factors, $\delta^{15}N$ and $\delta^{13}C$ as covariates. For between-year comparisons the models were similar except that colony and sex were replaced by individual (n = 21) and year as factors. For mercury levels in common prey items the dependent and covariates were as before with dietary category (n = 6) and colony as factors. Arithmetic means are given in all cases.

RESULTS

Mercury concentrations and isotope signatures measured in great skua tissues and regurgitated food samples are presented in Table 1.

Between-colony comparison

Breeding season intake. A GLM showed blood mercury levels to be significantly influenced by colony ($F_{1,101}$ = 13.29, p < 0.001) with the levels in St Kilda birds almost double those of Foula (Table 1). Blood $\delta^{13}C$ signatures ($F_{1,101}$ = 8.07, p = 0.005) had a negative effect on blood mercury and there was a significant interaction ($F_{1,101}$ = 11.76, p < 0.01) between colony and $\delta^{13}C$. Sex and $\delta^{15}N$ ratios had no significant effect.

Winter intake. Similarly, colony also had a significant influence on mercury levels measured in secondary 8 ($F_{1,89}$ = 4.37, p = 0.039) although this was much reduced and concentrations in great skuas from Foula were higher than those from St Kilda (Table 1). In this case $\delta^{13}C$ signatures of secondary 8 were the dominant influence on mercury levels ($F_{1,89}$ = 19.72, p < 0.001), showing a negative relationship. The interaction between $\delta^{13}C$ and colony was also much reduced compared to blood ($F_{1,89}$ = 4.73, p = 0.032). Sex and $\delta^{15}N$ ratios had no significant influence.

Long-term intake. In body feathers, colony again had a weak effect ($F_{1,67}$ = 4.69, p = 0.034) with mercury levels in Foula birds greater than St Kilda by about 1.5 µg g^{-1} (Table 1). A significant negative relationship existed between $\delta^{13}C$ and mercury concentration ($F_{1,67}$ = 10.59, p = 0.002). In addition $\delta^{15}N$ values in body

Table 1. Total mercury concentrations (μg g^{-1} dry weight) and stable isotope ratios (‰) in tissue and diet samples from great skuas at 2 northeast Atlantic colonies. CV: coefficient of variation

Sample	n	Mean $\delta^{13}C \pm SD$	Mean $\delta^{15}N \pm SD$	Mean Hg ± SD	CV Hg, $\delta^{13}C$, $\delta^{15}N$
Foula					
Blood	57	−16.6 ± 0.4	12.1 ± 0.6	3.49 ± 1.83	52.4, 2.1, 4.9
Secondary 8	58	−14.4 ± 1.2	15.1 ± 1.2	6.04 ± 5.81	96.0, 8.6, 9.9
Body feathers	57[a]	−14.3 ± 1.4	14.1 ± 0.9	6.19 ± 4.15	67.0, 9.7, 6.6
Auk muscle	3	−12.8 ± 0.2	11.7 ± 1.1	0.38 ± 0.05	13.0, 1.2, 9.0
Herring muscle	1	−16.7	9.8	0.21	–
Sandeel	4	−14.8 ± 3.4	7.8 ± 0.5	0.04 ± 0.01	20.0, 22.8, 6.6
Whitefish muscle	2	−14.0 ± 0.9	13.1 ± 0.4	0.16 ± 0.04	25.0, 6.1, 2.7
St Kilda					
Blood	56[a]	−17.3 ± 0.5	13.1 ± 0.9	6.71 ± 3.08	45.9, 2.6, 6.5
Secondary 8 (1997)	57[a]	−13.9 ± 1.3	13.9 ± 1.5	4.26 ± 3.53	82.9, 9.2, 10.7
Body feathers (1997)	57[a]	−13.9 ± 1.2	14.2 ± 1.4	4.72 ± 3.13	66.3, 8.7, 9.8
Primary 1 (1997)	21	−15.2 ± 0.4	14.3 ± 0.8	12.05 ± 3.96	32.9, 2.5, 5.0
Auk muscle	2	−14.8 ± 3.9	11.1 ± 0.3	0.89 ± 0.09	10.1, 26.4, 2.5
Herring muscle	3	−16.9 ± 2.2	9.9 ± 0.3	0.10 ± 0.07	70.0, 13.0, 2.6
Whitefish muscle	2	−12.1 ± 0.5	12.9 ± 0.2	0.34 ± 0.06	17.7, 4.2, 1.6
Mackerel muscle	3	−15.2 ± 2.9	11.6 ± 1.1	0.17 ± 0.09	52.9, 19.2, 9.6
Petrel muscle	1	−12.4	12.0	0.23	–
Secondary 8 (1996)	21	−14.0 ± 1.4	13.9 ± 1.3	4.87 ± 2.83	58.1, 9.6, 9.2
Body feathers (1996)	21	−13.9 ± 1.1	13.8 ± 1.0	5.48 ± 2.39	43.6, 7.8, 7.2
Primary 1 (1996)	21	−15.2 ± 1.0	13.9 ± 0.9	12.89 ± 5.21	40.4, 6.3, 6.1

[a]Sample sizes differ for mercury measurements. Foula body feathers n = 38; St Kilda blood n = 33, secondary 8 n = 36, body feathers n = 33

feathers ($F_{1,67}$ = 7.23, p = 0.009) were positively correlated with mercury concentration (Fig. 1). There was significant interaction between $\delta^{13}C$ and $\delta^{15}N$ ($F_{1,67}$ = 7.19, p = 0.009) and sex had no significant effect.

Between-year comparison

There were highly significant positive correlations between years for mercury concentrations in all 3 feather types (Table 2). This was also the case for isotope signatures with the exception of primary 1 (Table 2). Paired *t*-tests showed that there were no significant between-year differences for any of the variables in any tissues, apart from $\delta^{15}N$ signatures in body feathers which were slightly higher in 1997 by about 0.4‰ (t_{20} = 3.91, p = 0.001).

GLMs showed that differences between individuals best explained variability in mercury levels, being highly significant in all 3 feather types ($F_{20,60} > 5.19$ in all cases, p < 0.001). It was the only significant factor

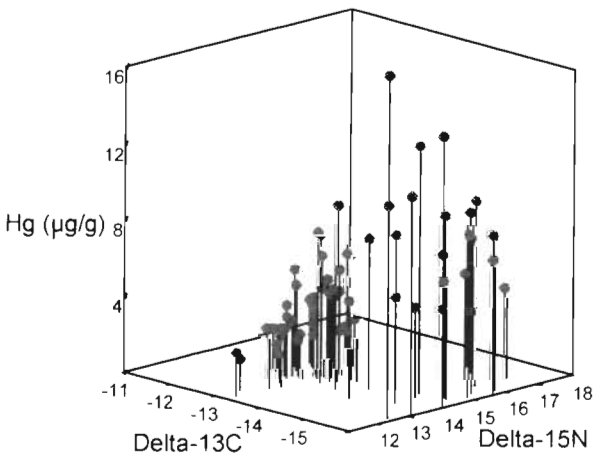

Fig. 1 Relationship between mercury concentrations, $\delta^{15}N$ and $\delta^{13}C$ in great skua body feathers

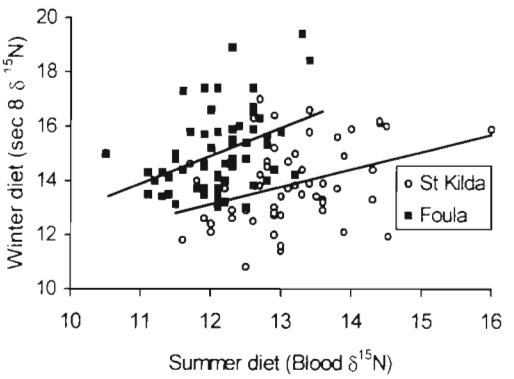

Fig. 2. Relationships between $\delta^{15}N$ values of great skua tissues indicating summer (blood) and winter (secondary 8) diets from 2 colonies

Table 2. Correlations between variables measured in the same feather type taken from the same individuals in 2 consecutive years. ns: not significant

Tissue	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Mercury ($\mu g\ g^{-1}$)
Secondary 8	$r^2 = 0.62$; $F_{1,19} = 30.89$; $p < 0.001$	$r^2 = 0.51$; $F_{1,19} = 19.84$; $p < 0.001$	$r^2 = 0.41$; $F_{1,19} = 12.62$ $p < 0.002$
Body feathers	$r^2 = 0.70$; $F_{1,19} = 44.86$; $p < 0.001$	$r^2 = 0.55$; $F_{1,19} = 23.23$; $p < 0.001$	$r^2 = 0.97$; $F_{1,19} = 34.54$; $p < 0.001$
Primary 1	ns	ns	$r^2 = 0.957$; $F_{1,19} = 23.38$; $p < 0.001$

for the between year comparison of body feathers, accounting for 87.2% of the variation in mercury levels in this tissue. Year had no significant effect on mercury levels in any of the 3 feather types. $\delta^{13}C$ ratios had a significant effect on mercury levels in primary feathers ($F_{1,18} = 19.59$, $p < 0.001$) but was not significant in any other models. There were significant positive relationships between $\delta^{15}N$ signatures and mercury levels in primary 1 ($F_{1,18} = 11.18$, $p = 0.004$) and secondary 8 ($F_{1,18} = 8.81$, $p = 0.008$), but not in body feathers.

Between-season comparison

Among different tissue types, there were very few significant relationships between the variables measured. Blood $\delta^{15}N$ signatures were significantly and positively correlated with those in secondary 8 (Fig. 2) for both Foula ($r = 0.40$, $F_{1,56} = 10.51$, $p = 0.002$) and St Kilda ($r = 0.35$, $F_{1,54} = 7.58$, $p = 0.008$). Blood mercury levels of Foula birds were significantly correlated with those in body feathers ($r = 0.62$, $F_{1,35} = 21.18$, $p < 0.001$). Finally, blood mercury levels of St Kilda birds were significantly correlated with those in primary feathers ($r = 0.49$, $F_{1,33} = 10.13$, $p = 0.003$).

Diet

A GLM showed that colony ($F_{1,7} = 33.12$, $p = 0.001$) and dietary category ($F_{4,7} = 17.96$, $p = 0.001$) had the greatest effect on mercury levels measured in dietary items of great skuas with concentrations measured in St Kilda dietary items being generally higher than those on Foula (Table 1). There was a very strong interaction between these 2 variables ($F_{2,7} = 86.82$, $p < 0.001$). $\delta^{13}C$ ratios had a relatively minor effect ($F_{1,7} = 7.07$, $p = 0.033$), but there was significant interaction between this parameter and species ($F_{4,7} = 8.16$, $p = 0.009$). $\delta^{15}N$ values of dietary items had no significant effect.

DISCUSSION

In previous papers authors have speculated on the causes underlying the high levels of intra-specific variation in mercury concentrations (Walsh 1990, Monteiro & Furness 1995). Here we provide quantitative evidence of the influence of a number of these factors and find that trophic status is a relatively minor contributor to this variation. Diet and colony also have some explanatory power; however the vast majority of variation is attributable to individual characteristics that are consistent across years, which is contrary to previous suggestions.

The observation that mercury levels in blood (taken to indicate breeding season intake) were primarily influenced by colony (St Kilda levels higher than Foula) is not surprising, as previous studies had found that mercury levels in the tissues of seabird species from St Kilda were higher than in the same species from Foula (Thompson et al. 1992). The reasons for this become clearer when the analysis of mercury levels in dietary items is considered (diet GLM). This GLM suggests that in addition to mercury concentrations in the St Kilda food web being higher than at Foula, the prey items favoured at the St Kilda colony tend to be ones with larger mercury burdens. These findings demonstrate that parallel to feeding specialisation among seabird species being a major source of inter-specific variation in mercury concentrations (Monteiro et al. 1998), feeding specialisation within a species can be a source of intra-specific variation in mercury levels. As predicted, primary 1 (one of the first feathers to be moulted) had the highest mercury concentrations since it reflects uptake and storage through the breeding season.

It was not expected that colony would still have a significant effect on winter mercury concentrations (as indicated by secondary 8). This relationship is almost certainly not a result of mercury accumulated during the breeding season being excreted into the feathers at this time as the levels in secondaries from Foula birds were higher than those from St Kilda. Since the comparison between individuals in consecutive years showed that mercury and isotope values in this feather were highly correlated (Table 2) and not significantly different from one another between years, we suggest 2 possible explanations (or a combination of these). First, great skuas from St Kilda may winter in a different region from Foula birds. The great skua is known to have several discrete wintering areas (Furness 1987). Birds in different areas may experience

different degrees of mercury exposure. For example it has been shown that Cory's shearwater *Calonectris diomedea* from the Mediterranean have much higher levels of mercury in their tissues than those from the Atlantic (Renzoni et al. 1986). The second possibility is that differences in feeding habits between the 2 colonies during the summer are maintained during winter. Great skuas at St Kilda feed predominantly on other seabirds whereas at Foula whitefish discarded from commercial trawlers are more common (Phillips et al. 1997, S.B. unpubl. data).

The significant interaction between colony and $\delta^{13}C$ (secondary 8 GLM) is consistent with both of these mechanisms. $\delta^{13}C$ ratios in feathers reflect diet at time of growth (Hobson & Clark 1992), therefore colony *per se* cannot influence these values in a feather grown in winter away from the breeding area. The feeding preference hypothesis is further supported by significant relationships, for birds from both colonies (Fig. 2), between trophic status in summer (blood $\delta^{15}N$) and trophic status in winter (secondary 8 $\delta^{15}N$). Most seabird species moult during the winter (Ginn & Melville 1983) and their tissue mercury levels decline substantially during this period (Braune & Gaskin 1987, Stewart et al. 1994). Fish cannot excrete assimilated mercury and so tissue levels tend to accumulate with age (Monteiro et al. 1991). Therefore it is possible that great skuas that feed on seabirds would experience lower mercury intake during winter months while those feeding on fish discards would not, and such a seasonal pattern is what the mercury data indicate (Table 1).

A further factor influencing mercury levels in secondary 8 may be the degree of pelagic feeding. There was a strong negative correlation between $\delta^{13}C$ and mercury concentration. Hobson et al. (1994) demonstrated that carbon isotope signatures of inshore foraging seabirds are ^{13}C-enriched compared species with pelagic feeding habits. It is also known that mesopelagic organisms have elevated mercury concentrations due to increased methylation rates beneath the thermocline (Monteiro et al. 1996). Correspondingly, seabirds feeding on these organisms have higher mercury concentrations in their tissues (Monteiro et al. 1998). Thus, pelagic feeding great skuas (with lower $\delta^{13}C$ ratios) could have higher mercury burdens due to increased influence of mesopelagic fish, either in the birds' diet or the diets of their prey.

Body feather mercury levels were also weakly influenced by colony, and again there was a negative relationship with $\delta^{13}C$ (Fig. 1) probably via the same mechanisms as described for secondary 8. However, the significant positive relationship between mercury concentrations and $\delta^{15}N$ ratios is particularly interesting (Fig. 1). Several recent studies have reported positive relationships between $\delta^{15}N$, as a measure of trophic status, and mercury concentrations, indicating biomagnification and bioaccumulation (Cabana & Rasmussen 1994, Jarman et al. 1996, Atwell et al. 1998). However, Thompson et al. (1998b) found no such relationship in great skua body feathers. They argued that isotope values and mercury concentrations in these feathers were 'uncoupled' because mercury levels in body feathers reflect varying periods of accumulation (including the breeding season) depending on what stage of the moult cycle the feather was grown, whereas isotope ratios represent diet only at time of growth. While it is clear that $\delta^{15}N$ ratios in randomly sampled body feathers cannot reflect diet during the breeding season (moult does not occur during this period), they should reflect diet over the extended period during which body feathers are moulted (August to March). Therefore, despite the fact that information on mercury accumulation and $\delta^{15}N$ information contained within body feathers reflect slightly different temporal scales, it may still be possible to detect a relationship between the 2 variables, particularly if birds do maintain feeding specialisation into the winter. However, as we have already seen, the region in which birds are foraging is very important in determining the degree of exposure an individual will experience. Thus by incorporating variables that account for area effects into the model ($\delta^{13}C$ and colony), trophic effects can become apparent as indicated by the significant positive relationship between $\delta^{15}N$ and mercury concentration in this tissue (Fig. 1).

In contrast, $\delta^{15}N$ ratios had no significant effect on mercury concentrations in blood. The half times for mercury in avian blood are weeks or months while isotope half times in blood are 11.4 d for $\delta^{13}C$ (Hobson & Clark 1992) and between 10 and 15 d for $\delta^{15}N$ (S.B., S.W., S. Votier & R.W.F. unpubl. data). In addition great skua diet is known to change in response to prey availability throughout the breeding season (Furness 1987, S.B. unpubl. data) and therefore in this instance we feel that there is uncoupling of the 2 information sources. Positive relationships between mercury concentration and $\delta^{15}N$ were detected in the analysis of mercury levels in feathers from the same individual in consecutive years (in primary 1 and secondary 8), when individual was included as a factor, again indicating that trophic effects can be masked by other influences.

Individual variation may be very important in determining mercury concentrations in tissues. Individual great skuas appear to be very conservative in terms of their feeding preferences from year to year. The coefficients of variation for the 2 isotope ratios are generally low in all of the skua tissues analysed (Table 2). Yet we found highly significant correlations between the isotope ratios in the same feather type taken from the same individual in consecutive years (Table 2). In the

case of the primary 1 the standard deviations (Table 1) are very close to accuracy limits of the analyser (see 'Methods') and it is probably not surprising that no correlations between isotope signatures in different years were detected. The coefficients of variation for mercury concentration in these feather types (Table 1) are many times greater than those for $\delta^{15}N$ and $\delta^{13}C$, which is further evidence for influences beyond foraging region and trophic status.

The importance of individual variation gains further credence in that mercury levels in the feathers of a given bird were highly correlated between years (Table 2) and that they were not significantly different from one another between years. Further, year was not a significant factor in any of the between-year GLMs whereas individual was; indeed, in the GLM for body feathers individual accounted for 87.2% of the variation in mercury concentration. Sex was not a significant factor in any of the models, so it seems unlikely that differences between males and females are driving the relationship; besides, previous studies of mercury levels in great skuas have failed to find any differences between the sexes (Thompson et al. 1991). It is possible that differences in the amount of mesopelagic prey in individual diets could account for some of this variation. However, individual was the major influence on primary 1 mercury levels in consecutive years and this represents great skua diet at a time (breeding season) when conventional studies show mesopelagic prey to be extremely rare (Phillips et al. 1997, Thompson et al. 1998a). Therefore some other factor is extremely important in determining intra-specific variability in mercury concentrations. Differences in individual physiology are generally considered unimportant in influencing intra-specific variability in tissue mercury concentrations. Nevertheless is has been demonstrated that rates of mercury excretion in humans are very variable (Al-Shahristani & Shihab 1974) and it is possible that individual seabirds might vary in the efficiency with which they excrete mercury into the feathers, but this would require further investigation.

It is clear that there are a number of interacting factors determining intra-specific variation in mercury concentrations and that the importance of these factors is variable both temporally and spatially. Foraging region, perhaps not surprisingly, seems to be an important factor, with trophic status effects being relatively minor, and the possibility of physiological differences among individuals should be considered. This study highlights the utility of stable isotopes in the evaluation of suitable species to act as biomonitors and the tissues to choose as monitoring units. In the case of great skuas, blood would seem to be a good indicator of mercury intake during the breeding season. Body feathers, as suggested by Furness et al. (1986), are probably good indicators of long-term intake (in the order of 1 yr). However, despite the attractiveness of gathering information on mercury intake and diet during winter months when birds are away from the colonies through stable isotope analyses, detailed information on the seasonal movements of biomonitor species is required before the potential for flight feathers can be fully realised.

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