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Spatial variations in winter Hg contamination affect egg volume in an Arctic seabird, the great skua (*Stercorarius skua*)

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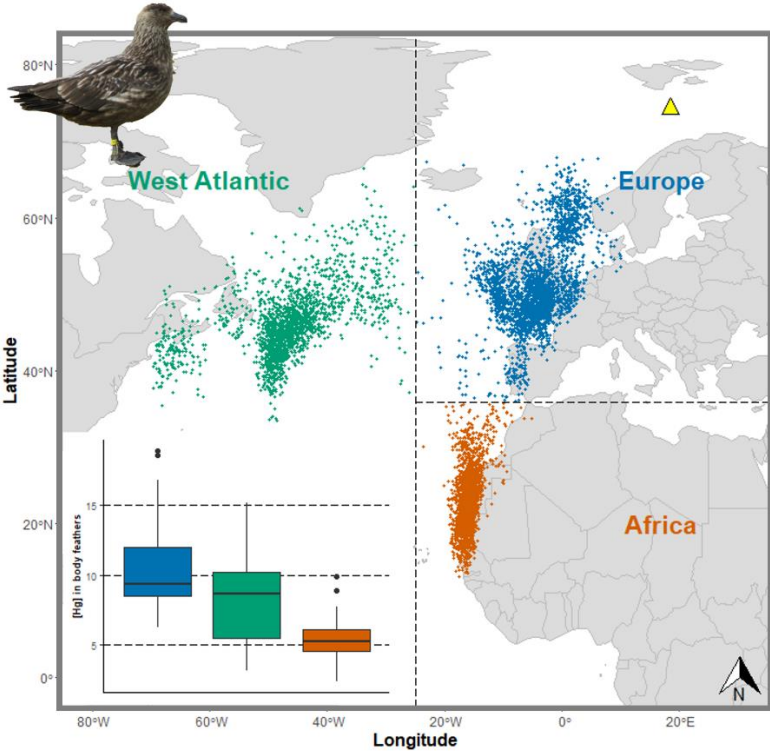
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Graphical abstract



Abstract: Knowledge of the ecology and at-sea distribution of migratory species like seabirds has substantially increased over the last two decades. Furthermore, an increasing number of studies have recently focused on chemical contamination of birds over their annual cycle. However, the understanding of the combined effects of spatial movements and contamination on seabirds' life-history traits is still scarce. During winter, seabirds can use very different areas, at the large-scale. Such overwintering strategies and distribution may expose individuals to contrasting environmental stressors, including pollutants. Here, we studied the winter distribution and contamination with mercury (Hg), and their combined effects on reproduction, in a great skua (*Stercorarius skua*) population breeding in Bjørnøya, Svalbard. We confirmed that individuals of this specific population overwinter in three different areas of the North Atlantic, namely Africa, Europe and northwest Atlantic. The highest Hg concentrations in feathers were measured in great skuas wintering off Europe (Linear Mixed Models - mean value \pm SD = $10.47 \pm 3.59 \mu\text{g g}^{-1}\text{dw}$), followed by skuas wintering in northwest Atlantic (8.42 ± 3.70) and off Africa (5.52 ± 1.83). Additionally, we found that female winter distribution and accumulated Hg affected the volume of their eggs (Linear Mixed Models), but not the number of laid and hatched eggs (Kruskal-Wallis tests). This study provides new insights on the contamination risks that seabirds might face according to their overwinter distribution and the possible associated carry-over effects.

Keywords: Mercury, Reproduction, Spatial ecotoxicology, Carry-over effects, Biologging

Synopsis: The combination of large-scale geo-tracking and ecotoxicology reveals spatial differences in Hg contamination and associated carryover effects on seabird reproduction.

INTRODUCTION

The use of geo-tracking technology has substantially improved our understanding of pressures that wildlife has to face in the marine environment. For instance, knowledge about winter ecology and at-sea distribution of migratory species like seabirds has increased considerably in recent decades. Yet, our understanding of the effects of this period on bird life-history traits is still scarce ([Strøm et al., 2021](#)). During the non-breeding period, seabirds travel long distances, and individuals from the same breeding population can use highly different wintering areas ([Leat et al., 2013](#)). Such different overwinter strategies and distributions may expose individuals to contrasting environmental stressors, like human activities ([Dupuis et al., 2021](#)), resource availability ([Frederiksen et al., 2012](#)), extreme climatic events ([Clairbaux et al., 2021](#); [Guéry et al., 2019](#)) or pollutants ([Fort et al., 2014](#); [Leat et al., 2013](#)), which may affect individual fitness and ultimately shape population processes ([Clairbaux et al., 2021](#)).

Among those stressors, pollutants like mercury (Hg) are of particular concern. Mercury is a metallic trace element naturally occurring in the environment but its concentrations have dramatically increased since the industrial revolution because of human activities ([UN Environment Programme, 2019](#)). It is in aquatic environment that Hg is the most problematic as it can be easily transformed into its most toxic form (methylmercury – MeHg) by microorganisms ([Hsu-Kim et al., 2013](#)). Hence, once incorporated in the marine food webs, this pollutant bioaccumulates in organisms and biomagnifies along the trophic pathways ([Morel et al., 1998](#)), making long-lived top predators like seabirds highly exposed to Hg and thus susceptible to its toxic effects ([Chastel et al., 2022](#); [Dietz et al., 2013](#)). Furthermore, emitted Hg is transported over large distances through oceanic, atmospheric or riverine currents, leading to its global, but heterogeneous distribution in the marine environments ([Zhang et al., 2020](#)). For instance, Hg concentrations in marine food webs show an east-west increasing gradient across the North Pacific ([Fleishman et al., 2019](#)) and the North Atlantic ([AMAP, 2011](#); [Provencher et](#)

al., 2014; UN Environment Programme, 2019). Hence, contrasting winter distributions adopted by seabirds could lead to variable Hg exposure and subsequent fitness effects (Albert et al., 2021).

Mercury can have various eco-toxico-physiological impacts on seabirds and wildlife in general (Chastel et al., 2022; Wolfe et al., 1998). Nonetheless, reproduction is one of the main endpoints for Hg toxicity, which can affect parental behavior or breeding success. For instance, in black-legged kittiwakes (*Rissa tridactyla*), males with the highest Hg concentrations were more likely to neglect their eggs (Tartu et al., 2015) and had a lower breeding success (Tartu et al., 2016). In grey-headed albatrosses (*Thalassarche chrysostoma*), individuals with the highest feather Hg concentrations experienced higher reproduction failure (Mills et al., 2020). Ultimately, Hg can affect seabird population dynamics such as in black-legged kittiwakes and both south polar (*Catharacta maccormicki*) and brown skuas (*C. lonnbergi*) where Hg was negatively related to breeding probability (Goutte et al., 2015) and breeding success (Goutte et al., 2014), respectively. However, specific effects of the non-breeding contamination on breeding success is still poorly known, especially when considering winter distribution. In little auks (*Alle alle*), Fort et al., (2014) suggested a carry-over effect with individuals with the highest Hg concentrations, overwintering off the Grand Banks of Newfoundland, laying smaller eggs.

In this context, the present study aimed to investigate how different wintering strategies and non-breeding distributions by individuals sharing the same breeding site influence their Hg contamination during winter and their subsequent body condition and reproduction. More specifically, we tested the hypothesis that different winter Hg concentrations, under the influence of contrasting winter distributions, negatively impact individual body mass and reproduction, studied through the egg volume, laying and hatching success. To this end, we focused on great skuas (*Stercorarius skua*) breeding on Bjørnøya, Svalbard. Bjørnøya is known

as a sink for contaminants such as Persistent Organic Pollutants (POPs) in the North Atlantic, where high concentrations were recorded in seabirds (e.g., glaucous gull *Larus hyperboreus* (Bustnes et al., 2003), great skua (Bourgeon et al., 2012; Leat et al., 2013)). However, information about Hg concentrations in the region are still limited. Great skuas are large top predators endemic to the northeast Atlantic that have seen their numbers increasing since the beginning of the 20th century. The great skua was first recorded breeding on Bjørnøya in 1970. Since then, the population has been growing rapidly and the total North Atlantic breeding population was in 2015 estimated at 16,300 to 17,200 breeding pairs (BirdLife International, 2015).

MATERIAL AND METHODS

Study site and sampling

Fieldwork was conducted on Bjørnøya in Svalbard, Norway (74°29'N, 18°49'E) (Fig 1) from 2014 to 2017. Geolocators (hereafter “GLS”) (< 0.4% of birds' body mass), attached on a color leg ring, were deployed from 2014 to 2016 and retrieved every following year (**Table A.1**). At the GLS retrieval, three body feathers (back or chest) were sampled on each individual and stored into a Ziploc® plastic bag at ambient temperature until analyses. Feathers have proven their efficiency as proxy of Hg concentrations during different periods of the year (Albert et al., 2019). In great skuas, feathers are moulted from August to March and therefore possibly inform about both breeding and non-breeding periods (Bearhop et al., 2000). Mercury concentrations in feathers represent the Hg accumulated between two molts and inform about the Hg body burden at the molting time (Agusa et al., 2005; Furness et al., 1986). As a consequence, Hg concentrations in feathers are not affected by the age of the individual (Bustamante et al., 2016; Honda et al., 1986). In total, 67 tracking and associated Hg contamination datasets were collected (2015 (n = 14), 2016 (n = 12) and 2017 (n = 41)), with

some individuals recaptured several years (**Table A.2.**). Individuals with undefined sex were removed (n = 13) leaving a dataset composed of 27 individuals and 40 observations (9 individuals captured from 2 to 3 years). Additionally, body mass (with Pesola weight, precision ± 5 g), skull length (head + bill, with caliper, precision ± 0.5 mm) and wing length (with wing ruler, precision ± 1 mm) were measured at the GLS deployment. The number of eggs was monitored when the GLS was retrieved, eggs' length (L) and breadth (B) were measured and eggs' volume calculated following the equation $V = \pi /6 x LB^2 / 1000$ (Stempniewicz et al., 1996). Skua sampling and measurements were performed during the incubation (**Table A.3.** for average and range dates). Each nest was then monitored to record the hatching success.

Sample preparation and analysis

Before Hg analyses, the calamus and down were first removed. The three feathers were then cleaned to remove external contamination in a 3 min ultrasonic bath of 2:1 methanol:chloroform solution, then rinsed twice in a methanol bath, dried for 48 hours at 45°C and homogenized with alcohol-rinsed stainless steel scissors. Total Hg analyses were done on subsamples of 0.28 ± 0.09 mg (mean \pm SD) (range: 0.15 - 0.63) of homogenized feathers using an Advanced Mercury Analyzer spectrophotometer (Altec AMA 254) at the laboratory Littoral Environnement et Sociétés (LIENSs, La Rochelle, France) and as described in Chouvelon et al.(2009). Total Hg concentrations are used as a proxy of MeHg as more than 80 % of the Hg excreted into feathers is under its organic and toxic MeHg form (Bond and Diamond, 2009; Renedo et al., 2017; Thompson and Furness, 1989). Two replicates were measured per sample, and we controlled that for all samples the relative standard deviation was $< 10\%$ (mean \pm SD = 3.80 ± 0.03 %). The mean value of these two measurements was then used for statistical analyses. Measurements' accuracy was ensured using a Certified Reference Materials (CRM) analysed each 15 samples. The CRM was a dogfish liver DOLT-3, NRCC (reference value =

0.337 $\mu\text{g g}^{-1}$, mean measured \pm SD = $0.349 \pm 0.004 \mu\text{g g}^{-1}$, % recovery = 104 %, n = 6). Mercury concentrations (mean \pm SD) are expressed in $\mu\text{g g}^{-1}$ dw (i.e., dry weight). Blanks were run prior analyses and the detection limit of the AMA was 0.05 ng.

Spatial analysis

To obtain locations from raw light levels, we followed the procedures described in Bråthen et al. (2021), but adapted to the great skuas, described here in **Table A.4**. Briefly, we used a threshold method to estimate twilights events, from which two positions could be calculated per day, based on the length of day and night (latitudes) and the timing of noon and midnight (longitudes). Using an approach by Hanssen et al. (2016), the suns' angle to the horizon during twilight was determined for each non-breeding season, which is necessary for estimating reliable latitudes from length of day and night. Due to the number of factors that can interfere with timing of twilights (e.g. cloud cover, shading of the sensor and artificial light), twilights and positions was filtered for erroneous data, before positions were smoothed to limit the influence large and rapid migratory movements may have on timing of twilights. Latitudes derived from day and night length gets increasingly unreliable in weeks close to the September (21st –24th) and March (19th - 21st) equinoxes, because in the daylength gets similar across a very wide latitudinal gradient. Therefore, latitudes were disregarded for a period in autumn (8th Sep – 20th Oct) and spring (20nd Feb – 3rd Apr). Finally, we used daily mean positions to determine the winter distribution of each individual. Based on the distance to the colony, calculated as great circle distances and considering spherical Earth (**Fig. A.2.**), we assumed that skuas were on their wintering ground from 21th October to 19th February each year. Therefore, this is the period of the year that was defined as winter.

Following results on skua distribution (see results for more details), three wintering areas were defined: northwest Africa (corresponding to positions $\leq 35.94^\circ\text{N}$ and $\geq 25.01^\circ\text{W}$),

Europe ($\geq 35.97^{\circ}\text{N}$ and $\geq 25.01^{\circ}\text{W}$) and northwest Atlantic ($\leq 25.00^{\circ}\text{W}$) (**Fig. 1**). Each individual was considered to overwinter in one of these three areas if more than 75 % of all its wintering positions were located within the area and disregarded from statistical analyses otherwise (i.e. individuals considered having an intermediate winter period - 14 individuals) (**Table A.5**). Nine individuals caught for 2 to 3 years are included in the dataset. One individual (female) spent $>75\%$ of winters 2014-2015 and 2015-2016 in Africa. However, in 2016-2017, it spent 65% of its time in Africa for 31% in Canadian waters. Therefore, the 2016-2017 winter was removed for this individual. The remaining 8 individuals for which we had several years of tracking data kept a constant wintering ground, in which 5 repeatedly overwintered in Africa, 3 in Europe and 1 in West Atlantic.

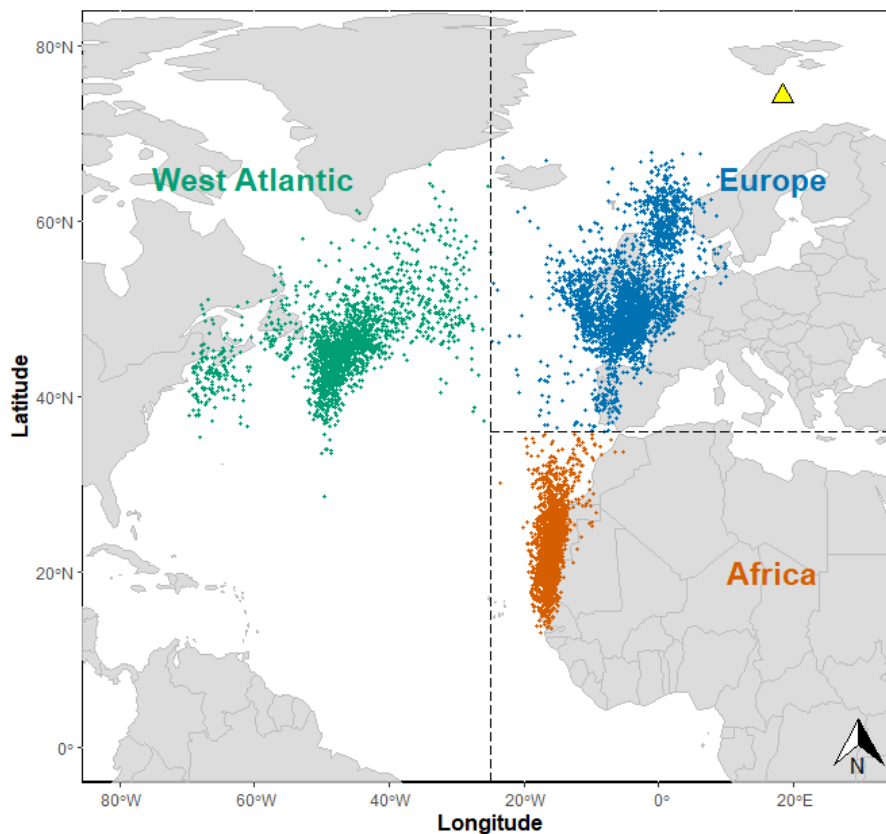


Figure 1. Winter distribution (November-January) of the tracked great skuas (i.e. both females and males, $n = 59$) breeding in Bjørnøya in winters 2014-2015 to 2016-2017 (yellow triangle) and wintering in Africa (orange), Europe (blue) and West Atlantic (green). Each dot represents daily distribution per individual from November to January (see methods).”

Statistical analysis

We used single Linear Mixed Models (LMMs) to account for repeated sampling of individuals, having ID Bird as a random factor. Hg concentrations were log_e-transformed to meet the parametric assumptions of normality and homoscedasticity of residual distribution. As there were no inter-annual variation in Hg concentrations (LMM1, $F_{2,17.05} = 2.591$, $p = 0.104$, **Fig. A.1., Table 1**) Hg data for all three years were pooled in subsequent analyses. We tested whether Hg concentrations differed according to the used wintering areas and sex (LMM2), under the form: Hg concentrations ~ winter distribution * sex + (1|ID Bird). LMM1 and LMM2 included 40 annual winter distributions represented by 27 individuals (21 females, 6 males), in which 9 skuas had been tracked over 2 or 3 non-breeding seasons.

Table 1. Full models and model selections (for LMM3 and LMM4 only) of the Linear Mixed Models used in the present study. ID Bird was added as a random effect as females could lay up to 2 eggs for up to 3 years. The table includes the AICc, Δ AICc, weight and df (number of parameters) for LMM3 and LMM4.

Variable	Model	AICc	Δ AICc	Weight	df
LMM1					
Hg concentrations	~ sampling year + (1 ID Bird)	-	-	-	-
LMM2					
Hg concentrations	~ winter distribution * sex + (1 ID Bird)	-	-	-	-
LMM3					
Egg volume	~ Hg concentrations * winter distribution + (1 ID Bird)	870.2	0	0.71	8
	~ Hg concentrations + (1 ID Bird)	875.0	4.8	0.07	4
	~ 1 + (1 ID Bird)	875.2	5.0	0.06	3
	~ winter distribution + (1 ID Bird)	875.4	5.2	0.05	5
	~ Hg concentrations + winter distribution + (1 ID Bird)	876.4	6.2	0.03	6
	~ Hg concentrations + body mass + (1 ID Bird)	877.1	6.9	0.02	5
	~ body mass + (1 ID Bird)	877.4	7.2	0.02	4
	~ body mass + winter distribution + (1 ID Bird)	877.6	7.4	0.02	6
	~ Hg concentrations + body mass + winter distribution + (1 ID Bird)	878.5	8.3	0.01	7
	~ Hg concentrations * body mass + (1 ID Bird)	878.8	8.6	0.10	6
	~ Hg concentrations * body mass + winter distribution + (1 ID Bird)	880.5	10.3	0.004	8
	~ body mass * winter distribution + (1 ID Bird)	882.9	12.7	0.001	8
	~ Hg concentrations + body mass * winter distribution + (1 ID Bird)	883.8	13.6	<0.001	9
~ Hg concentrations * body mass * winter distribution + (1 ID Bird)	885.2	15.0	<0.001	14	
LMM4					
Body mass	~ Hg concentrations * winter distribution + (1 ID Bird)	602.5	0	0.99	8
	~ 1 + (1 ID Bird)	615.1	12.6	0.00	3
	~ Hg concentrations + (1 ID Bird)	617.4	14.9	<0.001	4
	~ winter distribution + (1 ID Bird)	618.5	16.0	<0.001	5
	~ Hg concentrations + winter distribution + (1 ID Bird)	621.0	18.5	<0.001	6

The number of eggs laid and hatched per individuals ($n = 34$ and 29 , respectively) was compared between wintering areas using Kruskal-Wallis tests. As Hg concentrations were different between sexes (LMM2 - $F_{1,31.72} = 16.87$, $p < 0.001$) and as our focus is on breeding success, males were disregarded for the following statistical analyses. Additionally, only female laying two eggs (21 individuals for 29 observations) were considered in the analysis for “hatching success”, as mixing females laying both 1 egg (for which 0 or 1 egg only could hatch) and 2 eggs (for which 0, 1 or 2 eggs could hatch) would bias obtained results. All females laid 2 eggs at least once. We tested the effect of the wintering areas and Hg concentrations in female feathers on eggs’ volume (with females laying 1 or 2 eggs) using a model under the form: egg volumes \sim winter distribution * Hg concentrations * body mass + (1|ID Bird) (LMM3). Then, we investigated the effects of female skua body mass (g), winter distribution and Hg concentrations on the egg volumes using body mass (g) as a proxy (LMM4). Indeed, we could not use the scaled mass index (SMI - adjust body mass to body size) or regression method as proxy of body condition as none of the relationships between the body mass (g) and the wing (mm) or the head bill (mm) were significant ($F_{1,50} = 3.223$, $p = 0.079$; $F_{1,50} = 0.109$, $p = 0.742$, respectively – female only, laying one or two eggs). To do so, we tested if body mass was affected by Hg concentrations and winter distribution. The full model was under the form: body mass (female only) \sim Hg concentrations * winter distribution + (1|ID Bird).

We used the Akaike Information Criterion corrected for small sample sizes (AICc) (Burnham and Anderson, 2002) to compare models, using the package “bbmle” (Bolker and R Development Core Team, 2021). When two models had close AICc values ($\Delta\text{AICc} < 2$), the model with the lowest number of factors were selected following the principle of parsimony (Burnham & Anderson, 2002). Otherwise, the model with the lowest AICc was selected. (Burnham & Anderson, 2002). The linear mixed models were performed with packages “lme4” (Bates et al., 2015) and “LmerTest” (Kuznetsova et al., 2017). Statistical analyses were

performed with R version 3.4.3 (R Core Team, 2017). Mean values are reported with standard deviation (mean \pm SD) and model estimates with standard error (mean \pm SE). When required, statistical significance was assumed at $p < 0.05$.

RESULTS & DISCUSSION

Great skuas from Bjørnøya overwintered in three different areas: off Africa, off Europe and in northwest Atlantic, which confirms previous results for this specific population (Leat et al., 2013; Magnusdottir et al., 2012). Out of the 27 studied individuals, 11 spent the winter mostly off Europe (9 females, 2 males) while 9 of them overwintered mostly off Africa (7 females, 2 males) or 7 in West Atlantic (5 females, 2 males). On the 9 individuals tracked for several years, 8 of them consistently overwintered in the same area (see **Material and Methods section** for details). In the present study, trophic data, through the use of nitrogen stable isotopes were not used. Indeed, Hg concentrations in feathers represent an intermolt period, whereas nitrogen stable isotopes represent the period of feather growth only. Therefore, as they do not provide information for the same time periods, the isotopic values cannot be directly compared with Hg measurements in the feathers (Bond, 2010).

Mercury concentrations measured in feathers of great skuas were on average $7.84 \pm 3.64 \mu\text{g g}^{-1} \text{ dw}$ (range: 2.39 to $18.88 \mu\text{g g}^{-1} \text{ dw}$, $n = 40$) and varied significantly according to the winter distribution (LMM2, $F_{2,23.52} = 18.51$, $p < 0.001$) and the sex of the individuals (LMM2, $F_{1,31.72} = 16.87$, $p < 0.001$). A model selection of LMM2 showed that the best model comprises both winter distribution and sex, but without interactions (**Table A.6.**). More specifically, mean Hg concentrations were statistically different between all regions with the highest concentrations for skuas wintering off Europe (estimates \pm SE = $2.40 \pm 0.11 \mu\text{g g}^{-1} \text{ dw}$ – mean value \pm SD = $10.47 \pm 3.59 \mu\text{g g}^{-1} \text{ dw}$), followed by northwest Atlantic (estimates \pm SE = $2.16 \pm 0.11 \mu\text{g g}^{-1} \text{ dw}$ – mean value \pm SD = $8.42 \pm 3.70 \mu\text{g g}^{-1} \text{ dw}$) and skuas wintering off Africa

(estimates \pm SE = $1.71 \pm 0.08 \mu\text{g g}^{-1} \text{dw}$ – mean value \pm SD = $5.52 \pm 1.83 \mu\text{g g}^{-1} \text{dw}$) (**Fig. 2**). Spatial variations in Hg concentrations in seabirds have been highlighted in most of the North Atlantic ([Albert et al., 2019](#); [AMAP, 2021](#); [Provencher et al., 2014](#)), and previous studies suggested Hg hotspots off Newfoundland ([Fort et al., 2014](#)) and a positive east-west Hg gradient in the North Atlantic ([Albert et al., 2019](#); [AMAP, 2018](#); [Provencher et al., 2014](#)). However, such a knowledge was still scarce for the southern part of Europe or northern parts of Africa. Our results are in agreement with previous investigations for the North Atlantic, but also highlight that great skuas strongly contaminate when overwintering off the European coasts. This supports previous work suggesting that wintering grounds play a major role in the contamination of wildlife by pollutants ([Albert et al., 2021](#); [Fort et al., 2014](#); [Leat et al., 2013](#)) and that species with similar winter diet as skuas can have the same exposure. These new results are important as many seabird species are known to use European waters during winter ([Fauchald et al., 2021](#)) and species with similar diet as skuas could therefore experience a similar high environmental Hg contamination. Conversely, northwest Africa could represent a less Hg contaminated area to wintering seabirds with similar winter diet of great skuas, although low Hg concentrations do not necessarily mean no toxicological impacts. Additionally, spatial variations in other pollutants (e.g., poly-brominated diphenyl ethers - PBDEs) were reported between three different wintering grounds used by skuas, with for instance lower concentrations of PBDE 47 in skuas wintering off Africa than in northwest Atlantic or Europe ([Leat et al., 2013](#)).

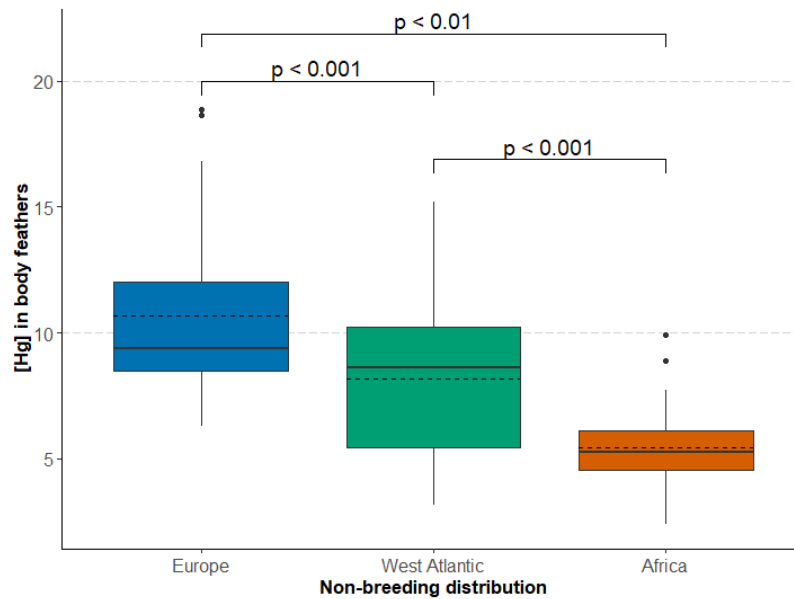


Figure 2. Mean Hg concentrations ($\mu\text{g g}^{-1}\text{ dw}$) measured in body feathers in relation to bird winter distribution. Mean Hg concentrations are represented by dashed black lines and are $10.61 \pm 3.60 \mu\text{g g}^{-1}\text{ dw}$ for Europe, $8.37 \pm 3.49 \mu\text{g g}^{-1}\text{ dw}$ for West Atlantic and $5.19 \pm 1.91 \mu\text{g g}^{-1}\text{ dw}$ for Africa. Boxplots show the median (horizontal black line within the boxes), 1st and 3rd quartiles, the minimum (1st-1.5x interquartile range) and maximum (3rd-1.5x interquartile range) concentrations (lower and upper whiskers) and outliers.

Mercury concentrations measured in female feathers were higher (estimates \pm SE = $1.71 \pm 0.08 \mu\text{g g}^{-1}\text{ dw}$ – mean value \pm SD = $8.30 \pm 3.61 \mu\text{g g}^{-1}\text{ dw}$) than in males (estimates \pm SE = $1.15 \pm 0.13 \mu\text{g g}^{-1}\text{ dw}$ – mean value \pm SD = $5.23 \pm 2.78 \mu\text{g g}^{-1}\text{ dw}$). This influence of sex on Hg concentrations found in great skuas has been shown in other seabird species, but males were generally found to have higher concentrations than females (but see [Mills et al., 2022](#); [Provencher et al., 2016](#)). Similarly, Leat and colleagues (2013) studied contamination with POPs for the same population of great skuas, and also found that males had higher concentrations of POPs (i.e., organochlorines, PBDEs) than females. These differences between our study and the literature likely result from the different tissues investigated. In the present study, Hg was measured in feathers (i.e., representing an integrated annual contamination), while Hg and POPs in previous studies were assessed in blood during the breeding time (i.e., indicating shorter-term contamination) only. Such contrasting sexual patterns in different

periods thus suggest that female are more contaminated during winter, but then partly excrete Hg into their eggs at the onset of the breeding period (Leat et al., 2013; Mills et al., 2022; Robinson et al., 2012), decreasing their body loads below the ones of males in summer as reflected by blood. Higher contamination during the non-breeding period found in female great skuas could also partly result from a trophic segregation (Carravieri et al., 2014a) with females feeding at higher trophic level or in different feeding habitats. However, data about diet and its variation between sexes are too scarce to support this hypothesis. A sexual dimorphism occurs in the species with females being bigger than males (Catry et al., 1999; Dunning, 2007), which could also partly explain the obtained results.

Interaction between the non-breeding distribution and the sex of the individuals were not supported in our model selection (**Table A.6.**), suggesting that the observed sex difference could not be explained or accentuated by the three different wintering areas. Like for previous studies performed on great skuas from Bjørnøya (Leat et al., 2013; Magnúsdóttir et al., 2012), we should stress that females were overrepresented in our dataset (21 for 6 males – 2 males wintering in each area), mainly because (1) 13 individuals had to be removed from our initial dataset because they could not be sexed, and (2) males spend more time foraging than females during the breeding period as they feed both females and chicks, decreasing catching and sampling opportunities (Caldow and Furness, 2000; Catry et al., 1999). This calls for further investigations with enhanced male sample sizes, although this bias in sex ratio should not affect our results regarding the effects of Hg and winter distribution on skua reproduction using female samples only (see below).

Feather mean Hg concentrations measured in the present study were higher than those measured in the same tissue for other European great skua populations, except when considering individuals wintering off Africa only. Indeed, in St Kilda archipelago, Foula and Shetland Islands (Scotland), feather Hg concentrations were 4.72 ± 3.13 , 6.19 ± 4.15 and 6.80

$\pm 4.40 \mu\text{g g}^{-1}$ dw, respectively (Bearhop et al., 2000; Thompson and Furness, 1989). These populational differences might be explained by the different seabird distributions and thus exposure to Hg, both during winter and during the breeding period. Skuas breeding in Shetland Islands (Scotland) are known to spend the winter in Europe or off Africa (but not in northwest Atlantic) (Leat et al., 2013). While individuals from Shetland Islands wintering off Africa show relatively similar Hg concentrations in their feathers than skuas from Bjørnøya, this is not the case for those wintering in Europe. These inter-population differences could be explained by historical variations of Hg in marine ecosystems. Indeed, studies on skuas from Scotland (Bearhop et al., 2000; Thompson and Furness, 1989) were conducted two to three decades ago when Hg concentrations may have been lower in the marine environment than nowadays (AMAP, 2018; Tartu et al., 2022). Such a temporal increase in North Atlantic seabird Hg contamination has for instance been observed in several seabirds population of the North-Atlantic Arctic (Fort et al., 2016; Morris et al., 2022). On the other hand, such spatial differences could also be explained by a higher exposition in Bjørnøya during summer, area known to be a sink for pollutants (Bourgeon et al., 2012; Bustnes et al., 2003; Leat et al., 2013), compared to the Shetland Islands.

Beyond skuas, Hg concentrations measured in the present study are some of the highest found in Arctic and North Atlantic seabirds (AMAP, 2021) and highlight potential associated toxicity risks, especially for skuas wintering in the European waters and in the northwest Atlantic. Within our sampled individuals, 81 % showed Hg concentrations above the toxicity benchmark set up at $5 \mu\text{g g}^{-1}$ dw in feathers (Eisler, 1987). Among potential reproductive effects of winter Hg contamination, reduced egg volume has been reported in little auks (Fort et al., 2014). Here, mean values suggest that female skuas wintering in the most contaminated areas laid the highest number of eggs (West Atlantic: 2.00 ± 0.00 ; $n = 6$; Europe: 1.92 ± 0.29 ; $n = 12$; Africa: 1.75 ± 0.45 egg laid per nest; $n = 16$), but had the lowest hatching success (Europe: 1.25

± 0.75 ; $n = 11$; West Atlantic: 1.33 ± 1.03 ; $n = 6$; Africa: 1.38 ± 0.72 egg hatched per nest; $n = 12$). However, in both cases, inter-wintering site values were not significant (number of eggs laid: Kruskal-Wallis chi-squared = 2.69, $df = 2$, $p = 0.26$; number of eggs hatched: chi-squared = 0.44, $df = 2$, $p = 0.80$). Furthermore, we showed a linear relationship between female egg volumes and feather Hg concentrations, which differed according to their wintering areas, independently of their body mass (LMM3, $AICc = 870.2$) (Table 1) (Fig. 3). Indeed, our best model showed that egg volumes were affected by Hg concentrations ($F_{1,47.81} = 9.86$, $p < 0.01$), non-breeding distribution ($F_{2,42.86} = 6.24$, $p < 0.01$) and the interaction between those two variables ($F_{2,44.25} = 6.48$, $p < 0.01$). More specifically, egg volumes in relation to Hg concentrations showed a negative linear relationship for females overwintering off Africa and in the northwest Atlantic, but a positive linear relationship for females overwintering off Europe (Fig.3). In addition, female body mass was related to both Hg concentrations and winter distributions (LMM4, $AICc = 602.5$) (Table 1) (Fig. 4), as recently demonstrated in free-ranging birds (Carravieri et al., 2022). Indeed, following the model LMM3, our best model showed that female body mass was affected by Hg concentrations ($F_{1,34.58} = 11.13$, $p < 0.01$), non-breeding distribution ($F_{2,40.09} = 14.79$, $p < 0.001$) and the interaction between those two variables ($F_{2,34.69} = 30.60$, $p < 0.001$) (Fig. 4). Altogether, our results therefore suggest a carry-over effect, with Hg contamination during the non-breeding period impacting skuas during their reproduction. Although highest Hg concentrations were measured in skuas which overwintered in Europe, this contamination did not affect either the volume of their eggs (Fig. 3) or the female body mass (Fig. 4), but was associated with a lower hatching success. Conversely, females overwintering off Africa had the lowest mean Hg concentrations and the highest hatching success, but both female body mass and egg volume were negatively related to Hg concentrations. Those results highlight that winter distribution and subsequent Hg contamination differently affect the reproduction of great skuas breeding in Bjørnøya. The

hypothesis of a carry-over effect is supported by our earlier discussion about sexual dimorphism in great skuas. Hg contamination during the breeding period is not always associated with impacts on reproduction in seabirds, as showed in Leach's storm-petrels (*Oceanodroma leucorhoa*) or Antarctic petrel (*Thalaccoica antarctica*) (Carravieri et al., 2018; Pollet et al., 2017). However, our results support a previous study which also suggested carry-over effects of Hg on the reproduction of little auks (Fort et al., 2014) with a specific influence of female winter distribution and Hg contamination on egg volume.

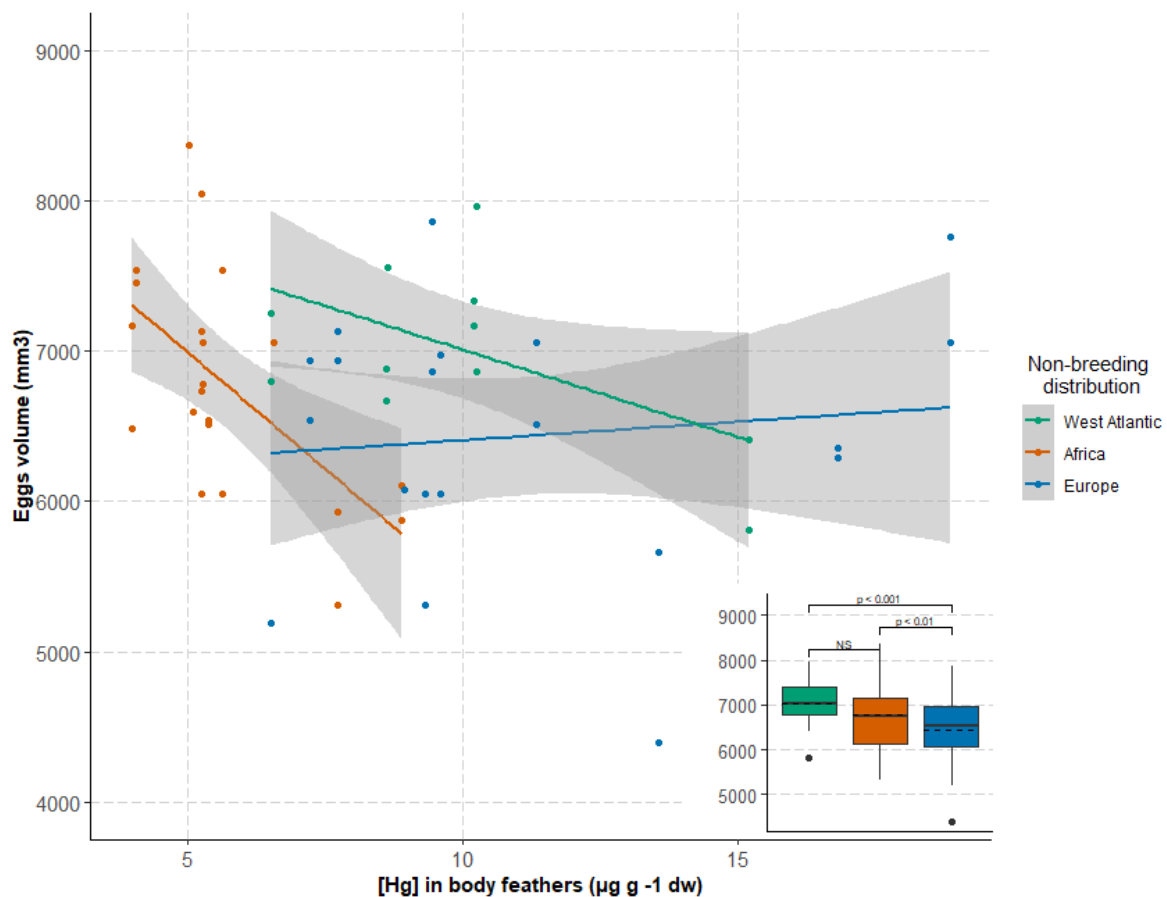


Figure 3. Egg volume (mm^3) in relation to Hg concentration ($\mu\text{g g}^{-1} \text{dw}$) in body feathers, depending on female winter distribution. Mean egg volume was $6439 \pm 815 \text{ mm}^3$ for females wintering in Europe, $6900 \pm 687 \text{ mm}^3$ for female wintering off Africa and 7022 ± 579 for those wintering in West Atlantic. Egg volume is represented using the same colour code as in Fig. 1. The shaded grey area represents the 95 % confidence interval.

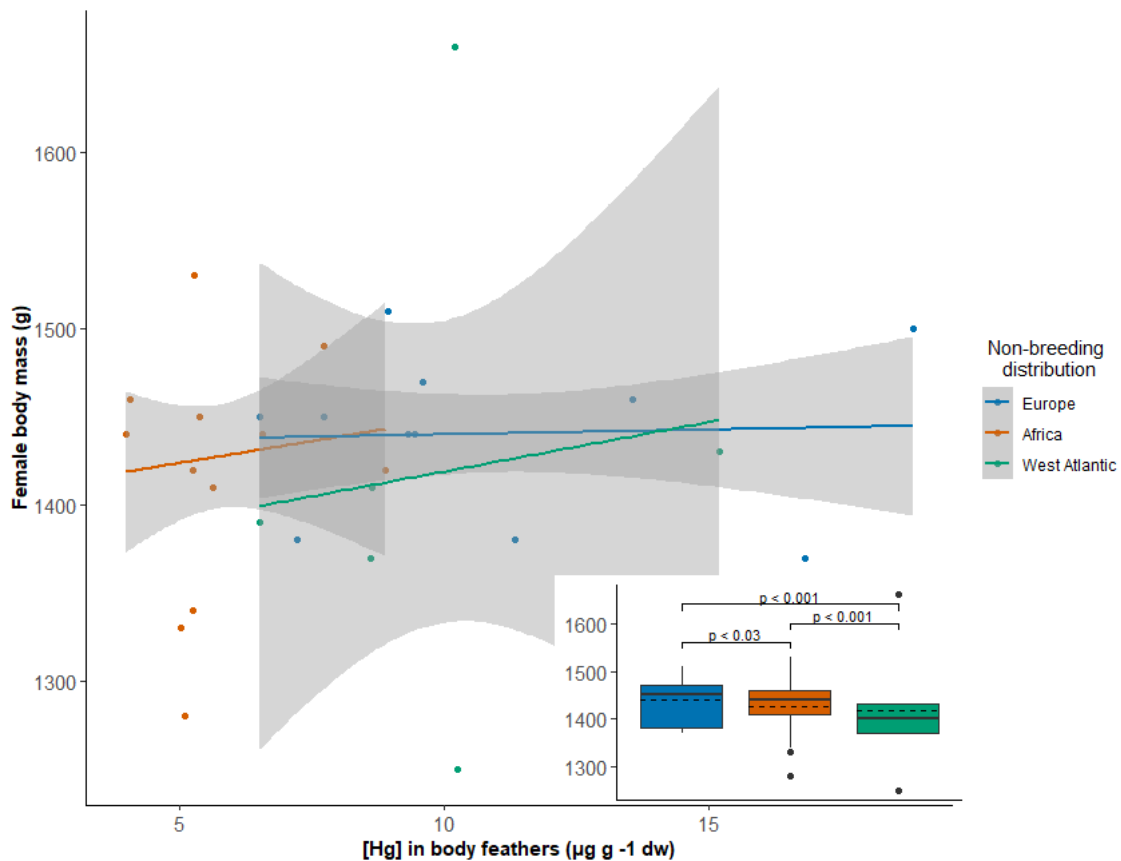


Figure 4. Female body mass (g) in relation to Hg concentration ($\mu\text{g g}^{-1} \text{ dw}$) in body feathers and their winter distribution. Mean values of female body mass were 1443.0 ± 45.6 g for female wintering in Europe, 1420.5 ± 62.9 g for female wintering off Africa and 1418.3 ± 128.0 g for female wintering in West Atlantic. Female body masses are represented using the same colour code as in Fig. 1. The shaded grey area represents the 95 % confidence interval.

Conclusion

By focusing on great skuas from Bjørnøya the present study demonstrated spatial variations in Hg contamination during the non-breeding period of seabirds and the associated ecotoxicological effects on reproduction. It thereby highlights the need to maintain long-term monitoring efforts at large spatial scales considering the different adopted overwintering strategies and the associated contamination. Additional environmental factors which could influence bird diet and selenium (Se) uptakes during winter should nonetheless also be explored, to further understand observed results, Hg effects and spatial patterns. Hg contamination of individual is indeed closely related to its diet, which could vary in space and

time (Carravieri et al., 2014b). Additionally, Se is an antagonist of Hg that actively participates in Hg detoxification and therefore protects against Hg toxicity (Khan and Wang, 2009; Manceau et al., 2021). However, no information exists regarding spatial variations of Se in seabirds and whether contrasting wintering grounds also result in different Se concentrations. Finally, although the study population of great skua has been increasing since 1971 (from 68 pairs in 2005 to 175 pairs in 2020 in Bjørnøya), our results highlight the potential risks for bird reproduction, which could ultimately result in long-term effects on population (Amélineau et al., 2019; Goutte et al., 2015). It therefore appears important to continue the close monitoring of this population, its contamination and demographic trends in order to ensure appropriate conservation measures.

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