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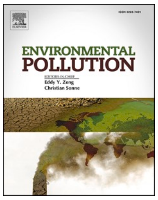

Carryover effects of winter mercury contamination on summer concentrations and reproductive performance in little auks

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ABSTRACT

Many animals migrate after reproduction to respond to seasonal environmental changes. Environmental conditions experienced on non-breeding sites can have carryover effects on fitness. Exposure to harmful chemicals can vary widely between breeding and non-breeding grounds, but its carryover effects are poorly studied. Mercury (Hg) contamination is a major concern in the Arctic. Here, we quantified winter Hg contamination and its carryover effects in the most abundant Arctic seabird, the little auk *Alle alle*. Winter Hg contamination of birds from an East Greenland population was inferred from head feather concentrations. Birds tracked with Global Location Sensors (GLS, $N = 28$ of the total 92) spent the winter in western and central North Atlantic waters and had increasing head feather Hg concentrations with increasing longitude (*i.e.*, eastward). This spatial pattern was not predicted by environmental variables such as bathymetry, sea-surface temperature or productivity, and needs further investigation. Hg concentrations in head feathers and blood were strongly correlated, suggesting a carryover effect of adult winter contamination on the consequent summer concentrations. Head feather Hg concentrations had no clear association with telomere length, a robust fitness indicator. In contrast, carryover negative effects were detected on chick health, as parental Hg contamination in winter was associated with decreasing growth rate of chicks in summer. Head feather Hg concentrations of females were not associated with egg membrane Hg concentrations, or with egg volume. In addition, parental winter Hg contamination was not related to Hg burdens in chicks' body feathers. Therefore, we hypothesise that the association between parental winter Hg exposure and the growth of their chick results from an Hg-related decrease in parental care, and needs further empirical evidence. Our results stress the need of considering parental contamination on non-breeding sites to understand Hg trans-generational effects in migrating seabirds, even at low concentrations.

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1. Introduction

Many animals migrate, commuting between breeding and non-breeding grounds to adapt to seasonal environmental changes (Newton, 2010). In long-lived birds such as seabirds, the non-breeding period is essential to renew the plumage, recover from the past breeding season and prepare for the upcoming one (Dunn et al., 2020; Reynolds et al., 2011). Environmental conditions experienced on non-breeding grounds can differ substantially from those encountered during breeding (Lambert and Fort, 2022), and can have carryover effects on subsequent reproductive performance and survival (Norris, 2005; Szostek and Becker, 2015). For instance, non-breeding habitat and diet quality can affect body condition, survival probability, breeding propensity and success in seabirds (*e.g.*, Bogdanova et al., 2011; Sorensen et al., 2009). Migration to distant non-breeding grounds can also expose seabirds to patterns or/and quantities of harmful chemical contaminants that are different to those encountered during breeding (*e.g.*, Lavoie et al., 2014; Miller et al., 2020). However, despite well-known toxic effects of contaminants on reproduction and survival (Walker et al., 2012), the carryover effects of non-breeding contamination on seabird reproductive performance have been sparsely studied, with mixed results (*e.g.*, Bustamante et al., 2016; Mills et al., 2020). This gap of knowledge limits our capacity to quantify the effect of multiple environmental pressures along the annual cycle of seabirds.

Seabirds are exposed to a plethora of chemical contaminants (*e.g.*, Walker et al., 2012). Among these, mercury (Hg) is of high environmental concern, especially in its methylated and most toxic form (MeHg), which is easily bioaccumulated by marine biota, and biomagnifies in marine food webs (Eagles-Smith et al., 2018). In the Arctic, growing environmental change is modifying the Hg contamination of seabirds, with recently observed or predicted increases (*e.g.*, Foster et al., 2019; Tartu et al., 2022). Recent findings point to a net MeHg production at relatively shallow depths (20–200 m) in the Arctic Ocean, which is believed to contribute to the high total Hg concentrations measured in Arctic surface seawater, and in Arctic predators (Dietz et al., 2022; Heimbürger et al., 2015). In addition, Arctic seabirds can acquire MeHg outside the Arctic during the non-breeding period. Previous work has shown that the oceanic waters off Newfoundland in the western North Atlantic Ocean are a hotspot of MeHg transfer to several Arctic seabird species that spend the winter there (Albert et al., 2021; Fort et al., 2014; Renedo et al., 2020). However, the environmental drivers that determine these hotspots are yet to be identified. Several factors, such as latitude, primary productivity, climatic and weather indices, air and seawater temperature, can play a role in the transfer of MeHg to food webs (Foster et al., 2019; Fitzgerald et al., 2007). High MeHg quantities are found in both coastal and shelf sediments, and in subthermocline low-oxygen oceanic waters in the mesopelagic zone, notably in association with active populations of Hg methylating microorganisms (Fitzgerald et al., 2007). Consumers have higher MeHg burdens in oligotrophic rather than mesotrophic environments due to the bioconcentration effect, whereby MeHg partitions among fewer cells in low productivity systems (Chouvelon et al., 2018; Pickhardt et al., 2002). Also, top predators in complex food webs can have higher MeHg burdens than those in short food webs, because of enhanced biomagnification (Braune et al., 2014; Lavoie et al., 2013). Understanding which environmental drivers best explain Arctic seabird MeHg accumulation can help us predict future exposure and risk scenarios.

This study aims to understand the environmental drivers of winter MeHg contamination and its carryover effects on fitness proxies in Arctic-breeding little auks (or dovekies, *Alle alle*), the most abundant seabird in the North Atlantic (>40 million birds, Egevang et al., 2003). Auks experience two moults per year: all feathers are replaced at the end of the breeding season (complete moult), then head feathers are replaced again at the end of the non-breeding period (partial pre-breeding moult in winter) (Albert et al., 2019 and references therein). In birds, MeHg accumulates in blood and internal tissues after dietary exposure, and deposits into growing feathers during moult (*e.g.*, Furness et al., 1986). Therefore, feather Hg concentrations represent exposure during the inter-moult period, *i.e.* winter months for head feathers of auks sampled on breeding grounds (Albert et al., 2019; Fort et al., 2014). Auks are thus excellent models to identify MeHg hotspots over North Atlantic wintering grounds through feather sampling during the following breeding season (Albert et al., 2021; Fort et al., 2014; Renedo et al., 2020). On breeding sites, blood can also be sampled, and is often used as short-term integrator of MeHg (*e.g.*, Evers, 2018). Yet, blood MeHg concentrations represent a balance of recent and past dietary intake redistributed from internal tissues, and the contribution of past (*e.g.*, winter) and more recent (*e.g.*, summer) Hg exposure on blood Hg concentrations is rarely studied (*e.g.*, Lavoie et al., 2014). We used biologging (Global Location Sensor, GLS) to identify spatial differences in winter MeHg contamination, feather and blood Hg concentrations as proxy of winter and summer exposure, and multiple indicators of short-term reproductive performance and individual quality to quantify MeHg effects. Our specific aims were to assess whether: 1) wintering median position of GLS-tracked little auks affects their head feather Hg concentrations (proxy of winter MeHg contamination), and if environmental drivers (bathymetry, productivity, sea-surface temperature and mixed layer depth) can explain spatial differences in Hg concentrations; 2) winter MeHg contamination affects MeHg concentrations of breeding adults (blood Hg concentrations) and their offspring; 3) winter MeHg contamination is associated with short-term reproductive performance (egg volume, hatching date and success, chick growth rate and survival) and individual health and quality (body condition, *e.g.*, Peig and Green, 2009; and adult telomere length, *e.g.*, Angelier et al., 2019). Based on previous results, we expected winter MeHg contamination to increase westward (Renedo et al., 2020; Fort et al., 2014), and to increase with decreasing productivity (bioconcentration effect, Chouvelon et al., 2018; Pickhardt et al., 2002). MeHg concentrations were expected to be higher in head feathers (winter) than in blood (summer) (Albert et al., 2021), and to be significantly associated with each other because of retention of MeHg from winter to summer (Lavoie et al., 2014). Given MeHg toxic effects on bird health (Chastel et al., 2022; Whitney and Cristol, 2018), and interannual repeatability of Hg contamination in seabird feathers (Carravieri et al., 2013; Bertram et al., 2022), we expected winter Hg contamination to be negatively associated with telomere length measured in summer. As MeHg can be transferred from mothers to eggs in avian species (reviewed in Ackerman et al., 2020) and have negative effects on hatchability and chick health (Whitney and Cristol, 2018; Yu et al., 2016), MeHg concentrations were expected to be correlated between mothers, their offspring and their health. In addition, egg volume was expected to decrease with increasing maternal head feather MeHg concentrations, as previously found in this population (Fort et al., 2014).

2. Material and methods

2.1. Study site and sample collection

This study was conducted on the little auk population of Ukaleqarteq, Kap Höegh (East Greenland; 70°44′N, 21°35′W) in July–August of 2018 and 2019. The little auk is a long-lived seabird (>20 years) producing a single egg per year. Adults provide bi-parental care until late chick-rearing, when only males feed the chick. Little auks are zooplanktivorous and specialise on large copepods, diving at depths of 20–50 m during winter (Fort et al., 2010). A total of 92 breeding adults ($N = 62$ in 2018, 32 females, 29 males, one unknown sex; $N = 30$ in 2019, 10 females, 19 males, one unknown sex, see Section 2.4. for molecular sexing) were caught in the nest or in its proximity by hand or with noose traps during incubation or chick-rearing. Handling of birds for morphometric measurements (see Section 2.2), as well as blood and feather sampling, lasted ~10 min. Blood (approx. 0.5 ml) was collected from the brachial vein with heparinised syringes, and centrifuged for 10 min at 3500 rpm, within 6 h from collection. Red blood cells and plasma were separately stored at −20 °C until further analyses. Red blood cells were used for Hg (see Section 2.5) and telomere length (see Section 2.6) quantification, while plasma will be used in further investigations. Feathers (7–10 per individual) were collected from the throat (hereafter head feathers) and stored at ambient temperature in sealed plastic bags. To track wintering movements, 28 of the 92 sampled adults ($N = 11$ in 2018, 8 females, 3 males; $N = 17$ in 2019, 5 females, 12 males) had been equipped with a miniature GLS data-logger (F100 and C65-SUPER, Migrate Technology, mass of 1.5 g, ~1% of adult body mass), mounted on a conventional metal ring, in the previous year. All birds were sampled only once (no repeated observations).

2.2. Nest monitoring, reproductive output and morphological data

In 2018 and 2019, 70 and 39 nests, respectively, were monitored to quantify hatching date, success, chick growth and survival. When accessible, the single egg was measured to calculate its volume as detailed in Fort et al. (2014). Nests were checked every second day to determine the hatching date. Eggshell fragments were collected and stored in sealed plastic bags at −20 °C until Hg analyses. Once chicks were at least one day old, they were weighed (electronic scale to the nearest gram) every second day to quantify their growth. Chick growth rate was inferred from the slope of the relationship between chick mass and age during the linear phase of growth (4–14 days of age, Amélineau et al., 2016). Survival of chicks was estimated when they were 18 ± 3 days old (mean ± SD), *i.e.*, shortly before they left the nest. Chick age at survival estimation was accounted for in statistical analyses concerning chick growth rate (see Section 2.7). On the day of chick survival estimation, four breast feathers (hereafter chick body feathers) were sampled, following the same procedures as in adults (see Section 2.1). In 2018, one or both parents of 43 out of the 70 monitored nests were sampled for blood and head feathers to determine Hg contamination (see Section 2.1 and 2.5) and its fitness proxies' correlates (see Section 2.7). For logistical reasons, parents of only two out of the 39 monitored nests could be sampled for blood and head feathers in 2019, and were thus not included in statistical analyses looking at fitness proxies' correlates of Hg contamination. Adults and chicks were weighed (±1 g), measured with a calliper (head-bill, culmen, tarsus, ±1 mm), and a ruler (flattened wing, ±1 mm). Initially we considered calculating a scaled mass index (SMI, Peig and Green, 2009) in adults as proxy of body condition. However, slope estimates of the correlation between mass and the different length measures available (head-bill, culmen, tarsus, wing) were not significant. Therefore, we considered adult body mass alone as body condition index, which is a reliable condition indicator within a population (Peig and Green, 2009).

2.3. Movement and environmental data

GLS loggers measured daylight level intensity each minute and recorded its maximum intensity each 5 min. Following the standardised procedure described in Bråthen et al. (2021), we used a threshold method to estimate latitudes from the length of day and night and longitudes on the timing of noon and midnight (Hill, 1994; Wilson et al., 1992), giving a maximum of two locations per day, and subsequently filtered erroneous locations. We treated GLS tracking data from December 1 to January 31 (the "core wintering period", when all birds were at their wintering grounds, Fort et al., 2013). We extracted the following environmental variables on a daily basis over 1° × 1° cells: sea-surface temperature (SST), mixed-layer depth (MLD), sea-surface chlorophyll *a* concentration (chl*a*, as a proxy of productivity) and bathymetry. Environmental data was retrieved from Marine Copernicus (products: GLOBAL_ANALYSISFORECAST_PHY_CPL_001_015 for SST and MLD; and GLO_CHL_L4_REP_OBSERVATIONS_009_082 for chl*a*, https://resources.marine.copernicus.eu/products). Bathymetry was extracted using the NOAA dataset https://www.ncei.noaa.gov/maps/bathymetry/(GEBCO). We calculated the median of latitude and longitude, and extracted all environmental variables at this location, for each individual separately. These unique values per individual were used to test the influence of location and environmental characteristics on head feather (*i.e.*, winter) Hg concentrations (see Section 2.7).

2.4. DNA extraction and molecular sexing

Genomic DNA was extracted from calamus tips of plucked feathers stored at room temperature using NucleoSpin® Tissue Kit (Macherey-Nagel EURL, Hoerdt, France). DNA concentration was determined using a Nanodrop 2000. Molecular sexing was performed using primers 2550 F and 2718 R (Fridolfsson and Ellegren, 1999) that amplify portions of the CHD genes present on the Z and W sex chromosomes.

PCR reactions included 0–90 ng of DNA, 0.4 μM of each primer, 1X reaction buffer (biotechrabbit, Hennigsdorf, Germany), 1.5 mM $MgCL_2$, 0.2 mM of dNTPs, 0.32 mg/μL of bovine serum albumine and 1.2 U of *Taq* polymerase (biotechrabbit, Hennigsdorf, Germany) in a 30 μL final volume. The following PCR profile was performed on a TC-5000 (Techne) thermocycler: 94 °C for 1 min, followed by 35 cycles of 30 s at 94 °C, 45 s at 53 °C, and 45 s at 72 °C, and a final extension of 5 min at 72 °C. PCR products were separated by electrophoresis on a 2.5% agarose gel stained with GelRed. No-template negative controls were included in DNA extractions and PCR reactions.

2.5. Hg analysis

Quantification of total Hg (hereafter Hg) was carried out in adult head feathers and chick body feathers and adult red blood cells, and in eggshell membranes at the laboratory Littoral, Environment and Societies (LIENSs, CNRS-La Rochelle Université). Total Hg concentrations in these three tissues are a close approximation of MeHg concentrations, as they contain virtually 100% MeHg (Bond and Diamond, 2009; Renedo et al., 2021). In the blood compartment, Hg is preferentially found within red blood cells, and red blood cell Hg concentrations are a very close approximation of whole blood Hg concentrations (Tavares et al., 2013 and authors' unpublished data). Hereafter, red blood cell will be abbreviated to "blood" unless otherwise specified. Whole blood and red blood cell MeHg concentrations represent a balance of recent and past dietary intake redistributed from internal tissues. The biological half-life of Hg is 30–40 days during moult, and longer than 65 days outside moult (Monteiro and Furness, 2001). Feather synthesis is an important MeHg excretion pathway in birds; up to 90% of the body burden can be found in feathers after moult (Bond and Diamond, 2009; Braune and Gaskin, 1987). After completion of telomere length analysis on wet red blood cells (see Section 2.6), these were freeze-dried for 48 h and homogenised to enable Hg determination on the dry mass, which is necessary when using direct Hg analysers (see below). To remove external contamination, seven to 10 head feathers, and four chick body feathers, were cleaned in a 2:1 chloroform:methanol solution in an ultrasonic bath for 3 min, then rinsed twice with methanol before being dried in aluminium foil for 24 h at 45 °C (details in Carravieri et al., 2013). Three feathers of each type were randomly selected and homogenised by cutting them into small fragments with stainless scissors. Membranes were first separated from eggshells using stainless tweezers, and then placed in a net before cleaning, to avoid the loss of small particles in the cleaning mixture. The cleaning procedure was the same as for feathers. Head feather, red blood cells, and eggshell membrane Hg concentrations were quantified using an advanced Hg analyser (AMA-254, Altec) and are expressed as $\mu g\ g^{-1}$ dry weight (dw). All analyses were carried out in duplicate (relative standard deviation < 10%) and average values used in data analyses. The certified reference material (CRM) TORT-3 (certified Hg concentration: $0.292 \pm 0.022\ \mu g\ g^{-1}$ dw) was measured at the beginning and end of each set of analysis, and every 10–15 samples. Measured TORT-3 values were $0.284 \pm 0.010\ \mu g\ g^{-1}$ dw ($N = 7$) for the set of blood samples, $0.289 \pm 0.004\ \mu g\ g^{-1}$ dw ($N = 9$) for adult head feathers, 0.289 ± 0.003 μg g^{-1} (N = 15) for chick body feathers, and 0.290 ± 0.005 μg g^{-1} dw (N = 5) for eggshell membranes. CRM mass (and thus Hg quantity introduced in the analyser) was adjusted to mirror the Hg mass present in samples. Blanks were analysed at the beginning of each set of samples and the limit of detection of the Hg analyser was 0.05 ng.

2.6. Telomere length quantification

Telomeres are repetitive, non-coding DNA sequences found at the end of chromosomes, which protect genome integrity (Blackburn, 2005). These sequences shorten at each cell division, but also as a result of environmental stress (*e.g.*, Angelier et al., 2018). Telomere length was determined by quantitative PCR (qPCR; BioRad CFX 96, Bio-Rad USA) according to Cawthon (2002), and adapted for the little auk, at the Centre d'Etudes Biologiques de Chizé (CEBC, CNRS-La Rochelle Université). Briefly, 5 μL of red blood cells were digested with proteinase K and DNA was extracted using the Nucleospin Tissue Kit (Macherey-Nagel), following the manufacturer's instructions. DNA concentration and purity were assessed with a Nanodrop ND1000 spectrophotometer (Thermo Scientific). The telomere primers were similar to those previously used in other seabird species (*e.g.*, Sebastiano et al., 2020). The control single-copy gene Recombination Activating Gene 1 (RAG1) was selected and amplified using specific primers designed for the little auk. All qPCR runs were performed using 7.5 ng of DNA per reaction and using the BioRad SYBR Green Supermix. The universal telomere primers were used at a concentration of 800 nM, and RAG1-F/RAG1-R at 300 nM. To generate a six-point standard curve (from 20.0 ng to 0.62 ng) for controlling the amplifying efficiency of the reactions, serial dilutions of DNA from a pooled sampled of 10 little auks were included on the plate. All samples were randomly distributed across the PCR plates. The efficiency of the telomere and RAG1 assays ranged from 103.0 to 108.6% and 100.7–103.0%, respectively, and all r^2 were very high (>0.990). Three reference samples ('golden samples') were run in triplicate on all plates to account for inter-plate variation, and each sample was run in duplicate on every plate. The interplate repeatability was 0.959 (intra-class correlation coefficient). The relative telomere length was calculated as the telomere copy number (T) relative to single-copy gene (S), expressed as TS ratio.

2.7. Data analysis

Data exploration, visualisation and statistical analyses were performed in R version 4.0.5 (R Core Team, 2021). To address our aims, we used linear or generalised linear models with different specifications depending on the response variable and error distribution, and different explanatory variables depending on aims and sample size (*Table S1*, Supplementary Material). Model specification and fit were validated *via* residual analysis of initial models (*e.g.*, homoscedasticity of residuals). When multiple explanatory variables were continuous, we tested for the absence of collinearity (variance inflation factor, VIF <3) and standardised them (mean = 0, SD = 1) to facilitate comparison of effect sizes (Zuur et al., 2009).

2.7.1. Aim 1

The effect of the median latitude and longitude of adult position during the core winter, and the associated environmental variables, was tested on head feather (*i.e.*, winter) Hg concentrations. Environmental variables (bathymetry, chl*a*, MLD, SST) were strongly collinear (VIF >10). Therefore, chl*a*, MLD, and SST data were log-transformed to achieve a normal distribution (raw bathymetry data was normally distributed), and all variables were scaled, to perform a principal component analysis (PCA, R package *ade4*, (Dray and Dufour, 2007). The first and second axis of the PCA explained 93% of total variation in environmental data over wintering grounds (*Fig. S1*). Bathymetry was positively related to MLD (*i.e.*, deeper waters were associated with larger MLD) and these two variables were mainly associated with PC1 scores (decreasing PC1 scores indicated deeper waters and MLD). SST and chl*a* were not related and were mainly associated with PC2 (decreasing PC2 scores indicated higher SST and chl*a* values, *Fig. S1*). Principal component (PC) scores of PC1 and PC2 were extracted to obtain uncorrelated variables, and then used as explanatory variables of head feather Hg concentrations alongside latitude and longitude (no collinearity detected, all VIF <3).

2.7.2. Aim 2

The effect of adult head feather (*i.e.*, winter) Hg contamination, year, sex and their interaction (sex:Hg) was tested on adult blood (*i.e.*, summer) Hg concentrations. The sex:Hg interaction was considered because sexual differences in Hg accumulation and toxic effects have been previously described in seabirds (Robinson et al., 2011, 2012). We also tested whether (i) eggshell membrane Hg concentrations (*i.e.*, offspring contamination) were related to maternal head feather (*i.e.*, winter) Hg concentrations, (ii) maternal and paternal head feather Hg concentrations were related to chick body feathers (*Table S1*).

2.7.3. Aim 3

This aim tested (i) the effect of maternal head feather Hg contamination on egg volume; (ii) the effect of winter Hg concentrations, sex and their interaction, year and sampling date (as Julian day), on telomere length and body condition, which were measured in both 2018 and 2019; and (iii) the effect of winter Hg contamination, sex and their interaction on four variables of short-term reproductive performance (hatching date and success, chick growth and survival, only measured in 2018, *Table S1*). Sampling date was considered as explanatory because body condition can vary temporally across the breeding season (*e.g.*, Moe et al., 2002). Also, the proportion of breeders of different ages and/or quality, which can drive telomere length (Angelier et al., 2019), can vary across the breeding season in seabirds (*e.g.*, de Forest and Gaston, 1996; González-Solís et al., 2004). Birds were of unknown age, so accounting for sampling date can help controlling for the potential age bias. We only considered head feather Hg concentrations, and not blood Hg concentrations, to test carryover effects of winter Hg contamination on reproductive performance, as concentrations in blood also reflect shorter-term exposure (here the summer breeding season). For binomial models (response variables: hatching success and chick survival, *Table S1*), model fit was checked through the overdispersion term value. Chick age (days) at survival estimation was accounted for in chick survival models.

2.7.4. Model selection

For all our aims, we used Akaike's information criterion corrected for small sample sizes (AICc) to select the best models (R package *MuMIn,* Bartón, 2019). We compared a list of biologically meaningful initial candidate models. The initial and best models selected for each specific question within each aim, as well as their sample sizes, are presented in *Table S1*. The AICc, the difference between AICc of the specific model and the best model (ΔAICc), and the AICc weight (normalized weight of evidence in favour of the specific model), and the explained deviance (indicative of the proportion of variation explained by the model, similar to R^2 for linear models, Zuur et al., 2009) were calculated. If the null model ranked as the best model, the effects of all explanatory variables were considered statistically insignificant. When multiple models performed better than the null model and had ΔAICc <2, we applied model averaging on those models to make an inference. This produced averaged parameter estimates (β) of the predictor variables included in those models, weighted using AICc weights. AICc tables for candidate models with significant and insignificant effects are presented in Table 1 and *Table S2*, respectively. When model averaging was applied, the averaged β ± standard error (SE), and 95% confidence interval (CI), are also reported for each predictor in Table 1.

Table 1
Akaike tables including model specification and sample size of the models used to address the different aims of this study (see Introduction, and *Table S1*). This table includes response variables showing significant effects, while response variables showing insignificant effects are reported in *Table S2*. Only the five best ranked models and the null model are presented. When more than two models had similar support ($\Delta AIC_c < 2$), model averaging was applied, and averaged estimates (β) reported, to determine the explanatory variables with the clearest effect (in bold). Abbreviations: Lat and Lon, median latitude and longitude of wintering position; PC1 and 2, scores on axis 1 and 2 of a PCA of environmental variables (SST, sea-surface temperature; chl*a*, sea-surface chlorophyll *a* concentration; MLD, mixed-layer depth); Hg_HF, head feather (*i.e.*, winter) Hg concentrations; AICc, Akaike's information criterion corrected for small sample sizes; ΔAICc, difference between AICc of the specific model and the best model; *k*, number of parameters; w_i AICc weight; Exp. Dev., explained deviance.

GLM Gaussian (log)	***k***	**AIC$_c$**	**ΔAIC$_c$**	**w_i**	**Exp. Dev.**
Aim 1) Head feather Hg concentrations in GLS-tracked birds (N = 28)					
Initial model: Head feather Hg ~ Lat + Lon + PC1 + PC2 + Year + Sex					
Lon	3	90.3	0	0.29	0.30
Lon + Lat	4	92.1	1.78	0.12	0.29
Lon + PC2	4	92.7	2.32	0.09	0.28
Lon + Year	4	92.7	2.34	0.09	0.28
Lon + PC1	4	93.0	2.64	0.08	0.27
Null	2	98.3	7.93	0.01	0.00
Aim 2) Red blood cell Hg concentrations (N = 79)					
Initial model: Red blood cell Hg ~ Hg_HF + Year + Sex + Hg_HF:Sex					
Hg_HF + Year + Sex	5	−28.11	0	0.69	0.43
Initial model	6	−26.03	2.09	0.24	0.42
Hg_HF + Sex	4	−22.89	5.22	0.05	0.38
Hg_HF + Sex + Hg_HF:Sex	5	−20.74	7.37	0.02	0.37
Hg_HF + Year	4	−10.99	17.12	0.00	0.28
Null	2	12.66	40.77	0.00	0.00
Aim 3) Telomere length (TS ratio) (N = 77)					
Initial model: TS ratio ~ Hg_HF + Julian + Year + Sex + Hg_HF:Sex					
Julian + Sex + Year	5	−98.50	0.00	0.28	0.22
Julian + Year	4	−98.04	0.46	0.22	0.20
Hg_HF + Julian + Year	5	−97.70	0.81	0.19	0.21
Hg_HF + Julian + Sex + Year	6	−97.60	0.91	0.18	0.22
Julian + Sex	4	−95.23	3.27	0.05	0.22
Null	2	−83.27	15.24	0.00	0.00
Model averaging (full average)	*β* ± *SE* [*95% CI*]				
Intercept	0.955 ± 0.021 [0.912–0.997]				
Julian	**0.049 ± 0.014 [0.021–0.078]**				
SexM	0.024 ± 0.030 [-0.036–0.083]				
Year 2019	**0.078 ± 0.030 [0.017–0.138]**				
Hg_HF	−0.007 ± 0.012 [-0.032–0.017]				
Aim 3) Body mass (N = 80)					
Initial model: Body mass ~ Hg_HF + Julian + Year + Sex + Hg_HF:Sex					
Year + Julian	4	627.7	0	0.23	0.08
Julian	3	627.8	0.07	0.22	0.07
Hg_HF + Julian	4	628.8	1.06	0.14	0.07
Hg_HF + Julian + Year	5	629.2	1.47	0.11	0.08
Julian + Sex + Year	5	629.8	2.12	0.08	0.07
Null	2	632.1	4.42	0.03	0.00
Model averaging (full average)	β ± *SE* [*95% CI*]				
Intercept	304 ± 61 [183–425]				
Julian	**−0.74 ± 0.31 [-1.35–-0.13]**				
Year 2019	−4.05 ± 2.82 [-7.51–3.56]				
Hg_HF	−1.19 ± 1.21 [-2.21–1.37]				
Aim 3) Chick growth (N = 18)					
Initial model: Chick growth ~ Hg_HF + Sex + Hg_HF:Sex + Chick_age					
Hg_HF	3	58.37	0.00	0.53	0.23
Hg_HF + Sex	4	60.54	2.17	0.18	0.23
Initial	5	61.08	2.70	0.14	0.32
Null	2	61.30	2.93	0.12	0.00
Sex	3	63.63	5.25	0.04	0.00

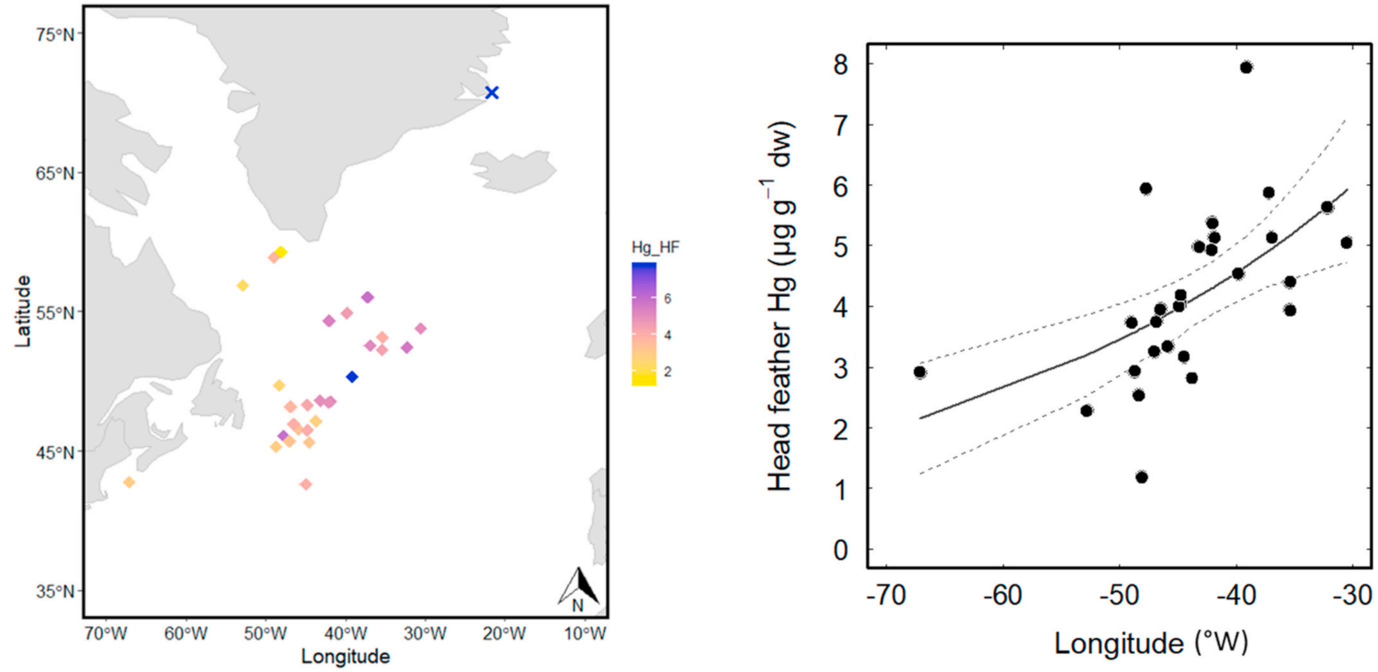

Fig. 1. Left panel: median positions of little auks wintering in the North Atlantic Ocean in 2017–18 and 2018–19 (1st December – 31st January), coloured by the Hg concentrations in their head feathers. The blue cross indicates the breeding colony at Ukaleqarteq, East Greenland. Right panel: Head feather Hg concentrations increase with decreasing longitude (eastward) in little auks wintering in the North Atlantic in 2017–18 and 2018–19 (1st December – 31st January) ($\beta \pm$ SE on unscaled values: slope 0.028 ± 0.008, intercept 2.621 ± 0.343, N = 28, $\Delta AICc_{Model\text{-}Null} = 7.93$, see Table 1).

3. Results

3.1. *Influence of wintering median position and environment on head feather Hg concentrations*

GLS-tracked little auks spent the core wintering period (1st December – 31st January) of 2018 and 2019 on average 2598 km (range 1743–3995 km) from their breeding colony, between latitudes 42.6°N and 59.3°N, and longitudes 67.1°W and 30.5°W (Fig. 1). Descriptive statistics of the environmental characteristics at these locations are presented in *Table S3*. The targeted environmental variables (represented by PC1 and PC2 scores) did not drive variation in head feather Hg concentrations, as models including them were not retained by AICc selection (Table 1). In contrast, the median longitude of winter location had a clear effect on head feather Hg concentrations ($\beta \pm$ SE on scaled values: 0.196 ± 0.058, 95% CI: 0.085–0.309): winter Hg exposure increased eastward (Fig. 1), with no effect of year or sex (Table 1).

3.2. *Association of head feather Hg concentrations with blood and offspring Hg concentrations*

Hg concentrations in head feathers (range 1.18–7.93 $\mu g\ g^{-1}$ dw, *Table S4*) were similar between sexes and years (Table 1). The best model explaining Hg concentrations in blood (range 0.4–2.0 $\mu g\ g^{-1}$ dw, *Table S4*) included head feather Hg concentrations, sex and year as predictors, with no sex:Hg interaction (Table 1). Blood Hg concentrations were significantly higher in males than females (sexM: 0.203 ± 0.046, 95% CI: 0.113–0.293), and in 2018 than 2019 (year 2019: 0.130 ± 0.048, CI: 0.222–0.034), and increased with increasing head feather Hg concentrations (0.145 ± 0.022, 95% CI: 0.101–0.189) (Table 1, Fig. 2). Eggshell membrane Hg concentrations were not related to maternal head feather Hg concentrations (*Table S2*). Maternal and paternal head feather Hg concentrations were not related to chick body feather Hg concentrations (*Table S2*).

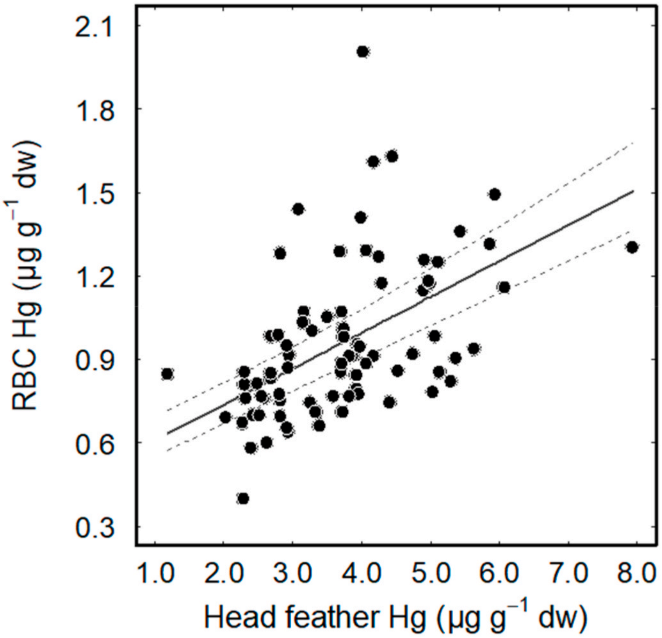

Fig. 2. Red blood cell (RBC) Hg concentrations increased with increasing head feather Hg concentrations in little auks breeding at Ukaleqarteq, East Greenland, in 2018 and 2019 ($\beta \pm$ SE: slope 0.145 ± 0.022, intercept 0.362 ± 0.080, N = 79, $\Delta AICc_{Model\text{-}Null} = 40.8$, see Table 1, sex and year effects are not represented for readability).

3.3. *Association of head feather Hg concentrations with fitness proxies*

Four models had similar support in explaining variation in telomere length (range of TS ratio: 0.65–1.32, *Table S4*), indicating that Julian day, year, sex and head feather Hg concentrations were significant predictors (Table 1). However, model averaging showed that only Julian

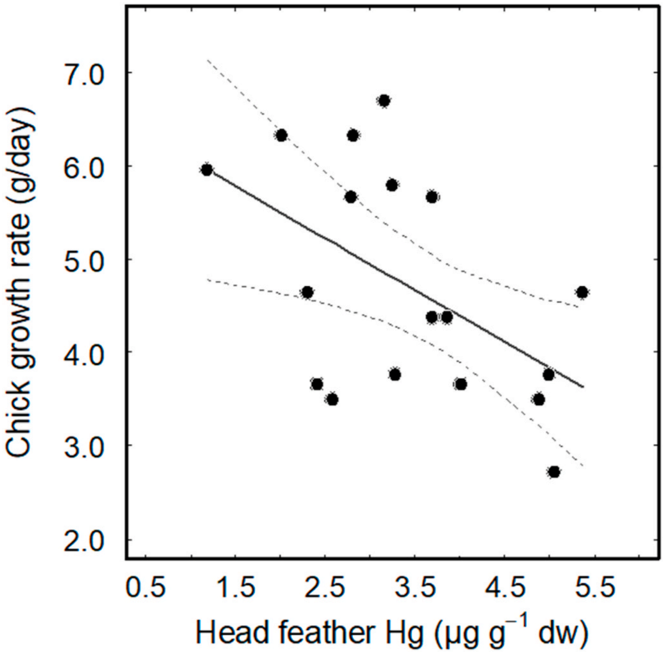

Fig. 3. Chick growth rate decreases with increasing head feather Hg concentrations of their parents in little auks breeding at Ukaleqarteq, East Greenland, in 2018 (slope −0.555 ± 0.215, intercept 6.615 ± 0.838, N = 18, $\Delta \mathrm{AICc}_{\mathrm{Model\text{-}Null}}$ = 2.93, see Table 1).

day and year had a clear statistical effect: telomere length increased as the sampling season progressed (averaged β ± SE, 0.049 ± 0.014, 95% CI: 0.021–0.078), and telomeres were on average longer in 2019 than 2018 (year 2019: 0.078 ± 0.030, 95% CI: 0.017–0.138, Table 1, *Fig. S2*). Telomere length showed a weak, decreasing trend with increasing head feather Hg concentrations, and tended to be longer in males than females (Table 1). Variation in adult body mass during the breeding period (range 125–182 g, *Table S4*) was explained by four models with similar support, including Julian day, year and head feather Hg concentrations as predictors (Table 1). However, model averaging showed that Julian day only had a clear statistical effect: body mass decreased with increasing Julian day (averaged β ± SE, −0.74 ± 0.31, 95% CI: 1.35–0.13, Table 1). In addition, all models explained very little of the total variation (maximum explained deviance of 8%, Table 1). Egg volume (range 21.9–31.0 cm^3, *Table S4*) was not related to female head feather Hg concentrations (Table S2). Hatching success was 64.3% and 87.2% of monitored nests (70 and 39), and chick survival was 72.5% and 85.3% of monitored chicks (30 and 34) in 2018 and 2019, respectively (*Table S4*). In 2018, hatching success and chick survival were not related to parental head feather Hg concentrations (Table S2). Chick growth rate (range 2.71–6.70 g day^{-1}) decreased with increasing parental head feather Hg concentrations (−0.555 ± 0.215, 95% CI: 0.976–0.123, Fig. 3), irrespective of parent sex (Table 1).

4. Discussion

By combining biologging, nest monitoring and molecular biomarkers, we showed that adult winter Hg exposure influences blood Hg concentrations during breeding, and is negatively associated with chick growth rate, without apparent effects on hatching success and chick survival. We hypothesise that trans-generational Hg effects may be mediated by a decrease in parental care, which should be confirmed by additional evidence from studies of parental behaviour and physiology during chick-rearing. Further investigations on a larger sample size are also needed to clarify the relationship between Hg contamination and telomere length, as well as telomere dynamics, in this population. Hg contamination was similar to previously published work in the same population for both summer (whole blood Hg concentrations around 0.8 µg g^{-1}, Fort et al., 2014) and winter (head feather Hg concentrations around 3.8 µg g^{-1}, Fort et al., 2014), which identifies little auks' Hg contamination as low when compared to other Arctic breeding seabirds (Albert et al., 2021; Chastel et al., 2022). This has two important implications: 1) ecological and physiological effects may arise even at low concentrations in this species (see also Grunst et al. Under review) and 2) further studies should look at similar potential Hg effects in other Arctic species.

4.1. Spatial differences in Hg exposure and potential environmental drivers

Head feather Hg concentrations in little auks breeding in East Greenland were driven by longitude of wintering position, but, contrary to our hypothesis and to results in other species (Albert et al., 2021; Amap, 2021), increased eastward. Namely, head feather Hg concentrations decreased eastward in the North Atlantic in wintering little auks from multiple Arctic colonies in 2015 and 2016 (Renedo et al., 2020). Results from the latter study included little data from longitudes farther west, *i.e.*, shelf waters off the United States and south Greenland, which were visited by birds of the present study. This could indicate that winter Hg exposure is low on shelf waters east of the United States and Greenland, and high in oceanic waters in the central North Atlantic. This is consistent with empirical and modelling studies on MeHg content in different marine matrices, which show a similar longitudinal trend in zooplankton MeHg content in North Atlantic waters (Zhang et al., 2020). Alternatively, environmental and/or ecological drivers of winter Hg contamination in little auks differ temporally in the North Atlantic, leading to variation in the spatial pattern of Hg exposure found in different years (Fort et al., 2014; Renedo et al., 2020, present study). Temporal variation in seawater Hg concentrations and/or in the transfer of Hg to food webs is likely, because they depend on several environmental (Foster et al., 2019; Stern et al., 2012) and trophic factors (Braune et al., 2014). However, none of the environmental variables that were studied here had a clear role in explaining the spatial pattern of little auks' winter Hg contamination. Previously, productivity has been associated with Hg biodilution in zooplankton (Pickhardt et al., 2002) and fish (Chouvelon et al., 2018), while Hg burden increases were detected at chl*a* low and high extremes in Arctic seabirds, likely as a result of bottom-up nutrients effects on fish communities (Tartu et al., 2022). In addition, MeHg transfer to food webs can vary with the depth of the ocean mixed-layer (Dietz et al., 2022; Heimbürger et al., 2015), with potential cascading effects on Hg contamination of consumers, including those feeding at relatively shallow depths like little auks (Fort et al., 2010). However, interactions between these environmental variables and the ecological processes that lead to Hg exposure in little auks are complex, likely work at different temporal scales, and might vary at a high rate under climate change (Stern et al., 2012; Tartu et al., 2022; Wang et al., 2019). Further studies on larger sample sizes associating wintering movements of seabirds and their Hg contamination are necessary to gain more insights on Hg hotspots, their environmental drivers, and their interannual variation in the North Atlantic. This is particularly important given the hotspot of seabird biodiversity found within this oceanic region, which sustains millions of birds every year (Davies et al., 2021).

4.2. Carryover effect of winter Hg exposure on concentrations in summer

Previous studies have shown that Hg exposure at distant migrating grounds can affect summer Hg concentrations in aquatic birds (*e.g.*, Bertram et al., 2022; Lavoie et al., 2014). In agreement with this, the correlation between head feather and blood Hg concentrations found here supports that part of Hg bioaccumulated during winter is still circulating in blood during summer. Hg contamination is higher over wintering than breeding grounds in several Arctic breeding seabirds, including little auks (Albert et al., 2021). Hg excretion into feathers is an efficient mechanism (Bond and Diamond, 2009), but winter moult only affects head feathers in little auks, *i.e.*, a small proportion of the whole plumage. In addition, excretion in feathers is known to be up to 90% of the body burden (Bond and Diamond, 2009; Braune and Gaskin, 1987). This can limit the total amount of Hg that can be eliminated from the organism. Furthermore, the biological half-life of Hg in seabirds can be longer than 65 days in non-moulting individuals (Monteiro and Furness, 2001). A correlation of Hg concentrations in head feathers and blood could also result from individuals consistently targeting prey of similar Hg content in both winter and summer. However, between- and within-individual variation in diet is small in this copepod specialist, at least in summer (Amélineau et al., 2016; Jakubas et al., 2020). In addition, little auk prey and its Hg content are poorly known at wintering grounds (Rosing-Asvid et al., 2013), further studies are thus necessary to confirm this hypothesis. Individuals may also differ in their physiological capacity to assimilate, bioaccumulate and excrete Hg, resulting in some birds consistently retaining more Hg than others, irrespective of exposure. Importantly, prey Hg content explains a large part of inter-annual variations in summer Hg concentrations in this population (Fort et al., 2016). Carryover effects of winter Hg exposure appear to be another important driver of summer Hg concentration, and should be considered when using little auks as bioindicators of temporal variations of Hg in Arctic food webs (Fort et al., 2016). The sex-related and inter-annual differences in summer Hg exposure can be related to trophic and abiotic factors, respectively (Carravieri et al., 2014; Hitchcock et al., 2019; Robinson et al., 2012).

4.3. Carryover effects on fitness proxies

4.3.1. Telomere length and body condition

Telomere length integrates the effect of multiple stressors and can predict reproductive performance and survival in a variety of taxa (Angelier et al., 2019; Chatelain et al., 2020; Louzon et al., 2019; Salmón and Burraco, 2022). Exposure to environmental contaminants can disrupt telomere dynamics, *e.g.*, through molecular oxidative damage, disruption of antioxidant defences, and/or impact on telomerase, the enzyme responsible for telomere elongation (reviewed in Louzon et al., 2019). *In vitro* and studies in humans have shown a general trend of decrease in telomere length after contaminant exposure (Chatelain et al., 2020; Louzon et al., 2019). Yet, the few studies on Hg-related variation of telomere length in birds showed contrasted results. A female-specific positive association between Hg contamination and telomere length was observed in black-legged kittiwakes *Rissa tridactyla* (Blévin et al., unpublished data in Angelier et al., 2018), while no association was found in Mandt's black guillemots *Cepphus grylle mandtii* (Eckbo et al., 2019). A potential indirect effect of Hg on telomere dynamics through impacts on corticosterone has been suggested in red kite *Milvus milvus* nestlings (Powolny et al., 2020). Other studies have shown no clear evidence of Hg effects on corticosterone (*e.g.*, Chastel et al., 2022 and references therein), the latter result should thus be taken with caution. Recently, Bauch et al. (2022) showed a clear, male-specific decreasing trend of telomere length with increasing winter Hg contamination in Cory's shearwaters *Calonectris borealis*. In our study, and irrespective of sex, little auk telomere length was not clearly related to winter Hg contamination, even though there was a negative, nonsignificant trend. Winter Hg concentrations are 1.5 times lower in little auks than Cory's shearwaters (Bauch et al., 2022), suggesting that Hg contamination might be too low to have a similarly strong and significant effect. This is consistent with low Hg risk identified for little auks when compared to other Arctic seabird species (Chastel et al., 2022). On the other hand, telomere length increased with sampling date, and varied significantly between years. These results could be explained by a confounding effect of age. Telomere length has been associated with biological and chronological age in birds (Bize et al., 2009; Young et al., 2013). Breeding phenology and performance can also vary with age, with older, more experienced seabirds breeding earlier than younger ones (*e.g.*, de Forest and Gaston, 1996; González-Solís et al., 2004). The observed increase in telomere length across the season could thus indicate that birds sampled later were younger. In addition, telomeres were on average shorter in birds sampled in 2018 than 2019, potentially because a larger proportion of old birds was sampled in 2018. Environmental conditions can drive annual changes in telomere length of adult birds (Mizutani et al., 2013; Young et al., 2013). Environmental conditions were likely challenging in 2018, as both hatching success and chick survival were lower in 2018 than 2019. Furthermore, chick growth rates were lower in 2018 compared to 2019 (*Fig. S3*), and to the long-term average (Amélineau et al., 2019). The more challenging year 2018 possibly allowed only older and experienced birds to breed, and thus be sampled, while several young birds may have failed early or skipped reproduction. Good conditions in the winter and/or summer of 2019 might also have promoted telomere restoration (*i.e.*, through telomerase activity, Louzon et al., 2019). Further investigation in birds of known age and quality are necessary to confirm or refute these interpretations. Quantifying the intrinsic and extrinsic drivers of telomere length and Hg contamination, which could co-vary (Bauch et al., 2022; Salmón and Burraco, 2022), is essential to rule out whether telomere length and/or dynamics are useful biomarkers of Hg health effects.

Body mass tended to decrease with increasing winter Hg contamination. This is consistent with one previous investigation showing a negative association between summer Hg concentrations and body condition in this population (Amélineau et al., 2019). Current (summer) Hg exposure may be more important than past contamination over wintering grounds for effects on body condition. Alternatively, the lack of statistical significance could be linked to small statistical power. A recent meta-analysis showed that Hg contamination effects on body condition are weak, can be confounded by several ecological and physiological factors, and are difficult to detect in wild birds (Carravieri et al., 2022).

4.3.2. Short-term reproductive performance

Reproduction is a sensitive endpoint of Hg toxicity in birds (reviewed in Evers, 2018; Whitney and Cristol, 2018). Effects on hatching success can result from Hg embryotoxicity (Whitney and Cristol, 2018; Yu et al., 2016), impacts on egg quality (Brasso and Cristol, 2008; Evers et al., 2003; Fort et al., 2014; but see Pollet et al., 2017), but also from disruption of parents' incubation behaviour, for example through egg neglect (Tartu et al., 2015, 2016 but see Blévin et al., 2018). Overall, Hg effects on hatching success are contrasted, with some studies showing declines (*e.g.*, Albers et al., 2007; Henny et al., 2002), no associations (*e.g.*, Carravieri et al., 2021; Weech et al., 2006; present study), or increases (Heinz et al., 2010). Stronger evidence exists on the association of Hg with breeding success in multiple avian taxa (*e.g.*, Brasso and Cristol, 2008; Goutte et al., 2014a,b, 2015). As Hg can decrease time spent in energy-demanding activities (reviewed in Whitney and Cristol, 2018), chick survival effects are thought to be mediated by disruption of parental care. Evidence of this comes from both behavioural observations (*e.g.*, decrease in chick provisioning rate, Merrill et al., 2005, increase in egg neglect behaviour, Tartu et al., 2015 at higher Hg exposure), and endocrine effects, such as disruption of the hormone prolactin (Tartu et al., 2015, 2016). Here, we showed that parental winter Hg contamination had no effect on egg volume, hatching success and chick survival, while chick growth was negatively affected. Potential confounding effects of embryonic Hg on chick health without impact on hatching success cannot be ruled out by the present study. However, there was no correlation between Hg concentrations in maternal head feathers and their eggshell membrane, and in parent head feathers and in their chicks' feathers (Table S2). This indicates that the association of parental winter Hg contamination with chick growth is not solely linked to Hg transfer to the egg. However, parental age and diet quality, or other factors not considered here, could also confound this association, calling for caution in the interpretation. Even though further evidence is needed, we hypothesise that trans-generational effects of Hg could act indirectly through parental care during chick-rearing.

5. Conclusions

The present study shows spatial variation in Hg transfer to mid-trophic consumers in the North Atlantic Ocean in winter, and calls for further investigations to identify the drivers of this. Importantly, we detected carryover effects of winter Hg exposure on summer breeding concentrations of adults and on the quality of their offspring. This suggests that whole-year exposure should be considered to quantify effects of Hg contamination on reproductive performance in migrating seabirds. Our results did not provide conclusive evidence of a negative effect of winter Hg contamination on telomere length. However, further studies on a larger sample size of known-age birds, and in other species, are warranted to confirm this. In addition, nutritional factors such as varying exposure to selenium, an essential metal necessary to contrast Hg deleterious effects (Manceau et al., 2021; Scheuhammer et al., 2008), should also be taken into account to understand Hg effects in the wild. Finally, variation in the association between Hg and reproductive performance could be driven by the interplay of multiple stressors (Bårdsen et al., 2018), which merits further investigation, in particular in the context of rapid environmental change.

Credit author statement

AC: draft conceptualisation and writing, sample and statistical analyses, data visualisation; SL, sample analysis and early discussions on the draft; FA, OC, MG, early discussions on the draft; CA, EB-C, MC, SP, fieldwork; VSB, KD, TP, assistance with spatial and environmental data analysis; CR, sample analysis; AV-P molecular sexing; DG, fieldwork, funding; PB, project management, early discussions on the draft; JF, project conceptualisation and management, funding, early discussions on the draft, fieldwork. All authors contributed to draft editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2022.120774.

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