

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

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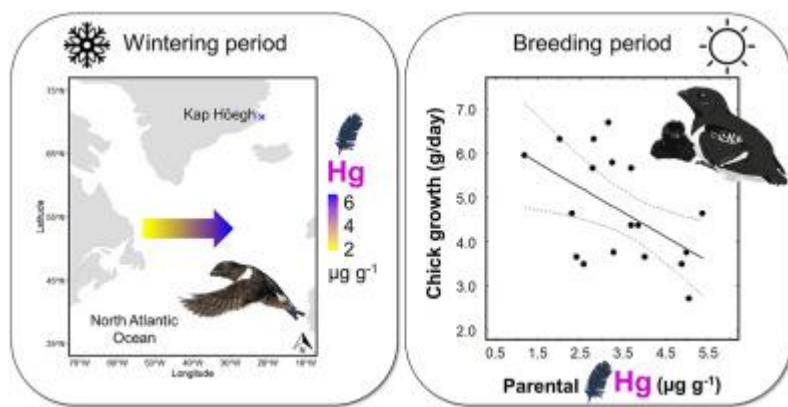
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Abstract :

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*. 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.

Graphical abstract



Highlights

► Winter Hg contamination and its carryover effects were quantified in little auks. ► Winter Hg contamination increased eastward in the North Atlantic Ocean. ► Blood Hg contamination in summer was predicted by winter Hg exposure. ► Winter Hg contamination had no clear effect on telomere length or body condition ► Parental winter Hg burdens were negatively associated with chick growth.

Keywords : blood, chick growth, feathers, reproduction, migration, seabird, telomeres

63 I. Introduction

64 Many animals migrate, commuting between breeding and non-breeding grounds to
65 adapt to seasonal environmental changes (Newton, 2010). In long-lived birds such as seabirds,
66 the non-breeding period is essential to renew the plumage, recover from the past breeding
67 season and prepare for the upcoming one (Dunn et al., 2020; Reynolds et al., 2011).
68 Environmental conditions experienced on non-breeding grounds can differ substantially from
69 those encountered during breeding (Lambert and Fort, 2022), and can have carryover effects
70 on subsequent reproductive performance and survival (Norris 2005; Szostek and Becker
71 2015). For instance, non-breeding habitat and diet quality can affect body condition, survival
72 probability, breeding propensity and success in seabirds (*e.g.*, Bogdanova et al., 2011;
73 Sorensen et al., 2009). Migration to distant non-breeding grounds can also expose seabirds to
74 patterns or/and quantities of harmful chemical contaminants that are different to those

75 encountered during breeding (*e.g.*, Lavoie et al., 2014; Miller et al., 2020). However, despite
76 well-known toxic effects of contaminants on reproduction and survival (Walker et al., 2012),
77 the carryover effects of non-breeding contamination on seabird reproductive performance
78 have been sparsely studied, with mixed results (*e.g.*, Bustamante et al., 2016; Mills et al.,
79 2020). This gap of knowledge limits our capacity to quantify the effect of multiple
80 environmental pressures along the annual cycle of seabirds.

81 Seabirds are exposed to a plethora of chemical contaminants (*e.g.*, Walker et al.,
82 2012). Among these, mercury (Hg) is of high environmental concern, especially in its
83 methylated and most toxic form (MeHg), which is easily bioaccumulated by marine biota, and
84 biomagnifies in marine food webs (Eagles-Smith et al., 2018). In the Arctic, growing
85 environmental change is modifying the Hg contamination of seabirds, with recently observed
86 or predicted increases (*e.g.*, Foster et al., 2019; Tartu et al., 2022). Recent findings point to a
87 net MeHg production at relatively shallow depths (20-200 m) in the Arctic Ocean, which is
88 believed to contribute to the high total Hg concentrations measured in Arctic surface
89 seawater, and in Arctic predators (Dietz et al., 2022; Heimbürger et al., 2015). In addition,
90 Arctic seabirds can acquire MeHg outside the Arctic during the non-breeding period. Previous
91 work has shown that the oceanic waters off Newfoundland in the western North Atlantic
92 Ocean are a hotspot of MeHg transfer to several Arctic seabird species that spend the winter
93 there (Albert et al., 2021; Fort et al., 2014; Renedo et al., 2020). However, the environmental
94 drivers that determine these hotspots are yet to be identified. Several factors, such as latitude,
95 primary productivity, climatic and weather indices, air and seawater temperature, can play a
96 role in the transfer of MeHg to food webs (Foster et al., 2019; Fitzgerald et al., 2007). High
97 MeHg quantities are found in both coastal and shelf sediments, and in subthermocline low-
98 oxygen oceanic waters in the mesopelagic zone, notably in association with active populations
99 of Hg methylating microorganisms (Fitzgerald et al., 2007). Consumers have higher MeHg

100 burdens in oligotrophic rather than mesotrophic environments due to the bio-concentration
101 effect, whereby MeHg partitions among fewer cells in low productivity systems (Chouvelon
102 et al., 2018; Pickhardt et al., 2002). Also, top predators in complex food webs can have higher
103 MeHg burdens than those in short food webs, because of enhanced biomagnification (Braune
104 et al., 2014; Lavoie et al., 2013). Understanding which environmental drivers best explain
105 Arctic seabird MeHg accumulation can help us predict future exposure and risk scenarios.

106 This study aims to understand the environmental drivers of winter MeHg
107 contamination and its carryover effects on fitness proxies in Arctic-breeding little auks (or
108 dovekies, *Alle alle*), the most abundant seabird in the North Atlantic (>40 million birds,
109 Egevang et al., 2003). Auks experience two moults per year: all feathers are replaced at the
110 end of the breeding season (complete moult), then head feathers are replaced again at the end
111 of the non-breeding period (partial pre-breeding moult in winter) (Albert et al., 2019 and
112 references therein). In birds, MeHg accumulates in blood and internal tissues after dietary
113 exposure, and deposits into growing feathers during moult (*e.g.*, Furness et al., 1986).
114 Therefore, feather Hg concentrations represent exposure during the inter-moult period, *i.e.*
115 winter months for head feathers of auks sampled on breeding grounds (Albert et al., 2019;
116 Fort et al., 2014). Auks are thus excellent models to identify MeHg hotspots over North
117 Atlantic wintering grounds through feather sampling during the following breeding season
118 (Albert et al., 2021; Fort et al., 2014; Renedo et al., 2020). On breeding sites, blood can also
119 be sampled, and is often used as short-term integrator of MeHg (*e.g.*, Evers 2018). Yet, blood
120 MeHg concentrations represent a balance of recent and past dietary intake redistributed from
121 internal tissues, and the contribution of past (*e.g.*, winter) and more recent (*e.g.*, summer) Hg
122 exposure on blood Hg concentrations is rarely studied (*e.g.*, Lavoie et al., 2014). We used
123 biologging (Global Location Sensor, GLS) to identify spatial differences in winter MeHg
124 contamination, feather and blood Hg concentration as proxy of winter and summer exposure,

125 and multiple indicators of short-term reproductive performance and individual quality to
126 quantify MeHg effects. Our specific aims were to assess whether: 1) wintering median
127 position of GLS-tracked little auks affects their head feather Hg concentrations (proxy of
128 winter MeHg contamination), and if environmental drivers (bathymetry, productivity, sea-
129 surface temperature and mixed layer depth) can explain spatial differences in Hg
130 concentrations; 2) winter MeHg contamination affects MeHg concentrations of breeding
131 adults (blood Hg concentrations) and their offspring; 3) winter MeHg contamination is
132 associated with short-term reproductive performance (egg volume, hatching date and success,
133 chick growth rate and survival) and individual health and quality (body condition, *e.g.*, Peig
134 and Green, 2009; and adult telomere length, *e.g.*, Angelier et al., 2019). Based on previous
135 results, we expected winter MeHg contamination to increase westward (Renedo et al., 2020,
136 Fort et al., 2014), and to increase with decreasing productivity (bio-concentration effect,
137 Chouvelon et al., 2018; Pickhardt et al., 2002). MeHg concentrations were expected to be
138 higher in head feathers (winter) than in blood (summer) (Albert et al., 2021), and to be
139 significantly associated with each other because of retention of MeHg from winter to summer
140 (Lavoie et al., 2014). Given MeHg toxic effects on bird health (Chastel et al., 2022; Whitney
141 and Cristol, 2018), and interannual repeatability of Hg contamination in seabird feathers
142 (Carravieri et al., 2013; Bertram et al., 2022), we expected winter Hg contamination to be
143 negatively associated with telomere length measured in summer. As MeHg can be transferred
144 from mother to the egg in avian species (reviewed in Ackerman et al., 2020) and have
145 negative effects on hatchability and chick health (Whitney and Cristol, 2018; Yu et al., 2016),
146 MeHg concentrations were expected to be correlated between mothers, their offspring and
147 their health. In addition, egg volume was expected to decrease with increasing maternal head
148 feather MeHg concentrations, as previously found in this population (Fort et al., 2014).

149 **II. Material and methods**

150 II.1. Study site and sample collection

151 This study was conducted on the little auk population of Ukaleqarteq, Kap Höegh
152 (East Greenland; 70°44'N, 21°35'W) in July-August of 2018 and 2019. The little auk is a
153 long-lived seabird (>20 years) producing a single egg per year. Adults provide bi-parental
154 care until late chick-rearing, when only males feed the chick. Little auks are zooplanktivorous
155 and specialise on large copepods, diving at depths of 20-50m during winter (Fort et al., 2010).
156 A total of 92 breeding adults (N = 62 in 2018, 32 females, 29 males, one unknown sex; N =
157 30 in 2019, 10 females, 19 males, one unknown sex, see Section II.4. for molecular sexing)
158 were caught in the nest or in its proximity by hand or with noose traps during incubation or
159 chick-rearing. Handling of birds for morphometric measurements (see Section II.2), as well as
160 blood and feather sampling, lasted ~10 min. Blood (approx. 0.5 ml) was collected from the
161 brachial vein with heparinised syringes, and centrifuged for 10 minutes at 3500 rpm, within
162 six hours from collection. Red blood cells and plasma were separately stored at -20°C until
163 further analyses. Red blood cells were used for Hg (see Section II.5.) and telomere length (see
164 Section II.6.) quantification, while plasma will be used in further investigations. Feathers (7-
165 10 per individual) were collected from the throat (hereafter head feathers) and stored at
166 ambient temperature in sealed plastic bags. To track wintering movements, 28 of the 92
167 sampled adults (N = 11 in 2018, 8 females, 3 males; N = 17 in 2019, 5 females, 12 males) had
168 been equipped with a miniature GLS data-logger (F100 and C65-SUPER, Migrate
169 Technology, mass of 1.5 g, ~1% of adult body mass), mounted on a conventional metal ring,
170 in the previous year. All birds were sampled only once (no repeated observations).

171 II.2. Nest monitoring, reproductive output and morphological data

172 In 2018 and 2019, 70 and 39 nests, respectively, were monitored to quantify hatching
173 date, success, chick growth and survival. When accessible, the single egg was measured to
174 calculate its volume as detailed in Fort et al. (2014). Nests were checked every second day to

175 determine the hatching date. Eggshell fragments were collected and stored in sealed plastic
176 bags at -20°C until Hg analyses. Once chicks were at least one day old, they were weighed
177 (electronic scale to the nearest gram) every second day to quantify their growth. Chick growth
178 rate was inferred from the slope of the relationship between chick mass and age during the
179 linear phase of growth (4–14 days of age, Amélineau et al., 2016). Survival of chicks was
180 estimated when they were 18 ± 3 days old (mean \pm SD), *i.e.*, shortly before they left the nest.
181 Chick age at survival estimation was accounted for in statistical analyses concerning chick
182 growth rate (see Section II.7.). On the day of chick survival estimation, four breast feathers
183 (hereafter chick body feathers) were sampled, following the same procedures as in adults (see
184 Section II.1). In 2018, one or both parents of 43 out of the 70 monitored nests were sampled
185 for blood and head feathers to determine Hg contamination (see Section II.1. and II.5.) and its
186 fitness proxies' correlates (see Section II.7.). For logistical reasons, parents of only two out of
187 the 39 monitored nests could be sampled for blood and head feathers in 2019, and were thus
188 not included in statistical analyses looking at fitness proxies' correlates of Hg contamination.
189 Adults and chicks were weighed (± 1 g), measured with a calliper (head-bill, culmen, tarsus,
190 ± 1 mm), and a ruler (flattened wing, ± 1 mm). Initially we considered calculating a scaled
191 mass index (SMI, Peig and Green, 2009) in adults as proxy of body condition. However, slope
192 estimates of the correlation between mass and the different length measures available (head-
193 bill, culmen, tarsus, wing) were not significant. Therefore, we considered adult body mass
194 alone as body condition index, which is a reliable condition indicator within a population
195 (Peig and Green, 2009).

196 II.3. Movement and environmental data

197 GLS loggers measured daylight level intensity each minute and recorded its maximum
198 intensity each 5 min. Following the standardised procedure described in Bråthen et al. (2021)
199 we used a threshold method to estimate latitudes from the length of day and night and

200 longitudes on the timing of noon and midnight (Hill 1994; Wilson et al., 1992), giving a
201 maximum of two locations per day, and subsequently filtered erroneous locations. We treated
202 GLS tracking data from December 1 to January 31 (the “core wintering period”, when all
203 birds were at their wintering grounds, Fort et al., 2013). We extracted the following
204 environmental variables on a daily basis over $1^\circ \times 1^\circ$ cells: sea-surface temperature (SST),
205 mixed-layer depth (MLD), sea-surface chlorophyll *a* concentration (chl_a, as a proxy of
206 productivity) and bathymetry. Environmental data was retrieved from Marine Copernicus
207 (products: GLOBAL_ANALYSISFORECAST_PHY_CPL_001_015 for SST and MLD; and
208 GLO_CHL_L4_REP_OBSERVATIONS_009_082 for chl_a,
209 <https://resources.marine.copernicus.eu/products>). Bathymetry was extracted using the NOAA
210 dataset <https://www.ncei.noaa.gov/maps/bathymetry/> (GEBCO). We calculated the median of
211 latitude and longitude, and extracted all environmental variables at this location, for each
212 individual separately. These unique values per individual were used to test the influence of
213 location and environmental characteristics on head feather (*i.e.*, winter) Hg concentrations
214 (see Section II.7.).

215 II.4. DNA extraction and molecular sexing

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

221 PCR reactions included 0 to 90 ng of DNA, 0.4 μ M of each primer, 1X reaction buffer
222 (biotechrabbit, Hennigsdorf, Germany), 1.5 mM MgCl₂, 0.2 mM of dNTPs, 0.32 mg/ μ L of
223 bovine serum albumine and 1.2 U of *Taq* polymerase (biotechrabbit, Hennigsdorf, Germany)
224 in a 30 μ L final volume. The following PCR profile was performed on a TC-5000 (Techne)

225 thermocycler: 94°C for 1 min, followed by 35 cycles of 30 s at 94 °C, 45 s at 53 °C, and 45 s
226 at 72 °C, and a final extension of 5 min at 72 °C. PCR products were separated by
227 electrophoresis on a 2.5% agarose gel stained with GelRed. No-template negative controls
228 were included in DNA extractions and PCR reactions.

229 II.5. Hg analysis

230 Quantification of total Hg (hereafter Hg) was carried out in adult head feathers and
231 chick body feathers and adult red blood cells, and in eggshell membranes at the laboratory
232 Littoral, Environment and Societies (LIENSs, CNRS-La Rochelle Université). Total Hg
233 concentrations in these three tissues are a close approximation of MeHg concentrations, as
234 they contain virtually 100% MeHg (Bond and Diamond, 2009; Renedo et al., 2021). In the
235 blood compartment, Hg is preferentially found within red blood cells, and red blood cell Hg
236 concentrations are a very close approximation of whole blood Hg concentrations (Tavares et
237 al., 2013 and authors' unpublished data). Hereafter, red blood cell will be abbreviated to
238 "blood" unless otherwise specified. Whole blood and red blood cell MeHg concentrations
239 represent a balance of recent and past dietary intake redistributed from internal tissues. The
240 biological half-life of Hg is 30-40 days during moult, and longer than 65 days outside moult
241 (Monteiro and Furness 2001). Feather synthesis is an important MeHg excretion pathway in
242 birds; up to 90% of the body burden can be found in feathers after moult (Bond and Diamond,
243 2009; Braune and Gaskin, 1987). After completion of telomere length analysis on wet red
244 blood cells (see Section II.6.), these were freeze-dried for 48h and homogenised to enable Hg
245 determination on the dry mass, which is necessary when using direct Hg analysers (see
246 below). To remove external contamination, seven to 10 head feathers, and four chick body
247 feathers, were cleaned in a 2:1 chloroform:methanol solution in an ultrasonic bath for 3 min,
248 then rinsed twice with methanol before being dried in aluminium foil for 24h at 45°C (details
249 in Carravieri et al., 2013). Three feathers of each type were randomly selected and

250 homogenised by cutting them into small fragments with stainless scissors. Membranes were
251 first separated from eggshells using stainless tweezers, and then placed in a net before
252 cleaning, to avoid the loss of small particles in the cleaning mixture. The cleaning procedure
253 was the same as for feathers. Head feather, red blood cells, and eggshell membrane Hg
254 concentrations were quantified using an advanced Hg analyser (AMA-254, Altec) and are
255 expressed as $\mu\text{g g}^{-1}$ dry weight (dw). All analyses were carried out in duplicate (relative
256 standard deviation <10%) and average values used in data analyses. The certified reference
257 material (CRM) TORT-3 (certified Hg concentration: $0.292 \pm 0.022 \mu\text{g g}^{-1}$ dw) was measured
258 at the beginning and end of each set of analysis, and every 10-15 samples. Measured TORT-3
259 values were $0.284 \pm 0.010 \mu\text{g g}^{-1}$ dw (N = 7) for the set of blood samples, $0.289 \pm 0.004 \mu\text{g g}^{-1}$
260 dw (N = 9) for adult head feathers, $0.289 \pm 0.003 \mu\text{g g}^{-1}$ (N = 15) for chick body feathers,
261 and $0.290 \pm 0.005 \mu\text{g g}^{-1}$ dw (N = 5) for eggshell membranes. CRM mass (and thus Hg
262 quantity introduced in the analyser) was adjusted to mirror the Hg mass present in samples.
263 Blanks were analysed at the beginning of each set of samples and the limit of detection of the
264 Hg analyser was 0.05 ng.

265 II.6. Telomere length quantification

266 Telomeres are repetitive, non-coding DNA sequences found at the end of
267 chromosomes, which protect genome integrity (Blackburn, 2005). These sequences shorten at
268 each cell division, but also as a result of environmental stress (*e.g.*, Angelier et al., 2018).
269 Telomere length was determined by quantitative PCR (qPCR; BioRad CFX 96, Bio-Rad
270 USA) according to Cawthon (2002), and adapted for the little auk, at the Centre d'Etudes
271 Biologiques de Chizé (CEBC, CNRS-La Rochelle Université). Briefly, 5 μL of red blood
272 cells were digested with proteinase K and DNA was extracted using the Nucleospin Tissue
273 Kit (Macherey-Nagel), following the manufacturer's instructions. DNA concentration and
274 purity were assessed with a Nanodrop ND1000 spectrophotometer (Thermo Scientific). The

275 telomere primers were similar to those previously used in other seabird species (*e.g.*,
276 Sebastiano et al., 2020). The control single-copy gene Recombination Activating Gene 1
277 (RAG1) was selected and amplified using specific primers designed for the little auk. All
278 qPCR runs were performed using 7.5 ng of DNA per reaction and using the BioRad SYBR
279 Green Supermix. The universal telomere primers were used at a concentration of 800 nM, and
280 RAG1-F/RAG1-R at 300 nM. To generate a six-point standard curve (from 20.0 ng to 0.62
281 ng) for controlling the amplifying efficiency of the reactions, serial dilutions of DNA from a
282 pooled sampled of 10 little auks were included on the plate. All samples were randomly
283 distributed across the PCR plates. The efficiency of the telomere and RAG1 assays ranged
284 from 103.0 to 108.6% and 100.7 to 103.0%, respectively, and all r^2 were very high (>0.990).
285 Three reference samples ('golden samples') were run in triplicate on all plates to account for
286 inter-plate variation, and each sample was run in duplicate on every plate. The interplate
287 repeatability was 0.959 (intra-class correlation coefficient). The relative telomere length was
288 calculated as the telomere copy number (T) relative to single-copy gene (S), expressed as TS
289 ratio.

290 II.7. Data analysis

291 Data exploration, visualisation and statistical analyses were performed in R version
292 4.0.5 (R Core Team, 2021). To address our aims, we used linear or generalised linear models
293 with different specifications depending on the response variable and error distribution, and
294 different explanatory variables depending on aims and sample size (**Table S1**, Supplementary
295 Material). Model specification and fit were validated *via* residual analysis of initial models
296 (*e.g.*, homoscedasticity of residuals). When multiple explanatory variables were continuous,
297 we tested for the absence of collinearity (variance inflation factor, $VIF < 3$) and standardised
298 them (mean = 0, SD = 1) to facilitate comparison of effect sizes (Zuur et al., 2009).

299 *II.7.a Aim 1*

300 The effect of the median latitude and longitude of adult position during the core
301 winter, and the associated environmental variables, was tested on head feather (*i.e.*, winter)
302 Hg concentrations. Environmental variables (bathymetry, *chl_a*, MLD, SST) were strongly
303 collinear ($VIF > 10$). Therefore, *chl_a*, MLD, and SST data were log-transformed to achieve a
304 normal distribution (raw bathymetry data was normally distributed), and all variables were
305 scaled, to perform a principal component analysis (PCA, R package *ade4*, Dray and Dufour,
306 2007). The first and second axis of the PCA explained 93% of total variation in environmental
307 data over wintering grounds (**Fig. S1**). Bathymetry was positively related to MLD (*i.e.*, deeper
308 waters were associated with larger MLD) and these two variables were mainly associated with
309 PC1 scores (decreasing PC1 scores indicated deeper waters and MLD). SST and *chl_a* were
310 not related and were mainly associated with PC2 (decreasing PC2 scores indicated higher SST
311 and *chl_a* values, **Fig. S1**). Principal component (PC) scores of PC1 and PC2 were extracted to
312 obtain uncorrelated variables, and then used as explanatory variables of head feather Hg
313 concentrations alongside latitude and longitude (no collinearity detected, all $VIF < 3$).

314 *II.7.c Aim 2*

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

322 *II.7.d Aim 3*

323 This aim tested (i) the effect of maternal head feather Hg contamination on egg
324 volume; (ii) the effect of winter Hg concentrations, sex and their interaction, year and

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

340 *II.7.d Model selection*

341 For all our aims, we used Akaike's information criterion corrected for small sample
342 sizes (AICc) to select the best models (R package *MuMIn*, Bartón 2020). We compared a list
343 of biologically meaningful initial candidate models. The initial and best models selected for
344 each specific question within each aim, as well as their sample sizes, are presented in **Table**
345 **S1**. The AICc, the difference between AICc of the specific model and the best model
346 (ΔAICc), and the AICc weight (normalized weight of evidence in favour of the specific
347 model), and the explained deviance (indicative of the proportion of variation explained by the
348 model, similar to R^2 for linear models, Zuur et al., 2009) were calculated. If the null model
349 ranked as the best model, the effects of all explanatory variables were considered statistically

350 insignificant. When multiple models performed better than the null model and had $\Delta\text{AICc} <$
351 2, we applied model averaging on those models to make an inference. This produced averaged
352 parameter estimates (β) of the predictor variables included in those models, weighted using
353 AICc weights. AICc tables for candidate models with significant and insignificant effects are
354 presented in **Table 1** and **Table S2**, respectively. When model averaging was applied, the
355 averaged $\beta \pm$ standard error (SE), and 95% confidence interval (CI), are also reported for each
356 predictor in **Table 1**.

357 **III. Results**

358 III.1. Influence of wintering median position and environment on head feather Hg 359 concentrations

360 GLS-tracked little auks spent the core wintering period (1st December – 31st January)
361 of 2018 and 2019 on average 2598 km (range 1743–3995 km) from their breeding colony,
362 between latitudes 42.6°N and 59.3°N, and longitudes 67.1°W and 30.5°W (**Fig. 1**).
363 Descriptive statistics of the environmental characteristics at these locations are presented in
364 **Table S3**. The targeted environmental variables (represented by PC1 and PC2 scores) did not
365 drive variation in head feather Hg concentrations, as models including them were not retained
366 by AICc selection (**Table 1**). In contrast, the median longitude of winter location had a clear
367 effect on head feather Hg concentrations ($\beta \pm$ SE on scaled values: 0.196 ± 0.058 , 95% CI:
368 0.085–0.309): winter Hg exposure increased eastward (**Fig. 1**), with no effect of year or sex
369 (**Table 1**).

370 III.2. Association of head feather Hg concentrations with blood and offspring Hg 371 concentrations

372 Hg concentrations in head feathers (range 1.18–7.93 $\mu\text{g g}^{-1}$ dw, **Table S4**) were similar
373 between sexes and years (**Table 1**). The best model explaining Hg concentrations in blood
374 (range 0.4–2.0 $\mu\text{g g}^{-1}$ dw, **Table S4**) included head feather Hg concentrations, sex and year as

375 predictors, with no sex:Hg interaction (**Table 1**). Blood Hg concentrations were significantly
376 higher in males than females (sexM: 0.203 ± 0.046 , 95% CI: 0.113–0.293), and in 2018 than
377 2019 (year2019: -0.130 ± 0.048 , CI: -0.222–0.034), and increased with increasing head
378 feather Hg concentrations (0.145 ± 0.022 , 95% CI: 0.101–0.189) (**Table 1, Fig. 2**). Eggshell
379 membrane Hg concentrations were not related to maternal head feather Hg concentrations
380 (**Table S2**). Maternal and paternal head feather Hg concentrations were not related to chick
381 body feather Hg concentrations (**Table S2**).

382 III.3. Association of head feather Hg concentrations with fitness proxies

383 Four models had similar support in explaining variation in telomere length (range of
384 TS ratio: 0.65–1.32, **Table S4**), indicating that Julian day, year, sex and head feather Hg
385 concentrations were significant predictors (**Table 1**). However, model averaging showed that
386 only Julian day and year had a clear statistical effect: telomere length increased as the
387 sampling season progressed (averaged $\beta \pm SE$, 0.049 ± 0.014 , 95% CI: 0.021–0.078), and
388 telomeres were on average longer in 2019 than 2018 (year2019: 0.078 ± 0.030 , 95% CI:
389 0.017–0.138, **Table 1, Fig. S2**). Telomere length showed a weak, decreasing trend with
390 increasing head feather Hg concentrations, and tended to be longer in males than females
391 (**Table 1**). Variation in adult body mass during the breeding period (range 125–182 g, **Table**
392 **S4**) was explained by four models with similar support, including Julian day, year and head
393 feather Hg concentrations as predictors (**Table 1**). However, model averaging showed that
394 Julian day only had a clear statistical effect: body mass decreased with increasing Julian day
395 (averaged $\beta \pm SE$, -0.74 ± 0.31 , 95% CI: -1.35–0.13, **Table 1**). In addition, all models
396 explained very little of the total variation (maximum explained deviance of 8%, **Table 1**). Egg
397 volume (range 21.9–31.0 cm³, **Table S4**) was not related to female head feather Hg
398 concentrations (**Table S2**). Hatching success was 64.3% and 87.2% of monitored nests (70
399 and 39), and chick survival was 72.5% and 85.3% of monitored chicks (30 and 34) in 2018

400 and 2019, respectively (**Table S4**). In 2018, hatching success and chick survival were not
401 related to parental head feather Hg concentrations (**Table S2**). Chick growth rate (range 2.71–
402 6.70 g day⁻¹) decreased with increasing parental head feather Hg concentrations ($-0.555 \pm$
403 0.215 , 95% CI: -0.976 – 0.123 , **Fig. 3**), irrespective of parent sex (**Table 1**).

404 **IV. Discussion**

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

420 IV.1. Spatial differences in Hg exposure and potential environmental drivers

421 Head feather Hg concentrations in little auks breeding in East Greenland were driven
422 by longitude of wintering position, but, contrary to our hypothesis and to results in other
423 species (Albert et al., 2021; AMAP 2021), increased eastward. Namely, head feather Hg
424 concentrations decreased eastward in the North Atlantic in wintering little auks from multiple

425 Arctic colonies in 2015 and 2016 (Renedo et al., 2020). Results from the latter study included
426 little data from longitudes farther west, *i.e.*, shelf waters off the United States and south
427 Greenland, which were visited by birds of the present study. This could indicate that winter
428 Hg exposure is low on shelf waters east of the United States and Greenland, and high in
429 oceanic waters in the central North Atlantic. This is consistent with empirical and modelling
430 studies on MeHg content in different marine matrices, which show a similar longitudinal
431 trend in zooplankton MeHg content in North Atlantic waters (Zhang et al., 2020).
432 Alternatively, environmental and/or ecological drivers of winter Hg contamination in little
433 auks differ temporally in the North Atlantic, leading to variation in the spatial pattern of Hg
434 exposure found in different years (Fort et al., 2014; Renedo et al., 2020, present study).
435 Temporal variation in seawater Hg concentrations and/or in the transfer of Hg to food webs is
436 likely, because they depend on several environmental (Foster et al., 2019; Stern et al., 2012)
437 and trophic factors (Braune et al., 2014). However, none of the environmental variables that
438 were studied here had a clear role in explaining the spatial pattern of little auks' winter Hg
439 contamination. Previously, productivity has been associated with Hg bio-dilution in
440 zooplankton (Pickhardt et al., 2002) and fish (Chouvelon et al., 2018), while Hg burden
441 increases were detected at chl a low and high extremes in Arctic seabirds, likely as a result of
442 bottom-up nutrients effects on fish communities (Tartu et al., 2022). In addition, MeHg
443 transfer to food webs can vary with the depth of the ocean mixed-layer (Dietz et al., 2022;
444 Heimbürger et al., 2015), with potential cascading effects on Hg contamination of consumers,
445 including those feeding at relatively shallow depths like little auks (Fort et al., 2010).
446 However, interactions between these environmental variables and the ecological processes
447 that lead to Hg exposure in little auks are complex, likely work at different temporal scales,
448 and might vary at a high rate under climate change (Stern et al., 2012; Tartu et al., 2022;
449 Wang et al., 2019). Further studies on larger sample sizes associating wintering movements of

450 seabirds and their Hg contamination are necessary to gain more insights on Hg hotspots, their
451 environmental drivers, and their interannual variation in the North Atlantic. This is
452 particularly important given the hotspot of seabird biodiversity found within this oceanic
453 region, which sustains millions of birds every year (Davies et al., 2021).

454 IV.2. Carryover effect of winter Hg exposure on concentrations in summer

455 Previous studies have shown that Hg exposure at distant migrating grounds can affect
456 summer Hg concentrations in aquatic birds (*e.g.*, Bertram et al., 2022; Lavoie et al., 2014). In
457 agreement with this, the correlation between head feather and blood Hg concentrations found
458 here supports that part of Hg bioaccumulated during winter is still circulating in blood during
459 summer. Hg contamination is higher over wintering than breeding grounds in several Arctic
460 breeding seabirds, including little auks (Albert et al., 2021). Hg excretion into feathers is an
461 efficient mechanism (Bond and Diamond, 2009), but winter moult only affects head feathers
462 in little auks, *i.e.*, a small proportion of the whole plumage. In addition, excretion in feathers
463 is known to be up to 90% of the body burden (Bond and Diamond, 2009; Braune and Gaskin,
464 1987). This can limit the total amount of Hg that can be eliminated from the organism.
465 Furthermore, the biological half-life of Hg in seabirds can be longer than 65 days in non-
466 moulting individuals (Monteiro and Furness 2001). A correlation of Hg concentrations in
467 head feathers and blood could also result from individuals consistently targeting prey of
468 similar Hg content in both winter and summer. However, between- and within-individual
469 variation in diet is small in this copepod specialist, at least in summer (Amélineau et al., 2016;
470 Jakubas et al., 2020). In addition, little auk prey and its Hg content are poorly known at
471 wintering grounds (Rosing-Asvid et al., 2013), further studies are thus necessary to confirm
472 this hypothesis. Individuals may also differ in their physiological capacity to assimilate,
473 bioaccumulate and excrete Hg, resulting in some birds consistently retaining more Hg than
474 others, irrespective of exposure. Importantly, prey Hg content explains a large part of inter-

475 annual variations in summer Hg concentrations in this population (Fort et al., 2016).
476 Carryover effects of winter Hg exposure appear to be another important driver of summer Hg
477 concentration, and should be considered when using little auks as bioindicators of temporal
478 variations of Hg in Arctic food webs (Fort et al., 2016). The sex-related and inter-annual
479 differences in summer Hg exposure can be related to trophic and abiotic factors, respectively
480 (Carravieri et al., 2014; Hitchcock et al., 2019; Robinson et al., 2012).

481 IV.3. Carryover effects on fitness proxies

482 IV.3.1. Telomere length and body condition

483 Telomere length integrates the effect of multiple stressors and can predict reproductive
484 performance and survival in a variety of taxa (Angelier et al., 2019; Chatelain et al., 2020;
485 Louzon et al., 2019; Salmón and Burraco, 2022). Exposure to environmental contaminants
486 can disrupt telomere dynamics, *e.g.*, through molecular oxidative damage, disruption of
487 antioxidant defences, and/or impact on telomerase, the enzyme responsible for telomere
488 elongation (reviewed in Louzon et al., 2019). *In vitro* and studies in humans have shown a
489 general trend of decrease in telomere length after contaminant exposure (Chatelain et al.,
490 2020; Louzon et al., 2019). Yet, the few studies on Hg-related variation of telomere length in
491 birds showed contrasted results. A female-specific positive association between Hg
492 contamination and telomere length was observed in black-legged kittiwakes *Rissa tridactyla*
493 (Blévin et al., unpublished data in Angelier et al., 2018), while no association was found in
494 Mandt's black guillemots *Cepphus grylle mandtii* (Eckbo et al., 2019). A potential indirect
495 effect of Hg on telomere dynamics through impacts on corticosterone has been suggested in
496 red kite *Milvus milvus* nestlings (Powolny et al., 2020). Other studies have shown no clear
497 evidence of Hg effects on corticosterone (*e.g.*, Chastel et al., 2022 and references therein), the
498 latter result should thus be taken with caution. Recently, Bauch et al. (2022) showed a clear,
499 male-specific decreasing trend of telomere length with increasing winter Hg contamination in

500 Cory's shearwaters *Calonectris borealis*. In our study, and irrespective of sex, little auk
501 telomere length was not clearly related to winter Hg contamination, even though there was a
502 negative, nonsignificant trend. Winter Hg concentrations are 1.5 times lower in little auks
503 than Cory's shearwaters (Bauch et al., 2022), suggesting that Hg contamination might be too
504 low to have a similarly strong and significant effect. This is consistent with low Hg risk
505 identified for little auks when compared to other Arctic seabird species (Chastel et al., 2022).
506 On the other hand, telomere length increased with sampling date, and varied significantly
507 between years. These results could be explained by a confounding effect of age. Telomere
508 length has been associated with biological and chronological age in birds (Bize et al., 2009;
509 Young et al., 2013). Breeding phenology and performance can also vary with age, with older,
510 more experienced seabirds breeding earlier than younger ones (*e.g.*, de Forest and Gaston,
511 1996; González-Solís et al., 2004). The observed increase in telomere length across the season
512 could thus indicate that birds sampled later were younger. In addition, telomeres were on
513 average shorter in birds sampled in 2018 than 2019, potentially because a larger proportion of
514 old birds was sampled in 2018. Environmental conditions can drive annual changes in
515 telomere length of adult birds (Mizutani et al., 2013; Young et al., 2013). Environmental
516 conditions were likely challenging in 2018, as both hatching success and chick survival were
517 lower in 2018 than 2019. Furthermore, chick growth rates were lower in 2018 compared to
518 2019 (**Fig. S3**), and to the long-term average (Amélineau et al., 2019). The more challenging
519 year 2018 possibly allowed only older and experienced birds to breed, and thus be sampled,
520 while several young birds may have failed early or skipped reproduction. Good conditions in
521 the winter and/or summer of 2019 might also have promoted telomere restoration (*i.e.*,
522 through telomerase activity, Louzon et al., 2019). Further investigation in birds of known age
523 and quality are necessary to confirm or refute these interpretations. Quantifying the intrinsic
524 and extrinsic drivers of telomere length and Hg contamination, which could co-vary (Bauch et

525 al., 2022; Salmón and Burraco, 2022), is essential to rule out whether telomere length and/or
526 dynamics are useful biomarkers of Hg health effects.

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

535 IV.3.2 Short-term reproductive performance

536 Reproduction is a sensitive endpoint of Hg toxicity in birds (reviewed in Evers, 2018;
537 Whitney and Cristol, 2018). Effects on hatching success can result from Hg embryotoxicity
538 (Whitney and Cristol, 2018; Yu et al., 2016), impacts on egg quality (Brasso and Cristol,
539 2008; Evers et al., 2003; Fort et al., 2014; but see Pollet et al., 2017), but also from disruption
540 of parents' incubation behaviour, for example through egg neglect (Tartu et al., 2015, 2016
541 but see Blévin et al., 2018). Overall, Hg effects on hatching success are contrasted, with some
542 studies showing declines (*e.g.*, Albers et al., 2007; Henny et al., 2002), no associations (*e.g.*,
543 Carravieri et al., 2021; Weech et al., 2006; present study), or increases (Heinz et al., 2010).
544 Stronger evidence exists on the association of Hg with breeding success in multiple avian taxa
545 (*e.g.*, Brasso and Cristol, 2008; Goutte et al., 2014ab, 2015). As Hg can decrease time spent in
546 energy-demanding activities (reviewed in Whitney and Cristol, 2018), chick survival effects
547 are thought to be mediated by disruption of parental care. Evidence of this comes from both
548 behavioural observations (*e.g.*, decrease in chick provisioning rate, Merrill et al., 2005,
549 increase in egg neglect behaviour, Tartu et al., 2015 at higher Hg exposure), and endocrine

550 effects, such as disruption of the hormone prolactin (Tartu et al., 2015, 2016). Here we
551 showed that parental winter Hg contamination had no effect on egg volume, hatching success
552 and chick survival, while chick growth was negatively affected. Potential confounding effects
553 of embryonic Hg on chick health without impact on hatching success cannot be ruled out by
554 the present study. However, there was no correlation between Hg concentrations in maternal
555 head feathers and their eggshell membrane, and in parent head feathers and in their chicks'
556 feathers (**Table S2**). This indicates that the association of parental winter Hg contamination
557 with chick growth is not solely linked to Hg transfer to the egg. However, parental age and
558 diet quality, or other factors not considered here, could also confound this association, calling
559 for caution in the interpretation. Even though further evidence is needed, we hypothesise that
560 trans-generational effects of Hg could act indirectly through parental care during chick-
561 rearing.

562 **V. Conclusions**

563 The present study shows spatial variation in Hg transfer to mid-trophic consumers in
564 the North Atlantic Ocean in winter, and calls for further investigations to identify the drivers
565 of this. Importantly, we detected carryover effects of winter Hg exposure on summer breeding
566 concentrations of adults and on the quality of their offspring. This suggests that whole-year
567 exposure should be considered to quantify effects of Hg contamination on reproductive
568 performance in migrating seabirds. Our results did not provide conclusive evidence of a
569 negative effect of winter Hg contamination on telomere length. However, further studies on a
570 larger sample size of known-age birds, and in other species, are warranted to confirm this. In
571 addition, nutritional factors such as varying exposure to selenium, an essential metal
572 necessary to contrast Hg deleterious effects (Manceau et al., 2021; Scheuhammer et al.,
573 2008), should also be taken into account to understand Hg effects in the wild. Finally,
574 variation in the association between Hg and reproductive performance could be driven by the

575 interplay of multiple stressors (Bårdsen et al., 2018), which merits further investigation, in
576 particular in the context of rapid environmental change.

577

578 **Conflict of interest**

579 The authors declare that there are no conflicts of interest.

580

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1059 **Table 1.** Akaike tables including model specification and sample size of the models used to
 1060 address the different aims of this study (see Introduction, and Table S1). This table includes
 1061 response variables showing significant effects, while response variables showing insignificant
 1062 effects are reported in Table S2. Only the five best ranked models and the null model are
 1063 presented. When more than two models had similar support ($\Delta AIC_c < 2$), model averaging
 1064 was applied, and averaged estimates (β) reported, to determine the explanatory variables with
 1065 the clearest effect (in bold). Abbreviations: Lat and Lon, median latitude and longitude of
 1066 wintering position; PC1 and 2, scores on axis 1 and 2 of a PCA of environmental variables
 1067 (SST, sea-surface temperature; chl a , sea-surface chlorophyll a concentration; MLD, mixed-
 1068 layer depth); Hg $_{HF}$, head feather (*i.e.*, winter) Hg concentrations; AIC $_c$, Akaike's
 1069 information criterion corrected for small sample sizes; ΔAIC_c , difference between AIC $_c$ of
 1070 the specific model and the best model; k , number of parameters; w_i AIC $_c$ weight; Exp. Dev.,
 1071 explained deviance.

Aim 1) Head feather Hg concentrations in GLS-tracked birds (N = 28)

Initial model: Head feather Hg ~ Lat + Lon + PC1 + PC2 + Year + Sex

GLM Gaussian (log)	k	AIC $_c$	ΔAIC_c	w_i	Exp. Dev.
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

1072

Aim 2) Red blood cell Hg concentrations (N = 79)

Initial model: Red blood cell Hg ~ Hg $_{HF}$ + Year + Sex + Hg $_{HF}$:Sex

GLM Gamma (identity)	k	AIC $_c$	ΔAIC_c	w_i	Exp. Dev.
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

1073

Aim 3) Telomere length (TS ratio) (N = 77)

Initial model: TS ratio ~ Hg $_{HF}$ + Julian + Year + Sex + Hg $_{HF}$:Sex

GLM Gamma (identity)	k	AIC $_c$	ΔAIC_c	w_i	Exp. Dev.
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) $\beta \pm SE$ [95% CI]

Intercept	0.955 \pm 0.021 [0.912–0.997]
Julian	0.049 \pm 0.014 [0.021–0.078]
SexM	0.024 \pm 0.030 [-0.036–0.083]

Year2019 0.078 ± 0.030 [0.017–0.138]
Hg_HF -0.007 ± 0.012 [-0.032–0.017]

1074

Aim 3) Body mass (N = 80)

Initial model: Body mass ~ Hg_HF + Julian + Year + Sex + Hg_HF:Sex

GLM Gamma (identity)	k	AIC_c	ΔAIC_c	w_i	Exp. Dev.
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) $\beta \pm SE$ [95% CI]

Intercept	304 ± 61 [183–425]
Julian	-0.74 ± 0.31 [-1.35– -0.13]
Year2019	-4.05 ± 2.82 [-7.51–3.56]
Hg_HF	-1.19 ± 1.21 [-2.21–1.37]

1075

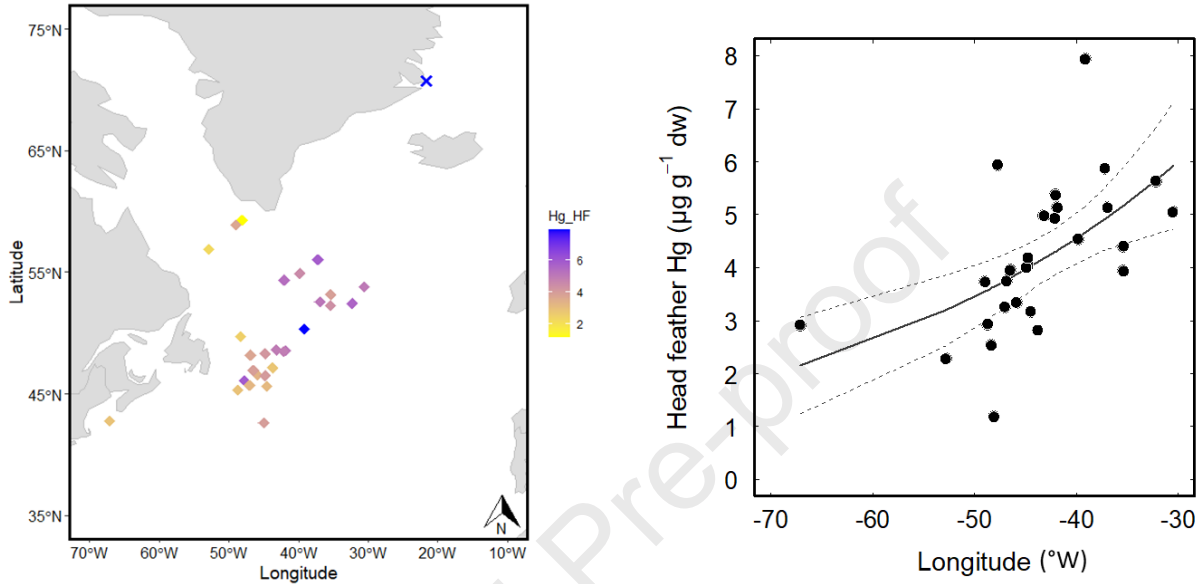
Aim 3) Chick growth (N = 18)

Initial model: Chick growth ~ Hg_HF + Sex + Hg_HF:Sex + Chick_age

GLM Gamma (identity)	k	AIC_c	ΔAIC_c	w_i	Exp. Dev.
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

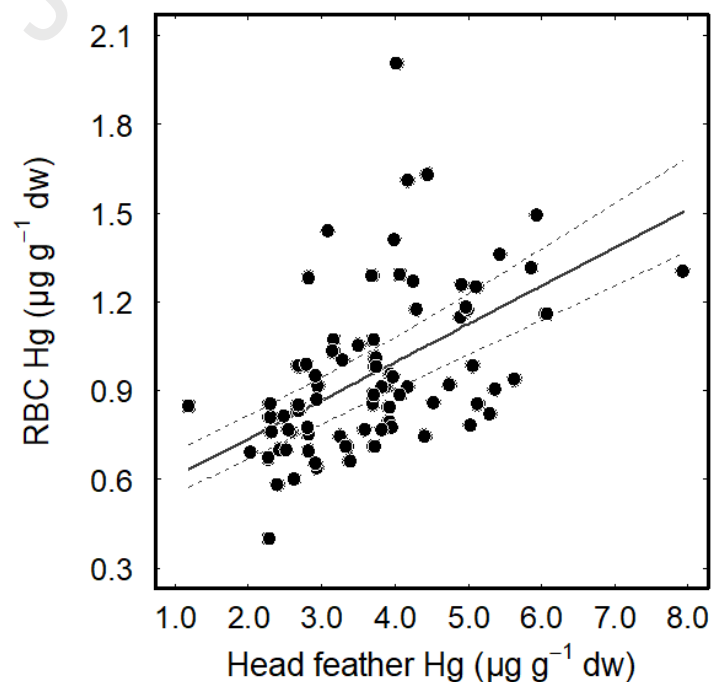
1076

1077 **Fig. 1.** Left panel: median positions of little auks wintering in the North Atlantic Ocean in
 1078 2017-18 and 2018-19 (1st December – 31st January), coloured by the Hg concentrations in
 1079 their head feathers. The blue cross indicates the breeding colony at Ukaleqarteq, East
 1080 Greenland. Right panel: Head feather Hg concentrations increase with decreasing longitude
 1081 (eastward) in little auks wintering in the North Atlantic in 2017-18 and 2018-19 (1st
 1082 December – 31st January) ($\beta \pm SE$ on unscaled values: slope 0.028 ± 0.008 , intercept $2.621 \pm$
 1083 0.343 , $N = 28$, $\Delta AIC_{CModel-Null} = 7.93$, see **Table 1**).



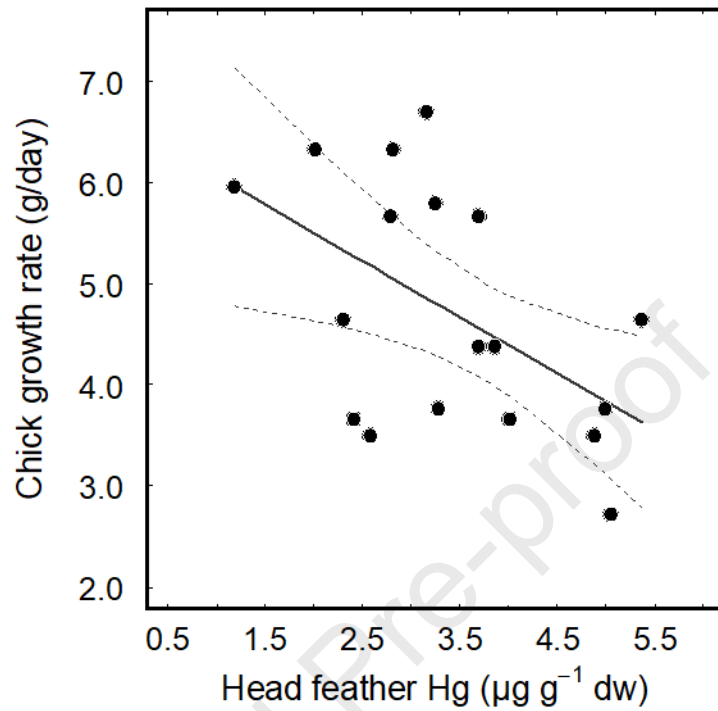
1084

1085 **Fig. 2.** Red blood cell (RBC) Hg concentrations increased with increasing head feather Hg
 1086 concentrations in little auks breeding at Ukaleqarteq, East Greenland, in 2018 and 2019 ($\beta \pm$
 1087 SE : slope 0.145 ± 0.022 , intercept 0.362 ± 0.080 , $N = 79$, $\Delta AIC_{CModel-Null} = 40.8$, see **Table 2**,
 1088 sex and year effects are not represented for readability).



1089

1090 **Fig. 3.** Chick growth rate decreases with increasing head feather Hg concentrations of their
1091 parents in little auks breeding at Ukaleqarteq, East Greenland, in 2018 (slope -0.555 ± 0.215 ,
1092 intercept 6.615 ± 0.838 , $N = 18$, $\Delta AIC_{\text{Model-Null}} = 2.93$, see **Table 2**).



1093

Highlights

- Winter Hg contamination and its carryover effects were quantified in little auks
- Winter Hg contamination increased eastward in the North Atlantic Ocean
- Blood Hg contamination in summer was predicted by winter Hg exposure
- Winter Hg contamination had no clear effect on telomere length or body condition
- Parental winter Hg burdens were negatively associated with chick growth

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; 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 interests

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.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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