Factors influencing mercury levels in Leach's storm-petrels at northwest Atlantic colonies

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HIGHLIGHTS

- Potential role of mercury in contributing to population declines of Leach's storm-petrels is not fully understood
- We analyzed associations among geotracking, stable isotope, and mercury concentration data
- Blood mercury levels were higher with increasing foraging depth, trophic level, and latitude
- Leach's storm-petrels can be biomonitors of pelagic marine food webs
- Effects of mercury on the species should be further investigated

GRAPHICAL ABSTRACT
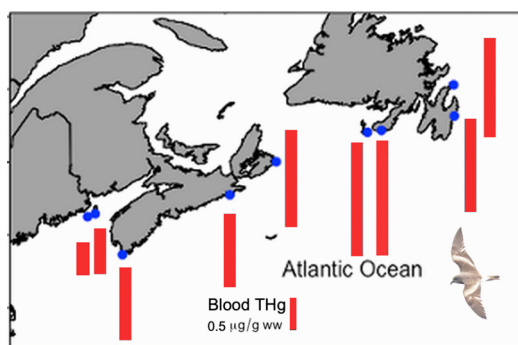
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ABSTRACT

Mercury (Hg) is a globally distributed heavy metal, with negative effects on wildlife. Its most toxic form, methylmercury (MeHg), predominates in aquatic systems. Levels of MeHg in marine predators can vary widely among individuals and populations. Leach's storm-petrels (Hydrobates leucorhous) have elevated levels of Hg but the role of Hg in storm-petrel population declines is unknown. In this study, we used egg and blood samples to study variation in Hg exposure among several northwest Atlantic colonies during breeding seasons, thereby evaluating relative toxicity risk within and among colonies. Total mercury (THg) concentrations were higher with increasing colony latitude, and were more pronounced in blood than in eggs. THg concentrations in blood were mostly associated with low toxicity risk in birds from the southern colonies and moderate risks in birds from the northern colonies; however, those values did not affect hatching or fledging success. THg concentrations in both eggs and blood were positively correlated with $\delta^{34}S$, emphasizing the role of sulfate-reducing bacteria in methylation of THg acquired through marine food webs, which is consistent with enriched $\delta^{34}S$ profiles. By associating tracking data from foraging trips with THg from blood, we determined that blood THg levels were higher when storm-petrels intensive search locations were over deeper waters. We conclude that spatial variation in THg concentrations in Leach's storm-petrels is attributable

to differences in ocean depth at foraging locations, both at individual and colony levels. Differences in diet among colonies observed previously are the most likely cause for observed blood THg differences. As one of the few pelagic seabird species breeding in Atlantic Canada, with limited overlap in core foraging areas among colonies, Leach's storm-petrels can be used as biomonitors for less sampled offshore pelagic regions. The global trend in Hg emissions combined with legacy levels warrant continued monitoring for toxicity effects in seabirds.

1. Introduction

Mercury (Hg) occurs naturally in the environment, but its main source is anthropogenic activities, primarily associated with burning of fossil fuels and small-scale gold mining operations (UN Environment, 2019). Upon release to the environment, Hg is highly volatile and is atmospherically transported long distances to remote regions, making Hg contamination a pervasive global issue (Schroeder and Munthe, 1998). In aquatic environments, Hg is transformed into methylmercury (MeHg) primarily by bacteria. MeHg is more toxic to organisms than is inorganic Hg (Lehnherr, 2014) and is persistent and biomagnifies up the food web. As a result, top predators, especially those associated with aquatic food webs, often have high MeHg concentrations in their tissues (Boening, 2000; Spencer et al., 2011). MeHg concentrations can vary among and within species due to age, sex, and dietary differences and habitat-specific foraging (Becker et al., 2002; Loseto et al., 2008; Bond and Diamond, 2009; Burgess et al., 2013; Tartu et al., 2014; Peterson et al., 2015; Ackerman et al., 2020). For example, herring gulls (*Larus argentatus*) foraging in urban and coastal areas had lower blood MeHg concentrations than those foraging in offshore waters (Thorne et al., 2021), and deeper and farther offshore foraging trips of northern elephant seals (*Mirounga angustorostris*) resulted in higher Hg concentrations than those from shallower and more coastal ones (Peterson et al., 2015). Whereas some studies combining tracking data and Hg levels in seabirds have focused on large spatial scales (i.e., migratory movements, Fort et al., 2014; Albert et al., 2021a), the few studies that assessed spatial difference in Hg levels during the breeding season (Clatterbuck et al., 2021; Thorne et al., 2021; Jouanneau et al., 2022) compared ocean versus terrestrial foraging habitats.

In marine ecosystems, Hg has been the focus of considerable research in fish, notably in relation to human consumption (Xue et al., 2007), but also in marine mammals (Wagemann et al., 1998) and seabirds (Monteiro and Furness, 1995). Toxic effects of Hg in birds have been detected in eggs and blood at concentrations as low as 0.2 μg/g of wet weight (ww). Hg can negatively affect nervous, hormonal, and reproductive systems, and may cause motor or behavioral deficiencies (Wolfe et al., 1998; Scheuhammer et al., 2015; Evers, 2018). Patterns of Hg contamination in tissues and relative toxicity are likely species-specific, making it difficult to predict effects. For seabirds, elevated Hg concentrations are sometimes positively correlated with egg neglect and negatively with reproductive success (e.g., Tartu et al., 2013, 2015; Fort et al., 2014), and rates of lesions in tissues such as kidneys (Nicholson and Osborn, 1983), or in some cases can be associated with starvation and death (Fort et al., 2015). Among many other marine risk factors, chronic exposure to Hg could play a role in population declines of seabirds by reducing their probability of breeding successfully (Goutte et al., 2014a).

Leach's storm-petrel (*Hydrobates leucorhous*) is a ~45-g seabird that breeds in the North Atlantic and Pacific Oceans, with the majority breeding in the Northwest Atlantic (Pollet et al., 2020). The population has experienced a decline of ≥30 % over the last three generations (39 years), leading the International Union for the Conservation of Nature (IUCN) to reclassify their status to "Vulnerable" in 2016 and the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) to assess the eastern Canadian population of Leach's storm-petrel as "Threatened" in 2020 (COSEWIC, 2020; BirdLife International, 2021). Causes of declines are not fully quantified, but may include predation at colonies by avian predators (Stenhouse et al., 2000; Pollet and Shutler, 2019; Hoeg et al., 2021), interactions with onshore or offshore structures presumably caused by disorientation due to lights (Ronconi et al., 2015; Gjerdrum et al., 2021; Wilhelm et al., 2021), changing global ocean temperatures (Mauck et al., 2018), and

perhaps influences of long-term, natural atmospheric-oceanic cycles (Duda et al., 2020a). Threats are likely cumulative (Dias et al., 2019), but currently it is not known what role contaminants may play in this decline.

Leach's storm-petrels in the Gulf of Maine (Northwest Atlantic) have high Hg concentrations compared to other seabirds in the region (Goodale et al., 2008; Bond and Diamond, 2009). However, Pollet et al. (2017) did not find a direct, negative relationship between blood Hg concentrations and return rates of adults or reproductive parameters in Leach's storm-petrels from one colony situated at the mouth of the Gulf of Maine, in southern Nova Scotia. In contrast, such effects have been detected in other seabird species breeding farther north (Fort et al., 2014; Tartu et al., 2016). Spatial ecology of Leach's storm-petrels may play a role in Hg accumulation, and our aim was to better describe this relationship. Despite close proximities among some colonies in the Northwest Atlantic, individuals from different colonies experience different ocean conditions and diet because there is little overlap in their core foraging areas (Hedd et al., 2018; Frith et al., 2020), which could lead to colony-based differences in accumulation of Hg.

To complement data on their spatial ecology, stable isotope values measured in the same tissues as Hg can often be informative as to whether observed differences in contaminants are the result of diet (Burgess et al., 2013, but see Bond, 2010). Stable isotopes are naturally occurring stable forms of elements, differing in their nuclear masses. They are incorporated from the diet into an animal's tissues and vary among tissues depending on their metabolic turnover rate (Bearhop et al., 2002). Typically, $\delta^{15}N$ is used to estimate an animal's trophic position, normally increasing from prey to predator (Rubenstein and Hobson, 2004; Burgess et al., 2013), whereas $\delta^{13}C$ gives an indication of general foraging locations (Carvalho et al., 2022). Within marine diets, depleted $\delta^{34}S$ may indicate benthic versus pelagic food webs (Hobson, 1999), whereas high $\delta^{34}S$ may result from foraging in parts of the ocean where sulfate-reducing bacteria convert Hg to MeHg (Góngora et al., 2018). Generally, isotopic analyses indicate that $\delta^{15}N$ increases with trophic position, $\delta^{13}C$ is higher in benthic compared to pelagic feeders, and $\delta^{34}S$ increases in parts of the ocean where sulfate-reducing bacteria convert Hg to MeHg (Góngora et al., 2018).

In this study, we compared total Hg (THg) concentration (a strong correlate of MeHg in eggs and whole blood, Rimmer et al., 2005; Ackerman et al., 2013) in eggs and adult blood among Leach's storm-petrels breeding in different colonies in the northwestern Atlantic, and assessed relationships between THg values and stable isotopes. Then, we tested whether THg concentrations in adult blood were associated with hatching and fledging success. Following Ackerman et al. (2016a), we compared relative levels of THg in a toxicity risk framework. Finally, using data from global positioning system loggers (hereafter GPS) deployed on adults during foraging trips combined with THg values from blood samples, we determined what oceanographic variables might explain THg differences. We hypothesized that (1) egg and blood THg concentrations would vary among colonies due to differences in foraging locations; (2) adults with high blood THg would have lower reproductive success, and (3) Leach's storm-petrels foraging over deep waters, where a high methylation rate occurs in mesopelagic prey, would have higher blood THg concentrations than birds foraging over shallower waters.

2. Methods

2.1. Field sites

We studied nine Leach's storm-petrel colonies in the Northwest Atlantic (Fig. 1) between 2013 and 2019. For THg and stable isotope analysis, we
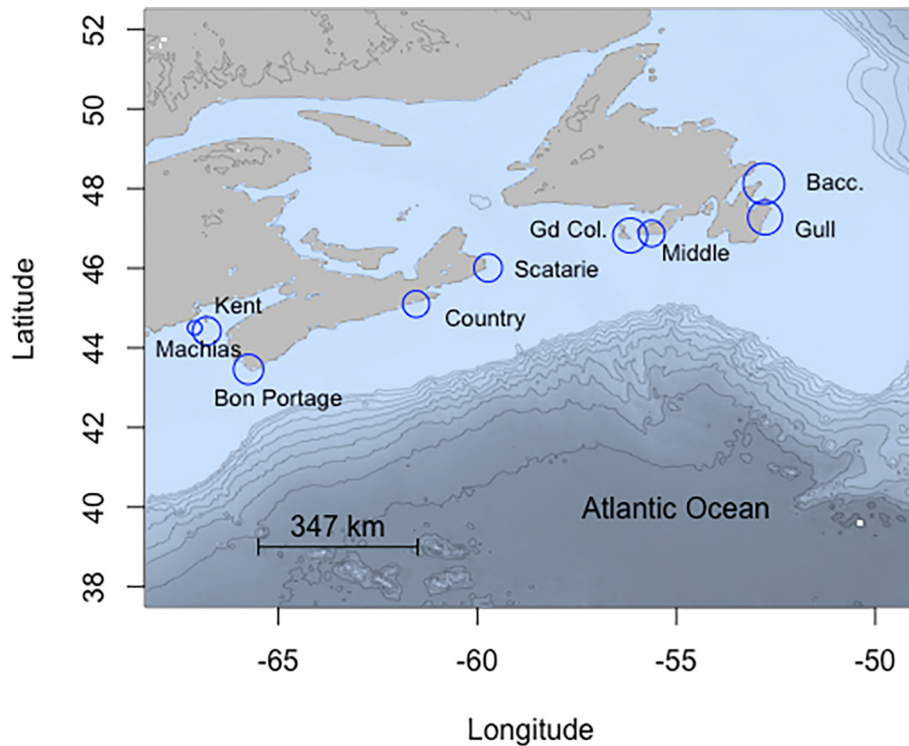
Fig. 1. Locations of the Leach's storm-petrel colonies in this study. Circle size relates to colony population size (Table 1). Bacc.: Baccalieu Island; Middle: Middle Lawn Island; Gd Col.: Grand Colombier Island. Light blue areas represent the extent of the continental shelf (< 200 m deep), with progressively darker gray representing deeper waters.

collected between 12 June and 1 July a minimum of 15 fresh eggs, at each of five colonies (Table 1). Stage of embryo development in eggs was determined by candling (Weller, 1956). In addition, over several years at all colonies, blood samples of breeding adults (max: 300 μl) were collected from the brachial vein in capillary tubes for Hg and stable isotope analysis. Blood samples and eggs were taken from different burrows, so we did not have matching data from adult tissues and their eggs. At selected colonies (Table 1), burrows where adults had been blood-sampled were checked for hatching success from mid to late July. In mid-September those burrows were checked again

for fledging success. Fledging was deemed to have occurred if nestlings were present in their burrow eight weeks post-hatching, with a minimum wing length of 120 mm. All handling procedures were approved by the Animal Care Committee of Environment and Climate Change Canada.

2.2. GPS tracking and spatial analysis

Leach's storm-petrels were tracked at six colonies (Table 1) during the breeding seasons (June–September) using GPS loggers (nanoFix™,

Table 1
Summary of information from Leach's storm-petrel colonies for this study, including the years for which data were collected. Province or country abbreviations are: NB: New Brunswick; NS: Nova Scotia; FR: France; NL: Newfoundland and Labrador. Colonies are arranged from west to east. "THg" indicates samples taken for total mercury.

Colony (Lat/long)	Population (pairs)	Population trend	THg egg (n)	Reproductive success	GPS	THg blood	d13C/d15N blood	δ³⁴S blood
Machias Seal, NB 44.50/−67.10	150	↓		No		2014–2015 (10)	2015	
Kent, NB 45.42/−66.80	21,643[a]	↓	2016 (15) 2018 (15)	Yes	2018–2019	2013–2015 (47) 2017–2019 (93)	2014–2015 2017–2019	2017–2019
Bon Portage, NS 43.46/−64.16	38,916[b]	↓	2017 (30)	Yes	2017–2019	2014–2015 (29) 2017–2019 (124)	2014–2015 2017–2019	2017–2019
Country, NS 45.1/−61.54	11,990[c]		2017 (16)	Yes	2017–2019	2017–2019 (130)	2017–2019	2017–2019
Scatarie, NS 46.01/−59.73				No	2019	2019 (5)	2019	2019
Grand Colombier, FR 46.82/−56.16	199,935[d]	↑?		No		2015 (17)	2015	
Middle Lawn, NL 46.87/−55.62	10,791[c]			No		2014–2015 (21)	2014–2015	
Baccalieu, NL 48.12/−52.8	1,976,665[e]	↓	2017 (30)	No	2016–2017	2013–2018 (50)	2014–2018	2017
Gull, NL 47.27/−52.77	179,743[c]	↓	2016 (15) 2017 (15)	Yes	2016–2018	2013–2019 (153)	2014–2019	2017–2019

[a] d'Entremont et al., 2020.
[b] Pollet and Shutler, 2018.
[c] Wilhelm, 2017.
[d] Duda et al., 2020b.
[e] Wilhelm et al., 2019.

PathTrack Limited, Otley, UK, 0.95 g), which were between 1.7 % and 2.2 % of body mass (range 42–56 g). Depending on the colony, we had one to three years of tracks (2016–2019, Table 1). GPS loggers were deployed between the scapulae with subcutaneous sutures following methods described in Pollet et al. (2014). Loggers were programmed to take one position every 2 h and were deployed for one or two foraging trips during incubation, and up to five foraging trips during the chick-rearing period. After GPS loggers were retrieved and data were downloaded, GPS loggers were recharged for deployment on another bird. Upon recovery of loggers, blood samples were collected for Hg and stable isotope analyses, and sex determination. Hg in whole blood corresponds to recent (a few weeks) dietary intake and any residual burden not yet depurated during feather molt or other means (Bearhop et al., 2000).

Using the tracking data, we calculated distance (km) from the colony of origin for each position. All statistical analyses were performed using R version 4.0.2 within R Studio version 1.4.1106. We characterized spatial distributions of Leach's storm-petrels from each colony using kernel density estimation with the 'kernelUD' function in the "adehabitatHR" package (Calenge, 2006) using all locations to illustrate colony-specific foraging areas. Locations were delineated into individual foraging trips before we applied a Hidden Markov Model (HMM). Hidden Markov Models are versatile and commonly used tools to analyze time series typical of telemetry data (McClintock and Michelot, 2018; McClintock et al., 2020); they rely on step length (km) and turning angle (radians) to classify each location into a behavioral class. We used the package "momentuHMM" (McClintock and Michelot, 2018), and modeled step lengths and turning angles with, respectively, a 'gamma' distribution and a 'von Mises' distribution. Starting parameters used in the three states model were 5, 25, and 60 km for the step length, and 0.1, 1, and 1 rad for the angle parameter. Starting parameters were verified by comparing different models using different starting parameters to test if results were similar. Given that mean ± s.d. for each parameter within each behavior state was the same among models, we kept the initial values assuming that they were able to distinguish behavior states in the trajectories. We then built different models considering different covariates, and following a lowest Akaike Information Criterion (AIC), we chose our final model built with three states and hour of the day as a covariate (i.e., the influence of hour of the day on the probability of switching from one behavior state to another). Given the temporal resolution of the data (location every 2 h), we delineated the first behavioral state as 'intensive searching' which included foraging in a restricted area and resting behavior where step lengths are short and tortuosity in trajectory is maximal. The second state: 'extensive searching' was delineated as more extensive searching movement, and the third state 'transiting' corresponded to traveling in a directional pattern with very little tortuosity. Moreover, this method is robust for classifying behavioral states in foraging seabirds, even with long intervals between sampling (Bennison et al., 2018; Collins et al., 2022), and has been used previously with this species (Mauck et al., 2022).

2.3. Environmental data

For each location classified as "intensive searching", we acquired the following environmental data through the Env-DATA function of the MoveBank website (www.movebank.org): 1. Ocean depth (i.e., bathymetry (m)); 2. Chlorophyll A (Chl-a) concentration (mg.m^{-3}) from MODIS Ocean Aqua OceanColor 4 km daily; 3. Daytime Sea Surface Temperature (SST; °C) from MODIS Ocean Aqua OceanColor 4 km daily.

2.4. Mercury and stable isotope analysis

In birds, > 90 % of all Hg in eggs and blood is in MeHg form (Evers et al., 2005; Ackerman et al., 2013); therefore, we used total Hg (THg) as a proxy for MeHg concentration. Egg and blood samples were shipped to the Environment and Climate Change Canada laboratory at the National Wildlife Research Centre in Ottawa for THg analysis. Upon arrival in the laboratory, blood samples were stored at −30 °C prior to analysis. Samples were

weighed into tared quartz boats and placed in the autosampler of a direct Hg analyser (DMA-80, Milestone Inc., Shelton, CT, USA).

Accuracy was evaluated before each day of analysis with 5–6 of the same certified reference materials (CRM) used to prepare the calibrations. These included: NIST 2976 mussel tissue from the National Institute of Standards and Technology (NIST), reference value 0.061 ± 0.0036 μg/g dry wet, measured (mean ± SD) 0.061 ± 0.002 μg/g dry wet; NIST 995c Caprine blood reference value 0.032 ± 0.0017 μg/g dry wet, measured 0.035 ± 0.001 μg/g dry wet; NRC TORT-3 Lobster hepatopancreas from the National Research Council of Canada (NRCC), reference value of 0.292 ± 0.022 μg/g dry wet, measured 0.285 ± 0.004 μg/g dry wet (mean, SD); BCR-463 Tuna fish from the Institute for Reference Materials and Measurements (IRMM), reference value 2.85 ± 0.16 μg/g dry wet, measured 2.74 ± 0.09 μg/g dry wet, IAEA-436 Fish flesh from the International Atomic Energy Agency (IAEA), reference value 4.20 ± 0.36 μg/g dry wet, measured 4.34 ± 0.12 μg/g dry wet. Precision was measured by replicate analyses of the same randomly selected aliquot and quantified by calculating the %RSD. Precision of our samples ranged from 0.3 to 22.0 %. Precision may have been affected by the lack of homogenization. However, multiple colonies were sampled each year and all colonies were analyzed the same way; therefore, it is unlikely that there is was bias in precision among colonies. Furthermore, the mean and the median of THg values were identical, implying zero skewness. Background contamination was checked by analyzing five blank samples at the start of every set. Accuracy was measured by recoveries of THg in three different CRMs and ranged from 83.3 to 104.0 %. Recovery of the three alternate source CRMs, including the two blood CRMS, ranged from 91.1 to 106.0 %. THg in all samples was greater than the practical detection limit of 0.0003 μg/g.

Upon arrival at the laboratory, egg samples were stored at 4 °C. Following cracking, albumen and yolk were homogenized and aliquots were retained at −40 °C prior to analysis. Samples were weighed in tared nickel boats and placed in the autosampler (DMA-80). Accuracy was evaluated at the start of each day of analysis with at least four readings of a selection of standard reference materials (SRMs). To ensure accuracy was maintained over the course of analyses, an appropriate SRM was analyzed at regular intervals throughout. Precision was measured by replicate analyses of the same randomly selected aliquot and quantified by calculating the relative percent difference, which ranged between 0.05 and 2.77 %.

Stable isotope analyses were carried out at the Ján Veizer Stable Isotope Laboratory at the University of Ottawa. Freeze-dried blood samples were encapsulated in tin capsules and analyzed with a Vario EL Cube interfaced to an isotope ratio mass spectrometer (Delta Advantage IRMS) by a Conflo III. Homogeneity of samples was checked by analyzing in duplicate one random sample in every 10 samples. Stable isotopes were quantified as the deviation from a standard using the equation:

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

with X being either ^{13}C, ^{15}N, or ^{34}S and R the corresponding ^{13}C/^{12}C, ^{15}N/^{14}N, ^{34}S/^{32}S. $R_{standard}$ for δ^{13}C is Vienna Pee-Dee Belemnite and normalized to internal standards calibrated to international standards IAEA-CH-6, NBS-22, and USGS-40. $R_{standard}$ for δ^{15}N is air and normalized to internal standards calibrated to international standards IAEA-N1. Data for δ^{34}S are normalized to different standards (IAEA-NBS-127, IAEA-S1 and S6). Random duplicate samples had variation in stable isotope values of 0.2 % for ^{13}C, 2.0 % for ^{15}N and 0.7 % for ^{34}S in blood samples.

2.5. Molecular sex determination

As is the case for many seabirds, Leach's storm-petrels are sexually monomorphic; therefore, sex determination is not reliable with field measurements. Genetic sex determination was performed through polymerase chain reaction (PCR) using a 2550/2718 primer set described previously (Fridolfsson and Ellegren, 1999). Products of PCR run through a gel electrophoresis revealed a single band (Z) in males and a double band (Z and W) in

females. Sex determination was only carried out on the subset of blood samples collected from adults with GPS tags, so sample sizes vary among tests.

2.6. Data analysis

THg values were log-transformed. To maximize data available, we first compared THg concentrations separately in eggs and blood among years and colonies, and between sexes and colonies for blood, using non-parametric Kruskal-Wallis rank sum tests, followed by a post-hoc Dunn's test with P values corrected using the Benjamin-Hochberg method, to identify significantly different values. Then, for the subset of samples for which we had stable isotope data, THg concentrations in eggs and blood were analyzed separately by a linear mixed-effects model fitted by restricted maximum likelihood (REML) using the 'lmer' function from the "lme4" package (R Development Core Team, 2012) with stable isotope values as predictors, and colonies (for eggs) and colonies and year (for blood) as random factors. Based on toxicity benchmarks and risk categories for THg concentrations in avian blood (Ackerman et al., 2016a), we calculated percentages of birds within each toxicity ranking (no, low, moderate, high, and severe) at each colony.

To determine potential effects of blood THg on incubating adult reproductive success, logistic regressions were used with hatch (no: 0, yes: 1) or fledge (no: 0, yes:1) as dependent variables and THg concentrations of adults as a predictor variable and location and year as random factors. Burrows where one adult was equipped with a GPS logger were not included in this analysis. Sex was not included in the models because sex of birds was not determined for those burrows.

To understand ocean factors associated with differences in blood THg levels, we used linear mixed-effects models. We included SST, Chl-a, distance from colony, and depth at locations classified as intensive searching by the HMM model and sex as a fixed effect in our models, including biologically meaningful interactions among those variables. To account for multiple trips among individuals and colonies, bird and colony were treated as random effects. Models were compared using the second-order Akaike Information Criterion adjusted for small sample size (AICc), and selected following Burnham and Anderson (2004).

3. Results

3.1. THg in eggs

We collected 121 eggs from five colonies, with overall geometric mean concentration of THg being 2.02 ± 1.50 µg/g dw. For the two colonies with multiple years of egg sampling, there was no difference among years (t-test: Kent Island: $t_{25} = 1.6$, $P = 0.11$; Gull Island: $t_{24} = -0.3$, $P = 0.73$), so we pooled data across years. Mercury concentrations differed among colonies (Kruskal-Wallis rank sum test, $x^2 = 41.1$, df = 4, $P < 0.001$) with THg in eggs from Kent Island lower than in all other colonies (Table 2). $\delta^{34}S$ was the only stable isotope in eggs significantly associated with egg THg values ($\delta^{13}C$: estimate 0.009 ± 0.08, CI: -0.15, 0.16; $\delta^{15}N$: estimate $-0.06 \pm$
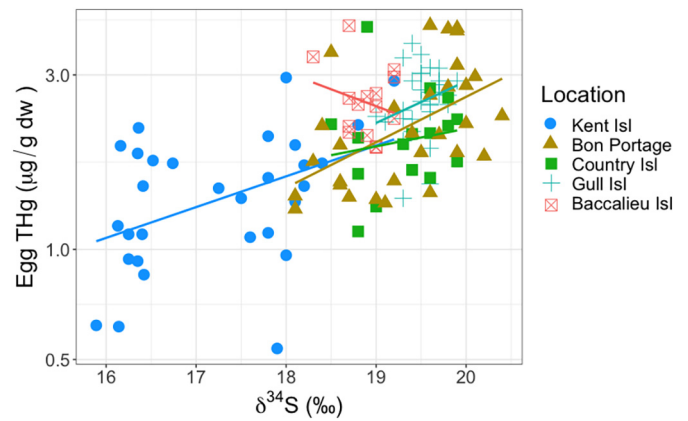

Fig. 2. Relationship between Leach's storm-petrel egg THg and $\delta^{34}S$ among different colonies with linear regressions for each colony.

0.13, CI: -0.31, 0.18; $\delta^{34}S$: estimate 0.39 ± 0.11, CI: 0.19, 0.61; Fig. 2; see also stable isotope values in the Supplemental Materials). The 95 % prediction intervals for the colonies varied from -0.05 for Country Island to 0.06 for Baccalieu Island. After accounting for the effect of egg $\delta^{34}S$, colony explained an additional 10 % of the variance in egg Hg concentrations.

3.2. THg in blood

We collected 742 blood samples over seven years from nine colonies. The overall geometric mean concentration of THg in blood was 0.76 ± 1.62 µg/g ww, with a strong relationship between mean egg and mean blood THg values by colony ($F_{1,3} = 12.9$, $R^2 = 0.81$, $P = 0.04$). THg concentrations in blood differed among colonies ($x^2 = 302.1$, df = 8, $P < 0.001$; Table 2) and years ($x^2 = 28.9$, df = 6, $P < 0.001$), with a significant interaction ($x^2 = 358.1$, df = 31, $P < 0.001$). Across five colonies, blood $\delta^{34}S$ was related to THg blood values ($\delta^{34}S$: estimate 0.09 ± 0.01, CI: 0.05, 0.12), but $\delta^{13}C$ and $\delta^{15}N$ had negligible associations with THg blood values ($\delta^{13}C$: estimate -0.04 ± 0.02, CI: -0.08, -0.008; $\delta^{15}N$: estimate 0.08 ± 0.01, CI: 0.05, 0.11). The 95 % prediction intervals for the colonies varied from -0.24 for Kent Island to 0.12 for Scatarie Island, and from -0.03 for 2017 to 0.07 for 2018. After accounting for the association with blood $\delta^{34}S$, colony and year explained an additional 42 % and 9.5 % of the variance, respectively.

3.3. Toxicity

Based on toxicity risk categories (Ackerman et al., 2016a), most (73–97 %) individuals from the southern colonies (Kent, Machias Seal, Bon Portage, and Country) had blood Hg concentrations associated with low risk, whereas most (51–88 %) individuals from northern colonies (Scatarie, Grand Colombier, Gull, Middle Lawn, and Baccalieu) had blood Hg concentrations associated with moderate risk (Table 3). Blood THg in adults was not associated with hatching success (estimate = 1.58 ± 1.20, $Z = 1.32$, $P = 0.19$) or fledging success (estimate = 0.45 ± 1.28, $Z = 0.35$, $P = 0.72$; Table 4), but this analysis had little power (19.7 %). Using a randomization procedure in the "simr" package (MacLeod, 2016), we estimated that over 1000 samples would be required for a minimum power of 80 %.

3.4. GPS telemetry data

Leach's storm-petrels tracked from the different colonies foraged in different areas (Fig. 3) and experienced different habitat and environmental conditions during their foraging trips (Table 5). These different foraging conditions were also observed at the colony level. The best model explaining variance in blood THg included as significant terms ocean depth, distance from colony, Chl-a at intensive searching locations, and

Table 2
Geometric mean (G. mean) of THg in egg and blood samples of Leach's storm-petrels at different northwest Atlantic colonies. Values within a column sharing the same letter are not statistically different($P > 0.05$).

Colony	THg egg µg/g dry weight				THg blood µg/g wet weight			
	n	G. mean	min	max	n	G. mean	min	max
Machias Seal, NB					6	0.34 [a]	0.17	0.57
Kent, NB	30	1.37 [a]	0.54	2.95	170	0.47 [a]	0.19	1.16
Bon Portage, NS	30	2.15 [b]	1.29	4.10	153	0.73 [b]	0.14	2.33
Country, NS	16	1.98 [b]	1.12	4.04	130	0.79 [b]	0.31	1.52
Scatarie, NS					5	1.07 [bc]	0.89	1.42
Grand Colombier, FR					17	1.26 [c]	0.91	1.56
Middle Lawn, NL					21	1.21 [c]	0.42	2.12
Baccalieu, NL	30	2.52 [b]	1.90	4.09	180	1.07 [bc]	0.33	1.73
Gull, NL	30	2.53 [b]	1.38	3.66	60	1.00 [c]	0.34	2.09

Table 3

Percent of Leach's storm-petrels at each colony within each risk category (as defined in Ackerman et al., 2016a) and corresponding blood Hg values (THg µg/g ww). Colonies are arranged in order of increasing latitude.

Location	N	Blood THg (µg/g ww)				
		< 0.20	0.20–1.00	1.00–3.00	3.00–4.00	> 4.00
		Risk				
		None	Low	Moderate	High	Severe
Kent Isl.	170	0.6	97.1	2.3	0.0	0.0
Machias Seal	6	16.7	83.3	0.0	0.0	0.0
Bon Portage	152	0.7	72.4	26.9	0.0	0.0
Country Isl.	130	0.0	73.1	26.9	0.0	0.0
Scatarie Isl.	5	0.0	40.0	60.0	0.0	0.0
Grand Colombier	17	0.0	11.8	88.2	0.0	0.0
Gull Isl.	179	0.0	48.6	51.4	0.0	0.0
Middle Lawn	21	0.0	19.1	80.9	0.0	0.0
Baccalieu Isl.	59	0.0	42.4	57.6	0.0	0.0

the interaction between distance from colony and sex (Table 6). The next best model had a ΔAICc of 6.14 and according to the selection criteria of Burnham and Anderson (2004), such a model has little support. Overall, THg was positively correlated with ocean depth at foraging locations and distance from colony, with a stronger slope for females than males, and negatively correlated with Chl-a (Table 7). In general, females foraged farther from their colonies than did males (Table 5; Fig. 3).

4. Discussion

We documented THg concentrations in Leach's storm-petrels across the northwest Atlantic, where the bulk of the species' population breeds. Through combined tracking and THg analysis, we determined that ocean depth at foraging locations was positively associated with THg concentrations in adult storm-petrel blood. To our knowledge, the is the first study to associate ocean conditions during foraging to THg levels during the breeding season, although biologging devices have been used previously to link THg levels in seabirds to their year-round movements (Fort et al., 2014; Renedo et al., 2020; Albert et al., 2021b; Shoji et al., 2021), and to compare oceanic and terrestrial habitats (Clatterbuck et al., 2021; Thorne et al., 2021; Jouanneau et al., 2022). Despite the relatively close proximity of Leach's storm-petrel colonies in Atlantic Canada (1160 km between Machias Seal Island and Baccalieu Island), there is limited spatial overlap in their home ranges (Fig. 3; Hedd et al., 2018), and ocean depth at their foraging locations differ by sex and among colonies (Table 5). Previous studies have shown these colony-based differences in space use are associated with differences in diet (Hedd and Montevecchi, 2006; Frith et al., 2020; Hebert et al., 2022). Differences in THg values among colonies observed in our study may also be a result of dietary differences which were greater in blood than in egg samples, possibly due to a sample size effect. Yet, THg values in eggs and blood samples by colony were strongly correlated. Females deposit Hg into their eggs proportional to Hg concentration in their

body at the time of egg formation (Ackerman et al., 2016b, 2020) whereas Hg in blood is more likely to vary based on diet during blood formation (i.e., in the previous weeks; Bearhop et al., 2002; Evans Ogden et al., 2004), residual Hg from other tissues since the last molt, and body condition (Fort et al., 2015; Mallory et al., 2018), as well as foraging locations (Carravieri et al., 2014, this study). Egg formation in procellariiforms occurs during a pre-laying exodus during which females forage far from their breeding colony (Hedd et al., 2014; Gatt et al., 2019). We do not know where females Leach's storm-petrels forage during their pre-laying exodus, nor the degree of spatial overlap among colonies during this period.

Leach's storm-petrels breeding at colonies farther north had comparatively elevated blood THg levels. Presumably, this is in part due to differences in diet among colonies, and origin of prey items. Deep, mesopelagic prey in diets can contribute to elevated mercury levels in seabirds (Monteiro and Furness, 1997; Thompson et al., 1998). Birds from Kent Island feed almost exclusively on euphausiid crustaceans, birds from Bon Portage Island feed on merluccid and myctophid fish as well as crustaceans in some years, and birds from Country Island feed on a mix of myctophids and euphausiids (Frith et al., 2020). In contrast, diets of Leach's storm-petrels from Newfoundland colonies consists primarily of myctophids such as glacier lanternfish (*Benthosema glaciale*) and other fish (Hedd and Montevecchi, 2006; Hedd et al., 2009). Lanternfish are diel migrants, moving near the surface of the ocean at night (Dypvik et al., 2012), but spending the day in deep, low-oxygen waters where sulfate-reducing bacteria produce MeHg (Blum et al., 2013), which is consistent with our result that blood THg levels increase with ocean depth at foraging locations. Deep water, sulfate-reducing bacteria could also explain why we found a strong positive relationship between Hg values and $\delta^{34}S$, both in eggs and in blood. We should also note that birds from Kent Island, with the lowest egg and blood THg levels feed in a more neritic zone, where $\delta^{34}S$ values are generally lower than in more oceanic waters, compared to foraging locations of birds from other colonies (Peterson and Fry, 1987; Suppl. material). This difference in Hg concentrations in individuals relative to their prey origin (epipelagic versus mesopelagic) has also been documented in fish (Choy et al., 2009; Madigan et al., 2018). A diet with a higher proportion of myctophids (i.e., mesopelagic fish with high Hg levels) compared to euphausiids is likely to explain relative differences in THg among colonies and individuals within colonies. We could have expected a relationship between THg and $\delta^{15}N$ given differences in diet among colonies; however, the scale at which Leach's storm-petrels forage (Pollet et al., 2014; Hedd et al., 2018) probably results in large differences in baseline $\delta^{15}N$, and could explain the absence of a relationship between THg and $\delta^{15}N$. The relatively small difference in latitude among colonies might not enable us to detect a variation in $\delta^{13}C$ among individuals of those colonies (Kelly, 2000). Compound-specific stable isotope analysis might be a better option for future studies to overcome the constraint of differences in isotopic baseline values (Quillfeldt et al., 2017, 2022; Elliott et al., 2021; Thébault et al., 2021).

Models to explain differences in THg values with environmental variables suggested that depth at foraging locations and distance from colony

Table 4

Summary table from binary logistic regression for hatching and fledging success with year and location as random factors.

| Predictors	Hatch					Fledge				
	Odds ratios	Std. error	CI	Statistic	p	Odds ratios	Std. error	CI	Statistic	p
(Intercept)	0.81	0.96	0.08–8.28	−0.18	0.856	2.02	0.71	1.02–4.03	2.01	**0.044**
THg	4.88	5.85	0.47–51.09	1.32	0.186	4.23	4.93	0.43–41.55	1.24	0.216
Random effects										
σ^2	3.29					3.29				
τ_{00}	1.48 Colony					0.22 Colony				
	1.93 years					0.00 year				
Inter-class correlation	0.51					0.06				
N	4 Colony					4 Colony				
	2 years					2 years				
Observations	180					165				
Marginal R^2/conditional R^2	0.013/0.516					0.021/0.083				
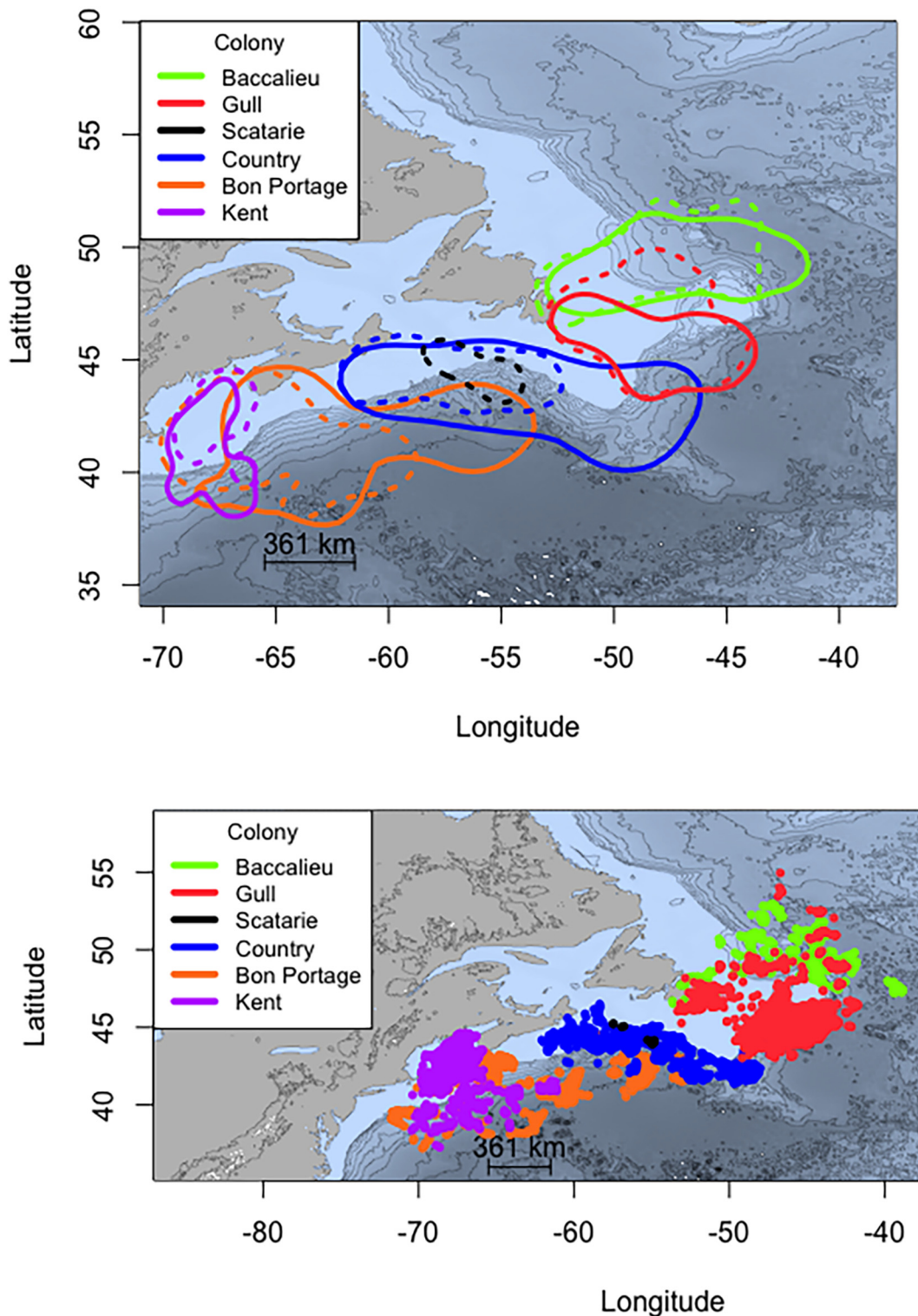
Fig. 3. Top panel: Kernel density contour lines (75 %) of Leach's storm-petrels tracked with GPS at different colonies during breeding seasons. Solid lines: Females; Dashed lines: Males. Numbers of tracked birds per island are presented in Table 5. Bottom panel: locations of intensive searching classified with Hidden Markov Model.

were important variables in determining blood THg levels in tracked Leach's storm-petrels. Birds from more southerly colonies (Kent Island and Bon Portage Island) tend to forage closer to their breeding colony and had lower THg blood concentrations than birds from more northerly colonies. Female Leach's storm-petrels foraged over deeper waters and farther from their colony than males, and generally had higher THg blood values (Table 5). Females alternate between short and long foraging trips,

possibly to replenish energy spent producing a relatively large egg for their body size (Mauck et al., 2022; Tyson et al., 2022).

In a range of bird species from western North America, toxic effects of Hg were detected at values as low as 0.2 μg/g ww of blood equivalent THg (Ackerman et al., 2016a). In a previous study focusing on one island, we failed to see a relationship between blood THg concentrations in adult Leach's storm-petrels and egg volume, chick growth, or adult return rate

Table 5

Geometric mean THg (μg/g ww), trip duration (days) and marine foraging habitat characteristics (depth, distance from colony, SST, chl-a) of locations classified as "intensive searching" with Hidden Markov Model for GPS-tracked Leach's storm-petrels (females and males) from the different colonies. Number of individuals tracked and sampled for Hg for each colony in parentheses.

Colony	Sex	THg (μg/g ww)	SST (°C)	Chl-a (mg.m^{-3})	Depth (m)	Distance (km)	Trip duration (days)
Kent NB	F (4)	0.47 ± 1.82	19.66 ± 5.28	0.80 ± 0.52	1716 ± 1827	250 ± 61	6.25 ± 2.52
	M (10)	0.44 ± 1.39	15.34 ± 2.65	1.01 ± 0.36	618 ± 1184	158 ± 92	4.65 ± 1.54
Bon Portage NS	F (14)	0.81 ± 1.49	19.99 ± 4.08	0.37 ± 0.21	3458 ± 1925	613 ± 427	5.48 ± 2.26
	M (6)	0.64 ± 1.54	16.26 ± 3.71	0.76 ± 0.43	1333 ± 2099	259 ± 209	5.29 ± 1.31
Country NS	F (4)	0.87 ± 1.64	13.41 ± 2.01	0.43 ± 0.07	3176 ± 1069	1247 ± 452	5.75 ± 0.59
	M (11)	0.83 ± 1.28	11.41 ± 2.19	0.45 ± 0.09	1401 ± 1277	535 ± 355	5.01 ± 0.77
Scatarie NS	M (1)	0.88	13.83 ± 1.13	0.50 ± 0.02	2637 ± 1277	487 ± 113	2.92
Gull NL	F (26)	0.84 ± 1.28	15.03 ± 1.72	0.42 ± 0.14	3136 ± 1425	734 ± 221	3.09 ± 0.83
	M (22)	1.06 ± 1.22	12.75 ± 3.24	0.43 ± 0.12	2471 ± 1491	668 ± 258	3.29 ± 0.64
Baccalieu NL	F (19)	1.05 ± 1.15	10.15 ± 2.32	0.97 ± 0.33	2902 ± 1450	797 ± 368	3.92 ± 0.89
	M (13)	1.18 ± 1.20	10.63 ± 1.65	0.90 ± 0.55	2281 ± 1557	602 ± 350	3.20 ± 0.51

Table 6

Results of linear mixed-effects models for explaining blood Hg concentrations in Leach's storm-petrels tracked with GPS from several colonies. For all models, number of random-effects terms k = 2 (colony and bird). Models were compared using the Akaike Information Criterion corrected for small sample size (AICc); ΔAICc: difference between AICc value of each model with the most parsimonious model (in bold); * denotes interaction between terms; df: number of estimated parameters; weight: explanatory power of models.

Models	AICc	ΔAICc	logLik	df	Weight
depth + dist * sex + Chl-a + (1| bird) + (1|colony)	**−917.40**	**0.00**	**488.3**	**8**	**0.896**
depth + dist + Chl-a + sex + (1| bird) + (1|colony)	−911.26	6.14	483.6	7	0.041
depth * Chl-a + dist* sex + (1| bird) + (1|colony)	−909.97	7.43	480.4	9	0.022
depth + dist + Chl-a + (1| bird) + (1|colony)	−909.45	7.95	480.1	6	0.016
depth + dist + Chl-a + sst + (1| bird) + (1|colony)	−909.10	8.30	479.9	7	0.014
depth + dist + Chl-a + sst + sex + (1| bird) + (1|colony)	−907.67	9.73	475.1	8	0.007
depth * Chl-a + dist + sex + (1| bird) + (1|colony)	−904.16	13.24	467.2	8	0.001
depth + dist + (1| bird) + (1|colony)	−903.70	13.70	465.4	5	0.001
depth * Chl-a + dist + (1| bird) + (1|colony)	−902.93	14.47	460.8	7	0.001
depth + Chl-a + (1| bird) + (1|colony)	−901.58	15.82	425.6	5	0.001
Null model: 1 + (1| bird) + (1|colony)	−713.84	203.56	361.7	3	<0.001

(Pollet et al., 2017). In this current study, average values were above Ackerman et al.'s (2016a) risk threshold in all colonies, and some individuals in eight of the nine colonies had blood THg concentrations above 1 μg/g ww of THg, the lower value for moderate risk effects. At this concentration (1 μg/g ww of THg in blood), we might expect impaired reproduction and a decrease in egg hatchability, possibly through egg neglect (Tartu et al., 2015). However, we know petrel's eggs are more adapted to egg neglect than other species to compensate for bad weather and missed incubation exchange duties (Boersma and Wheelwright, 1979). We found no effect of THg concentration on hatching or fledging success, but our analysis had little power and would require a much larger sample size to detect an effect. THg levels might have some effect on other parameters that we did not measure. For example, adults with high levels of Hg may skip breeding (Tartu et al., 2013; Goutte et al., 2015) and therefore would not have been sampled in this study, or have lower breeding probability and lower breeding success the following years (Goutte et al., 2014a, 2014b).

Table 7

Parameter estimates for AICc-selected model given in Table 6 for total mercury blood data.

Parameter	β	SE	T	Significance	Effect size	95 % confidence interval	
					d	Lower bound	Upper bound
Intercept	−0.14	0.056	−2.65	0.042	1.115	−0.26	−0.03
Depth	0.05	0.007	7.10	<0.001	0.389	0.04	0.07
Distance	0.04	0.007	5.83	<0.001	0.333	0.03	0.06
Sex (M)	0.03	0.010	3.41	0.001	0.257	0.01	0.06
Chla	−0.03	0.008	−4.68	<0.001	−0.292	−0.05	−0.02
Distance × * sex (M)	−0.04	0.011	−3.94	<0.001	0.330	−0.06	−0.02

Other studies have recorded higher Hg concentrations in procellariiform birds than those reported here (Thompson et al., 1993; Cherel et al., 2018), but in those studies, reproductive success was not investigated. At all colonies from our study, concentrations of THg in eggs were below the threshold of 1 μg/g ww that is associated with impaired hatchability (Scheuhammer et al., 2007). Although Baccalieu Island had high THg levels in eggs and adults (this study), a previous study found low hepatic concentrations of THg in recently fledged Leach's storm-petrels from this colony (Krug et al., 2021; but note that failed chicks were not assessed), perhaps because the birds shunt Hg into their growing feathers. Dietary Hg is thought to be transferred to eggs in a dose-dependent manner (Wolfe et al., 1998), and THg concentrations in eggs of Leach's storm-petrels are high compared to other seabirds breeding in the same region (Bond and Diamond, 2009). Perhaps some detoxification mechanisms permit seabirds to withstand these high concentrations (see El Hanafi et al., 2022). THg in feathers represents Hg accumulated in internal tissues since the last molt, but also from recent diets; as such, it is a powerful way to lower Hg concentrations in birds. In several Arctic seabird species, Hg concentrations in feathers molted during the non-breeding period were higher than in feathers molted during the breeding period (Albert et al., 2021b).

Leach's storm-petrels from northwest Atlantic colonies do not all migrate to the same over-wintering locations (Pollet et al., 2019). To determine areas associated with high mercury contamination during the non-breeding season, Hg concentrations in feathers grown during the non-breeding period could be linked to GLS-tracked birds. As such, the molt pattern of the studied species has to be clearly determined before we can correctly assign Hg feather values to any meaningful conclusions. Feathers, however, can have some value, when looking at historical data, through the use of museum specimens (see Thompson et al., 1992; Vo et al., 2011; Fairhurst et al., 2014; Bond et al., 2015).

In long-lived seabird species, adult survival is a key demographic parameter to maintain population viability, and is generally expected to be >90 % (Hamer et al., 2002). However, apparent adult survival of Leach's storm-petrels in several northwest Atlantic colonies is low (~ 78–86 %; Fife et al., 2015; Pollet et al., 2020), which is likely contributing to population declines. Limited data from Pacific colonies suggest a much higher apparent survival than in the Atlantic region (~ 97 %) with similar THg values in eggs (Elliott and Elliott, 2016; Rennie et al., 2020). Thus, we speculate that adverse effects of elevated Hg levels may interact with other stressors in Atlantic Leach's storm-petrels and contribute to declines caused by low adult return rates. More toxicological studies on the Pacific colonies would be required to test this hypothesis.

5. Conclusion

This study provides important new insights into colony-specific Hg levels in Leach's storm-petrels in the northwest Atlantic Ocean. This species forages farther offshore than most other seabirds in the northwest Atlantic (Ronconi et al., 2022) and core foraging areas do not noticeably overlap among colonies (Hedd et al., 2018). Tissue Hg concentrations vary strongly by colony and are predictably influenced by foraging locations, which could be explained by differences in diet. In addition, the species has several characteristics that make it a good bioindicator (Zhou et al., 2008), and can serve as a biomonitor for seldom sampled, offshore pelagic regions (Goodale et al., 2008; Bond and Diamond, 2009; Krug et al., 2021). Considering declines in Leach's storm-petrel populations, further research should test for a role of Hg in low adult survival rate at breeding colonies in the northwest Atlantic.

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CRediT authorship contribution statement

Ingrid L. Pollet: Investigation, Data curation, Formal analysis, Writing – original draft. **Laura McFarlane-Tranquilla:** Funding acquisition, Investigation, Writing – review & editing. **Neil M. Burgess:** Conceptualization, Funding acquisition, Project administration, Investigation, Methodology, Writing – review & editing. **Antony W. Diamond:** Investigation, Writing – review & editing. **Carina Gjerdrum:** Investigation, Writing – review & editing. **April Hedd:** Investigation, Writing – review & editing. **Rielle Hoeg:** Investigation, Writing – review & editing. **Patricia L. Jones:** Investigation, Writing – review & editing. **Robert A. Mauck:** Investigation, Writing – review & editing. **William A. Montevecchi:** Supervision, Writing – review & editing. **Isabeau Pratte:** Data curation, Writing – review & editing. **Robert A. Ronconi:** Investigation, Writing – review & editing. **Dave Shutler:** Supervision, Writing – review & editing. **Sabina I. Wilhelm:** Writing – review & editing. **Mark L. Mallory:** Funding acquisition, Supervision, Writing – review & editing.

Data availability

Data will be made available on request.

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.

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