



Bioaccumulation of trace elements by Leach's storm-petrels (*Hydrobates leucorhous*) in the North and South Atlantic Ocean during the non-breeding period

Catherine Potvin^{a,b,*}, Manon Sorais^{c,d}, Robert A. Ronconi^e, Katharine R. Studholme^f, April Hedd^g, Alexander L. Bond^h, Vegard S. Bråthenⁱ, Sydney M. Collins^j, Laura Crick^k, Joshua T. Cunningham^g, Anne N.M.A. Ausems^{d,l}, David A. Fifield^g, Carina Gjerdrum^e, Rielle Hoeg^{b,m}, Patricia L. Jonesⁿ, Laura A. McFarlane Tranquilla^{m,o}, William A. Montevecchi^j, Jennifer C. Rock^o, Dave Shutler^b, Sarah N.P. Wong^e, Glenn T. Crossin^d

^a Department of Earth and Environmental Science, Dalhousie University, Halifax, Nova Scotia, B3H 4R2, Canada

^b Department of Biology, Acadia University, Wolfville, Nova Scotia, B4P 2P8, Canada

^c Eeyou Marine Region Wildlife Board, Waskaganish, Quebec, J0M 1R0, Canada

^d Department of Biology, Dalhousie University, Halifax, Nova Scotia, B3H 4R2, Canada

^e Canadian Wildlife Service, Environment and Climate Change Canada, Dartmouth, Nova Scotia, B2Y 2N6, Canada

^f Biodiversity Research Division, Environment and Climate Change Canada, Dartmouth, Nova Scotia, B2Y 2N6, Canada

^g Biodiversity Research Division, Environment and Climate Change Canada, Mount Pearl, Newfoundland and Labrador, A1N 4T3, Canada

^h Bird Group, Natural History Museum, Akeman Street, Tring, Hertfordshire, HP23 6AP, United Kingdom

ⁱ Norwegian Institute for Nature Research, Trondheim, 7485, Norway

^j Cognitive and Behavioural Ecology Program, Psychology Department, Memorial University, St. John's, Newfoundland and Labrador, Canada

^k Imaging and Analysis Centre, Natural History Museum, Cromwell Road, London, SW7 5BD, United Kingdom

^l Department of Ecoscience, Aarhus University, Aarhus, 8000, Denmark

^m Birds Canada, Sackville, New Brunswick, E4L 1G6, Canada

ⁿ Department of Biology, Bowdoin College, Brunswick, ME, United States

^o Canadian Wildlife Service, Environment and Climate Change Canada, Sackville, New Brunswick, E4L 1G6, Canada

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ABSTRACT

Trace elements occur naturally in the environment, but anthropogenic activities can amplify their release, increasing exposure and bioaccumulation in marine predators such as seabirds. Mercury (Hg) in liver, blood, and eggs of Leach's storm-petrels (*Hydrobates leucorhous*), has been investigated as a short-term exposure indicator of hatching and fledging success. However, chronic Hg intake and exposure to other trace elements during the non-breeding period remain poorly understood. This study assessed geographic variation in trace element exposure and relative trophic position in Leach's storm-petrels from five overwintering locations in the Atlantic Ocean, using secondary feathers (S4s) and geolocation data. Hg concentrations and trophic position ($\delta^{15}\text{N}$) varied significantly among overwintering locations, whereas other trace elements varied without clear spatial patterns. Sea surface temperature was positively correlated with Hg concentrations, whereas dietary origin ($\delta^{13}\text{C}$) and year were associated with relative trophic position. Colony of origin had no effect on Hg or trophic position, likely reflecting high intra-colony variability in wintering locations. Additionally, Hg concentrations were highest in birds overwintering in oligotrophic regions where $\delta^{15}\text{N}$ values were low, suggesting lower nitrogen baselines in areas dominated by diazotrophic organisms and enhanced methylmercury availability via sulfate-reducing bacteria. In contrast, storm-petrels overwintering in productive upwelling regions such as the Benguela system exhibited lower Hg concentrations, consistent with Hg biodilution driven by rapid decaying phytoplankton export to deep sediments. These findings provide baseline information on trace element exposure during the non-breeding period of Leach's storm-petrels and inform future studies on migratory carry-over effects influencing adult survival and reproductive success.

* Corresponding author at: Department of Earth and Environmental Science, Dalhousie University, Halifax, Nova Scotia, B3H 4R2, Canada.

E-mail address: catherine.potvin@dal.ca (C. Potvin).

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1. Introduction

Globally, seabirds have been experiencing some of the fastest declines of all bird groups, and indeed of all vertebrates (Phillips et al., 2023). Seabirds are characterized by a slow life history and possess several traits that make them more vulnerable at a population level than terrestrial birds, including late sexual maturity and low fecundity (Brooke et al., 2018; Dias et al., 2019; Weimerskirch, 2007). The wide foraging range of pelagic seabirds also makes them vulnerable to fluctuations in climate and oceanographic conditions that influence availability of prey (Boyd et al., 2017; Devney et al., 2009). Additionally, because pelagic marine resources are unpredictable and unevenly distributed, adaptive strategies such as interannual consistency in migration behaviours may influence the decisions seabirds make regarding migratory routes and overwintering locations (Cerveira et al., 2020; Collins, 2025). Although migration is an adaptive trait, the wide-ranging distribution of seabirds across ocean basins increases their susceptibility to spatially heterogeneous threats.

There is growing evidence of the impacts arising from human activities on seabirds, including threats posed by commercial fisheries (Croxall et al., 2012; Phillips et al., 2023), introduction of predators to remote islands (Gutowsky et al., 2023), and light pollution (Heswall et al., 2022). Other anthropogenic activities such as fossil fuel combustion, agricultural runoff, and mining are known point source contributors to marine pollution (Gilmour et al., 2023) and can enhance environmental concentrations to potentially toxic levels to seabirds (Fahimirad and Hatami, 2017). Depending on the regions they occupy throughout the year, seabirds may be exposed to a variety of contaminants at differing concentrations. Mercury (Hg) and other trace elements are contaminants frequently quantified in seabirds (Albert et al., 2024; Ebert et al., 2020; Laranjeiro et al., 2025) in attempts to assess exposure and effects.

Prolonged exposure to various contaminants can affect the physiology and behaviours of seabirds, ultimately affecting their reproduction and survival (Mills et al., 2020). Although the effects of marine pollution on seabirds are largely sublethal, the chronic impacts of trace elements on seabirds' health remain unclear (Gilmour et al., 2023). Trace element biomagnification within the food webs of some seabirds has been documented, including for petrels and shearwaters, and seems to add environmental pressure during the breeding season (Rodríguez et al., 2019). Identifying where seabirds are exposed to elevated trace element concentrations during both breeding and non-breeding periods may help future studies link contaminant exposure to individual and population-level fitness outcomes.

Procellariiformes such as petrels and shearwaters forage year-round across neritic and oceanic zones (Pollet et al., 2023a; Thébault et al., 2020). These habitats vary in prey composition and contaminant signatures, which may be particularly important during the non-breeding period when individuals occupy distinct overwintering locations. Stable isotope ratios of carbon and nitrogen ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) can be useful in distinguishing these foraging zones and can also provide insights to the trophic levels at which seabirds feed (Silva et al., 2024). Several studies on pelagic seabirds have shown that the $\delta^{15}\text{N}$ tends to be higher in apex predators (Ishii et al., 2017; Pollet et al., 2023a). Additionally, $\delta^{13}\text{C}$ tends to be lower at higher latitudes and higher in benthic compared to pelagic zones, patterns which can also indicate seabirds' foraging ecology and spatial distribution (Ceia et al., 2018; Carvalho et al., 2022). Determining the trophic position and foraging behaviour of seabirds, during both breeding and non-breeding periods, can provide information about the location and mechanisms of potential exposure to contaminants.

Leach's storm-petrels (*Hydrobates leucorhous*) are small oceanic seabirds found extensively across the Pacific and Atlantic Ocean basins. The North American Atlantic population is listed as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC; COSEWIC, 2020), having faced a substantial decline of over 50% in the

past three generations (1974–2018). Potential threats similar to those of other wide-ranging seabirds have been identified on their breeding grounds (Pollet et al., 2023b; Calvert et al., 2024) but the threats to which they are exposed during the non-breeding period remain unclear. No contaminants assessment other than Hg has been done for Leach's storm-petrels during the non-breeding season. Tracking data from this species show that there is low migratory connectivity, reflecting high inter-individual plasticity around decisions of overwintering destination (Pollet et al., 2019). However, Leach's storm-petrels show strong fidelity to overwintering sites across years within individuals (Collins, 2025). These behaviours likely lead to differential and repeated exposure to contaminants among some individuals, potentially amplifying bioaccumulation in birds consistently overwintering in highly contaminated regions.

Despite growing concern about contaminant exposure in seabirds, little is known about how overwintering locations influence contaminant exposure in Leach's storm-petrels. This study quantifies trace element concentrations and stable isotopes values in Leach's storm-petrels during the non-breeding season and integrate those data with individual tracking information to assess spatial variation in exposure and diets among overwintering locations. We tested the hypothesis that the choice of overwintering location influenced the bioaccumulation of contaminants and the relative trophic level. By sampling winter-grown secondary feathers (S4) from Leach's storm-petrels that were tracked using geolocation from six breeding colonies in Atlantic Canada, we i) measured the concentrations of trace elements (As, Cd, Co, Cu, Hg, Mn, Pb, V, Zn) and stable isotope composition ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) in feathers grown on their wintering grounds; and ii) examined whether trace element concentrations or trophic level (inferred from $\delta^{15}\text{N}$) were influenced by overwintering locations, proxies of food production in these locations (chlorophyll-a [Chl-a], sea surface temperature [SST]), or colony of origin. Given the extensive migration range of individuals and the high degree of colony mixing in winter (Pollet et al., 2023b), we predicted that the choice of wintering location by individual Leach's storm-petrels would be independent of colony of origin, and that these locations would influence the concentration of contaminants in their feathers, due in part to expected spatial variation in foraging conditions. We also predicted that dietary origin (inferred from $\delta^{13}\text{C}$) and wintering locations of Leach's storm-petrels would influence $\delta^{15}\text{N}$ values due to spatial variation in prey availability.

2. Methods and materials

2.1. Study sites and data collection

Post-breeding Leach's storm-petrels ($n = 151$) from six breeding colonies in Atlantic Canada were successfully tracked with global location sensors (GLS) during two non-breeding seasons, in 2019–2020 and 2021–2022 (Fig. 1). Colonies included Baccalieu Island (48°07'N, 052°48'W), Gull Island (47°15'N, 052°46'W), and Middle Lawn Island (46°52'N, 055°36'W) in Newfoundland and Labrador, Country Island (45°06'N, 061°31'W) and Bon Portage Island (43°28'N, 065°44'W) in Nova Scotia, and Kent Island (44°34'N, 066°45'W) in New-Brunswick. GLS loggers were retrieved and the fourth secondary feathers (S4) were sampled between June and July when birds returned from over-winter migrations in 2020 and 2022. Main moult is thought to occur through the winter, with secondary feather moult starting 30 days after primary (Ginn and Melville, 1983); S4 feathers are among the last moulted, grown during mid-winter, assumed to be approximately February (Ainley et al., 1976; Pyle 2008, Part 2).

All bird handling and sampling protocols were approved by Environment & Climate Change Canada's Animal Care Committee (19GR01, 20GR01, 21GR01, 22GR01, 23GR01, 19JR01, 20JR01, 21JR01, 22JR02) or academic institutions (Acadia University: 03-17R#2, 03-17R#3, 03-21, 03-21R#1; Memorial University: 22-01-WM). Research was conducted under permits issued by the Canadian Wildlife Service

(banding permit numbers: 10851, 10559, 10934, 10695, 02109, 10922, 10332 K, 10332 U, 10695 P, 10559 AJ) and the Newfoundland Parks and Natural Areas Division (PNAD permit “Tracking coastal and marine birds in Newfoundland and Labrador”).

2.2. Capture, GLS deployment, and sampling

To track year-round movements, GLS loggers were deployed on adults during the late stages of incubation from mid-August to late September 2019 and 2021. In total, 128 GLS loggers were deployed in 2019 and 132 in 2021 across the 6 colonies (Table 1).

GLS loggers (Intigeo-W30A9-SEA, Migrate Technology Ltd.), weighed 0.45 g, measured $12 \times 5 \times 4$ mm and had a battery life of 12

months. The loggers were programmed to record in Mode 6B (light levels checked every minute, maximum value recorded every 5 min). Each logger was glued to a custom-built 3D printed nylon leg ring and then further secured using monofilament line threaded through two holes in the band prior to field deployment (Hedd et al., 2025). The logger assembly was fitted to the bird's left tarsus, and the band opening was glued closed. A stainless-steel band (USGS Bird Banding Lab size 1B) with a unique identification number was fitted to the opposite leg to identify the bird. Handling and attachments took approximately 5 min per bird, which was then returned to its burrow. The total mass of a tag with attaching material was ~ 0.6 g (1.3% mean body mass), well below the accepted 3% recommendation (Phillips et al., 2003). In 2020 and 2022, deployment burrows were revisited during the incubation period

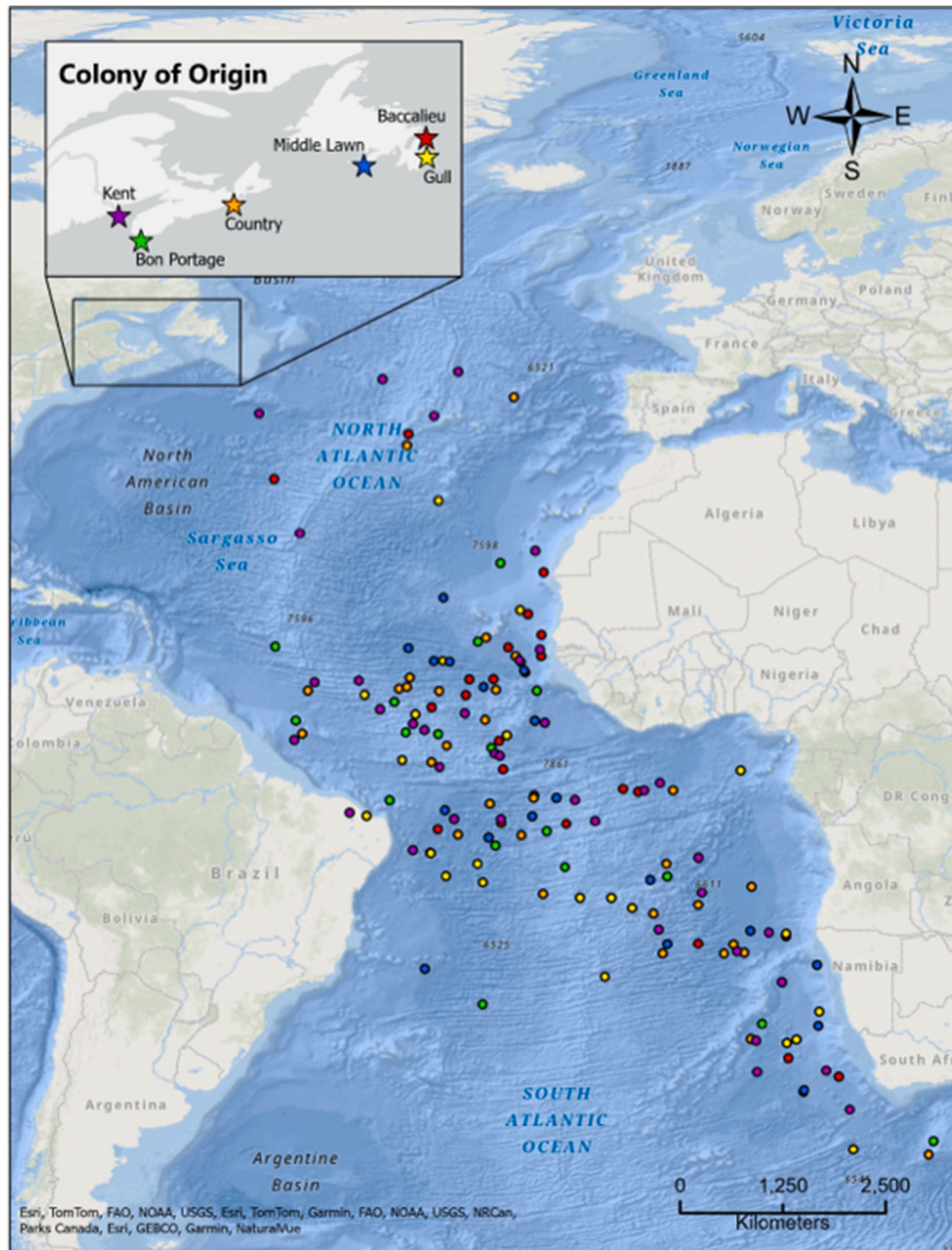


Fig. 1. Distribution of Leach's storm-petrel (*Hydrobates leucorhous*) centroids in February. Individual centroids are coloured by their colony of origin, with breeding colony locations shown in the Atlantic Canadian.

Table 1

Summary of bird and logger recovery data and deployment effort for Leach's storm-petrels (*Hydrobates leucorhous*) from six colonies in Southeastern Atlantic Canada, in each study year. Bird sex data reflects individuals that were identified as female or male only and omit missing data.

Year	Colony	N GLS deployed	N birds recaptured	N GLS recovered	Bird recapture rate (%)	GLS recovery rate (%)	N GLS analyzed	Known sex of birds analyzed	
								F	M
2019–2020	Baccalieu	25	15	10	60	40	4	0	2
	Gull	38	27	24	71	63	11	4	6
	Country	20	17	17	85	85	16	7	9
	Bon Portage	25	19	17	76	68	17	7	9
	Kent	20	19	18	95	90	13	6	6
2021–2022	Baccalieu	25	21	20	84	80	19	9	10
	Gull	20	17	17	85	85	11	2	9
	Middle Lawn	26	19	19	73	73	18	5	13
	Country	30	17	17	57	57	16	3	13
	Kent	31	27	27	87	87	26	9	16
Totals		260	198	186	76	72	151	52	93

The number of GLS analyzed was dictated by both the presence of February tracking data and complete trace element data.

(May–June) to find birds that had been tagged the previous year. Regular checks were made of occupied nests until the tagged individuals were recovered. Once recaptured, GLS loggers were removed, and two secondary flight feathers (S4) were collected for stable isotope and trace element analyses (details below). Of the 260 deployed GLS loggers, we recovered 186 (72%; Table 1). Because some birds lost their GLS logger, logger batteries died, or trace element data were incomplete, a total of 151 tracked individuals were analyzed in this study (Table 1).

2.3. GLS processing

Data from GLS loggers were processed by SEATRACK (seatrack.net), using a threshold method to identify twilight events with the 'twilightCalc' function in the 'GeoLight' package (Lisovski and Hahn, 2012) in R (version 4.4.1; R Core Team, 2024). Positional data were then derived and filtered through a set of standardized routines, removing unreasonable positions by filtering routines based upon equinox period, travel speed, distribution, angle, and distance (Bråthen et al., 2021). Resulting final positions were then double smoothed (Bråthen et al., 2021). Using methods adapted from Hanssen et al. (2016) and Van Bemmelen et al. (2017), sun elevation angle was chosen individually for each track by examining plots of latitude versus time for a variety of sun angles (−1.5° to −6.5°, at 0.5° intervals).

2.4. Stable-isotope analysis

Stable isotope composition was determined for each individual bird using the tip (~2 cm distal end) of one of the S4 feathers collected (remaining feather was reserved for other analyses not presented here). Each feather was soaked in a 2:1 chloroform:methanol solution for 24 h to remove external contamination such as surface oils (Lavers et al., 2013; Tate et al., 2021). Feathers were then rinsed twice with a fresh solution of grade 3 deionized water (DI) and air dried in a fume hood. Feather tips were sub-sampled using stainless steel scissors to cut small feather fragments which were packed into tin capsules for analysis at the Ján Veizer Stable Isotope Laboratory at the University of Ottawa.

Samples were quantified for stable carbon and nitrogen isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) using an Elemental Analyzer — Isotope Ratio Mass Spectrometer (Thermo Delta V), following the same methods used in Pollet et al. (2023b). Stable isotope values are expressed in δ notation as parts per thousand (‰) deviation from the international standards Vienna Pee Dee Belemnite (VPDB) for carbon ($\delta^{13}\text{C}$), and atmospheric air for nitrogen ($\delta^{15}\text{N}$), according to the following equation:

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

with X being either ^{13}C , or ^{15}N , and R the corresponding $^{13}\text{C}/^{12}\text{C}$ or

$^{15}\text{N}/^{14}\text{N}$. R_{standard} for $\delta^{13}\text{C}$ is VPDB normalized to secondary isotopic reference materials and calibrated to IAEA-CH-6, NBS-22, and USGS-40 (Carvalho et al., 2022). R_{standard} for $\delta^{15}\text{N}$ is air normalized to secondary isotopic reference materials IAEA-N1. Precision was assessed as the standard deviation of replicate analyses of three reference materials (NIST1577c, tilapia muscle and USGS 41) and was $\leq 0.14\text{‰}$ for $\delta^{13}\text{C}$ and $\leq 0.21\text{‰}$ for $\delta^{15}\text{N}$ values (Carvalho et al., 2022).

2.5. Trace elements analysis

For all birds, the second S4 feathers were sent to the Natural History Museum in London, United Kingdom for trace element analysis: arsenic (As), cadmium (Cd), cobalt (Co), copper (Cu), lead (Pb), manganese (Mn), mercury (Hg), vanadium (V), and zinc (Zn). Feathers were cleaned using a 2:1 (v/v) chloroform:methanol solution, rinsed three times with DI (18.2 M Ω resistivity) and dried at 55 °C. Following cleaning and drying, feathers were weighted and digested in a Milestone ultraWAVE Single Reaction Chamber (SRC) with 1 ml 15.7 M HNO₃ (Super pure Romil-SpA™) and ~1 ml DI water. After digestion, 0.1 ml 30% H₂O₂ (Suprapur®) was added and left capped for a minimum of 1 h. After this time samples were made up to volume with DI to a final matrix of 4% HNO₃. For mercury analysis a 5 ml aliquot of solution was taken and analyzed with the addition of L-cysteine to aid in stabilisation (Hight and Cheng, 2006; Li et al., 2006) and analyzed within 48 h.

Trace element concentrations were measured with an Agilent 7700 ICP-MS (Rf power: 1550 W; ICP-MS plasma gas flow: 15 l min^{−1}; auxiliary gas flow: 0.90 l min^{−1}; nebulizer gas flow: 1.15 l min^{−1}). Samples were measured both in no gas mode and in the presence of a helium collision cell, with solutions of gravimetrically determined concentration included every 10 to 15 samples to monitor instrumental drift. Values were corrected for background levels, such as atmospheric elemental concentrations not attributed to the analytical sample, using procedural blanks. Secondary reference materials were digested and analyzed in parallel with samples and their recoveries compared to certified values to verify the methodology. The secondary materials used as reference were certified human hair samples from the Institute for Reference Materials and Measurements (ERMDB001), oyster tissue from the National Institute of Standards and Technology (NIST1566b), and lobster hepatopancreas from National Research Council Canada (TORT-3). Secondary reference materials were certified for concentrations of some or all of the elements of interest: ⁷⁵As, ¹¹¹Cd, ⁵⁹Co, ⁶³Cu, ²⁰¹Hg, ⁵⁵Mn, ²⁰⁸Pb, ⁵¹V, and ⁶⁶Zn.

Cadmium was not included in our statistical analysis (Section 2.7) as bird feathers are not suitable for assessing total Cd burden due to frequent censored values (i.e., below detection limit) (Lavers et al., 2013; Bond and Lavers, 2020). Censored values from other trace elements were estimated using the 'clm' function from the 'censlm' package

(Marttila, 2023), in R (version 4.4.3; R Core Team, 2025), which fits censored maximum-likelihood models. This approach is preferred over substituting censored values with zeros or excluding them because it uses the observed distribution of the data to estimate plausible values below the censoring threshold, thereby avoiding bias and distortion of variance (Helsel, 2011). Concentrations below the limit of quantification (LOQ) were imputed individually using censored log-normal models fitted to uncensored data from the same year. Sample-specific LOQs were used as left-censoring thresholds, allowing multiple detection limits arising from differences in sample size, dilution, and analytical runs to be accommodated without data loss. Imputed values were then extracted from fitted models and used for statistical analysis. Censoring rate for each trace element that contained censored values can be found in supplementary material (Table S1).

2.6. Spatial analysis — assignment of overwintering locations and oceanographic variables

GLS data from February were visualized in ArcGIS Pro (version 3.4) since these positions likely correspond to the period of S4 feather growth in Atlantic Leach's storm-petrel (Ainley et al., 1976). For each individual, a mean center location (centroid) was calculated. Since the lack of variation in daylength can affect the accuracy of GLS logger -estimated latitudes several weeks before and after the spring equinox, we inspected the late February positions prior to calculating the centroid for each

bird to ensure we did not include any positions with clearly erroneous latitudes that would affect the location of the centroid. Individual February tracking maps are provided in the supplementary material (see SEATRACK February Maps file). February centroids from individual birds were used to generate a kernel density surface showing areas of high density in February. The cell size and search radius were set to 200 km to account for the error associated with GLS locations (Phillips et al., 2004; Pollet et al., 2019) and the geodesic option was selected to account for the curvature of the spheroid and minimize error for points near the poles. Five high-density hotspots emerged from visual interpretation of clustered areas of higher point density (Fig. 2), hereafter referred to as “overwintering locations”. Boundaries for each overwintering location were delineated using the outermost centroids within each cluster. The coordinates defining each overwintering location are provided in the supplementary material (see Overwintering Locations file). Each individual February centroid and the centroids of each overwintering location were compared, and individuals were assigned to an overwintering location based on minimum distance.

Two dynamic oceanographic variables were selected for their biological relevance to seabirds and ocean productivity: sea surface temperature (SST, °C) and chlorophyll-a (Chl- α , mg·m⁻³). These variables were chosen as they are frequently associated with habitat use by pelagic seabirds, contribute to underlying food availability in the oceans, and have the potential to explain some of the variation in trace element bioaccumulation in our models (Pollet et al., 2019; Pollet et al.,

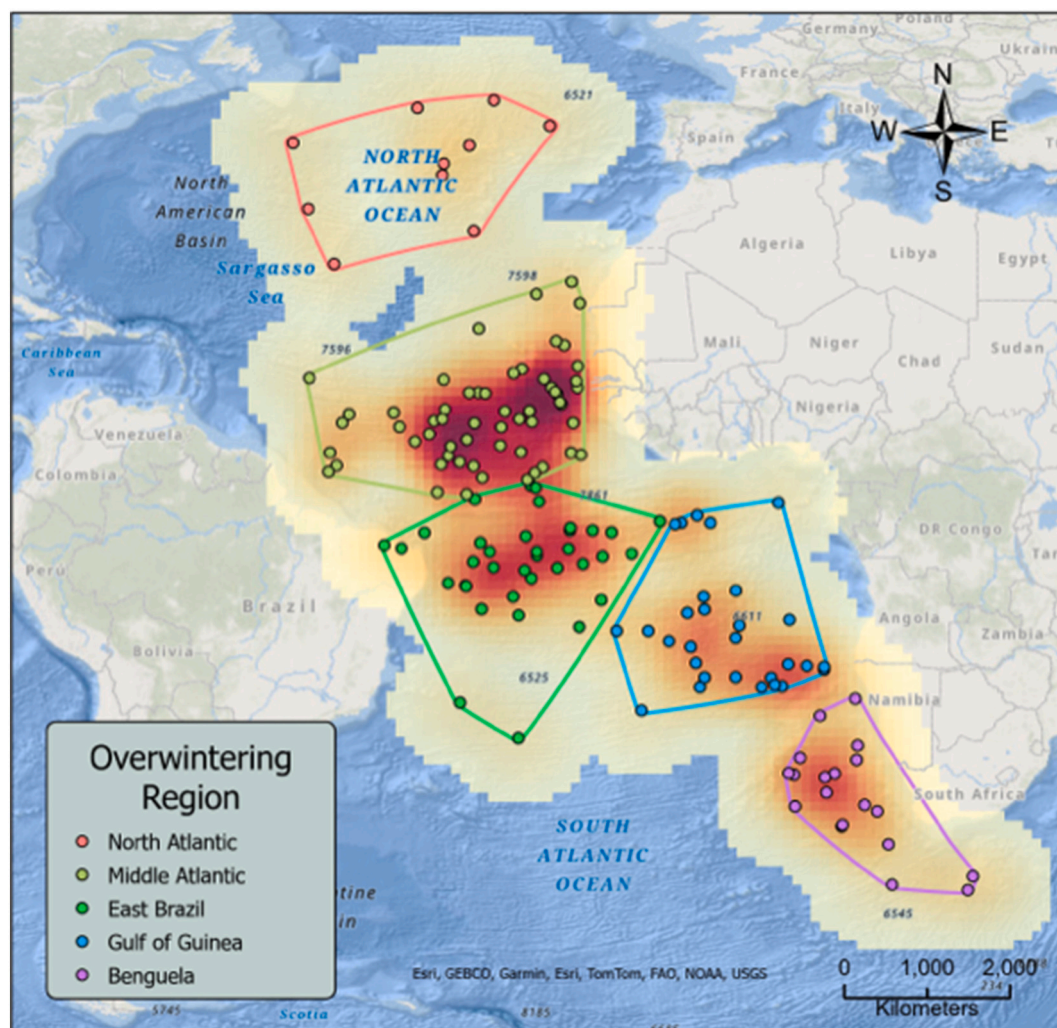


Fig. 2. Kernel density surface of Leach's storm-petrel (*Hydrobates leucorhous*) centroids in February, displaying five high-density hotspots (overwintering regions). Each centroid is coloured by the hotspot to which it is assigned.

2023b). These data were obtained as monthly averaged Copernicus Global Ocean Biogeochemistry Hindcast predictions at 0.25° (~28-km) resolution. SST and Chl-*a* values were extracted for each individual's February centroid. For the two centroids located on land, we assigned SST and Chl-*a* values from the nearest centroid situated in the marine environment.

2.7. Statistical analysis

All statistical analyses were conducted in R (version 4.4.3; R Core Team, 2025), with statistical significance assessed at $\alpha = 0.05$. To summarize the concentrations of trace elements in feathers, we calculated the mean $\pm$ SD of each trace element for each year and for both years combined, using the above-mentioned imputed values for censored values. Confidence intervals for fixed effects were estimated using profile likelihood from the “lme4” package. To assess significant differences between years, a Wilcoxon test was run for each trace element using the ‘stats’ package since these data were not normally distributed.

To test the hypothesis that the choice of overwintering location influenced trace element concentrations and relative trophic position, we built a series of linear mixed-effect models (LMM) to examine the influence of various independent variables on the bioaccumulation of trace element concentrations and $\delta^{15}\text{N}$ values in S4 feathers. Each trace element was analyzed separately with models fitted by maximum likelihood estimation (ML) using the ‘lmer’ function from the “lme4” package. Fixed effects (predictors) included overwintering locations (five hotspot identities, as defined by the spatial analyses above), oceanographic characteristics (Chl-*a*, SST), and year (2020, 2022). Colony of origin (determined by where the birds were captured) was treated as a random effect, given that we have no a priori expectation that provenance should influence migration behaviour (e.g., Shaffer et al., 2006; González-Solis et al., 2007; Albert et al., 2021a). Trophic position ($\delta^{15}\text{N}$) was modeled using the same methods, with the addition of dietary origin (measured by $\delta^{13}\text{C}$ values) as a fixed effect.

Leach's storm-petrels show sex differences in foraging strategies during the breeding season (Mauck et al., 2022) and sex can influence the distribution of non-breeding petrels (Phillips et al., 2017) and trace element concentrations (Robinson et al., 2012); however, exceptions exist, such as Sooty shearwaters (*Ardenna grisea*) which show no sexual segregation during winter (Hedd et al., 2014; Phillips et al., 2017). Although sex was determined by molecular analysis of blood samples, we did not include sex as a predictor in our linear mixed models because it had a negligible effect (variance = 0, SD = 0). Alternatively, to explore the effect of sex on trace element bioaccumulation, we ran a series of individual ANOVAs (analysis of variance, type III sums of squares), where each trace element was a dependent variable, with sex and overwintering location as fixed effects. The results showed no significant differences in trace element concentrations between sexes or in sex-by-overwintering location interactions, supporting the decision of removing the sex variable from the linear mixed models (Fig. S1; Table S2).

We were also interested in knowing whether there was evidence for spatial segregation between male and female storm-petrels. We therefore explored the effect of sex on spatial distributions by using ArcGIS Pro to run an ordinary least square (OLS) regression, with sex as the dependent variable and individual overwintering centroid coordinates (x,y) as explanatory variables. This allowed us to assess the relationship between sex and spatial distributions. Additionally, a Global Moran's I test was completed to test spatial autocorrelation of the OLS residuals. This test showed near perfect randomness in spatial distribution of the residuals (Moran's $I = -0.014$; $P = 0.87$) indicating a near equal distribution of females and males. A map showing the distribution of male and female Leach's storm-petrels can be found in the supplementary material (Fig. S2). Results of OLS regression and Global Moran's I test on OLS residuals outputs can also be found in the supplementary material

(Figs. S3, S4).

Each trace element and nitrogen stable isotope model was tested for parametric assumptions, including normality and homoscedasticity of residuals. Normality of residuals was assessed visually (Knief and Forstmeier, 2021). If the residuals were non-normally distributed, data were log-transformed for each dependent variable of interest and the model re-run. Following log transformation, we were unable to reliably model a few trace elements (Co, Cu, Zn) because model residuals remained non-normally distributed, preventing further interpretation of these elements. We also observed very high and very low values for Co, Cu and Pb. After visual exploration of the QQ-plots for these trace elements, we decided to remove a single extreme value for Pb that exceeded the mean by >10 SD. Trace element distributions rarely follow normal or log-normal distributions (Reimann and Filzmoser, 2000), and we acknowledge that this extreme value could still represent a true contamination event rather than a statistical anomaly. To address this uncertainty, we provide results for both scenarios, with and without this value included in the dataset, in the supplementary material (Table S3). All QQ-plots, histograms of best fit model's residuals, and Shapiro-Wilk test results can be found in the supplementary material (see exploratory plots file).

The global models for trace elements (1) and trophic position (2) from which variables were selected was structured as follows:

- 1) [Trace element] $\sim$ Overwintering Location + SST°C + Chl-*a* + Collection Year + (1 | Colony)
- 2) [$\delta^{15}\text{N}$] $\sim$ Overwintering Location + SST°C + Chl-*a* + $\delta^{13}\text{C}$ + Collection Year + (1 | Colony)

For each trace element and trophic position, models considering all possible combinations of covariates that were biologically meaningful were constructed and ranked using Akaike Information Criterion (AIC). Maximum likelihood was used when comparing models with different fixed effect structures because models using restricted maximum likelihood (REML) do not generate comparable estimates. Top models for each dependent variable were selected based on the lowest AIC score following Burnham and Anderson (2004). Once the top model was identified for each dependent variable, it was re-run using REML so that the magnitude of the random effect could be determined (discussed in Zuur et al., 2009). All LMM outputs including the AIC score for each trace element and nitrogen stable isotope can be found in the supplementary material (Table S3).

Finally, to compare variation in trace element bioaccumulation and trophic position within and among overwintering locations, an ANOVA was run (type III sums of squares) followed by a post-hoc Tukey test for pairwise comparisons.

3. Results

3.1. Trace elements concentrations

Trace element concentrations in the feathers of Leach's storm-petrels varied moderately between 2020 and 2022 (Table 2), differing significantly for As ($P < 0.001$), Cu ($P = 0.013$), Mn ($P = 0.036$), V ($P < 0.001$), and Zn ($P < 0.001$). With the exception of Hg (see next section), trace element concentrations did not significantly differ among overwintering locations (Table 3). In fact, most models did not show any significant effect of overwintering location, oceanographic characteristics (Chl-*a*, SST), or colony of origin (Table 3). While the null model was ranked as the best for Mn (Table 3), suggesting that the predictors considered in this study did not strongly influence its bioaccumulation, other models also failed to meet the normality assumption for residuals (Co, Cu, Zn). As no trace element other than Hg showed an association with overwintering location, and because we were unable to appropriately model some of the trace elements due to statistical limitations, we focus our discussion on Hg. However, model outputs for all trace elements can be

found in the supplementary material (Table S3).

3.2. Mercury (Hg)

Mercury varied significantly among overwintering locations (Fig. 3A, Table 3) and was the only trace element to show significant associations with our predictor variables other than year (Table 4). Among the five overwintering locations, Hg concentrations decreased with latitude: concentrations were highest in feathers grown in the north and mid-Atlantic Ocean region and lowest in the Benguela upwelling region (Fig. 3). Variance in the random effect of colony (SD = 1.17) was less than the individual (residual) variance (SD = 32.54) (Table 4). This suggests that some inherent traits among individual Leach's storm-petrels explained nearly 28 times the amount of variance in Hg concentration than colony of origin, after accounting for various fixed effects. There was also a weak but significant effect of SST on Hg concentrations ($R^2 = 0.04$, $P = 0.01$; Fig. 4). Although this relationship may reflect subtle underlying biological mechanisms, its explanatory power was very low and could be the result of Type I error. We therefore do not explore it further in the discussion.

3.3. Trophic position ($\delta^{15}\text{N}$)

Relative trophic position ($\delta^{15}\text{N}$) varied significantly among overwintering locations (Fig. 3B, Table 3) and showed significant associations with $\delta^{13}\text{C}$ and year (Table 5). Among the five overwintering locations, $\delta^{15}\text{N}$ values were highest in feathers grown in the Benguela upwelling region and lowest in the north and mid-Atlantic Ocean regions (Fig. 3B), following an increasing trend from north to south. Variance in the random effect of colony (SD = 0) was smaller in magnitude than the individual (residual) variance (SD = 0.92; Table 5), indicating that colony of origin did not explain any variance in $\delta^{15}\text{N}$ values, after accounting for various fixed effects. There was a significant effect of the dietary origin ($\delta^{13}\text{C}$) on $\delta^{15}\text{N}$ values (Table 5), with lower regional mean $\delta^{15}\text{N}$ generally associated with lower mean $\delta^{13}\text{C}$, except in the North Atlantic (Fig. S5).

4. Discussion

From GLS tracking of 151 Leach's storm petrels from five breeding colonies in eastern Canada, we identified five primary overwintering locations across the North and South Atlantic Ocean, similar to those observed previously (Pollet et al., 2019), and found that Hg was the only trace element that varied by location as well as relative trophic position. Further study would benefit from looking at the variability in the other trace elements that fit the model but were not explained by the factors considered in this study. In addition, interannual variability in trace elements such as As, Cu, Mn, V, and Zn should be investigated further, as year-to-year changes in oceanographic conditions may influence their bioaccumulation. These results support the hypothesis that Hg exposure and bioaccumulation in newly grown feathers is shaped by the individual choice of overwintering location and the bio-physical conditions therein. Specifically, feather concentrations of Hg were highest in Leach's storm-petrels wintering in the northern and mid-Atlantic regions

Table 3

Best ranked linear mixed-effect models explaining variation in each trace element concentration and nitrogen stable isotope values in fourth secondary (S4) feathers of Leach's storm-petrels (*Hydrobates leucorhous*). For all models, the number of random-effects terms (k) is one (colony). Models were compared using the Akaike Information Criterion (AIC). All variables (effects) were standardized by subtracting the mean and dividing by the standard deviation. Statistically significant effects ($\alpha = 0.05$) are indicated by an asterisk *. Trace element residuals were log-transformed if not normally distributed and are indicated by a caret ^. The models showing a regional effect are indicated in bold. Models for Co, Cu, and Zn failed to meet assumptions of normality and are not included. LMM output for all elements can be found in supplementary material Table S3.

Trace element	Model	Reference
Hg	Hg ~ Overwintering Location* + Chl-a + SST* + (1 Colony)	Table 4
$\delta^{15}\text{N}$	$\delta^{15}\text{N} \sim \text{Overwintering Location*} + \text{Chl-a} + \text{SST} + \delta^{13}\text{C}^* + \text{Year}^* + (1 \text{Colony})$	Table 5
As [*]	log(As) ~ Chl-a + SST + Year* + (1 Colony)	Table S3
Mn [*]	NULL MODEL: log(Mn) ~ 1 + (1 Colony)	Table S3
Pb [*]	log(Pb) ~ Chl-a + SST + (1 Colony)	Table S3
V [*]	log(V) ~ Chl-a + SST + Year* + (1 Colony)	Table S3

and decreased with latitude, with the lowest concentrations measured in birds wintering in the Benguela Current system off south-western Africa. In contrast, we found the inverse with trophic position, with the lowest $\delta^{15}\text{N}$ values measured in birds wintering in the northern and mid-Atlantic regions and highest in the Benguela. It has been widely reported that Hg biomagnification in most food webs increases with trophic level and $\delta^{15}\text{N}$ (Ivanova et al., 2025). The decoupling between these variables that we observed suggests that regional variation in Hg exposure among Leach's storm-petrels likely reflects regional differences in food-web structure and foraging conditions, driven by complex oceanographic processes, rather than trophic position alone.

A recent study of seven storm-petrel species concluded that Hg concentrations varied by species distribution and prey choice, whereby those populations foraging at higher trophic positions had increased Hg burdens (Quillfeldt et al., 2023). Consistent with Pollet et al. (2019) we also found spatial gradients in foraging trophic levels, in which $\delta^{15}\text{N}$ values were higher in birds wintering in the southern latitudes. But our results suggest that Leach's storm-petrels overwintering in areas where they obtained apparently high trophic level diets accumulated lower Hg concentrations. This is counterintuitive as organic Hg is known to biomagnify up the food chain. However, it is important to acknowledge that stable isotope concentrations may not be comparable among individuals from different regions when trying to explain trophic position (Rubenstein and Hobson, 2004). Additionally, while trace elements in blood are good representations of recent diet, the relationship between diet indicators (i.e., stable isotopes) and trace element burden is obscured in feathers, due to different integration periods (Bond, 2010). It is important to recognize that accumulated Hg in feathers does not solely reflect overwintering diet at the time of feather growth, but also integrates previously accumulated body burden mobilized between the previous and current moult (Bond and Diamond, 2009a). This represents a limitation of our study, as Hg concentrations in feathers reflect both

Table 2

Mean $\pm$ SD of trace elements concentrations accumulated in fourth secondary (S4) feathers of Leach's storm-petrels (*Hydrobates leucorhous*) grown during the non-breeding season at sea. Concentration units are reported as $\mu\text{g g}^{-1}$ dry weight. Trace elements that significantly differed between both years are indicated with an asterisk *.

Collect year	Sample size	As*	Co	Cu*	Hg	Mn*	Pb	V*	Zn*
2020	61	0.522 $\pm$ 0.324	0.033 $\pm$ 0.058	9.575 $\pm$ 1.162	14.846 $\pm$ 7.142	0.257 $\pm$ 0.164	0.123 $\pm$ 0.078	0.080 $\pm$ 0.035	99.536 $\pm$ 15.128
2022	90	1.948 $\pm$ 1.434	0.024 $\pm$ 0.028	9.028 $\pm$ 1.557	14.348 $\pm$ 7.334	0.233 $\pm$ 0.191	0.137 $\pm$ 0.116	0.057 $\pm$ 0.033	109.183 $\pm$ 25.060
Combined year	151	1.372 $\pm$ 1.325	0.028 $\pm$ 0.043	9.249 $\pm$ 1.432	14.549 $\pm$ 7.237	0.243 $\pm$ 0.180	0.131 $\pm$ 0.102	0.066 $\pm$ 0.036	105.286 $\pm$ 22.062

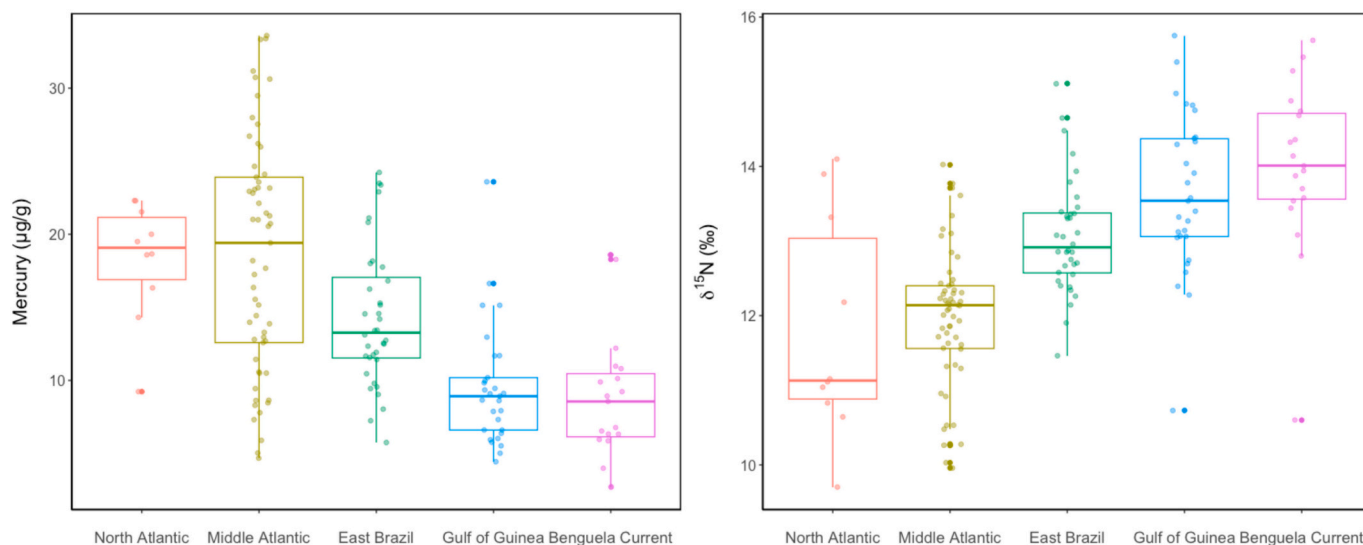


Fig. 3. Variation in A) Hg ($\mu\text{g/g}$ dry weight) and B) $\delta^{15}\text{N}$ (‰) of 151 Leach's storm-petrels (*Hydrobates leucorhous*) at 5 distinct overwintering locations, as inferred from kernel density analysis based on GLS locations. Regions are ordered from left to right by decreasing latitude. North Atlantic region $n = 10$, Middle Atlantic region $n = 57$, East Brazil region $n = 36$, Gulf of Guinea region $n = 29$, Benguela Current region $n = 19$.

Table 4

Statistical output from the linear mixed-effects model examining variation in Hg concentrations in fourth secondary (S4) feathers of Leach's storm-petrels (*Hydrobates leucorhous*), reflecting uptake during the period of feather growth in February. Statistically significant effects ($\alpha = 0.05$) are indicated by an asterisk *.

Fixed effects	Estimate	Standard error	95% CI		df	t-Value	p
			Lower	Higher			
Intercept*	25.37	2.83	19.60	30.81	132.67	8.91	<0.001
Chl-a	-0.77	0.64	-2.07	0.44	143.72	-1.21	0.23
SST ($^{\circ}\text{C}$)*	2.61	1.10	0.44	4.71	142.46	2.37	0.02
Overwintering location*							<0.001
Middle Atlantic	-7.08	3.08	-12.96	-0.87	143.85	-2.30	
East Brazil	-13.55	3.55	-20.33	-6.44	143.29	-3.81	
Southwest Africa	-16.22	3.11	-22.15	-9.98	143.15	-5.22	
South Atlantic	-13.05	2.40	-17.63	-8.18	142.28	-5.44	

Random effect		Standard deviation	Variance
Colony		1.08	1.17
Residual		5.70	32.54

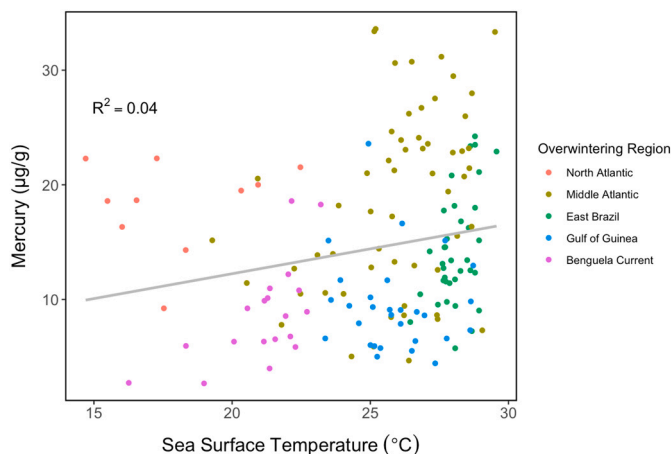


Fig. 4. Relationship between mercury ($\mu\text{g/g}$ dry weight) in fourth secondary (S4) feathers of Leach's storm-petrel (*Hydrobates leucorhous*) and sea surface temperature ($^{\circ}\text{C}$) at individual birds' February centroid locations across overwintering regions, with a linear regression fitted to all individuals ($n = 151$).

dietary exposure during feather formation and internal Hg stores. Consequently, variation in feather Hg among overwintering locations can only partially be attributed to differences in diet and should not be interpreted as a direct cause-and-effect relationship.

Despite uncertainty in dietary contribution to Hg in wintering grounds, we found that individuals' migratory choices accounted for more of the variance in Hg concentrations than the colony of origin, which reflects the high intra-colony variability in wintering destinations during the non-breeding period. This is evident in the high spatial variation of S4 Hg concentrations across the Atlantic Ocean among individuals from the same breeding colony, a pattern also observed in other seabirds with high inter-individual plasticity in non-breeding distributions, including northern fulmars (*Fulmarus glacialis*), Cory's (*Calonectris borealis*) and Sooty shearwaters (Shaffer et al., 2006; González-Solís et al., 2007; Albert et al., 2021a).

4.1. Biodilution effect and diazotrophs

In addition to the spatial variability in Hg availability known to exist in the Atlantic Ocean, other factors such as productive upwelling systems and sulfate enrichment may further affect Hg bioaccumulation in Leach's storm-petrels (Elliott and Elliott, 2016; Le Croizier et al., 2022).

Table 5

Statistical output from the linear mixed-effects model examining variation in nitrogen stable isotope concentrations in fourth secondary (S4) feathers of Leach's storm-petrels (*Hydrobates leucorhous*), reflecting uptake during the period of feather growth in February. Statistically significant effects ($\alpha = 0.05$) are indicated by an asterisk *.

Fixed effects	Estimate	Standard error	95% CI		df	t-Value	p
			Lower	Higher			
Intercept*	11.69	0.46	10.81	12.57	142	25.33	<0.001
$\delta^{13}\text{C}^*$	-0.20	0.09	-0.38	-0.03	142	-2.19	0.03
Chl-a	0.21	0.11	-0.00	0.42	142	1.89	0.06
SST ($^{\circ}\text{C}$)	-0.04	0.18	-0.38	0.30	142	-0.23	0.82
Overwintering location*					142		<0.001
Middle Atlantic	0.19	0.51	-0.78	1.17	142	0.38	
East Brazil	1.50	0.58	0.38	2.61	142	2.57	
Southwest Africa	2.04	0.51	1.07	3.01	142	4.02	
South Atlantic	2.27	0.40	1.50	3.03	142	5.68	
Year*					142		<0.001
2022	0.29	0.08	0.14	0.45	142	3.56	
Random effect			Standard deviation			Variance	
Colony			0			0	
Residual			0.85			0.92	

Studies have shown that the high levels of primary productivity, characteristic of upwelling zones, can have a biodilution effect on available Hg (Le Croizier et al., 2022; Zaferani and Biester, 2021). In such places, bioavailable Hg can be rapidly exported to deeper waters via zooplankton grazing and the sinking of fecal particles, thus increasing Hg sinking flux by upwards of 41% (Cui et al., 2024). Mercury is effectively “trapped” within decaying and sinking particles, resulting in a net flux from shallow to deeper waters and reduced availability in surface food webs (Cui et al., 2024; Le Croizier et al., 2022; Zaferani and Biester, 2021). This process likely reduces the biomagnification of Hg to higher trophic levels, which would result in lower Hg levels in seabirds foraging in these areas (Le Croizier et al., 2022). For example, Guanay cormorants (*Phalacrocorax bougainvillii*) and Peruvian boobies (*Sula variegata*) foraging in the highly productive Humboldt Current ecosystem had lower Hg concentrations despite having high $\delta^{15}\text{N}$ levels compared to birds foraging in more pelagic, oligotrophic ecosystems (Le Croizier et al., 2022).

Indeed, the lowest Hg concentrations recorded in this study were in Leach's storm-petrels overwintering in the South Atlantic region. This region overlaps with the Benguela current along the southwest African coast, a highly productive upwelling region with high nutrient availability (Martin et al., 2024) and an important foraging hotspot for many non-breeding seabirds and other marine taxa (González-Solís et al., 2007; Ronconi et al., 2018). Leach's storm-petrels wintering here had high $\delta^{15}\text{N}$ values compared to individuals overwintering in more oligotrophic, higher latitude regions, suggesting that petrels may have been foraging at a high trophic position in the Benguela during S4 feather growth (Pollet et al., 2019; Quillfeldt et al., 2023; Silva et al., 2024).

In contrast to the Benguela, $\delta^{15}\text{N}$ values were lower in the oligotrophic region of the mid-Atlantic, where Leach's storm-petrels also overwintered. In this pelagic region, diazotrophs (e.g. cyanobacteria) are responsible for atmospheric nitrogen (N_2) fixation, but provide only a small amount of bioavailable nitrogen to support primary productivity (Caffin et al., 2018; Chouvelon et al., 2018). Chouvelon et al. (2018) demonstrated that $\delta^{15}\text{N}$ values in oligotrophic waters were significantly lower at all trophic levels relative to more productive areas. Hence, the low $\delta^{15}\text{N}$ values that we measured in the feathers of Leach's storm-petrels here are more likely to reflect foraging in an oligotrophic ecosystem rather than foraging at a lower trophic level (Caffin et al., 2018). Additionally, $\delta^{15}\text{N}$ values may not strongly inform relative trophic positioning for a species that is so widely distributed. Ideally, we would correct for $\delta^{15}\text{N}$ baseline but this is not feasible considering the

area covered in our study and we acknowledge the limitations to interpreting trophic position based on $\delta^{15}\text{N}$ values in different regions. Future studies exploring Hg bioaccumulation in non-breeding Leach's storm-petrels should consider evaluating prey items digested by individuals from productive and oligotrophic regions.

4.2. Myctophid diet

As a general rule, Hg concentrations tend to increase with trophic position and are higher in subsurface fishes than surface fishes (Goodale et al., 2008; Elliott and Elliott, 2016). However, despite foraging upon the ocean surface, Leach's storm-petrels bioaccumulate more mercury than other seabirds (Elliott and Elliott, 2016; Pollet et al., 2022), including other storm-petrel species (Quillfeldt et al., 2023). This paradox may be explained by the fact that breeding Leach's storm-petrels are nocturnal foragers (Pollet et al., 2021) and feed on a variety of prey, predominantly vertically migrating fish such as myctophids (i.e. the lanternfishes [Myctophidae]) during the breeding season (Hedd and Montevecchi, 2006; Hedd et al., 2009 — non-breeding diet is unknown). During the daylight hours, these myctophids inhabit deep low-nutrient waters like those of the mesopelagic zone (i.e. the twilight zone, ~200–1000 m) which can contain an oxygen minimum zone, characterized by a sulfate-rich environment where high levels of anaerobic decomposition of organic matter occur through sulfate-reducing bacteria (Crichton et al., 2023; Elliott and Elliott, 2016). These bacteria play a crucial role in mercury methylation, as they transform inorganic Hg into the bioavailable form of methylmercury (Achá et al., 2011; Elliott and Elliott, 2016). Since myctophids spend most of their time in these methylmercury-rich depths, they bioaccumulate significant Hg levels before migrating to surface waters at night to feed (Blum et al., 2013; Elliott and Elliott, 2016; Pollet et al., 2023b).

Leach's storm-petrels are epipelagic feeders, and it is reasonable to assume that non-breeding individuals overwintering in pelagic regions like the mid-Atlantic have diets like those of breeding individuals (Silva et al., 2024). This could explain the elevated Hg concentrations that were found in the feathers of birds residing there. Nonetheless, breeding Leach's storm-petrels are also known to feed on a broad range of prey types (Frith et al., 2020), but their prey choices during non-breeding periods are wholly unknown. Future studies could further investigate these complex foraging dynamics by measuring both nitrogen and sulfur stable isotope concentrations in prey consumed during the breeding and non-breeding periods (Hedd et al., 2009; Hedd and Montevecchi, 2006). Combined with the results of our study, this would provide deeper

insights into the biogeochemistry of Hg and contaminant dynamics within Leach's storm-petrels' prey.

4.3. Toxicity

In this study, no speculation is made on the potential adverse physiological effects of elevated Hg concentrations on Leach's storm-petrels, partly due to the lack of studies quantifying Hg levels in flight feathers and how these relate to circulating levels (Elliott and Elliott, 2016; Pollet et al., 2022; Pollet et al., 2023b; Quillfeldt et al., 2023). However, it is known that birds can shunt circulating Hg into the matrix of newly growing feathers, and so feather moult and re-growth provide means for lowering their total Hg burden, potentially reducing any physiological impacts (Bond and Diamond, 2009b; Pollet et al., 2023b). Several Arctic seabirds are known to moult different sets of feathers at different times of the annual cycle (Albert et al., 2021b). In these birds, studies have shown that feathers grown during the non-breeding season can bioaccumulate up to three times more Hg than those grown during the breeding period (Albert et al., 2021b). From the few studies that have measured Hg in feathers of breeding Leach's storm-petrels (Bond and Diamond, 2009b; Pollet et al., 2022), Hg levels in breast feathers, which are almost entirely shed and regrown during the breeding season (Ainley et al., 1976) were ~3 times lower (THg = 4.855 µg/g dry weight) than those that we measured in the secondaries of non-breeding Leach's storm-petrels (Hg = 14.549 ± 7.237 µg/g dry weight). These results are consistent with those of the Arctic species mentioned above (Albert et al., 2021b).

5. Conclusion

This study provides important new insights into trace element bioaccumulation during the non-breeding period of Leach's storm-petrels and identifies potential contaminant exposure predictors, such as overwintering locations, the oceanographic processes therein, and trophic position. Although several trace elements were quantified, only Hg concentrations exhibited significant variability across five distinct overwintering locations. Potential negative effects of Hg bioaccumulation at the population level may be mediated by the high individual variability in overwintering locations (i.e. low migratory connectivity) and would not affect males and females differently based on their spatial distribution. Mercury also varies considerably across breeding sites of Leach's storm-petrels (Pollet et al., 2023b) and is potentially associated with decreased adult survival (Calvert et al., 2024), but carry-over effects of mercury from overwintering locations has not been widely tested (Pollet et al., 2017).

Leach's storm-petrels are important for marine pollution bio-monitoring due to their strong bioaccumulation abilities relative to other seabirds (Zhou et al., 2008; Pollet et al., 2023a) and are considered "sentinels" of ecosystem health (Francis, 2017; Pacyna et al., 2019; Velarde et al., 2019). The results of this study could serve as a baseline for future comparisons of trace element levels in offshore overwintering locations. Further tracking over additional years would enable exposure risk modeling, offering predictions on how this species may respond to changes in contamination over time. Such models could inform conservation and management strategies, helping to mitigate further population declines by identifying high-risk areas. The fate of many seabird species remains uncertain, as human activities have driven significant population declines (Xu et al., 2016; Dias et al., 2019; Phillips et al., 2023). With increasing anthropogenic pressures on the marine environment, the risks to seabirds are likely to escalate. Therefore, understanding the biogeochemistry of these contaminants and their physiological impacts should be prioritized in future research.

CRedit authorship contribution statement

Catherine Potvin: Writing – original draft, Visualization,

Investigation, Formal analysis, Data curation. **Manon Sorais:** Writing – review & editing, Supervision, Investigation, Data curation. **Robert A. Ronconi:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization. **Katharine R. Studholme:** Writing – review & editing, Supervision, Investigation, Data curation. **April Heddd:** Writing – review & editing, Investigation, Funding acquisition. **Alexander L. Bond:** Writing – review & editing, Investigation. **Vegard S. Bråthen:** Writing – review & editing, Formal analysis. **Sydney M. Collins:** Writing – review & editing, Investigation, Conceptualization. **Laura Crick:** Writing – review & editing, Investigation. **Joshua T. Cunningham:** Writing – review & editing, Investigation. **Anne N.M.A. Ausems:** Writing – review & editing, Formal analysis. **David A. Fifield:** Writing – review & editing, Investigation. **Carina Gjerdrum:** Writing – review & editing, Investigation. **Rielle Hoeg:** Writing – review & editing, Investigation. **Patricia L. Jones:** Writing – review & editing, Investigation. **Laura A. McFarlane Tranquilla:** Writing – original draft, Investigation. **William A. Montevocchi:** Writing – review & editing, Investigation. **Jennifer C. Rock:** Writing – review & editing, Investigation. **Dave Shutler:** Writing – review & editing, Investigation. **Sarah N.P. Wong:** Writing – review & editing, Investigation. **Glenn T. Crossin:** Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization.

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2026.119998>.

Data availability

The data analyzed in this study are publicly available on the Borealis repository at <https://doi.org/10.5683/SP3/X1HYCG>.

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