Bioaccumulation of Heavy Metals by Leach's Storm-Petrels (*Hydrobates leucorhous*) in the North and South Atlantic Ocean during the Non-breeding Period

by

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Abstract

Leach's storm-petrels (*Hydrobates leucorhous*) have experienced a significant decline in Atlantic Canada and are currently listed as "Threatened" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Many factors may underlie this decline, including exposure to heavy metals. While mercury (Hg) levels have been measured in blood and eggs of breeding storm-petrels, these short-term indicators have not been associated with impacts on hatching or fledging success. However, longer-term Hg intake and the extent of exposure to other heavy metals during the non-breeding period remain unknown. In this study, secondary feathers were assayed to assess variation in heavy metals concentration among five overwintering regions in the Atlantic Ocean. Using geolocation data, centroid locations for each overwintering region were calculated for February, when feathers are grown. Overwintering region was a significant predictor of Hg concentrations, whereas other heavy metal varied without a clear regional effect. Foraging indicators were also strong predictors of Hg concentrations, whereas colony of origin had no influence, likely due to high individual plasticity in non-breeding migration behavior. Hg concentrations were negatively correlated with $\delta^{15}N$ values, emphasizing the role of diazotrophic organisms in reducing baseline nitrogen levels in oligotrophic ecosystems such as the mid-Atlantic, while sulfate-reducing bacteria simultaneously enhance methylmercury bioavailability. In contrast, Hg concentrations were significantly lower in more productive upwelling regions like the Benguela system, where rapid export to deep sediments through decaying phytoplankton biomass and sinking particles drive Hg biodilution. Given their extensive migration across the Atlantic Ocean, Leach's storm-petrels serve as valuable bioindicators of heavy metal pollution. This study provides the first insight into exposure and bioaccumulation of heavy metals during the non-breeding period of Leach's storm-petrels. My results can serve as a baseline for assessing migration-to-breeding carry-over effects on adult survival and fledgling survival to maturity in the Atlantic population, as these factors remain unexamined. Furthermore, combining these findings with sulfate-isotope analysis could help future studies to better understand Hg biogeochemistry and contaminant dynamics within Leach's storm-petrel preys during the overwintering period.

Keywords: *Mercury biodilution effect; upwelling; oligotrophic region; sulfate reducing bacteria; diazotrophs; detoxification*

List of Abbreviations

ALAN	Artificial Light At Night
As	Arsenic
Cd	Cadmium
Chl *a*	Chlorophyll-a
Co	Cobalt
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
Cu	Cupper
GLS	Geolocation sensor
Hg	Mercury
IUCN	International Union for Conservation of Nature
LESP	Leach's storm-petrel
Mn	Manganese
MPAs	Marine Protected Areas
P10	10th primary flight feather
Pb	Lead
S4	4th secondary flight feather
Se	Selenium
SST	Sea Surface Temperature
V	Vanadium
Zn	Zinc
$\delta^{15}N$	Nitrogen stable isotope ratio
$\delta^{13}C$	Carbon stable isotope ratio

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Chapter 1: Introduction
1.1 Introduction

Globally, seabirds have been experiencing some of the fastest declines of all bird groups, and indeed of all vertebrates (Phillips et al. 2023) due to human activities such as bycatch and overfishing of prey items via commercial fisheries (Croxall et al. 2012; Cleeland et al. 2021; Richards et al. 2024) as well as climate change (Boyd et al. 2017; Dias et al. 2019). Seabirds are characterized by a slow life history, and possess several traits that make them vulnerable to exploitation, including late sexual maturity and low fecundity (Weimerskirch 2007; Brooke et al. 2018; Dias et al. 2019). The long-range foraging ecology of pelagic seabirds also makes them vulnerable to fluctuations in climate and oceanographic conditions that influence production of prey (Devney et al. 2009; Boyd et al. 2017). Additionally, because pelagic marine resources are known to be unpredictable and unevenly distributed, adaptative strategies such as interannual plasticity in migration behaviours may influence the decisions seabirds make for migratory routes and overwintering locations (Weimerskirch 2007; Cerveira et al. 2020). Although plasticity is an adaptative trait, the wide distribution of migration strategies across ocean basins makes seabirds susceptible to different threats. This vulnerability is especially pronounced during the fall migration initiated after the breeding season and during the spring migration following the wintering moult, amplifying the risk of exposure to contaminants (Amélineau et al. 2021; Bonnet-Lebrun et al. 2021).

Amongst seabirds, those from the Order Procellariiformes (albatrosses, petrels, etc.) are the most susceptible to human activities due to their wide-ranging migration biology (Dias et al. 2019; Phillips et al. 2023). Hamer (2001) reviewed the extensive distributional range of petrels and albatrosses across ocean basins during the non-breeding season when completing trans-equatorial migration. This review illustrated interspecific and individual plasticity in migration behaviours as some species or individuals might remain closer to their breeding colony with minimal change in latitude (Hamer 2001). Such far-ranging migrations increase the likelihood of exposure to pervasive marine pollution (Lopes et al. 2022; Navarro et al. 2023). Several anthropogenic activities such as fossil fuel combustion, agricultural runoffs, and mining are known point source contributors to marine pollution (Gilmour et al. 2023). Prolonged exposure to various contaminants resulting from these human activities 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, these effects are often overlooked when it comes to seabirds' body burden and health (Gilmour et al. 2023). Heavy metal biomagnification through the food chain has also been documented during the breeding season of some seabirds, including petrels and shearwater and seem to add environmental pressure (Rodríguez et al. 2019). Understanding how the exposure to and bioaccumulation of heavy metals affects individuals and populations requires knowledge on the distribution of these potential contaminants during the breeding and non-breeding period of pelagic seabirds.

Leach's storm-petrels (*Hydrobates leucorhous;* LESP) are a small oceanic seabird species within the Procellariiformes Order (COSEWIC 2020). They are found extensively across ocean basins such as the Pacific and Atlantic Oceans (COSEWIC 2020). Unfortunately, the Atlantic population has faced a substantial decline of over 50% in the past three generations, prompting investigations into the underlying causes of this decline (Pollet et al. 2023a; Calvert et al. 2024a). Potential threats have been identified on their breeding grounds but their behaviours and needs during the non-breeding period remain unclear. Mercury (Hg) exposure has been documented during the breeding period and showed that individuals from different colonies were exposed to different levels with higher concentration recorded in colonies from higher latitude in Atlantic Canada (Pollet et al. 2022; Pollet et al. 2023b). Additionally, LESP migrate long distances and show high individual- and colony-level plasticity in migration behavior during the wintering period, which could amplify their exposure to heavy metals during the non-breeding period (Fricke et al. 2015; Pollet et al. 2023a). Currently, no heavy metal assessment has been done on this Procellariiformes species during the non-breeding season which would be necessary to fully understand the possible threats that LESP are exposed to during their entire life cycle.

Pollet et al. (2023b) suggested that future studies should focus on birds tracked with geolocator sensors (GLS, i.e. birds for which year-round movements were recorded) and Hg concentration in feathers grown during the non-breeding period. This would allow identifying areas associated with high Hg exposure during the non-breeding period. Additionally, studies monitoring Hg in the environment have been motivated by several contextual aspects including health concerns of northern people feeding on wild seabirds (Pollet et al. 2022). Trans-Atlantic Hg monitoring schemes are required to coordinate research and better compare trends across a wide scale (Pollet et al. 2022). Therefore, a Trans-Atlantic group monitoring trends in contaminants could be beneficial to further assess reproductive success and population trends in LESP as well as informing indigenous communities on areas of exposure to contaminants (Pollet et al. 2022).

We currently know little about the links between overwintering locations and potential contaminant exposure in Leach's storm-petrels. The purpose of this study was to test the hypothesis that the choice of overwintering location influences the exposure to contaminants and their bioaccumulation. Using GLS-tracking data from six breeding colonies of Leach's storm-petrels in Atlantic Canada, I i) measured the concentrations of heavy metals (V, Mn, Co, Cu, Zn, As, Cd, Hg, Pb) in the feathers grown by individuals on their wintering grounds; and ii) examined whether choice of overwintering locations, trophic position ($\delta^{15}N$, $\delta^{13}C$), and (or) colony of origin predicted the heavy metal concentrations in feathers. Given the known extensive and highly plastic non-breeding migrations of Leach's storm-petrels (Pollet et al. 2023a), I predicted that individual choice of wintering location had a strong influence on contaminant exposure, due in part to variation in foraging conditions in different regions.

Through this research, I hope to document the spatial variability in the exposure to heavy metals during the non-breeding season and to fill gaps in the knowledge of this threatened seabird species. I also hope to contribute to future studies aimed at identifying the global point sources of potential contaminants to support the implementation of informed conservation policies in highly polluted areas.

Chapter 2: Literature Review

2.0 Overview

This literature review discusses the life history traits of seabirds, their foraging and migration biology, and several threats such as fisheries, predation, as well as light and marine pollution. Additionally, the present literature agrees that exposure to contaminants might be playing a role in the steep decline of seabird populations. An important emphasis on Leach's storm-petrels (*Hydrobates leucorhous*) highlights the need for studies focusing on their exposure to environmental contaminants, more importantly during their wintering months across the Atlantic Ocean. This review is informed by a diversity of sources, such as scientific journals and books, including bulletins, reviews, and novel research which are critical for understating the topics discussed.

2.1 Seabird Biology

2.1.1 Seabird Status and Life History Traits

Seabirds are undergoing one of the fastest declines among all bird species (Phillips et al. 2023). Indeed, almost half of the seabird species (47%) are considered globally threatened or near threatened by the International Union for Conservation of Nature (IUCN) with 31% and 11% of all seabird species respectively (Dias et al. 2019; Phillips et al. 2023). Species within the Procellariiformes Order are at higher risk of extinction than any other orders and include albatrosses, shearwater, petrels, and storm-petrels (Phillips et al. 2023). These pelagic seabirds have evolved with extreme life history traits such as late sexual maturity and low fecundity which make them more vulnerable than terrestrial birds (Weimerskirch 2007).

Procellariiformes species take several years to form a long-lasting pair-bond and premature breeding attempts are usually unsuccessful (Hamer 2001). Additionally, albatrosses and storm-petrels only lay a single-egg clutch once a year and in some cases, a second egg can be laid if the first one wasn't viable (Bond and Hobson 2015; Mauck et al. 2023). These extreme life history traits increase pelagic seabirds' vulnerability and could affect population recovery when facing substantial threats (Weimerskirch 2007; Brooke et al. 2018; Dias et al. 2019).

However, other factors such as foraging ecology and migration biology are important to understand to fully evaluate the causes that lead to their population decline.

2.1.2 Foraging Ecology

Prey accessibility can be affected by fluctuations in climate and oceanographic conditions, to which seabirds' long-range foraging ecology makes them particularly vulnerable (Devney et al. 2009; Boyd et al. 2017). Prey availability depends on several combined factors such as abundance, accessibility, patchiness and distance from a colony which are affected by oceanographic anomalies (Boyd et al. 2017). Marine resources are known to be unpredictable and unevenly distributed, further complicating prey availability (Cerveira et al. 2020). A study conducted in the western Pacific Ocean concluded that seabirds population decline was linked to El Niño anomalies which affect sea surface temperature and the thermocline, ultimately impacting ocean productivity and prey availability (Devney et al. 2009). While the foraging ecology of seabirds heighten their susceptibility to shifts in oceanographic conditions, migration to a wide range of overwintering locations can also increase this vulnerability.

2.1.3 Migration Biology

Adaptive strategies, such as interannual plasticity, can influence the migratory routes and overwintering sites selected by seabirds (Weimerskirch, 2007). While a study shows that it is common in some migratory seabirds to observe high interannual plasticity (Cerveira et al. 2020), consistency or fidelity to overwintering sites has also been documented, but as an extreme in the plasticity continuum (Phillips et al. 2017).

The choice of migration paths also makes seabirds vulnerable to a range of anthropogenic activities in areas with different management conservation statuses (Oppel et al. 2018). While some areas might have implemented better conservation policies such as Marine Protected Areas (MPAs), others might lack effective management leading to an increase in exposure risk where current or nonexistent conservation planning do not extent to the full range of migratory seabirds (Oppel et al. 2018). Therefore, it is important to identify the scale at which seabird’s range extent to implement efficient conservation areas (Oppel et al. 2018).

2.2 Threats to Seabirds

2.2.1 Anthropogenic Threats

The Anthropocene era is characterized by the significant impact humans have had on Earth's geology and ecosystems (Tong et al. 2022; Williams et al. 2024). This epoch reflects the dominance of human-driven changes in shaping the planet's systems (Tong et al. 2022). Some of these anthropogenic changes include ocean acidification, biodiversity loss, and pollution (Summerhayes et al. 2024; Williams et al. 2024). Specific human causal activities such as commercial fisheries (Croxall et al. 2012; Cleeland et al. 2021; Richards et al. 2024), climate change (Cleeland et al. 2021; Richards et al. 2024), light attraction (Rodríguez et al. 2019; Heswall et al. 2022), and marine pollution (Wilcox et al. 2015; Dias et al. 2019; Phillips et al. 2023) have negatively impacted seabirds' populations, especially those of albatrosses, shearwaters and petrels.

Bycatch, mostly from trawl fishing, is one of the main causes of population decline in seabirds, threatening several species of Procellariiformes including large-bodied albatrosses and petrels (Montevecchi 2023; Phillips et al. 2024). Artificial light at night (ALAN) from large cities and onshore and offshore oil and gas platforms is also an important threat to nocturnal seabirds such as shearwaters and petrels (Heswall et al. 2022). ALAN potentially attracts and disorients seabirds causing collisions with the anthropogenic structures often resulting in death (Rodriguez et al. 2019; Heswall et al. 2022). Marine pollution leading to exposure to contaminants such as plastic and heavy metals is also a threat to seabirds (Baak et al. 2020; Phillips et al. 2023; Pollet et al. 2023a). While the impact of fisheries and artificial light on seabirds are well documented, marine pollution seems to be an increasing environmental problem, and more research must be conducted to understand its impact on seabird population decline.

2.2.2 Marine Pollution

Plastic Pollution

Plastic consumption by seabirds is a growing environmental problem and the distribution of exposure should be assessed (Baak et al. 2020). Like marine resources, plastic pollution distribution is patchy across ocean basins (Clark et al. 2023). Baak et al. (2020) found that pelagic seabirds using surface-feeding strategies such as northern fulmar and black-legged kittiwakes, ingest more plastic than other seabird groups. This study also showed that seabirds' vulnerability to plastic ingestion was positively correlated with their trophic position and foraging range (Baak et al. 2020). Another study revealed that the exposure of oceanic seabirds such as petrels is disproportionally high compared to other families of seabirds especially outside the Exclusive Economic Zones (EEZs) where they generally forage (Clark et al. 2023).

Once plastic enters the marine environment, it gradually breaks down into smaller particles, releasing macro and microplastic-associated contaminants that can affect seabirds (Wang et al. 2021). The toxicological effect of these plastic-derived contaminants may impact different functions of seabirds' metabolism such as individual survival, growth and reproductive success (Wang et al. 2021).

Procellariiformes species, such as shearwater and storm-petrels, use surface-feeding strategies, have a high trophic position and cover large foraging ranges, which could potentially increase their exposure to plastic pollution (Muñoz et al. 2023). Although plastic ingestion in seabirds is becoming more widely documented, there is still a gap in research regarding the distribution of contaminants, such as plastic-derived chemicals and heavy metals, and their impacts on seabird metabolism.

Metallic Pollution

The extraction of Earth's mineral resources has significantly increased the release of heavy metals into the environment (Fashola et al. 2016; Hauton et al. 2017). Although these metals occur naturally, certain human activities, such as coal combustion and artisanal gold mining, have greatly accelerated their release into the atmosphere, contributing to higher deposition levels in marine ecosystems (Esdaile and Chalker 2018; Aziz et al. 2023). In high concentration, these contaminants can become harmful to seabirds as they are ingested directly and indirectly through prey and can cause important health problem (Mills et al. 2020; Gilmour et al. 2023). Chicks seems to be of higher concern as they are directly fed contaminated prey by seabird parents who offload their contaminant burdens (Gilmour et al. 2023).

As global emissions are expected to increase, it is crucial to find ways to evaluate temporal trends in global contamination (Pacyna et al. 2019). Bioindicator species can determine environmental health and conditions if their functions and populations are threatened (Francis 2017). Seabirds are known to be powerful sentinels to detect environmental pollution (Francis 2017; Pacyna et al. 2019). Feathers grown on different grounds can be used to evaluate contaminant exposure for different stage of seabird's annual life cycle as well as for different marine zones (Pacyna et al. 2019). Given the growing concern over the harmful effects of heavy metal contamination, understanding the spatial distribution and concentration of these pollutants is essential for assessing their impact on seabird populations.

2.3 Heavy Metals

2.3.1 Spatial Distribution

Recent studies have sought to measure concentrations of different heavy metals in seabirds and to localize environmental sources of exposure, ultimately aiming to assess the impact of heavy metals on population dynamics. Furthermore, it is known that the spatial variability of heavy metals in water bodies can lead to different levels of contamination and exposure (Irunde et al. 2022). For example, due to long-range transport pathways, the Arctic is considered a sink to atmospheric Hg deposition (Chastel et al. 2022).

A study conducted across the African continent focusing on the distribution of arsenic (As) concluded that this heavy metal has a high spatial variability, leading to different levels of contamination of several water bodies including the Atlantic Ocean (Irunde et al. 2022). Although this study didn't specifically involve seabirds, it clearly identified the provenance of this toxic contaminant from mining activities by disrupting the natural geological environment indeed, triggering the release of As into groundwater and surface water (Irunde et al. 2022).

Another study revealed that heavy metals such as chromium (Cr) and Hg, found in Kelp gulls (*Larus dominicanus)* along the coast of Santa Catarina in Brazil were below the detection level whereas lead (Pb) was significantly higher and maybe above toxicity levels (Ebert et al. 2020). Conversely, Albert et al. (2024) found that Hg level in most seabird species exceeded the toxicity threshold when conducting a study focusing on the marine distribution of mercury in the North Atlantic Ocean and the exposure level of breeding seabirds.

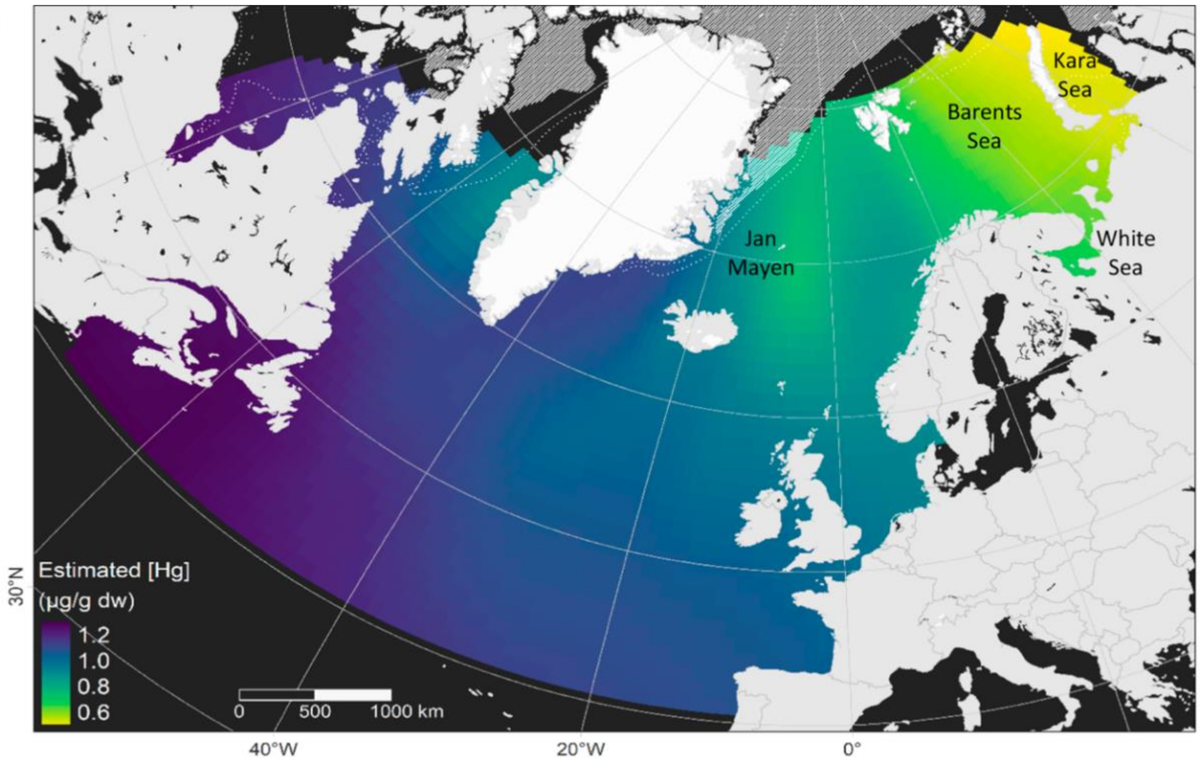

Figure 2.1 Predictions of the estimated Hg concentrations (log scale) for 1,000 iterations with highest values in dark purple and lowest predictions in yellow. (Albert et al. 2024)

It is known that Cr is released in the environment by the same processes as As when disrupting the geological setting through mining activities whereas Hg is mostly deposited in the atmosphere from coal burning and small-scale artisanal gold mining and transformed into its most toxic form by Hg methylation bacteria found in freshwater and marine environments (Fahimirad and Hatami 2017). As for Pb, it is found in different pesticides and paints but can also be released in the environment through the same processes as arsenic, chromium and mercury from mining and coal burning (Fahimirad and Hatami 2017). From these studies, we can conclude that seabirds are likely exposed to several heavy metals reaching their habitats at different concentration levels. However, the impact of these environment contaminants is also determined by several other factors, such as bioavailability, bioaccumulation, and contaminant interactions, all of which should be considered.

2.3.2 Bioaccumulation / Biomagnification

Heavy metals are bioaccumulated in several living organisms and biomagnified through the food chain (Furtado et al. 2019; Soliman et al. 2022). These metals can be measured in different tissues such as blood and feathers to infer their environmental dynamic over a given space and time (Ebert et al. 2020; Albert et al. 2024). It is known that the bioaccumulation of heavy metals in blood is representative of recent diet whereas the ones found in feathers represent recent diet during feather growth as well as from body burden accumulated since the last moult (Bond and Diamond 2009). For this reason, contaminant concentrations in feathers should be interpreted carefully as results are representative of a specific time frame, often prior to sample collection (Vizuete et al. 2019).

As heavy metals biomagnify through the food chain, they tend to reach higher concentrations in top predators (Furtado et al. 2019; Ashkoo et al. 2020). Interestingly, studies have shown that seabirds seem to tolerate higher concentrations of Hg compared to other groups of birds (Mills et al. 2020; Pollet et al. 2022). This tolerance might be in partly due to the interaction of Hg with selenium (Se) which seems to be playing a role in Hg detoxification in seabird's metabolism (El Hanafi et al. 2022a). Selenium also bioaccumulates through the food chain, further contributing to this complex relationship (El Hanafi et al. 2022a).

Furthermore, choices in prey items might have to be considered when trying to link bioaccumulation of heavy metals to the trophic level as lower concentration of bioaccumulated contaminants can be found in prey of higher trophic position (Quillfeldt et al. 2023). Additionally, Pollet et al. (2023b) found that total Hg (THg) was negatively correlated with Chlorophyll-a presuming that larger prey of higher trophic level might be found in environment other than high productivity areas. As Pollet et al. (2023b) suggested, other important information such as isotopic signatures of carbon and nitrogen can provide insights about the foraging location and trophic level to which individuals bioaccumulate potential contaminants and should be considered.

2.3.3 Stable Isotopes

Procellariiformes such as petrels and shearwater are known to forage in neritic and oceanic zones (Thebault et al. 2020; Pollet et al. 2023b). Stable isotopes analysis can be useful in distinguishing these foraging zones and can also provide insights on trophic levels at which seabirds feed by using carbon and nitrogen stable isotopes ratios, $\delta^{13}C$ and $\delta^{15}N$ respectively (Silva et al. 2024).

Several studies on pelagic seabirds have shown that the $\delta^{15}N$ tends to be higher in individual at the apex of the food chain (Ishii et al. 2017; Pollet et al. 2023b). However, nitrogen stable isotope ratio can be influenced by temporal predictors such as years due to potential annual variation in diet and baseline isotopic levels and should be considered during statistical analysis (Ceia et al. 2018). On the other end, other studies have shown that $\delta^{13}C$ tends to be lower in higher latitude from the Equator and higher in benthic compared to pelagic zones also informing seabirds' foraging ecology and spatial distribution (Ceia et al. 2018; Carvalho et al. 2022).

Determining the trophic position and foraging behaviour of seabirds can provide information about the location of potential exposure to contaminants. However, it is essential to assess exposure during both, breeding and non-breeding period of Procellariiformes to get a full picture of the risk that heavy metals pose to seabirds.

2.4 Leach's storm-petrels

2.4.1 Current State and Threats of the Atlantic Population

Leach's storm-petrel (*Hydrobates leucorhous*) are small, pelagic seabirds that occur extensively throughout the Pacific and Atlantic Oceans (COSEWIC 2020). Atlantic Canada hosts some of the largest breeding colonies of these birds on Earth, yet the species is currently listed as threatened (COSEWIC 2020). The factors underlying their decline are likely multicausal and remain not fully understood. However, predation pressure from gulls, corvids and voles (Hoeg et al. 2021; Bond et al. 2023; Calvert et al. 2024a), interspecific competition with Atlantic puffins (COSEWIC 2020), and light attraction by offshore oil and gas platforms, vessels, and industrial plants on land as well as Artificial Light At night (ALAN) are known threats, as is exposure to contaminants like mercury (Gilmour et al. 2023; Pollet et al. 2023a; Calvert et al. 2024). Literature describing the impact of land threats on LESP is well established, but the impact of Hg and other organic contaminants is not fully understood yet. Several contributing factors such as exposure to heavy metals could drive potential effects making it difficult to assess the impact.

2.4.2 Contaminant Levels and Exposure

Hg levels have been documented during the breeding season of Leach's storm-petrels in Atlantic Canada as well as the link between exposure and individual plasticity in migration behaviour (Pollet et al. 2019; Pollet et al. 2022). Tracking data from Leach's storm-petrels show that there is a low migratory connectivity based on individuals choosing to remain close to breeding areas off Newfoundland and Labrador meaning that there is high individual plasticity around decisions of overwintering destination (Pollet et al. 2019). This behaviour is likely causing an increase in exposure to contaminants as petrels are subjected to several different sites year after year with no consistency.

A study conducted on breeding colonies in the North Atlantic Ocean showed that individuals were exposed to substantial levels of Hg suggesting biomagnification through the food chain (Pollet et al. 2023b). THg concentrations were also observed to be higher with increasing colony latitude as shown in Figure 2.2 (Pollet et al. 2023b). Another study revealed that heavy metals such as As, Se, Hg, and Pb found in some migratory shorebirds and seabirds overwintering offshore West Africa, which are shared waters with Leach's storm-petrels, were below toxicity levels (Correia et al. 2023). It is likely that many other organic and inorganic contaminants, such as hydrocarbons or other heavy metals, are ubiquitous in Leach's storm-petrels' environment highlighting the importance to comprehensively assess the range and impact of contaminants on Leach's storm-petrels during the non-breeding season.

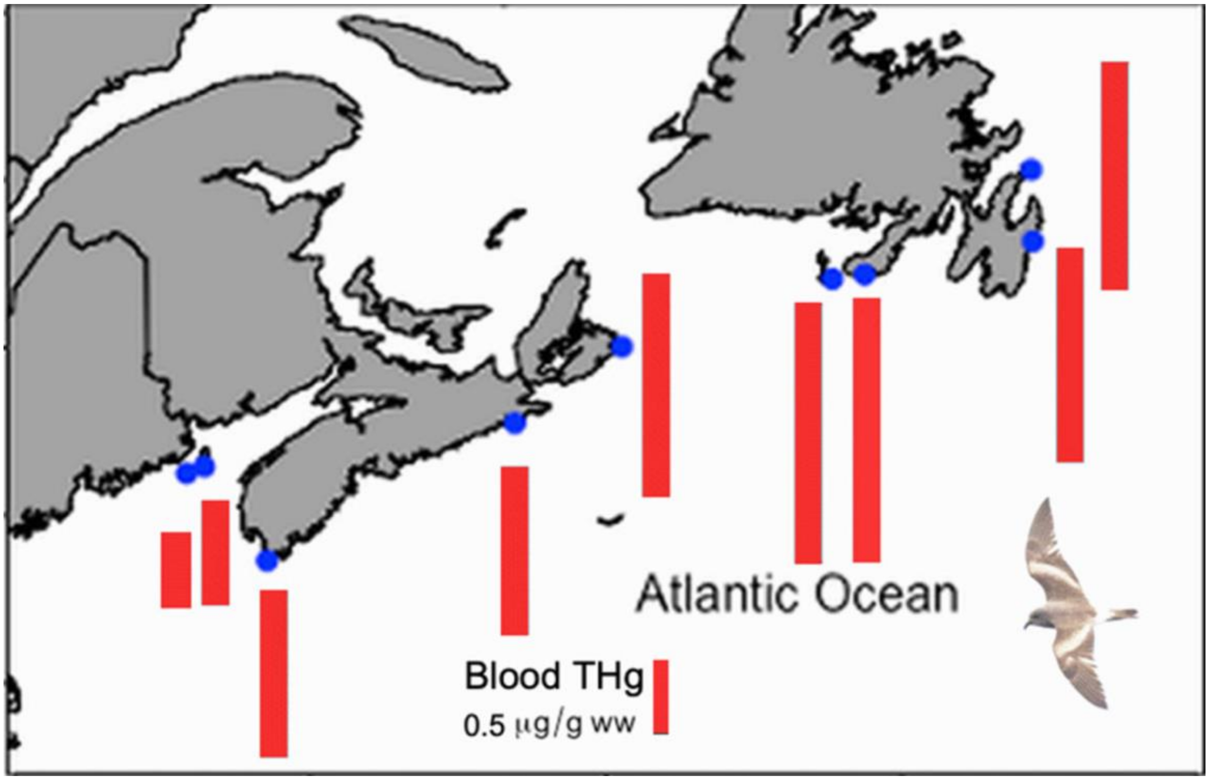

Figure 2.2 Total mercury (THg) concentrations in Leach's storm-petrels breeding in Atlantic Canada are shown by the red bars, and longer bars represent higher levels. Colony sites are represented by the blue dots and include (from right to left) Newfoundland: Baccalieu, Gull, Middle Lawn, Grand Colombier; Nova Scotia: Scatarie, Country, Bon Portage; New-Brunswick: Kent, Machias Seal. (Pollet et al. 2023b)

2.4.3 Moult Pattern

Moulting is an important annual process that allows seabirds to replace their feathers to maintain efficient flight and waterproofness (Ausems et al. 2021). This process is energetically costly and is usually initiated after the breeding period (Ausems et al. 2021). While some seabirds, such as penguins, undergo a catastrophic moult (Lewden et al. 2024), other species such as Leach's storm-petrel undergo sequential moult allowing them to keep their flight ability and migrate towards wintering grounds (Ainley et al. 1976). In fact, Ainley et al (1976) describes how there is only little overlap between moult and migration. Since LESP are oceanic seabirds, it is hard to capture them during their overwintering period to evaluate their moult stage. However, Ainley et al. (1976) concluded that most Leach's storm-petrels complete their yearly moult before returning to their breeding colony the following year.

Immature LESP were found to begin moult earlier than adults while the later were still in the laying or incubation stage (Ainley et al. 1976). Breeding adults initiate their body moult at about egg-hatching followed by tail moult, primary flight feathers, and end with secondary flight feather moult requiring an average of 274 days (Ainley et al. 1976). Finally, the last feathers to complete growth were found to be primary 10 (P10) and secondaries 4 (S4) and 9 (S9) which coincided with the month of February (Ainley et al. 1976) (Figure 2.3). As mentioned by Pollet et al. (2023b), moult patterns are important to identify when trying to link exposure to different contaminants to area in which a feather was grown.

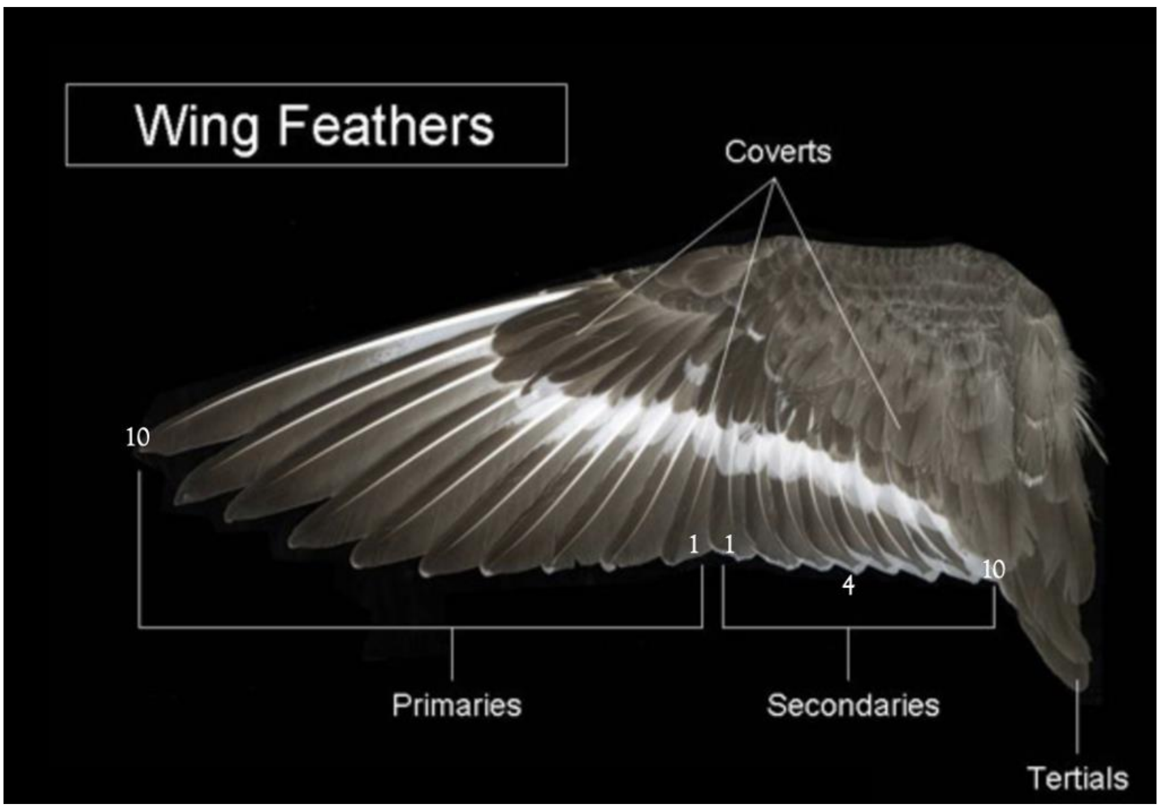

Figure 2.3 Bird wing that display the general feather arrangement. The primaries are read from the middle outward whereas the secondaries are read from the middle inward. (US Fish and Wildlife Service, Accessed November, 2024)

2.5 Conclusion

This literature review has placed the important role of heavy metals as a potential threat to Leach's storm-petrels and a possible contributing factor for their population decline in Atlantic Canada. The importance of both identifying the distribution of contaminants and understanding how overwintering location can predict exposure and bioaccumulation of heavy metals has become apparent throughout this literature review.

Several threats to Leach's storm-petrels including predation, light pollution and interspecific competition have been well studied in the past decade. Mercury, as part of marine pollution, has also been documented during the breeding season of this seabird species. However, other heavy metals have yet to be quantified in Leach's storm-petrels to further assess their potential impact.

Through this review, I have highlighted the need to assess the exposure to heavy metals during the overwintering period of Leach's storm-petrels in the Atlantic Ocean, as well as the impact of wintering locations on the variability of exposure to heavy metal bioaccumulation. I hope to fill these knowledge gaps and inform decision-makers to contribute to future implementation of informed conservation policies in highly polluted areas.

Chapter 3: Materials and Methods

3.1 Study Sites and Data Collection

The overwintering range of LESP is the primary study area, extending across the entire Atlantic Ocean (Figure 3.1). Post-breeding Leach's storm-petrels (*n*=151) were successfully tracked and sampled during two non-breeding seasons, in 2020 and 2022, from six breeding colonies in Atlantic Canada (Figure 3.1). Colonies from Newfoundland and Labrador 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) (Fig.5). Colonies from Nova Scotia included Country Island (45°06'N, 061°31'W) and Bon Portage Island (43°28′N, 065°44′W) and finally, Kent Island (44°34'N, 066°45'W) from New-Brunswick (Figure 3.1). The birds were captured and sampled between June and July of each year.

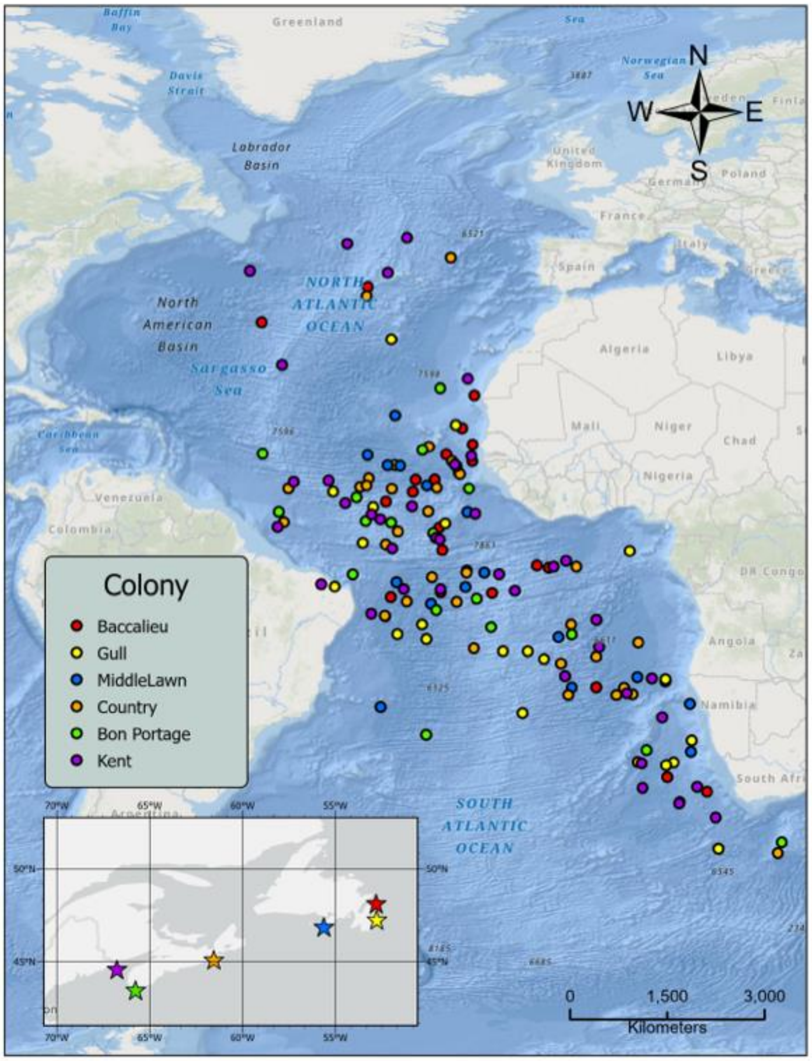

Figure 3.1 Distribution of Leach's storm-petrel (*Hydrobates leucorhous*) centroid across the Atlantic Ocean during the moulting period of S4 feathers (February). Individual centroids are coloured by their colony of origin and breeding colony locations are shown in the inset map of Southeastern Atlantic Canada.

3.2 GLS Tracking

GLS Deployment

To track year-round movements, GLS were deployed on randomly selected adults within the working plots during the late stages of incubation from mid-August to late September 2019 and 2021. Because LESP are a monomorphic species, adults were of unknown sex and age, and only one adult per burrow was tagged. A total of 61 individuals were deployed with GLS in 2019 and 90 individuals in 2021 across the 6 island colonies.

The loggers, (Figure 3.2; Intigeo-W30A9-SEA, Migrate Technology Ltd), weighed 0.45 g, measured 15 × 5 × 4 mm and had a battery life of 12 months (Migrate Technology, 2020). The tags were programmed to record in Mode 6 meaning that light levels were checked every minute and the maximum value encountered for every 5-minute period was recorded. Loggers were ground-truthed (i.e. run at known location in the colony) prior to deployment in 2019 and 2021.

Each tag was wrapped with a small amount of stretched self-amalgamating tape to provide grip to the UV-resistant zip tie passing through custom holes in a PVC ring (Migrate Technology, 2020). The tag was then attached to the bird's tarsus by slipping the ring, which had a small opening, around the leg (Migrate Technology, 2020). Care was taken to ensure that the light sensor was not covered. A stainless band size 1 was also applied to the other leg to identify the bird. Attachments took few minutes per bird, and adults were returned to their burrows immediately following the ring attachment. The total mass of a tag with attaching material was ~ 1.45 g, which was below the accepted 3 % rule (Phillips et al. 2003).

Figure 3.2 GLS tags used in this study. Model Intigeo-W30A9-SEA from Migrate Technology. (Source: Migrate Technology Limited, 2020)

GLS Retrieval

During the incubation period (June and July) of the year following GLS attachment, 2020 and 2022 respectively, burrows were surveyed to find birds that had been tagged the previous season. If an adult was present that had not received a GLS as above, entrances of burrows were latticed and daily checks were made until the lattice was disturbed, at which point burrows were checked for the presence of a tagged bird. To remove the GLS, the ring was cut and removed. At this point, two 4th secondary flight feather were collected for $\delta^{13}C$ and $\delta^{15}N$ stable-isotope analysis as well as heavy metal analysis. Bands number of birds without GLS were also checked to verify if individuals had lost their tags.

Logger data processing

The data retrieved from GLS were corrected for logger clock drift except in cases of battery failure. As explained by Studholme et al. (2019) daily sunrise and sunset event-times were estimated from light intensity curves in IntiProc 1.03 (Migrate Technology), with a lux threshold of 2. All light curves were visually inspected, and clearly erroneous event-times, such as program-defined sunrises or sunsets occurring within daylight or nighttime periods, or associated with severely truncated light curves, were identified and removed. A standard elevation angle was identified and used when calculating all positional data. This value was chosen by estimating the most appropriate angle for each ground-truthing period using the IntiProc calibration tool, calculating the mean of pre- and post-deployment estimates when available, and then calculating the mean for all loggers (Studholme et al. 2019).

As per Studholme et al. (2019), extensive logger data processing methods were applied in R and positional data were generated from event times using the 'coord' function in Geo-Light, yielding two positions per day when complete event-time data were available. As a final quality control step, the positional data for each bird were visualized in ArcGIS Pro 3.4 (ESRI) to identify and remove any positions that significantly deviated from the general distribution pattern, specifically those more than 350 km away from the nearest positions on the same date.

3.3 Stable-Isotopes Analysis

Stable isotope composition was determine using one S4 feather for each individual. Each feather was first washed in 0.25 M NaOH and rinsed thoroughly in grade 3 deionized water, or was soaked in a 2:1 chloroform:methanol solution for 24 hours to remove external contamination such as surface oils (Lavers et al. 2013; Tate et al. 2021). S4s were also rinsed twice with fresh solution and air dried in a fume hood at the Dalhousie University. Before shipment, feathers were cut into small pieces using stainless steel scissors, homogenized, and placed in a tin capsule.

Feathers were then sent to the Ján Veizer Stable Isotope Laboratory at the University of Ottawa for stable isotope analyses.

Upon arrival, encapsulated freeze-dried feather samples were quantified for stable carbon and nitrogen isotope ratios ($\delta^{13}C$, $\delta^{15}N$) using an Elemental Analyzer – Isotope Ratio Mass Spectrometer (Thermo Delta V). Stable isotope ratios are expressed in δ notation as parts per thousand (‰) deviation from the international standards Vienna Pee Dee Belemnite (PDB) for carbon ($\delta^{13}C$) and atmospheric air for nitrogen ($\delta^{15}N$), according to the following equation:

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

with X being either ^{13}C, or ^{15}N, and R the corresponding $^{13}C/^{12}C$, $^{15}N/^{14}N$. $R_{standard}$ for δ13C is Vienna Pee-Dee Belemnite and normalized to internal standards calibrated to international standards IAEA-CH-6, NBS-22, and USGS-40 (Carvalho et al. 2022; Pollet, McFarlane-Tranquilla, et al. 2023). $R_{standard}$ for $\delta^{15}N$ is air and normalized to internal standards calibrated to international standards IAEA-N1 (Pollet et al. 2023b). Precision was assessed as the standard deviation of replicate analyses of three standards (NIST1577c, tilapia muscle and USGS 41) and was ≤0.21‰ for $\delta^{15}N$ values and ≤0.14‰ for $\delta^{13}C$ values (Carvalho et al. 2022).

3.4 Heavy Metals Analysis

Feathers were weighed and washed (as per stable isotope analysis) and samples were then sent to a lab at the Natural History Museum in Tring, United Kingdom where all heavy metal analyses were conducted. Heavy metals analyzed in this study included vanadium (V), manganese (Mn), cobalt (Co), cupper (Cu), zinc (Zn), arsenic (As), cadmium (Cd), mercury (Hg), and lead (Pb). Extensive explanation on sample preparation can be found in Appendix A (Lavers et al. 2013).

Heavy metal concentrations were measured in a PerkinElmer ELAN DRCII ICP-MS (Rf power: 1200 W; ICP-MS plasma gas flow: 15 l min−1; auxiliary gas flow: 1 l min−1; nebulizer gas flow: 1 l min−1; sample uptake rate: 3.055 ml min−1). As described by Lavers et al. (2013), data acquisition was at peak-hopping mode, and each analyte mass was measured for 6 s based on protocols established by Friel et al. (1990). Procedural blanks and secondary reference materials were included every 15 to 20 samples to mitigate reading errors. The secondary materials used as reference were certified human hair samples from the Centre de Toxicologie du Québec, Institut National de Santé Publique du Québec. Secondary reference materials were certified for concentrations of each heavy metal we were interested in: ^{51}V, ^{55}Mn, ^{59}Co, ^{63}Cu, ^{66}Zn, ^{75}As, ^{111}Cd, ^{201}Hg, and ^{208}Pb. Statistical analyses were restricted to those elements that could be analysed reliably as assessed by the recovery of reference materials which in this case, all elements were reliable. However, Cd was removed from the statistical analysis as concentrations in feather samples were frequently below detection limits. This has also been observed in other studies quantifying Cd in bird feathers (Lavers et al. 2013; Bond and Lavers 2020). Bond and Lavers (2020) stated "Little of birds' Cd burden is sequestered into feathers (Honda et al. 1985; Burger 1993)" and so feathers are "not suitable for assessing total Cd burden".

Values were corrected for background levels such as atmospheric elemental concentrations not attributed to the analytical sample, using procedural blanks. For each element, the keratin reference material was used with the same magnitude of concentration as the unknowns to correct for recovery (Lavers et al. 2013).

3.5 Spatial Analysis

Clustering

All GLS tracking data for both collection years (2020 and 2022) were imported into ArcGIS Pro software version 3.4. Point features were created from this csv file using the latitude and longitude recorded data to obtain a visual representation. From there, coordinate points were filtered to only show data points corresponding to the month of February to match the time at which S4s are estimated to be grown (Ainley et al. 1976). A mean center location was calculated for each individual based on their February coordinate points and a centroid was obtained. The centroid of each individual was then used to generate a Kernel density map that shows areas of high point density. The cell size as well as the search radius was set at 200km to account for the error associated with GLS locations (Phillips et al. 2004; Pollet et al. 2018) and the geodesic option was selected to account for the curvature of the spheroid and minimize error for points near the poles. As explained by Tobler's first law, everything is related to everything else and near things are more related to each other (Waters 2017). Therefore, high-density hotspots were identified (*n*=5) and used as comparison areas (Figure 3.3). Each individual centroid was assigned to its closest hotspot. For centroids that weren't obvious to assign, their February coordinates were used to visualize the direction of the data points and decide on which hotspot would be the most appropriate to assign it to.

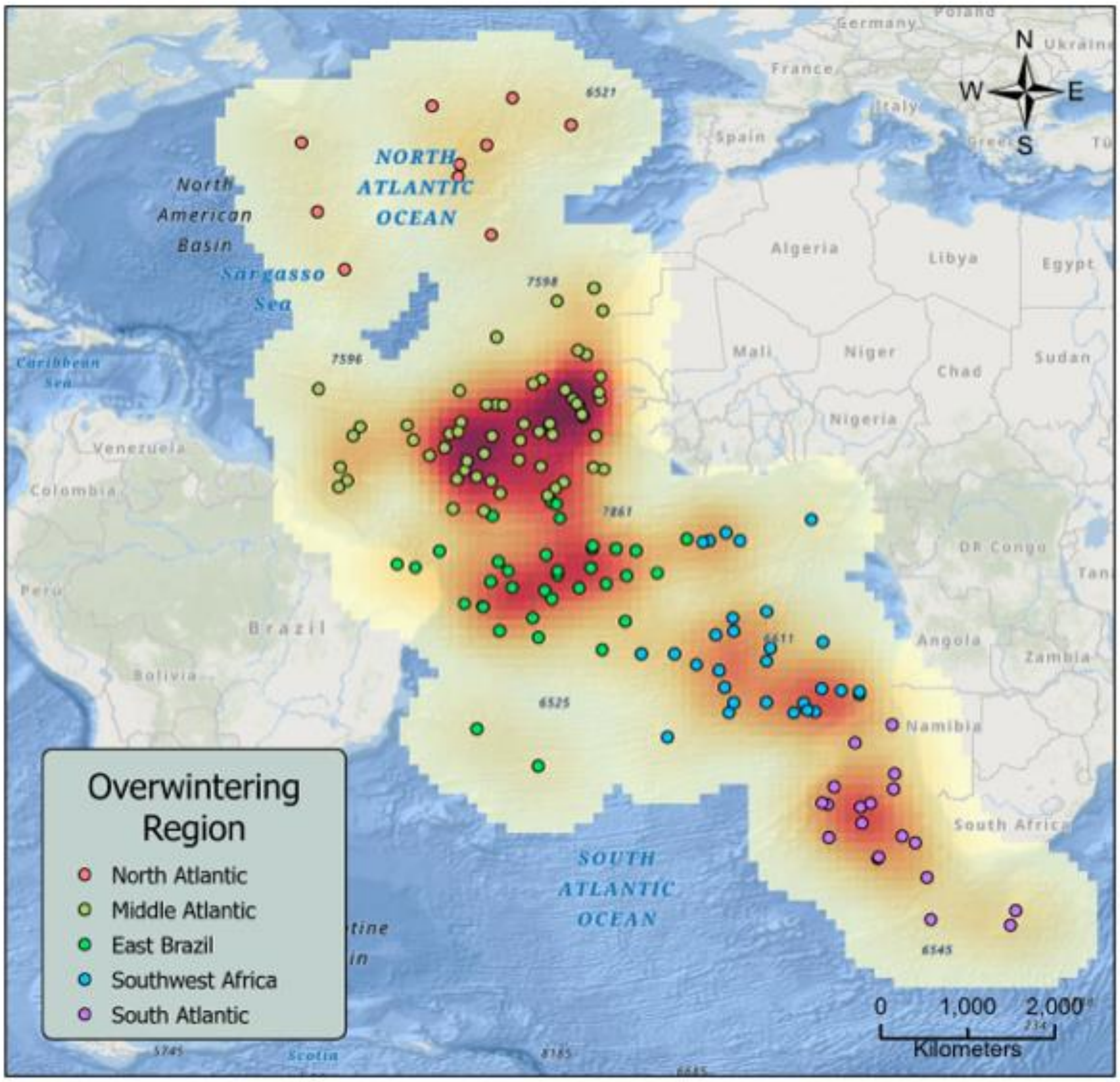

Figure 3.3 Kernel density estimates for Leach's storm-petrel (*Hydrobates leucorhous*) centroids, displaying hotspots of high-density areas. Each centroid is coloured by the hotspot it is assigned to and consist of n = 5 overwintering regions.

Oceanographic Variables

Two dynamic oceanographic variables were selected for their biological relevance to seabirds and ocean productivity; Sea surface temperature (SST, C°) and Chlorophyll-a (Chl-*a*, $mg \cdot m^{-3}$). Both layers were obtained from monthly average Aqua MODIS products mapped at 4-km resolution. Each centroid for February 2020 and 2022 was assigned to their respective layer and a zonal statistic was generated to extract the value of the layer for each centroid.

3.6 Statistical Analysis

The final variables included in the statistical analysis included heavy metals, stable isotopes ($\delta^{13}C$, $\delta^{15}N$), oceanographic variables (Chl-a, SST°C), overwintering regions, year sampled, colony of origin, and sex. For each overwintering location, the mean ± SD of each variable was calculated separately for each year and for both years combined, using Microsoft Excel and all individual centroid values within the area.

Using R software version 4.4.3, heavy metals concentrations were analyzed separately by linear mixed-effects models fitted by maximum likelihood (REML = FALSE) using the 'lmer' function from the "lme4" package (R Development Core Team, 2012) with stable isotope values, oceanographic variables values, overwintering regions and year as predictors. Individuals were sampled for one of the two non-breeding periods during the study period (2020/2022) at their colony. Hence, to address the potential non-independence among heavy metal concentrations taken within colonies, the colony of origin was treated as a random effect. Sex can influence the distribution of non-breeding petrels and other Procellariiformes (Phillips et al. 2017); however, exceptions exist, such as the Sooty Shearwaters, which show no sexual segregation during overwintering migration (Hedd et al. 2014). Initially, sex was included as a random effect in the global model for all heavy metals, but R returned a warning code due to negligeable effect (variance = 0, SD = 0). Using ArcGIS Pro, Ordinary Least Square (OLS) regression was run with sex as the dependent variable and coordinates (x,y) as explanatory variables to assess the relationship between sex and space. Additionally, a Global Moran's I test was completed to test spatial autocorrelation of the OLS residuals, also completed in ArcGIS Pro. This test showed near perfect randomness in spatial distribution of the residuals (*Moran's I* = -0.014; $p = 0.87$). Consequently, sex was removed from the model, assuming no sex effect. A map showing a near equal distribution of males and females across the North Atlantic is provided in Appendix B. OLS regression results and Global Moran's I on OLS residuals outputs are also provided in Appendix B, supporting the decision of removing the sex variable from the models.

Each heavy metal dataset was tested for parametric assumptions, including normality and homoscedasticity of residuals. If the residuals were non-normally distributed, raw data were transformed using logarithmic (log), square root, or inverse transformations depending on the most appropriate approach. The global model from which variables were selected was structured as follows:

$$\text{[Heavy Metal]} \sim \text{Overwintering Region} + \delta^{13}\text{C} + \delta^{15}\text{N} + \text{SST°C} + \text{Chl-}a + \text{Collection Year} + (1 \mid \text{Colony})$$

Akaike Information Criterion (AIC) was used to compare models, with each model assigned an AIC score as a ranking metric. Only biologically meaningful models were taken into consideration, and the best explanatory model was selected based on the lowest AIC score and was fit with restricted maximum likelihood estimation (REML = TRUE). A comprehensive statistical analysis of the final model was conducted in R, including a Type III (sums of square) ANOVA followed by a post-hoc Tukey test for pairwise comparisons to identify significant differences. This analysis tested the hypothesis that variability in heavy metal exposure was influenced by overwintering location.

3.7 Limitations of the Proposed Methods

Even if limited, few limitations were identified for this study. First, the GLS tracking devices have an error range of ~200 km (Phillips et al. 2004; Pollet et al. 2018). Therefore, the values attached to the centroids might be representative of a slightly different area. However, because the study is focusing on the entire Atlantic Ocean, 200km error range is considered of low impact. Second, the spatial resolution of the oceanographic variables of 5 km should also be considered when trying to link these values to geographic data point. However, due to the same reason as the GLS error range, the impact is considered of low significance. Misclassification, due to the 200km error range of the GLS devices, was also a possible limitation when assigning individual LESP to their closest hotspot. Centroids might have been assigned to a specific hotspot due to its close proximity but being more representative of another hotspot. Finally, while the exact timing at which S4 feathers are moult is unknown, it has been estimated to begin in February (Ainley et al. 1976). This estimation may influence the inferred timing of Leach's storm-petrels' exposure to heavy metals, subsequently affecting the identification of their exact exposure locations. These limitations were considered of low impact for this study, but considerations are important while interpreting results.

Chapter 4: Results

4.1 Heavy Metal Distribution

During the winter moult of S4 feathers, Leach's storm-petrels were widely distributed across the North and South Atlantic Ocean, with some individuals found in waters over the continental shelf and others in deeper oceanic waters (Figure 3.1). No discernible patterns were observed based on colony of origin or sex. Although sex was initially included as a random effect, it did not account for any unexplained variation within the models. While the effect of year was not significant for most heavy metals, it was retained as a predictor to account for potential year-to-year variation in the ocean's dynamic environment.

Heavy metal concentrations in the feathers of storm-petrels varied little by region and between years (Table 4.1), with the exception of Hg which varied widely amongst overwintering locations (Figure 4.1). However, while the hypothesis that exposure to contaminants is strongly influenced by individual choice of overwintering location, only Hg varied significantly by overwintering regions (Table 4.2). For all other metals (Appendix C), overwintering region was not a significant predictor; in fact, most models did not show any significant effect of wintering region, trophic position, and (or) colony of origin (Table 4.2). While the null model was ranked as the best for most heavy metals, suggesting that predictors considered in this study did not influence their bioaccumulation, the majority also failed to meet the normality assumption for residuals (Table 4.2). For these reasons, all metals except for Hg were discarded from the remainder of the results section.

Table 4.1 Mean ± SD of heavy metal concentrations bioaccumulated in S4 feathers of Leach's storm-petrels (*Hydrobates leucorhous*) grown during non-breeding season at sea. Concentration units are reported as μg g−1 dry weight. Heavy metals with year that significantly differed are indicated with an asterisk *

Collect Year	Sample size	V*	Mn	Co	Cu*	Zn*	As*	Pb	Hg
2020	61	0.080 ± 0.035	0.257 ± 0.164	0.034 ± 0.058	9.575 ± 1.162	99.536 ± 15.128	0.522 ± 0.324	0.123 ± 10.078	14.846 ± 7.142
2022	90	0.057 ± 0.031	0.236 ± 0.188	0.024 ± 0.028	9.028 ± 1.564	109.183 ± 25.061	1.950 ± 1.429	0.181 ± 0.345	14.348 ± 7.337
Combined Year	151	0.066 ± 0.035	0.245 ± 0.178	0.028 ± 0.043	9.249 ± 1.435	105.286 ± 22.068	1.373 ± 1.325	0.157 ± 0.271	14.549 ± 7.237

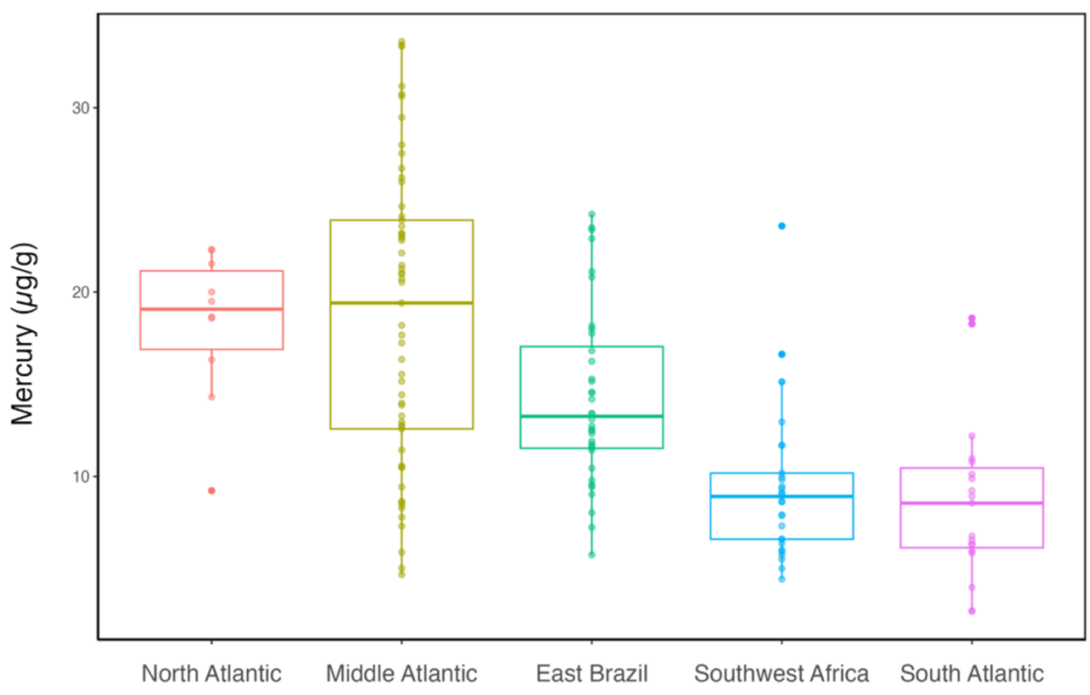

Figure 4.1 Variation in Hg (μg/g dry weight) of 151 Leach's storm-petrels (Hydrobates leucorhous) at 5 distinct overwintering location, as inferred from kernel density analysis based on GLS tags. Regions are ordered from left to right by decreasing latitude. North Atlantic region n=10, Middle Atlantic region n=57, East Brazil region n=36, Southwest Africa region n=29, South Atlantic region n=19.

Table 4.2 Best ranked linear mixed-effect models explaining variation in each heavy metal bioaccumulation in S4 feathers of Leach's storm-petrels (*Hydrobates leucorhous).* For all models, number of random-effects terms k = 1 (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 (α = 0.05) are indicated by an asterisk *. Heavy metal residuals were transformed if not normally distributed. The model showing a regional effect is indicated in bold. LMM output for Hg can be found in Table 4.3. LMM output for each other metal can be found in Appendix C.

Metal	Model	Reference
Hg	**Hg ~ δ^{13}C* + δ^{15}N* + Overwintering Location* + Chl-a* + SST + (1 | Colony)**	**Table 4.3**
V	log(V) ~ δ^{13}C + δ^{15}N + Chl-a + SST + Year* + (1 | Colony)	Appendix C
Mn	NULL MODEL: 1/(Mn) ~ 1 + (1 | Colony)	Appendix C
Co	NULL MODEL: 1/(Co) ~ 1 + (1 | Colony)	Appendix C
Cu	NULL MODEL: Cu ~ 1 + (1 | Colony)	Appendix C
Zn	NULL MODEL: Sqrt(Zn) ~ 1 + (1 | Colony)	Appendix C
As	log(As) ~ δ^{13}C + δ^{15}N + Chl-a + SST + Year* + (1 | Colony)	Appendix C
Pb	NULL MODEL: 1/(Pb) ~ 1 + (1 | Colony)	Appendix C

4.2 Predictors of Exposure

Hg concentrations varied widely among the five wintering hotspots from the North Atlantic Ocean to the South Atlantic Ocean, with the highest concentration recorded in feathers of individuals overwintering in the mid-Atlantic Ocean and the lowest concentration in individuals moulting in the South Atlantic waters (Figure 4.1). Individuals overwintering in the mid-Atlantic Ocean bioaccumulated significantly higher levels of Hg compared to storm-petrels overwintering in lower latitude regions. Overall, there was a significant effect of the foraging parameters (δ^{13}C, δ^{15}N, Chl-a), and of the wintering region, indicating that Leach's storm-petrels bioaccumulate different levels of Hg through diet based on their choice of overwintering location (Table 4.3). δ^{15}N, was strongly predictive of Hg bioaccumulation, such that individuals feeding at lower trophic level in the mid-Atlantic Ocean bioaccumulated more Hg than individuals overwintering in the South Atlantic region and feeding at higher tropic level (Figure 4.2). Variance in the random effect of colony (SD = 1.4) was smaller in magnitude than the individual (residual) variance (SD = 5.3) (Table 4.3). In other words, some inherent trait among individual Leach's storm-petrels explained nearly 4 times the amount of variance in Hg concentration as did colony of origin, after accounting for effects of trophic position ($\delta^{13}C$, $\delta^{15}N$), chlorophyll-a concentration, sea surface temperature, and overwintering location.

Table 4.3 Statistical output from a liner mixed-effects model examining variation in Hg concentrations in the S4 feathers of Leach's storm-petrels (*Hydrobates leucorhous),* reflecting uptake during the period of feather growth in February. Statistically significant effects (α = 0.05) are indicated by an asterisk *.

Fixed effects	**Estimate**	**Standard error**	**df**	**t-value**	***p***
Intercept*	24.45	3.00	140	8.16	<0.001
$\delta^{13}C$ *	1.65	0.52	140	3.19	<0.01
$\delta^{15}N$ *	-2.45	0.59	140	-4.15	<0.001
SST (°C)	1.80	0.95	140	1.89	0.059
Chl-a *	-1.05	0.52	140	-2.01	0.044
Overwintering location *					<0.001
Middle Atlantic	-7.95	3.12	140	-2.54	
East Brazil	-11.62	3.68	140	-3.16	
Southwest Africa	-13.46	3.28	140	-4.10	
South Atlantic	-10.50	2.68	140	-3.91	
Random effect	**Standard deviation**	**Variance**			
Colony	1.40	1.96			
Residual	5.33	28.37			

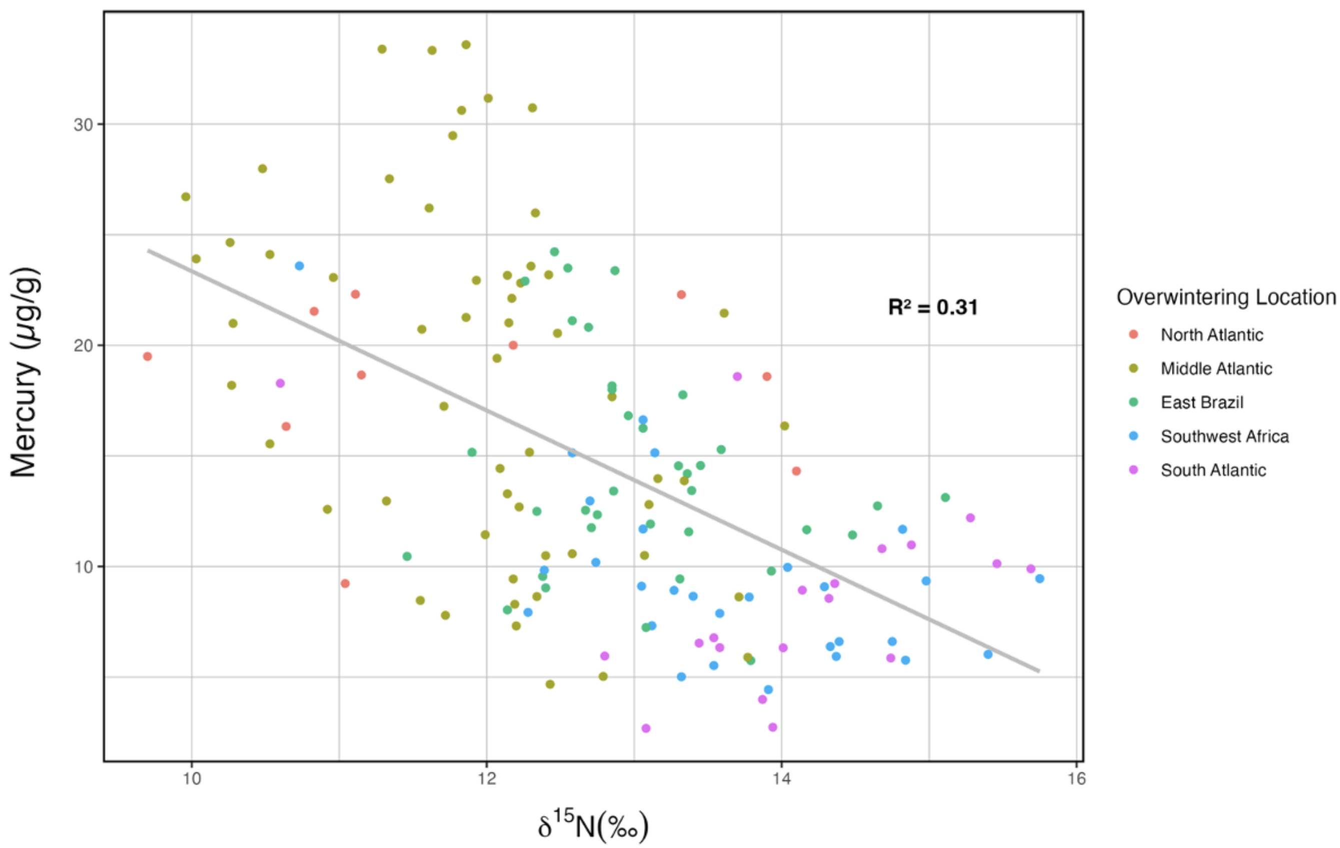

Figure 4.2 Relationship between Leach's storm-petrel (*Hydrobates leucorhous*) S4 feathers' Hg (µg/g dry weight) and $\delta^{15}N$ (‰) among different overwintering locations with linear regression for all individuals (*n* =151).

Chapter 5: Discussion
5.0 Summary

This is the first study to quantify the levels of multiple heavy metals in seabirds, including Leach's storm-petrels, and to identify areas of exposure across the Atlantic Ocean during the non-breeding period. Through combined analysis of geolocation tracking data, heavy metal concentrations in secondary flight feathers (S4), and foraging indicators ($\delta^{13}C$, $\delta^{15}N$, Chl-a), I identified five primary overwintering habitats spread trans-equatorially across the north and south Atlantic Ocean where exposure to Hg varied significantly. This result supports the prediction that exposure to Hg is influenced by the individual choice of overwintering habitat and the foraging conditions therein. Specifically, I found that Hg concentrations were the highest in Leach's storm-petrels wintering in the mid-Atlantic region and decreased with latitude, with the lowest concentrations recorded in birds wintering in the South Atlantic region. Additionally, because there was a significant relationship between Hg concentrations and $\delta^{15}N$ values, Hg variation in Leach's storm-petrels probably reflects regional differences in the foraging base available to these birds, which itself is the result of complex oceanographic processes. A study conducted on ten different species of storm-petrels showed positive correlation between nitrogen isotope and Hg concentrations where $\delta^{15}N$ values increased with higher trophic position (Quillfeldt et al. 2023). However, I found that dietary differences, as indicated by $\delta^{15}N$ values, were inversely related to Hg concentration which is counterintuitive as organic Hg is known to biomagnify up the food chain. Elliott and Elliott (2016) found similar results where herons and cormorants feeding on larger fish had lower Hg levels than partial planktivores such as storm-petrels and ancient murrelets, showing a negative relationship between Hg levels and trophic position. Such phenomenon can be explained by trophic characteristics of different overwintering areas. Additionally, Pollet et al. (2019) also found higher $\delta^{15}N$ values in Leach's storm-petrels migrating in the South Atlantic Ocean relative to birds overwintering in higher latitude areas such as the North Atlantic Ocean. Finally, I found that individuals' inherent traits accounted for more of the variance in Hg concentrations than the colony of origin, which reflects the high individual plasticity of the migration behaviour during the non-breeding period. This is evident in the high spatial variation in Hg levels across the Atlantic Ocean amongst individuals from the same breeding colony, a pattern also observed in other seabirds with high individual plasticity in non-breeding distribution including northern fulmars, Cory's and Sooty shearwaters (Shaffer et al. 2006; González-Solís et al. 2007; Albert et al. 2021a).

5.1 Biodilution Effect and Diazotrophs

In addition to the spatial variability in Hg availability known to exist in the Atlantic Ocean (e.g. Figure 2.1), prey choice within a given region may be playing a role in Hg intake (Le Croizier et al. 2022; Albert et al. 2024). However, 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). Studies have shown that the high levels of primary productivity, characteristic of upwelling zones, can have a biodilution effect on available Hg (Zaferani and Biester 2021; Le Croizier et al. 2022). 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). Hg 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 (Zaferani and Biester 2021; Le Croizier et al. 2022; Cui et al. 2024). This process likely reduces the biomagnification of Hg to higher tropic levels, which would predict lower Hg levels in seabirds foraging in these areas (Le Croizier et al. 2022). Indeed, the lowest Hg concentrations recorded in my 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 $\delta^{15}N$ values compared to individuals overwintering in more oligotrophic, higher latitude regions, suggesting that petrels were foraging at a high trophic position in the Benguela (Pollet et al. 2019; Quillfeldt et al. 2023; Silva et al. 2024).

Hg biodilution was also observed in upwelling regions of the Pacific Ocean (Le Croizier et al. 2022). For example, Guanay cormorants (*Phalacrocorax bougainvillii*) and Peruvian boobies (*Sula variegata*) foraging in the Humboldt Current ecosystem had lower Hg concentrations despite having high $\delta^{15}N$ levels compared to birds foraging in more pelagic, oligotrophic ecosystems (Le Croizier et al. 2022). In contrast to the Benguela, $\delta^{15}N$ levels 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 $\delta^{15}N$ values in oligotrophic waters were significantly lower at all trophic levels relative to more productive areas. Hence, the lowest $\delta^{15}N$ values that I 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). To test this hypothesis, 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.

5.2 Myctophid Diet

As a general rule, Hg concentrations tend to increase with trophic position, and for example 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). This paradox may be explained by the fact that breeding Leach's storm-petrels are nocturnal foragers (COSEWIC 2020) and feed on a variety of prey, including vertically migrating fish such as myctophid fishes (i.e. the lanternfishes [Myctophidae]) (Hedd and Montevecchi 2006; Hedd et al. 2009). During the daylight hours, these fishes 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 (Elliott and Elliott 2016; Crichton et al. 2023). 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 middle Atlantic have diets similar to breeding individuals. This could explain the elevated Hg levels that I found in the feathers of birds residing there. 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 and Montevecchi 2006; Hedd et al. 2009). Combined with the results of my study, this would provide deeper insights into the biogeochemistry of Hg and contaminant dynamics within Leach's storm-petrels' prey.

5.3 Detoxification Mechanism

In this study, no speculation was 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 I 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 this those of the Arctic species mentioned above (Albert et al. 2021b). Hypotheses about how Leach's storm-petrels might cope with high Hg concentrations have been posed, including internal detoxification mechanisms (El Hanafi et al. 2022b; Pollet, McFarlane-Tranquilla, et al. 2023). Selenoneine, a Se-derived compound, was found in giant petrels at the highest concentrations ever recorded in animal tissues (El Hanafi et al. 2022b). This compound is known to be bioaccumulated through diet, biomagnified through the food chain, and plays a key role in the nervous system (El Hanafi et al. 2022b). El Hanafi et al. (2022) also identified a negative correlation between selenoneine and Hg concentrations in the brains of giant petrels, supporting the hypothesis that selenoneine plays a role in Hg detoxification. While selenoneine concentrations were not measured in this study, it is fair to assume that this compound is found in Leach's storm-petrels due to their relatively high trophic position in the food web (Hedd and Montevecchi 2006; Silva et al. 2024). The contribution of selenoneine could explain why relatively high levels of Hg are found in birds that are healthy enough to breed (Mills et al. 2020; Pollet et al. 2022).

5.4 Adult Survival

Regarding the maternal transfer of Hg to offspring, multiple tissue types have been used to infer the toxicological effect of Hg on hatching and fledglings' success in Leach's storm-petrels, but no significant effect have been found on these parameters (Pollet et al. 2022). Ultimate measures of breeding success, such as fledgling survival to maturity have not been assessed. As such, more comprehensive assessments of Hg in the context of migration-to-breeding carry-over effects should be conducted. This is especially salient given that Leach's storm-petrels breeding in Atlantic Canada have shown lower adult survival (~78-86%; Fife et al. 2015; Pollet et al. 2023) compared to their counterparts in the Pacific (~97%; Elliott and Elliott 2016; Rennie et al. 2020). While predation effects are known to have important impacts on adult survival in Leach's storm-petrel colonies in Atlantic Canada (Bond et al. 2023; Gutowsky et al. 2023), non-breeding contaminant exposure could also be playing a role and should be studied.

Chapter 6: Conclusion

This study provides important new insight into heavy metal bioaccumulation during the non-breeding period of Leach's Storm-Petrels and identifies potential contaminant exposure predictors, such as overwintering areas, the oceanographic processes therein, and trophic position. Although several heavy metals were quantified, only Hg concentrations exhibited significant variability across five distinct overwintering regions. Seabirds, such as Leach's storm-petrels, are important for marine pollution biomonitoring due to their strong bioaccumulation abilities relative to other seabirds (Zhou et al. 2008; Pollet et al. 2023), and are considered "sentinels" of ecosystem health (Francis 2017; Pacyna et al. 2019; Velarde et al. 2019). In future research, the results of this study could serve as a baseline for comparisons of heavy metal levels in offshore overwintering regions. 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. Additionally, these predictions could support decision-makers in establishing new MPAs that encompass regions of elevated contaminant exposure. The fate of many seabird species in the future remains uncertain, as human activities have driven significant population declines (Xu et al. 2016; Dias et al. 2019; Phillips et al. 2023). With increasing heavy metal released into the 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.

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Appendices

Appendix A: Feather sample preparation for heavy metal analysis

"We weighed and washed (as per stable-isotope analysis) 2 feathers per bird (~15 to 25 mg per sample) and placed samples into clean Savillex 15 ml Teflon screw-cap vessels. We analysed 2 feathers per sample, as individual feathers can be highly variable in metal concentrations (Bond & Diamond 2008). We added ~1 ml of 8 M HNO3 (Fisher Scientific, 16 M, distilled in-house using Teflon stills) to the vessels, and capped and heated them on a hotplate at 70°C for 60 min. After 60 min, an additional 1 ml of 8 M HNO3 was added, and the feathers were pushed down with clean disposable plastic pipettes until fully submerged in the acid and were capped and heated for 24 h. After 24 h, the hotplate was cooled to 50°C, the vessels were uncapped, and 1 ml of H2O2 (Fisher Scientific, 30 % certified, American Chemical Society) was added. When the feathers had completely digested, the vessels were recapped and left on the hotplate for 3 h more at 70°C. We then diluted the sample 500× with distilled deionized water in clean, sealed containers. For inductively coupled plasma mass spectrometry (ICP-MS) analysis, 1 ml of the sample solution was pipetted into clean 10 ml tubes, and 4 ml of distilled, deionised water were added to make a final tube dilution of ~2500×." (Lavers et al. 2013)

Appendix B: Distribution of male and female birds across the North Atlantic Ocean

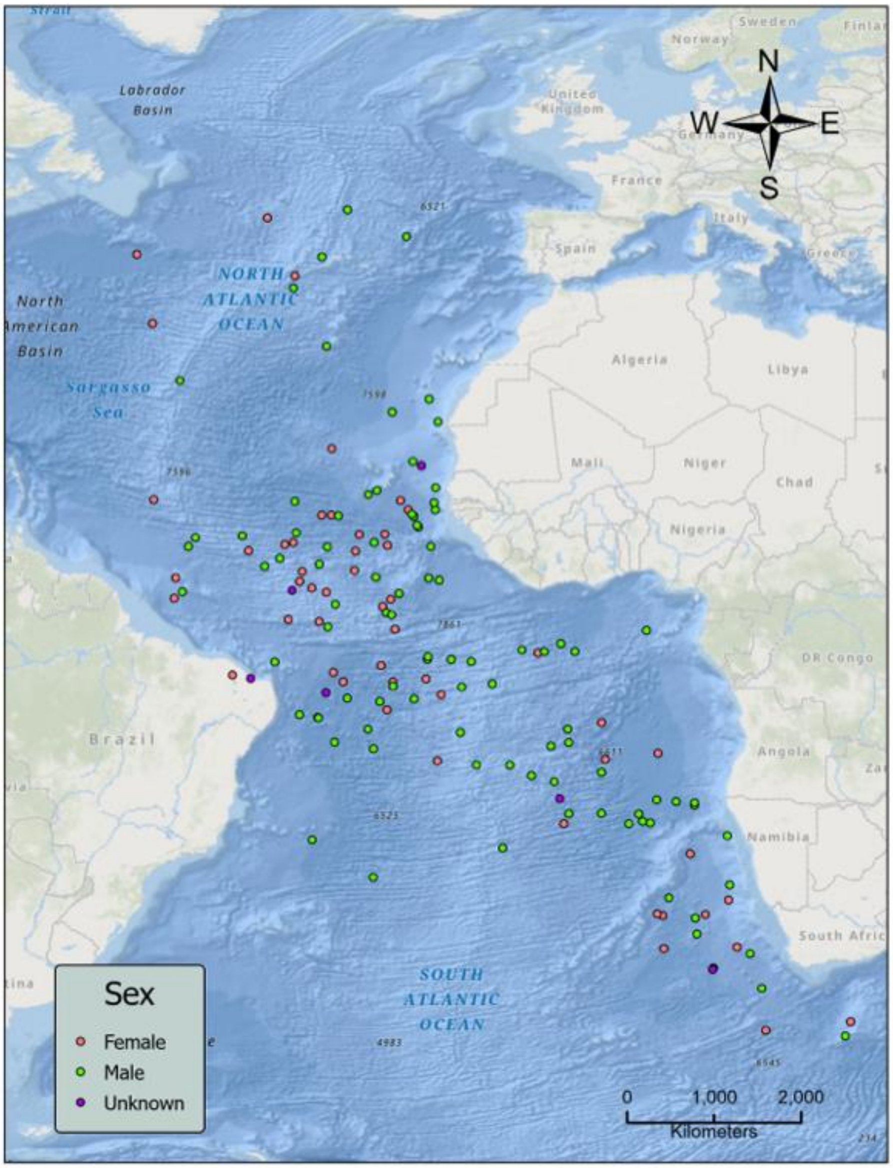


Figure B1 Distribution of male (n=93), female (n=52), and unknown sex (n=6) Leach's storm-petrels (*Hydrobates leucorhous)* across the North Atlantic Ocean and showing near perfect randomness of distribution.

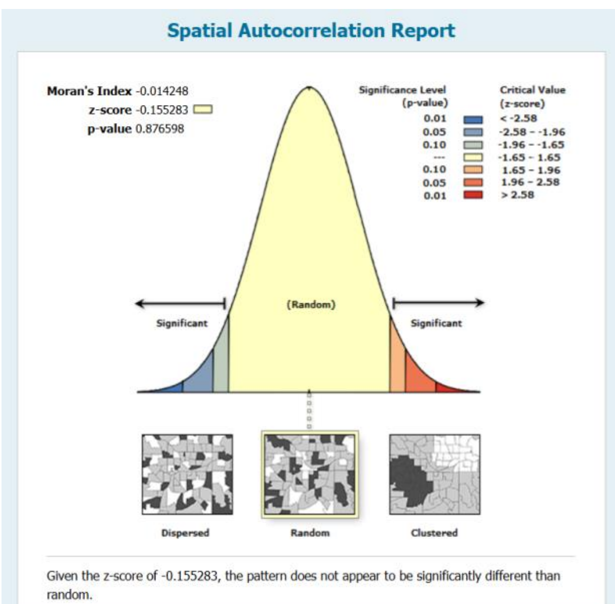
Summary of OLS Results

Variable	Coefficient[a]	StdError	t-Statistic	Probability[b]	Robust_SE	Robust_t	Robust_Pr[b]	VIF[c]
Intercept	1.251924	0.092889	13.477699	0.000000*	0.085473	14.647009	0.000000*	--------
XCOORD	-0.008952	0.004199	-2.131893	0.034659*	0.004255	-2.103808	0.037079*	2.285106
YCOORD	-0.006353	0.003872	-1.640824	0.102967	0.003847	-1.651519	0.100762	2.285106

OLS Diagnostics

Input Features	Colony_GLS_XYTableToPoint	Dependent Variable	SEXC
Number of Observations	151	Akaike's Information Criterion (AICc)[d]	261.889442
Multiple R-Squared[d]	0.029820	Adjusted R-Squared[d]	0.016709
Joint F-Statistic[e]	2.274506	Prob(>F), (2,148) degrees of freedom	0.106432
Joint Wald Statistic[e]	4.439123	Prob(>chi-squared), (2) degrees of freedom	0.108657
Koenker (BP) Statistic[f]	3.880542	Prob(>chi-squared), (2) degrees of freedom	0.143665
Jarque-Bera Statistic[g]	20.390110	Prob(>chi-squared), (2) degrees of freedom	0.000037*

Figure B2 Ordinary Least Square (OLS) regression results of sex as a dependent variable and coordinates (x,y) as explanatory variables. The OLS residuals were used to test spatial autocorrelation using Global Moran's I test in ArcGIS Pro 3.4 (ESRI) .



Global Moran's I Summary

Moran's Index	-0.014248
Expected Index	-0.006667
Variance	0.002384
z-score	-0.155283
p-value	0.876598

Dataset Information

Input Feature Class:	Colony_GLS_XYTableToPoint_OrdinaryLeastSquares
Input Field:	STDRESID
Conceptualization:	INVERSE_DISTANCE
Distance Method:	EUCLIDEAN
Row Standardization:	True
Distance Threshold:	856569.2207 meters
Weights Matrix File:	None
Selection Set:	False

Figure B3 Global Moran's I results on OLS residuals showing randomness in residual distribution (*Moran's I* = -0.014; *p* = 0.87)

Appendix C: LMM output for all heavy metals (Hg, V, Mn, Co, Cu Zn As, Cd, Pb)

(Hg)

Model	Intercept	δ13C	Chl-a	δ15N	Overwintering Location	SST	Year	REML	Df	logLik	AICc	Delta	Weight
δ13C + δ15N + Chl-a + SST + Overwintering Location + (1 | Colony)	12.84	1.63	-1.06	-2.45	+	1.78	NA	FALSE	11.00	-465.11	954.12	0.00	0.50
δ13C + δ15N + Chl-a + Overwintering Location + (1 | Colony)	14.20	1.64	-1.52	-2.66	+	NA	NA	FALSE	10.00	-466.91	955.39	1.26	0.27
δ13C + δ15N + Chl-a + SST + Overwintering Location + Year + (1 | Colony)	-922.10	1.78	-1.12	-2.62	+	1.76	0.46	FALSE	12.00	-464.71	955.68	1.56	0.23
δ13C + δ15N + Overwintering Location + (1 | Colony)	14.72	1.33	NA	-2.73	+	NA	NA	FALSE	9.00	-472.29	963.86	9.73	0.00
δ13C + δ15N + Chl-a + SST + Year + (1 | Colony)	-2103.71	1.87	-1.42	-4.38	NA	-0.17	1.05	FALSE	8.00	-475.04	967.10	12.98	0.00
δ13C + δ15N + Chl-a + SST + (1 | Colony)	14.63	1.56	-1.25	-4.21	NA	-0.12	NA	FALSE	7.00	-477.15	969.08	14.95	0.00
δ13C + δ15N + (1 | Colony)	14.66	1.41	NA	-4.17	NA	NA	NA	FALSE	5.00	-480.37	971.16	17.04	0.00
Chl-a + SST + Overwintering Location + (1 | Colony)	12.10	NA	-0.73	NA	+	2.52	NA	FALSE	9.00	-476.57	972.42	18.30	0.00
Overwintering Location + (1 | Colony)	14.41	NA	NA	NA	+	NA	NA	FALSE	7.00	-483.67	982.13	28.01	0.00
Chl-a + SST + (1 | Colony)	14.55	NA	-0.60	NA	NA	0.98	NA	FALSE	5.00	-509.95	1030.32	76.20	0.00
NULL MODEL	14.61	NA	NA	NA	NA	NA	NA		3.00	-512.21	1030.58	76.45	0.00

log(V)

Model	Intercept	δ13C	Chl-a	δ15N	Overwintering Location	SST	Year	REML	Df	logLik	AICc	Delta	Weight
δ13C + δ15N + Chl-a + SST + Year + (1 | Colony)	441.75	-0.06	0.01	-0.01	NA	0.06	-0.22	FALSE	9.00	-94.85	208.98	0.00	0.97
δ13C + δ15N + Chl-a + SST + Overwintering Location + Year + (1 | Colony)	412.32	-0.04	0.02	-0.04	+	0.11	-0.21	FALSE	13.00	-93.72	216.10	7.11	0.03
Chl-a + SST + (1 | Colony)	-2.86	NA	-0.02	NA	NA	0.05	NA	FALSE	6.00	-107.23	227.05	18.06	0.00
NULL MODEL	-2.85	NA	NA	NA	NA	NA	NA		4.00	-109.78	227.83	18.85	0.00
δ13C + δ15N + (1 | Colony)	-2.86	0.01	NA	-0.04	NA	NA	NA	FALSE	6.00	-107.79	228.16	19.17	0.00
δ13C + δ15N + Overwintering Location + (1 | Colony)	-3.01	0.02	NA	-0.12	+	NA	NA	FALSE	10.00	-104.41	230.39	21.41	0.00
δ13C + δ15N + Chl-a + SST + (1 | Colony)	-2.86	0.00	-0.02	-0.04	NA	0.05	NA	FALSE	8.00	-106.78	230.56	21.58	0.00
Overwintering Location + (1 | Colony)	-2.93	NA	NA	NA	+	NA	NA	FALSE	8.00	-107.23	231.47	22.49	0.00
δ13C + δ15N + Chl-a + Overwintering Location + (1 | Colony)	-2.98	0.03	-0.03	-0.12	+	NA	NA	FALSE	11.00	-104.16	232.22	23.23	0.00
Chl-a + SST + Overwintering Location + (1 | Colony)	-2.62	NA	0.00	NA	+	0.14	NA	FALSE	10.00	-105.66	232.89	23.90	0.00
δ13C + δ15N + Chl-a + SST + Overwintering Location + (1 | Colony)	-2.75	0.03	0.00	-0.11	+	0.10	NA	FALSE	12.00	-103.42	233.09	24.11	0.00

1/(Mn)

Model	Intercept	δ13C	Chl-a	δ15N	Overwintering Location	SST	Year	REML	Df	logLik	AICc	Delta	Weight
NULL MODEL	6.16	NA	NA	NA	NA	NA	NA		3.00	-364.59	735.34	0.00	0.80
δ13C + δ15N + (1 | Colony)	6.16	-0.07	NA	0.14	NA	NA	NA	FALSE	5.00	-364.95	740.32	4.98	0.07
Chl-a + SST + (1 | Colony)	6.15	NA	0.05	NA	NA	0.09	NA	FALSE	5.00	-365.12	740.64	5.31	0.06
Overwintering Location + (1 | Colony)	5.29	NA	NA	NA	+	NA	NA	FALSE	7.00	-363.79	742.36	7.03	0.02
δ13C + δ15N + Chl-a + SST + Year + (1 | Colony)	-1019.73	-0.01	0.03	0.11	NA	0.13	0.51	FALSE	8.00	-362.86	742.72	7.39	0.02
δ13C + δ15N + Overwintering Location + (1 | Colony)	5.15	-0.33	NA	0.45	+	NA	NA	FALSE	9.00	-361.94	743.17	7.83	0.02
δ13C + δ15N + Chl-a + SST + (1 | Colony)	6.15	-0.13	0.10	0.16	NA	0.16	NA	FALSE	7.00	-364.76	744.31	8.97	0.01
δ13C + δ15N + Chl-a + Overwintering Location + (1 | Colony)	5.11	-0.34	0.05	0.45	+	NA	NA	FALSE	10.00	-361.92	745.41	10.07	0.01
Chl-a + SST + Overwintering Location + (1 | Colony)	4.62	NA	-0.06	NA	+	-0.30	NA	FALSE	9.00	-363.57	746.42	11.08	0.00
δ13C + δ15N + Chl-a + SST + Overwintering Location + (1 | Colony)	4.71	-0.33	0.01	0.43	+	-0.17	NA	FALSE	11.00	-361.85	747.60	12.26	0.00
δ13C + δ15N + Chl-a + SST + Overwintering Location + Year + (1 | Colony)	-768.04	-0.22	-0.03	0.31	+	-0.18	0.38	FALSE	12.00	-360.84	747.95	12.61	0.00

1/(Co)

Model	Intercept	δ13C	Chl-a	δ15N	Overwintering Location	SST	Year	REML	Df	logLik	AICc	Delta	Weight
NULL MODEL	64.21	NA	NA	NA	NA	NA	NA		3.00	-759.92	1526.00	0.00	0.44
Overwintering Location + (1 | Colony)	65.14	NA	NA	NA	+	NA	NA	FALSE	7.00	-756.35	1527.47	1.47	0.21
Chl-a + SST + (1 | Colony)	64.29	NA	-0.29	NA	NA	-7.81	NA	FALSE	5.00	-758.91	1528.24	2.24	0.14
δ13C + δ15N + Overwintering Location + (1 | Colony)	68.87	-0.45	NA	5.41	+	NA	NA	FALSE	9.00	-755.37	1530.02	4.02	0.06
Chl-a + SST + Overwintering Location + (1 | Colony)	49.01	NA	-0.34	NA	+	-6.95	NA	FALSE	9.00	-755.62	1530.52	4.52	0.05
δ13C + δ15N + Chl-a + SST + (1 | Colony)	64.30	0.93	-0.29	4.00	NA	-7.81	NA	FALSE	7.00	-757.96	1530.70	4.70	0.04
δ13C + δ15N + Chl-a + Overwintering Location + (1 | Colony)	67.69	-0.72	1.29	5.36	+	NA	NA	FALSE	10.00	-755.28	1532.14	6.14	0.02
δ13C + δ15N + (1 | Colony)	64.25	-1.55	NA	4.78	NA	NA	NA	FALSE	5.00	-760.89	1532.20	6.20	0.02
δ13C + δ15N + Chl-a + SST + Year + (1 | Colony)	1984.88	0.65	-0.16	4.10	NA	-7.75	-0.95	FALSE	8.00	-757.92	1532.86	6.86	0.01
δ13C + δ15N + Chl-a + SST + Overwintering Location + (1 | Colony)	55.30	-0.61	-0.08	4.69	+	-5.43	NA	FALSE	11.00	-754.92	1533.74	7.74	0.01
δ13C + δ15N + Chl-a + SST + Overwintering Location + Year + (1 | Colony)	3127.42	-1.14	0.08	5.21	+	-5.46	-1.52	FALSE	12.00	-754.83	1535.93	9.93	0.00

(Cu)

Model	Intercept	δ13C	Chl-a	δ15N	Overwintering Location	SST	Year	REML	Df	logLik	AICc	Delta	Weight
NULL MODEL	9.30	NA	NA	NA	NA	NA	NA		3.00	-268.46	543.08	0.00	0.35
δ13C + δ15N + Chl-a + SST + Year + (1 | Colony)	699.86	-0.14	0.00	0.12	NA	0.11	-0.34	FALSE	8.00	-263.36	543.74	0.66	0.25
Chl-a + SST + (1 | Colony)	9.29	NA	-0.06	NA	NA	0.07	NA	FALSE	5.00	-267.05	544.52	1.43	0.17
δ13C + δ15N + (1 | Colony)	9.29	-0.02	NA	0.06	NA	NA	NA	FALSE	5.00	-267.40	545.22	2.13	0.12
Overwintering Location + (1 | Colony)	9.38	NA	NA	NA	+	NA	NA	FALSE	7.00	-265.93	546.65	3.57	0.06
δ13C + δ15N + Chl-a + SST + (1 | Colony)	9.29	-0.05	-0.05	0.06	NA	0.09	NA	FALSE	7.00	-266.86	548.50	5.41	0.02
Chl-a + SST + Overwintering Location + (1 | Colony)	9.71	NA	-0.03	NA	+	0.13	NA	FALSE	9.00	-265.63	550.53	7.45	0.01
δ13C + δ15N + Chl-a + SST + Overwintering Location + Year + (1 | Colony)	722.89	-0.11	0.01	0.16	+	0.16	-0.35	FALSE	12.00	-262.25	550.76	7.68	0.01
δ13C + δ15N + Overwintering Location + (1 | Colony)	9.38	0.00	NA	0.01	+	NA	NA	FALSE	9.00	-265.93	551.14	8.05	0.01
δ13C + δ15N + Chl-a + Overwintering Location + (1 | Colony)	9.45	0.01	-0.07	0.01	+	NA	NA	FALSE	10.00	-265.77	553.11	10.02	0.00
δ13C + δ15N + Chl-a + SST + Overwintering Location + (1 | Colony)	9.77	0.01	-0.03	0.03	+	0.14	NA	FALSE	11.00	-265.60	555.11	12.02	0.00

sqrt(Zn)

Model	Intercept	δ13C	Chl-a	δ15N	Overwintering Location	SST	Year	REML	Df	logLik	AICc	Delta	Weight
NULL MODEL	10.28	NA	NA	NA	NA	NA	NA		3.00	-225.38	456.92	0.00	0.42
δ13C + δ15N + (1 | Colony)	10.27	0.03	NA	-0.11	NA	NA	NA	FALSE	5.00	-223.83	458.07	1.15	0.23
Chl-a + SST + (1 | Colony)	10.27	NA	0.01	NA	NA	-0.05	NA	FALSE	5.00	-224.45	459.30	2.38	0.13
δ13C + δ15N + Chl-a + SST + Year + (1 | Colony)	-395.79	0.10	-0.04	-0.14	NA	-0.09	0.20	FALSE	8.00	-221.54	460.09	3.17	0.09
Overwintering Location + (1 | Colony)	10.52	NA	NA	NA	+	NA	NA	FALSE	7.00	-222.80	460.38	3.46	0.07
δ13C + δ15N + Chl-a + SST + (1 | Colony)	10.28	0.06	-0.02	-0.12	NA	-0.08	NA	FALSE	7.00	-223.45	461.69	4.77	0.04
δ13C + δ15N + Overwintering Location + (1 | Colony)	10.55	0.05	NA	-0.06	+	NA	NA	FALSE	9.00	-222.55	464.38	7.46	0.01
Chl-a + SST + Overwintering Location + (1 | Colony)	10.30	NA	-0.01	NA	+	-0.10	NA	FALSE	9.00	-222.65	464.57	7.65	0.01
δ13C + δ15N + Chl-a + Overwintering Location + (1 | Colony)	10.55	0.05	0.01	-0.06	+	NA	NA	FALSE	10.00	-222.55	466.67	9.75	0.00
δ13C + δ15N + Chl-a + SST + Overwintering Location + Year + (1 | Colony)	-404.58	0.11	-0.05	-0.15	+	-0.13	0.21	FALSE	12.00	-220.50	467.26	10.34	0.00
δ13C + δ15N + Chl-a + SST + Overwintering Location + (1 | Colony)	10.27	0.05	-0.03	-0.08	+	-0.12	NA	FALSE	11.00	-222.34	468.57	11.65	0.00

log(As)

Model	Intercept	δ13C	Chl-a	δ15N	Overwintering Location	SST	Year	REML	Df	logLik	AICc	Delta	Weight
δ13C + δ15N + Chl-a + SST + Year + (1 | Colony)	-1138.26	-0.08	-0.05	0.01	NA	-0.09	0.56	FALSE	8.00	-168.44	353.90	0.00	0.92
δ13C + δ15N + Chl-a + SST + Overwintering Location + Year + (1 | Colony)	-1136.36	-0.12	-0.07	-0.01	+	-0.24	0.56	FALSE	12.00	-166.28	358.82	4.92	0.08
δ13C + δ15N + (1 | Colony)	-0.11	-0.24	NA	0.09	NA	NA	NA	FALSE	5.00	-197.76	405.93	52.03	0.00
δ13C + δ15N + Overwintering Location + (1 | Colony)	-0.18	-0.30	NA	0.22	+	NA	NA	FALSE	9.00	-194.35	407.97	54.08	0.00
δ13C + δ15N + Chl-a + SST + (1 | Colony)	-0.11	-0.23	0.05	0.09	NA	-0.06	NA	FALSE	7.00	-197.09	408.95	55.05	0.00
δ13C + δ15N + Chl-a + Overwintering Location + (1 | Colony)	-0.23	-0.31	0.06	0.22	+	NA	NA	FALSE	10.00	-194.05	409.67	55.77	0.00
δ13C + δ15N + Chl-a + SST + Overwintering Location + (1 | Colony)	-0.69	-0.31	0.01	0.19	+	-0.20	NA	FALSE	11.00	-193.18	410.27	56.37	0.00
Chl-a + SST + (1 | Colony)	-0.11	NA	-0.02	NA	NA	-0.16	NA	FALSE	5.00	-201.35	413.11	59.21	0.00
NULL MODEL	-0.11	NA	NA	NA	NA	NA	NA		3.00	-204.35	414.86	60.96	0.00
Overwintering Location + (1 | Colony)	0.11	NA	NA	NA	+	NA	NA	FALSE	7.00	-201.92	418.62	64.72	0.00
Chl-a + SST + Overwintering Location + (1 | Colony)	-0.47	NA	-0.05	NA	+	-0.26	NA	FALSE	9.00	-200.56	420.40	66.50	0.00

1/(Pb)

Model	Intercept	δ13C	Chl-a	δ15N	Overwintering Location	SST	Year	REML	Df	logLik	AICc	Delta	Weight
NULL MODEL	9.93	NA	NA	NA	NA	NA	NA		3.00	-426.81	859.77	0.00	0.73
Chl-a + SST + (1 | Colony)	9.94	NA	0.49	NA	NA	-0.09	NA	FALSE	5.00	-426.26	862.93	3.15	0.15
δ13C + δ15N + (1 | Colony)	9.93	0.23	NA	-0.20	NA	NA	NA	FALSE	5.00	-427.19	864.80	5.02	0.06
δ13C + δ15N + Chl-a + SST + (1 | Colony)	9.94	0.24	0.41	-0.21	NA	-0.20	NA	FALSE	7.00	-425.89	866.57	6.79	0.02
Overwintering Location + (1 | Colony)	10.33	NA	NA	NA	+	NA	NA	FALSE	7.00	-426.83	868.44	8.67	0.01
δ13C + δ15N + Chl-a + SST + Year + (1 | Colony)	-472.58	0.30	0.38	-0.23	NA	-0.22	0.24	FALSE	8.00	-425.71	868.44	8.67	0.01
Chl-a + SST + Overwintering Location + (1 | Colony)	8.07	NA	0.30	NA	+	-0.89	NA	FALSE	9.00	-424.72	868.72	8.94	0.01
δ13C + δ15N + Overwintering Location + (1 | Colony)	10.69	0.22	NA	0.02	+	NA	NA	FALSE	9.00	-426.65	872.57	12.80	0.00
δ13C + δ15N + Chl-a + Overwintering Location + (1 | Colony)	10.24	0.10	0.51	0.01	+	NA	NA	FALSE	10.00	-425.53	872.63	12.85	0.00
δ13C + δ15N + Chl-a + SST + Overwintering Location + (1 | Colony)	8.10	0.12	0.28	-0.11	+	-0.92	NA	FALSE	11.00	-424.66	873.21	13.44	0.00
δ13C + δ15N + Chl-a + SST + Overwintering Location + Year + (1 | Colony)	-330.96	0.17	0.26	-0.16	+	-0.93	0.17	FALSE	12.00	-424.57	875.41	15.64	0.00