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Global drivers of variation in blood mercury of seabirds revealed by a meta-analysis

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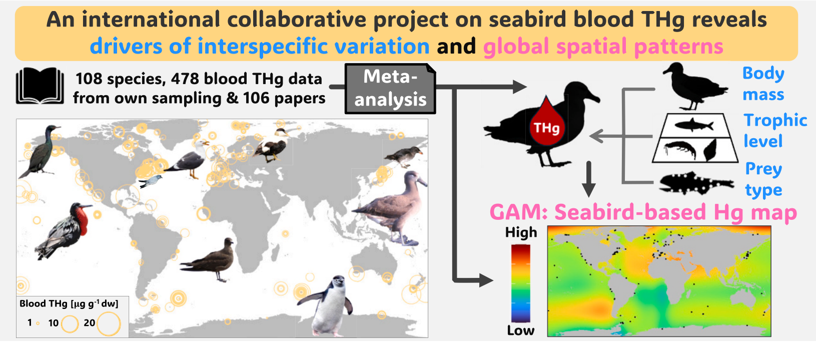
HIGHLIGHTS

- We conducted a global meta-analysis using blood total Hg (THg) from 108 seabird species.
- Blood THg was higher in seabirds feeding on higher trophic levels or mesopelagic prey consumers.
- Seabird THg spatial patterns differed from modeled THg in particulate organic matter.
- We showed seabirds' utility as Hg bio-monitors and a path to understand global ocean Hg pollution

GRAPHICAL ABSTRACT



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ABSTRACT

Mercury (Hg) is a global contaminant that biomagnifies in marine food webs. Seabirds can serve as valuable bioindicators of marine Hg pollution due to their high trophic positions and broad distributions. However, the

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Environmental pollution
Heavy metal pollution
Marine ecosystem
Top predator

biological and spatial drivers of variation in seabird Hg levels remain unclear, and few studies have validated whether seabird-derived estimates of the spatial distribution of Hg are consistent with predictions from biogeochemical-ocean models. We conducted a global meta-analysis of total Hg (THg) concentrations in adult seabird blood. Based on our own fieldwork and a literature review, we compiled 478 mean THg values from 108 species representing >11,000 individuals. Blood THg increased in species feeding at higher trophic levels, with larger body mass, and those more likely to consume mesopelagic prey in oceanic waters. Additionally, blood THg might further increase in regions with low chlorophyll-a level, likely due to greater methylmercury uptake in areas with low-productivity. We subsequently developed models to predict global spatial variation in seabird blood THg, either from all species or only epipelagic prey feeders. Only our epipelagic prey feeder-based model showed a weak significant positive correlation with THg in particulate organic matter from biogeochemical-ocean models. However, the low correlation coefficient ($r = 0.23$) indicates potential discrepancies between the two models. We suggest that future studies adopt our integrative approach, combining biological data and large-scale modeling, to improve our understanding of global marine Hg pollution. Together, these findings clarify the biological and environmental drivers of Hg exposure in seabirds and highlight the value of seabirds for global monitoring of marine Hg pollution.

1. Introduction

Mercury (Hg) is a heavy metal that has historically been released into the environment through natural processes such as volcanic activity (Rice et al., 2014). Since the Industrial Revolution, anthropogenic emissions of Hg (e.g., from mining and the combustion of fossil fuels), have increased significantly (UNEP, 2019), leading to a substantial rise in the global cycling of Hg among terrestrial, atmospheric, and oceanic cycles, globally (Selin, 2009). Anthropogenic Hg emissions are estimated to have increased by 330 % between 1960 and 2021 (Qiu et al., 2025) and now exceed natural emissions by more than six times (UNEP, 2019). Approximately 90 % of Hg released from natural and anthropogenic sources is transported via the atmosphere on hemispheric to global scales, more than half of which eventually deposits into the world's oceans (Fitzgerald et al., 1998; UNEP, 2019). The deposited Hg can remain in the marine environment for centuries, and a portion of it is transformed into methylmercury (MeHg) through biological and abiotic processes (Fitzgerald et al., 2007). MeHg bioaccumulates in organisms and biomagnifies through aquatic food webs. Due to its high toxicity, MeHg can adversely affect neurological and behavioral functions, ultimately impacting reproduction and survival in both wildlife and humans (Chételat et al., 2020; Espejo et al., 2017; Whitney and Cristol, 2017). In response to growing concerns about Hg pollution and its negative impacts, the Minamata Convention on Hg was adopted in 2013 (Kesser, 2013), requiring a better understanding of the global dynamics of Hg pollution and the suggestion of effective and efficient management strategies.

In marine ecosystems, top predators can be valuable bioindicators for assessing pollution including Hg contamination (Elliott and Elliott, 2013). Because they occupy higher trophic levels, they exhibit strong biomagnification of Hg and other contaminants in their tissues (Seco et al., 2021), making it easier to detect and quantify contamination levels compared to measurements in seawater or organisms occupying lower trophic levels. By considering when and where contaminants are incorporated into their tissues, top predators can provide an integrated signal of Hg contamination across specific spatial and temporal scales (Shoji et al., 2021; Cusset et al., 2023; Albert et al., 2024). Seabirds are top marine predators that occupy high trophic levels in oceanic food webs and integrate chemical and ecological signals across broad spatial scales. They represent a diverse taxonomic assemblage of species adapted to life in marine environments and primarily dependent on oceanic food webs (Schreiber and Burger, 2002). They are widely distributed across the world's oceans, and their diverse foraging modes, such as diving and dynamic gliding, enable them to exploit a wide range of marine habitats—from coastal zones to the open ocean (Gaston, 2004). Moreover, most seabirds form dense breeding colonies on land during the breeding period, which allows researchers to collect samples that reflect contamination at defined spatial and temporal scales—an advantage over other marine top predators. Tissue samples such as blood and feathers can often be collected in a non-lethal manner (Ackerman et al., 2016). These traits make seabirds highly effective bioindicators of pollution across extensive marine regions. Indeed, Hg concentration data have been reported for numerous seabird species worldwide (Evers et al., 2024), and their utility as bioindicators of marine Hg pollution has gained increasing attention over the past decades (Lopes et al., 2022).

Previous studies have frequently reported interspecific and spatial variation in seabird Hg levels (Albert et al., 2019; Bahamonde et al., 2023). Comparative studies, often limited to specific taxonomic groups or ocean regions, have suggested that biological factors such as trophic level and reliance on mesopelagic prey (Carravieri et al., 2014; Pollet et al., 2022), as well as environmental factors such as the productivity of foraging areas (Renedo et al., 2020) contribute to these differences. However, few studies have provided a comprehensive overview of the fundamental mechanisms driving Hg exposure across the full diversity of seabirds worldwide. To address this gap, it is necessary to analyze Hg concentrations across a wide range of seabird species inhabiting different oceanic regions, while simultaneously incorporating both biological and environmental explanatory variables. To minimize the influence of tissue-specific variation in Hg concentrations across species (Eagles-Smith et al., 2008), it is further necessary to focus on the same tissue type for comparison. Moreover, using tissues in which the duration and area of Hg uptake can be more reliably inferred, such as blood (Ackerman et al., 2016; Shoji et al., 2019), can further improve the validity of interspecific comparisons. Blood represents Hg exposure over a relatively short to medium time frame, typically integrating Hg uptake over the preceding several weeks to 1–2 months (Bearhop et al., 2000; Monteiro and Furness, 2001) and therefore reflects conditions experienced during the period (Albert et al., 2019).

By compiling Hg concentration data from seabirds across ocean regions and accounting for both interspecific and intraspecific variation, we may be able to extract spatial patterns that provide insights into regional differences in marine Hg contamination. Using this approach, several recent studies have identified localized Hg "hotspots" within specific ocean regions (Table 1). Extending such methodology to a global scale may allow us to estimate broad-scale trends in oceanic Hg pollution, including less-studied regions. So far, large-scale assessments of marine Hg distribution have primarily relied on global emission inventories combined with ocean circulation models (Kawai et al., 2020; Zhang et al., 2020; Wang et al., 2023). In addition, cruise-based observational programs such as GEOTRACES have provided valuable direct measurements of Hg and its species in various oceanic basins, contributing essential data for model validation and improving our understanding of global Hg cycling (e.g., Bowman et al., 2020). However, few studies have used biological data to estimate global ocean Hg contamination and to validate ocean biogeochemical model estimates. Comparing seabird-derived Hg estimates with predictions from ocean biogeochemical models could serve as a valuable validation step, enhancing our understanding of global ocean Hg contamination while taking biological effects into account. Such comparisons are particularly valuable in the framework of the Minamata Convention and the evaluation of its effectiveness (Evers et al., 2016, 2024).

We conducted a meta-analysis by compiling total Hg (THg) concentrations in the blood of adult seabirds worldwide, including our own sampling and an extensive literature review. Our dataset encompassed a wide range of seabird species that forage across diverse marine environments—from coastal (e.g., skuas, sea ducks) to oceanic habitats (e.g., storm-petrels, albatrosses)—and occurring across regions from the tropics to the poles (Table 2). These species also represent a broad spectrum of trophic levels and prey preferences, including those feeding on low-trophic-level prey like zooplankton, and others that consume higher-trophic-level prey such as small fish, squid, and mesopelagic organisms (Table 2). Based on THg concentrations in the blood of these seabird species, we addressed two main objectives. First, we aimed to identify which types of species and linked environments are associated with elevated THg concentrations. We hypothesized that THg levels would be higher in species feeding at higher trophic levels due to biomagnification (Pollet et al., 2022; Padilha et al., 2023), and in those consuming mesopelagic prey, where MeHg is more concentrated compared to epipelagic prey (Monteiro et al., 1996; Thompson et al., 1998; Choy et al., 2009). We also expected higher Hg concentrations in regions with lower marine productivity, where Hg is more concentrated in lower-trophic level organisms, thereby enhancing biomagnification through the food web (Chen and Folt, 2005; Chouvelon et al., 2018). Secondly, we aimed to predict the spatial distribution of environmental THg by controlling for interspecific variation in seabird THg concentrations. We then compared these seabird-based predictions with those from a biogeochemical ocean model to evaluate their consistency. Based on this comparison, we considered the potential utility of using seabirds as bioindicators for estimating global patterns of marine Hg pollution.

2. Materials & methods

We included only species or populations in our study that primarily forage in marine environments following the list of seabird species in Dias et al. (2019). We followed the taxonomy of the eBird/Clements Checklist (Clements et al., 2024) for common species names and scientific names. The technical terms related to the marine environment used in this study are defined in Fig. 1.

2.1. Blood THg in seabirds

We focused our analysis on THg in the blood of adults, with the majority of samples obtained at seabird breeding colonies and additional samples collected from non-breeding area. Blood of adults is particularly valuable for monitoring recent Hg exposure because it can be collected non-lethally and serves as a reliable indicator of Hg exposure (Ackerman et al., 2016). While blood of chicks can reflect Hg exposure around the colony, it can change rapidly as chicks age due to mass dilution and Hg transfer into growing feathers, making interpretation more difficult than in adults (Ackerman et al., 2016). The half-life of THg in whole blood is estimated to be approximately 30–60 days (slow terminal phase) based on experimental studies (Bearhop et al., 2000; Monteiro and Furness, 2001), allowing for relatively accurate inference of uptake timing. Furthermore, collecting samples during the breeding period, when seabird foraging ranges are more restricted, makes it possible to evaluate regional Hg exposure based on average concentrations from multiple individuals. Feathers, like blood, can be collected non-lethally and have been widely used to assess Hg exposure (Monteiro and Furness, 1995; Table 1). However, challenges remain in using feathers, due to inter- and intraspecific variation in molt timing and location, differences in Hg content among feather types, and difficulties in interpreting the spatial scale of uptake in wide-ranging species (Ackerman et al., 2016; Chastel et al., 2022). Other tissues such as eggs and chick down can also offer temporal and spatial resolution similar to blood (Ackerman et al., 2016), but converting those values into equivalent blood Hg concentrations introduces uncertainties due to interspecific variation. Further, some seabird species forage in different areas depending on chick provisioning and self-feeding (e.g., short vs. long trips in petrels, Phillips et al., 2023) and thus simple conversions may not be straightforward. For these reasons, focusing on THg in adult blood is valuable to clearly define the spatiotemporal scale of Hg uptake and to avoid errors stemming from tissue-specific differences in bioaccumulation rates.

2.2. Collection and collation of blood Hg data

We collected data on THg in the red blood cells or whole blood of seabirds worldwide through our own field sampling and a literature review. Since THg in blood in chicks and immature birds may be lower than those in adults (Carravieri et al., 2014), we included only data from adults in our analysis.

Table 1

Examples of studies that estimated the spatial distribution of mercury contamination using top predators across different marine regions. This table includes studies that assessed the spatial distribution of mercury contamination at the ocean-basin scale or at a comparable spatial scale.

Biomonitor type	Specific species or group	Tissue type	Ocean region (Latitude; Longitude)	Is spatial trend consistent with this study?	References
Seabird	Penguins	Blood; Feathers	Southern hemisphere	Yes	Gimeno et al., 2024
Seabird	Penguins	Feathers	Southern Indian Ocean (−70––35°; 60–80°)	Yes	Carravieri et al., 2016
Seabird	Various species	Various tissues	North Atlantic (15–80°; −100–40°)	Yes	Pollet et al., 2022
Seabird	Little auk	Feathers	North Atlantic (40–60°; −70°–30°)	Yes	Carravieri et al., 2023
Seabird	Great skua	Feathers	North Atlantic (10–65°; −60°–10°)	No	Albert et al., 2022
Seabird	Various species	Feathers	North Atlantic (10–40°; −80–40°)	No	Albert et al., 2024
Seabird	Common tern	Feathers	North and South Atlantic (−35–25°; −20–20°)	Yes	Bertram et al., 2022
Seabird	Short-tailed shearwater	Feathers	North Pacific (30–70°; 120–180°& -180°–-150°)	No	Watanuki et al., 2015
Seabird	Streaked shearwater	Feathers	North and South Pacific (−20–20°; 100–150°)	Yes	Watanuki et al., 2016
Seabird	Red-legged kittiwake	Feathers	North Pacific (40–60°; 150–170°)	No	Fleishman et al., 2019
Large fish	Tunas	Muscle	North and South Pacific (−30–40°; 120–180°& -180°–-50°)	No	Médieu et al., 2022
Large fish	Tunas	Muscle	North and South Pacific (−40–10°; 140–180°& -180°–-120°)	No	Houssard et al., 2019
Seabird	Thick-billed murre	Feathers	Arctic Ocean	No	AMAP, 2021

Table 2
The number of species included in our dataset, the main feeding habitat, the latitudinal range of the sampling locations, and the number of blood total mercury (THg) values categorized into each potential health risk level associated with THg exposure for each family (Ackerman et al., 2016). See Supplementary Material 3 for detailed feeding attributes of each species.

Order	Family	No. of species	Feeding habitat[a]	Trophic level index[b]	Mesopelagic prey consumption[c] Yes, No	Latitudinal range of sampling location (°)	No. of blood THg values for each potential health risk level					
							No	Low	Moderate	High	Severe	Total
Anseriformes	Anatidae	5	C	1	0, 5	41–79	36	32	0	0	0	68
Charadriiformes	Alcidae	12	C, B, O	1–2	6, 6	41–80	36	53	0	0	0	89
	Laridae	29	C, B, O	1–3	4, 25	-4–82	40	67	14	0	1	122
	Stercorariidae	4	C	2.5–3	0, 4	−67–-48, 58–79	2	5	3	0	0	10
Phaethontiformes	Phaethontidae	2	O	2	0, 2	−18–-4	4	1	0	0	0	5
Procellariiformes	Diomedeidae	6	B, O	1.5–2	5, 1	−54–-46, 28	0	4	6	0	1	11
	Hydrobatidae	3	B, O	1.5	1, 2	32–48	2	25	16	0	0	43
	Oceanitidae	4	O	1–1.5	2, 2	−62–-44	5	2	0	0	0	7
	Procellariidae	24	C, B, O	1–3	10, 14	−72–-4, 28–77	20	34	4	0	0	58
Sphenisciformes	Spheniscidae	9	C, B, O	1–2	3, 6	−69–-15	18	8	0	0	0	26
Suliformes	Fregatidae	2	O	2	0, 2	5–26	0	5	2	0	0	7
	Phalacrocoracidae	2	B	2	0, 2	−12, 59	4	3	0	0	0	7
	Sulidae	6	B, O	2	2, 4	−22–-4, 6–45	14	10	1	0	0	25
Total		108			33, 75		181	249	46	0	2	478

[a] Feeding habitat classification: Coastal (C), Oceanic (O), and Both (B).
[b] 1 for zooplankton and benthos; 2 for nekton such as fish and squid; and 3 for birds, mammals, scavenging, and fishery discards.
[c] No. of species which consume mesopelagic prey.

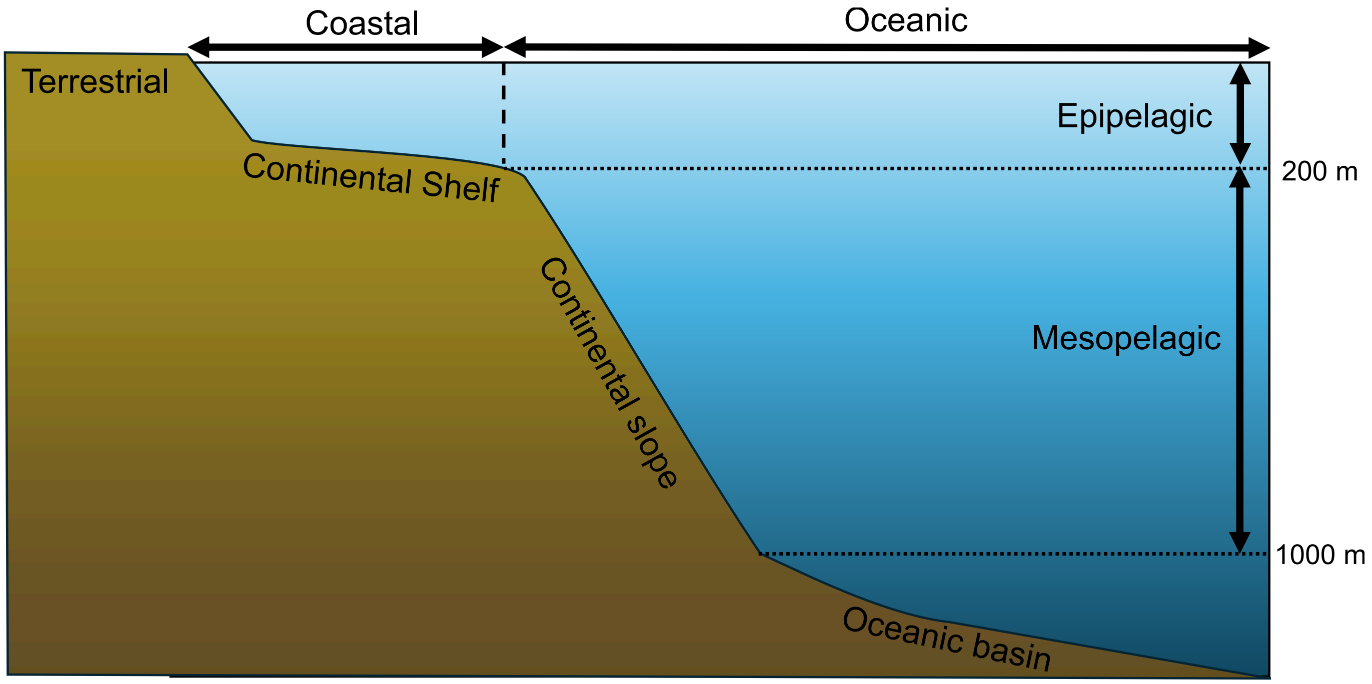

Fig. 1. Schematic diagram of the horizontal and vertical habitat classifications in the ocean used in this study.

For our own field sampling, we collected blood samples during the breeding period between 2017 and 2024 from 659 individuals, representing 10 seabird species breeding in Japan, Alaska, and Aotearoa New Zealand: Antipodean albatross (subspecies *Diomedea antipodensis antipodensis*, $n = 20$; *D. a. gibsoni*, $n = 20$), black-legged kittiwake *Rissa tridactyla* ($n = 29$), Leach's storm-petrel *Hydrobates leucorhous* ($n = 1$), pelagic cormorant *Urile pelagicus* ($n = 30$), rhinoceros auklet *Cerorhinca monocerata* ($n = 306$), streaked shearwater *Calonectris leucomelas* ($n = 20$), tufted puffin *Fratercula cirrhata* ($n = 66$), common diving petrel *Pelecanoides urinatrix* ($n = 70$), South Georgia diving petrel (subspecies: *Pelecanoides georgicus whenuahouensis*, $n = 77$), and Westland petrel *Procellaria westlandica* ($n = 20$) (Table S1). For all species except Leach's storm-petrel, we caught adult birds and collected 0.3 to 1 mL of blood from a wing or leg vein using a heparinized syringe. In some cases, blood samples were centrifuged to separate red blood cells and plasma (Table S1). For Leach's storm-petrel, we collected 0.3 mL of clotted blood from the heart of a dead adult bird collected during chick-rearing period in 2021. All blood samples were stored at −20 °C or below until analysis. Some samples were preserved as is, while others were preserved in 70 % ethanol (Table S1). We measured THg in these samples using atomic absorption spectrometry with a Hg analyzer (MA-3000, Nippon Instruments Corporation, Kyoto, Japan or Altec AMA 254, LECO, Michigan, USA) after drying and homogenizing them. Detailed information on the THg measurement process for our own samples is provided in Supplementary Materials 1A.

From our literature review, we collated data on THg in seabird blood using Web of Science, Google Scholar, and Scopus, up to 1 March 2025. For the search, we used the keywords "seabird* AND mercury* AND blood*". We screened articles that reported data on THg concentrations in blood of adult seabirds. Supplementary Materials 1A including Table S2 contain details on search conditions and the literature screening process information. We recorded seabird blood THg data from both our field sampling and the literature review as the mean concentration of THg in blood for each site and year (or the median if the mean was not available). In addition, we compiled the sampling year, the latitude and longitude of the sampling location (e.g., breeding colony, wintering area), sampling period (i.e., breeding or non-breeding), the type of blood sample (whole blood or red blood cells) and the measurement unit (See Supplementary Materials 2 for all data).

2.3. Blood THg data

Studies have reported THg in seabird blood using various units, such as per dry weight, wet weight, or volume of whole blood or red blood cells. To enable comparisons, we standardized all measurements to THg concentration per gram of dry weight (μg g^{-1} dw) in whole blood. For conversion, we transformed values reported as wet weight basis into dry weight using water content values in blood (79.13 % for whole blood, Eagles-Smith et al., 2008; 67.84 % for red blood cells, Lavoie et al., 2010). We assumed that 1 mL of whole blood weighs 1 g (1 g mL^{-1}, Yamamoto et al., 2011). Furthermore, we assumed that the THg in red blood cells (wet weight basis) corresponds to 55.6 % of that in whole blood (Ma et al., 2020). Hereafter, unless otherwise specified, we define "blood THg" as the mean THg concentration in the whole blood of adult birds, per species, location, and year in μg g^{-1} dw.

Although not the primary focus of this study, evaluating the potential health risks associated with blood THg levels in seabird species may provide helpful reference information for informing future conservation measures. To assess the potential health risks, we thus classified each blood THg values in our dataset into five risk levels. We converted the risk thresholds originally proposed by Ackerman et al. (2016), which were based on wet weight, to dry weight units, using the water content of whole blood (79.13 %, Eagles-Smith et al., 2008). Based on a literature review examining Hg concentrations in various body tissues and their effects on health, behavior, and reproduction, Ackerman et al. (2016) categorized risk levels as follows: no risk (< 1.0 μg g^{-1} dw) corresponds to concentrations with no observed effects; low risk (1.0–4.8 μg g^{-1} dw) indicates levels where minor effects are evident; moderate risk (4.8–14.4 μg g^{-1} dw) refers to concentrations causing moderate impacts on health and reproduction; high risk (14.4–19.2 μg g^{-1} dw) is associated with serious impairments to health and reproduction; and severe risk (>19.2 μg g^{-1} dw) includes concentrations linked to reproductive failure or mortality.

2.4. Ocean region and sampling decade

To summarize the geographic distribution of the collected data, we divided the world's oceans into the following seven regions: North Pacific Ocean, South Pacific Ocean, North Atlantic Ocean, South Atlantic Ocean, Indian Ocean, Arctic Ocean, and Southern Ocean, based on the classification of the five oceans by International Hydrographic Organization (IHO, 1953), with a practical subdivision of the Pacific and Atlantic Oceans into northern and southern regions following Kawai et al. (2020).

2.5. Trophic level index

To investigate the influence of trophic level on THg concentration, we determined the primary prey species for each seabird and assigned them to three distinct trophic levels: 1 for zooplankton and benthos; 2 for nekton such as fish and squid; and 3 for birds, mammals, scavenging, and fishery discards. We determined the trophic level used by each species based on descriptions of primary diet provided in Birds of the World (https://birdsoftheworld.org/, accessed on 1 Jan 2025). For species that feed across multiple trophic levels, we used the mean of the relevant trophic level values (Supplementary Materials 3).

2.6. Body mass

We derived body mass of each seabird species from Schreiber and Burger (2002) and Birds of the World. When body mass differed between sexes, we used their mean values. When only mass ranges were reported, we used median values (Supplementary Materials 3).

2.7. Mesopelagic prey consumption

Mesopelagic organisms are known to contain higher concentrations of Hg compared to epipelagic species (Monteiro et al., 1996; Choy et al., 2009). We tested the hypothesis that seabirds that predominantly feed on mesopelagic prey (below 200 m of the water column) accumulate higher Hg concentrations than those that mainly feed on epipelagic prey (above 200 m) (Carravieri et al., 2014; Pollet et al., 2022). We assessed the dependence on mesopelagic prey for each species using a two-step approach. First, we examined the general diet of each species to determine whether they consume mesopelagic prey. We reviewed the depth distribution of each prey species from the literature describing seabird diets and determined whether the diet of each seabird species included at least one mesopelagic prey species, recording the presence or absence of mesopelagic prey as binary data (Supplementary Materials 3). Second, we assessed the pelagic dependency during foraging of each species. Mesopelagic prey is abundant in oceanic basins and continental slope habitats, species that frequently forage in oceanic areas likely have a higher proportion of mesopelagic prey in their diet (Watanuki and Thiebot, 2018). As a proxy of pelagic dependency for each seabird species included in this study, we separately compiled typical foraging range data for the breeding and non-breeding periods (the latter corresponding to the recorded home range in the wintering areas) based on tracking studies using GPS loggers, satellite transmitters, radio telemetry, and geolocators (methods: Supplementary Materials 1A, data: Supplementary Materials 4). Then, we included the mesopelagic prey consumption and foraging range as an interaction term (see Statistical analysis) and considered seabird species that include mesopelagic prey in their diet and strongly rely on pelagic habitats as those most likely to feed on mesopelagic prey.

2.8. Phytoplankton biomass within the seabird foraging range

To examine phytoplankton biomass within the seabird foraging range, we downloaded long-term average (2002−2023) images of sea surface chlorophyll *a* concentration (mg m^{-3}, chl-a, a proxy for local phytoplankton biomass) with a spatial resolution of 9 km from NASA's OceanColor Web (https://oceancolor.gsfc.nasa.gov/, accessed on 1 Dec 2024). We used Level-3 data derived from the MODIS-Aqua sensor using the OCL algorithm. The spatial mean of chl-a was extracted within a 300 km radius of each seabird colony (i.e., the average foraging range of all seabird species assumed from our data, Supplementary Materials 4).

2.9. Statistical analysis

We conducted all statistical analyses using R ver. 4.4.2 (R Core Team, 2024). In the following modeling analyses, we included only blood THg data that had corresponding foraging range information; This applied to data collected during the breeding period for all species, and during the non-breeding period for the common eider *Somateria mollissima*, but not to non-breeding data for other species.

To examine the biological and spatial factors influencing blood THg, we performed a General Linear Model (GLM) assuming a normal distribution. We used $\log_{10}$-transformed blood THg as the response variable and confirmed normality visually using a histogram. As explanatory variables, we included $\log_{10}$-transformed body mass, a trophic level index, and an interaction term of presence or absence of mesopelagic prey consumption and foraging range ($\log_{10}$-transformed, as a proxy for pelagic foraging). We also included two environmental or spatial factors: chl-a ($\log_{10}$-transformed) surrounding the sampling site and ocean region. We considered multicollinearity among the explanatory variables to be negligible based on the generalized variance inflation factor adjusted for degrees of freedom (< 1.34, *vif* function by the *car* package, Fox and Weisberg, 2019). We used the *emmeans* function and *contrast* function from the *emmeans* package (Lenth, 2024) to evaluate the significance of the deviation of each ocean region's mean from the overall mean in the best GLM selected through model selection. We adjusted the *p*-values using the Scheffe's method. We did not include taxonomic variables such as species or family as explanatory variables, because the taxonomic factors could obscure the specific effects of biological traits like body mass or trophic level by containing species-level variation (Carravieri et al., 2014). However, we also conducted phylogenetic generalized linear mixed models (PGLMMs), with species included as a random effect both with and without phylogenetic relationships included and confirmed that the explanatory variables showed similar trends to those obtained from the GLM analyses (see Supplementary Materials 1C for details). Additionally, we excluded sampling decade from explanatory variable because 93.7 % of the data originated from the 2000s or later, the dataset is unbalanced and inadequate for testing temporal trends. Preliminary analyses that included sampling year as an explanatory variable alongside other biological and spatial factors further suggested that sampling decade was not an important variable explaining model fit.

Understanding which seabird species serve as more effective indicators of marine Hg pollution is crucial. Species that exhibit low temporal variability in blood THg, even when sampled at the same location across different years, are potentially more suitable for monitoring. To investigate the variability, we calculated the coefficient of variation (CV) in blood THg within species, focusing only on sites where blood THg were available for more than three years. We then examined whether the CVs were associated with ecological factors of the species, including body mass, trophic level index, and the interaction between mesopelagic prey consumption and the foraging range using a generalized linear model assuming a beta distribution (*betareg* function in the *betareg* package, Cribari-Neto and Zeileis, 2010).

To estimate the spatial variation in Hg contamination based on blood THg in seabirds, we applied a generalized additive model (GAM) using the *mgcv* package (version 1.9.1; Wood, 2011). We used $\log_{10}$-transformed blood THg as the response variable. To extract spatial variation in blood THg while minimizing the influence of biological and environmental effects, we included the factors that were part of the best models in the GLM analyses as explanatory variables (i.e., body mass, trophic level index, the interaction term between the presence or absence of mesopelagic prey consumption and foraging range, and chl-a concentration), along with species (treated as a categorical variable), assuming linear effects. To estimate spatial variation in blood THg, we also included latitude, longitude, and their interaction as smooth terms. We applied a thin plate spline smoother to latitude and a cyclic cubic spline to longitude. For the interaction between latitude and longitude, we used a tensor product smoother combining a thin plate spline for latitude and a cyclic cubic spline for longitude to allow for two-dimensional spatial smoothing. When interpreting the results of such spatial modeling, it is important to consider which depth layers of oceanic Hg contamination the predicted patterns represent. While seabirds are generally considered to feed on prey in the epipelagic layer ($<$ 200 m) (Gaston, 2004), some species also consume prey from mesopelagic layer (Watanuki and Thiebot, 2018). Therefore, we constructed two separate models: one including all species, and another including only those species that do not feed on mesopelagic prey (hereafter "epipelagic prey feeder species"), to compare predicted spatial patterns.

We performed variable selection for both GLM and GAM using Akaike's Information Criterion (AIC). We compared all possible combinations of explanatory variables, and selected models with a $\Delta\text{AIC} < 2$ relative to the model with the lowest AIC (*dredge* function from the *MuMIn* package version 1.48.4, Bartoń, 2024). For the lowest AIC models, we validated model assumptions and fit by visually checking the normality of the model residuals, QQ-plot and plot of the residuals to the fitted values.

Using the best-fit GAM including all species and the GAM including only epipelagic prey feeder species, we estimated the spatial variation in Hg contamination inferred from the blood THg of seabirds, hereafter referred to as the "seabird-model THg". To control species-level effects, we fixed the species variable to a single species, rhinoceros auklet, as a representative species for consistent extrapolation, and conducted extrapolation across latitude and longitude. We then examined whether the seabird-model Hg values exhibited spatial patterns similar to those predicted by an oceanographic Hg distribution model that incorporates physical and chemical circulation, hereafter referred to as the "ocean-model THg". For the ocean-model THg, we used updated estimates based on the model by Kawai et al. (2020), specifically the average THg concentration in particulate organic matter (POM), such as phytoplankton and zooplankton, in the upper ocean layer (0–70 m), expressed in $\mu\text{g g}^{-1}$ wet weight ($3^\circ \times 3^\circ$ spatial resolution; Kawai et al., unpublished data). We used mean values of ocean-model THg for the year 2010 as representative values and did not account for temporal variation, as the seabird-model THg dataset consists mostly of samples collected after the 2000s. We extracted the ocean-model THg from the grid cells corresponding to each seabird sampling location and calculated the mean seabird-model THg within a 300 km radius around each location to match the spatial resolution of the ocean-model THg. Finally, we compared the THg from the two models using Pearson's correlation test, with statistical significance evaluated at $p < 0.05$.

3. Results

3.1. Dataset of blood THg in seabirds

Through a systematic literature review, we screened a total of 1571 publications and identified blood THg data for adult individuals of seabirds from 141 studies (Table S2). After excluding studies with duplicate data for the same species, year, and location, we used data from 105 species including at least 10,556 adult individuals from 106 publications for analysis. These studies were published between 1980 and 2025, with over 80 % published after 2010. We also added the blood THg values of 10 seabird species including 659 adult individuals from our own sampling (Table S1). Combined, our total dataset consisted of 478 blood THg values (defined by species/year/location) across 108 species from 6 orders and 13 families (Table S4). The most frequently represented families were Laridae (25.5 % of the 478 values), Alcidae (18.6 %), Anatidae (14.2 %), Procellariidae (12.1 %), and Hydrobatidae (9.0 %), with other families contributing between 1.0 % and 5.4 % to the dataset (Table S4). For the GLM and GAM analyses, we included only blood THg data that had corresponding foraging range information, resulting in a final dataset of 441 blood THg values across 100 species (see Supplementary Materials 5). We summarized the number of blood THg values by ocean region and decade in Table S3. Most data originated from the Arctic (28.9 %), North Atlantic (29.7 %), and North Pacific (15.5 %) regions, while data from the Indian Ocean and the three Southern Hemisphere regions were limited, accounting for only 5.0–8.2 % of the total. The sampling years ranged from the 1970s to the 2020s, but 93.7 % of the data were collected after 2000.

Among the 108 species analyzed, 76 were classified as Least Concern (LC), 12 as Near Threatened (NT), 14 as Vulnerable (VU), 5 as Endangered (EN), and 1 as Critically Endangered (CR) by the IUCN (Supplementary Materials 3). Among the 25 species with data indicating Moderate or Severe Hg health risks (see below), four Diomedeidae species, two Procellariidae species, one Hydrobatidae species, and one Laridae species fell into the NT or higher categories (NT: black-footed albatross *Phoebastria nigripes*, VU: Snowy albatross *Diomedea exulans*, Audouin's gull *Ichthyaetus audouinii*, Leach's storm-petrel, EN: Westland petrel, grey-headed albatross *Thalassarche chrysostoma*, Antipodean albatross, CR: Magenta petrel *Pterodroma magentae*).

3.2. Potential health risks

We categorized blood THg data into risk levels, with the majority classified as No risk (181 values, 37.9 %) or Low risk (249 values, 52.1 %), and a smaller proportion as Moderate risk (46 values, 9.6 %) (Table 2, Figs. 2 and 3). Values classified as High risk and Severe risk were zero (0 %) and two (0.4 %), respectively (Figs. 2 and 3). Among families of seabirds, all data from Phaethontidae, Spheniscidae, Oceanitidae, Anatidae, Phalacrocoracidae, and Alcidae were categorized as No risk or Low risk (Table 2, Fig. 3). The proportion of data classified as Moderate risk or higher ranged from 4.0 % to 12.3 % in Sulidae, Procellariidae, and Laridae; 28.6 % to 37.2 % in Fregatidae, Stercorariidae, and Hydrobatidae; and was highest in Diomedeidae at 63.6 % (Table 2, Fig. 3). The only two cases classified as Severe risk were a sooty tern *Onychoprion fuscatus* sampled in 1977 at Dry Tortugas, Florida (Stoneburner et al., 1980), and a black-footed albatross sampled in 2001 at Sand Island, Midway Atoll (Finkelstein et al., 2006).

3.3. Effects of biological and spatial factors on blood THg

Two models identifying factors influencing variation in blood THg in seabirds had ΔAIC values of less than 2 and we selected them as best-fitting models (Table 3). The model with the lowest AIC included all explanatory variables (Fig. 4; Table 3), while the other excluded chl-a (Table 3). In terms of individual effects, blood THg increased with higher trophic level index and greater body mass. We found that species with a larger foraging range exhibited higher Hg concentrations, and this trend was particularly significant in species that included mesopelagic prey in their diet. Additionally, blood THg might be higher in areas where surrounding chl-a were lower (Fig. 4; Table 4). The AIC of the model without chl-a, however, was comparable to that of the model with the lowest AIC (Table 3), suggesting that chl-a is a relatively less important variable compared to the others. We also found significant variation among ocean regions: according to the post-hoc test for deviation from the overall mean, the North Atlantic Ocean (estimate ± SE = 0.321 ± 0.045, $t = 7.09$, $p < 0.0001$) and the North Pacific Ocean (estimate ± SE = 0.259 ± 0.048, $t = 5.39$, $p = 0.0001$) showed a significantly higher mean, while the South Atlantic Ocean (estimate ± SE = −0.431 ± 0.068, $t = -6.37$, $p < 0.001$) and the Southern Ocean (estimate ± SE = −0.326 ± 0.076, $p = 0.0056$) had a significantly lower mean, and the other regions did not significantly differ from the overall mean (all $p > 0.9$).

In total, 30 datasets of blood THg spanning three or more years were available, encompassing 23 sites and 23 seabird species (four Alcidae, one Anatidae, one Hydrobatidae, five Laridae, one Phaethontidae, one Phalacrocoracidae, six Procellariidae, two Spheniscidae, and two Sulidae). The mean and standard deviation of the CVs of blood THg concentrations were 0.291 ± 0.236 (range: 0.007–0.906, $n = 30$). We applied a generalized linear model to examine whether CV was influenced by species-specific ecological traits. The null model showed the lowest AIC, followed closely by the model including body mass (ΔAIC = 1.7), indicating that none of the explanatory variables had a significant effect on the variation.

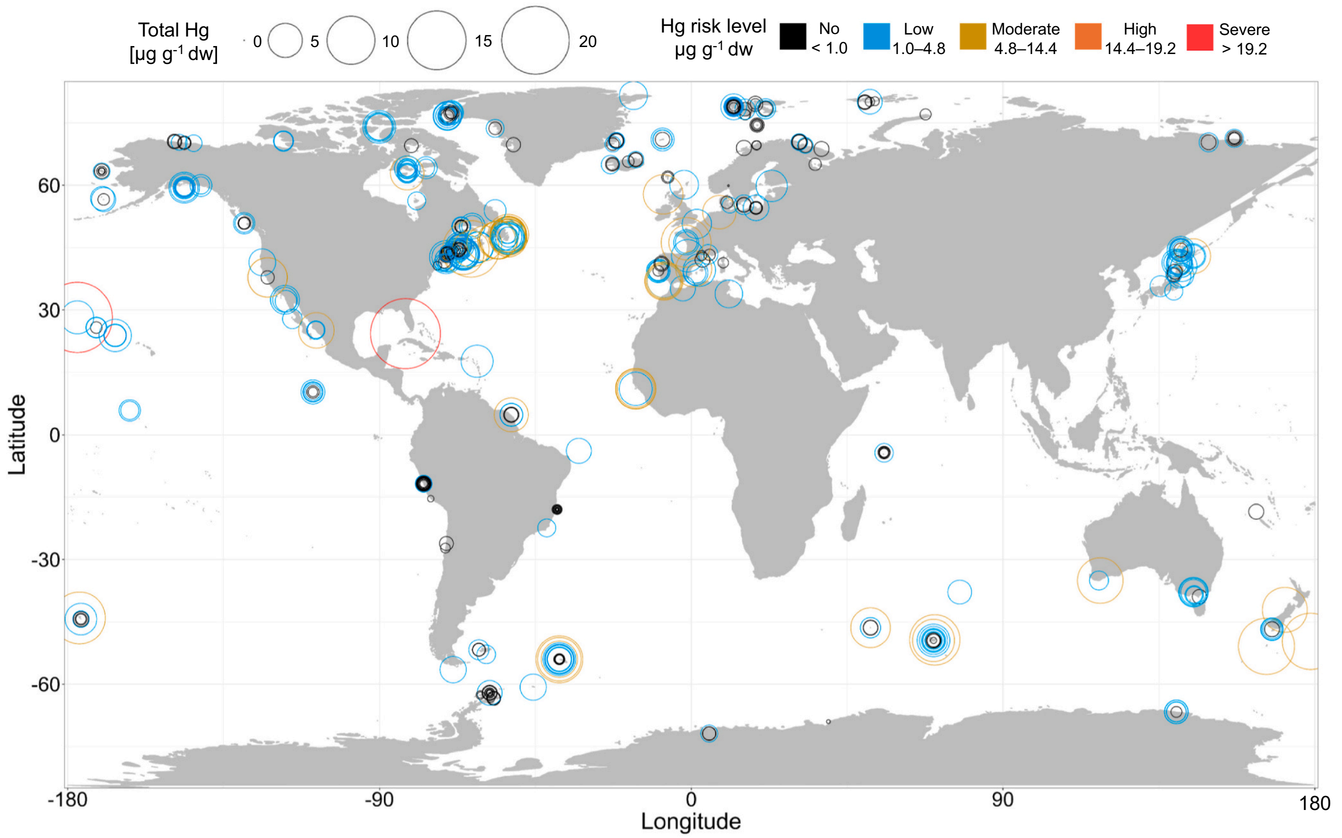

Fig. 2. Map showing total mercury in blood of seabirds and sampling locations for seabirds included in this study. Each circle represents the mean total mercury in blood (µg g^{-1} dw) for a given species/year/location. Circle size indicates the concentration level, while color denotes the associated health risk level (Ackerman et al., 2016).

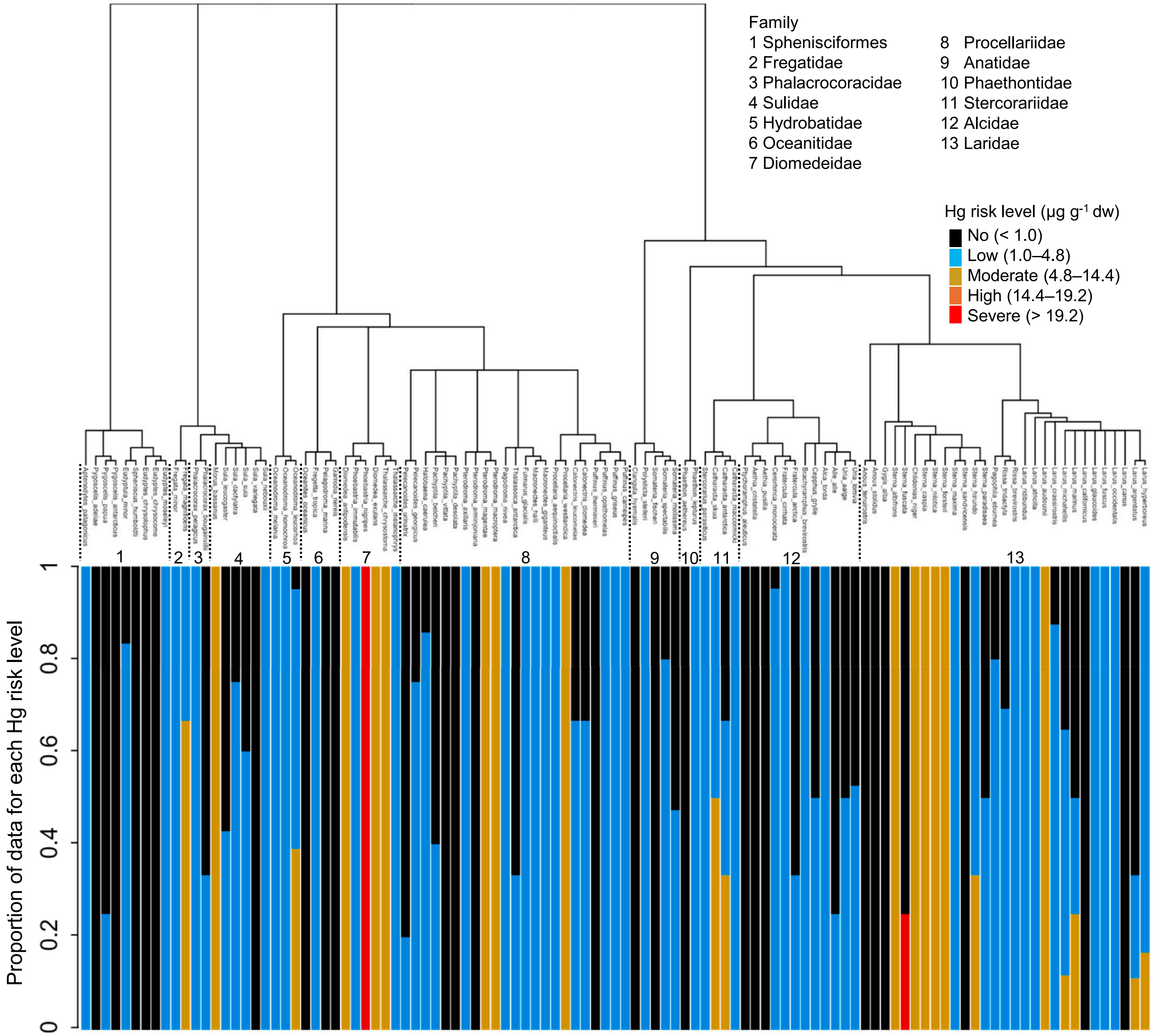

Fig. 3. Phylogenetic tree of seabirds analyzed in this study (top) and the proportion of species within each health risk category based on blood total mercury (bottom; Ackerman et al., 2016). The phylogenetic tree was constructed based on data from Jetz et al. (2012). Due to data constraints, scientific names follow the BirdLife V3 World List (June 2010, recognizing 9895 extant species). Therefore, *Calonectris diomedea* includes data for both the currently recognized *Calonectris diomedea* (Scopoli's shearwater) and *Calonectris borealis* (Cory's shearwater). Dashed lines and numbered labels below the tree indicate taxonomic families.

Table 3

Model selection results for general linear model (GLM) to examine the effects of biological and spatial factors on $\log_{10}$-transformed total mercury in blood of seabirds. Models include various combinations of the factors: trophic level index, $\log_{10}$-transformed body mass, interaction term of $\log_{10}$-transformed foraging range and presence of mesopelagic prey in the diet, $\log_{10}$-transformed chlorophyll-a concentration around the collection site, and ocean region. The table shows parameter estimates (or presence [+] of categorical variables), log-likelihood (Loglik), Akaike Information Criterion (AIC), and delta AIC from the lowest one (ΔAIC). The models with ΔAIC <2 are shown with the null model.

Model no.	Intercept	Trophic level index	$\log_{10}$ Body mass	$\log_{10}$ Foraging range: diet mesopelagic prey	$\log_{10}$ chlorophyll-a	Ocean region	Loglik	AIC	ΔAIC	Adjusted r^2
Best GLM 1	−0.761	0.254	0.116	+	−0.089	+	−207.171	440.3	0	0.302
Best GLM 2	−0.805	0.267	0.123	+		+	−208.217	440.4	0.09	0.300
Null GLM	0.0988						−292.124	588.2	147.72	0

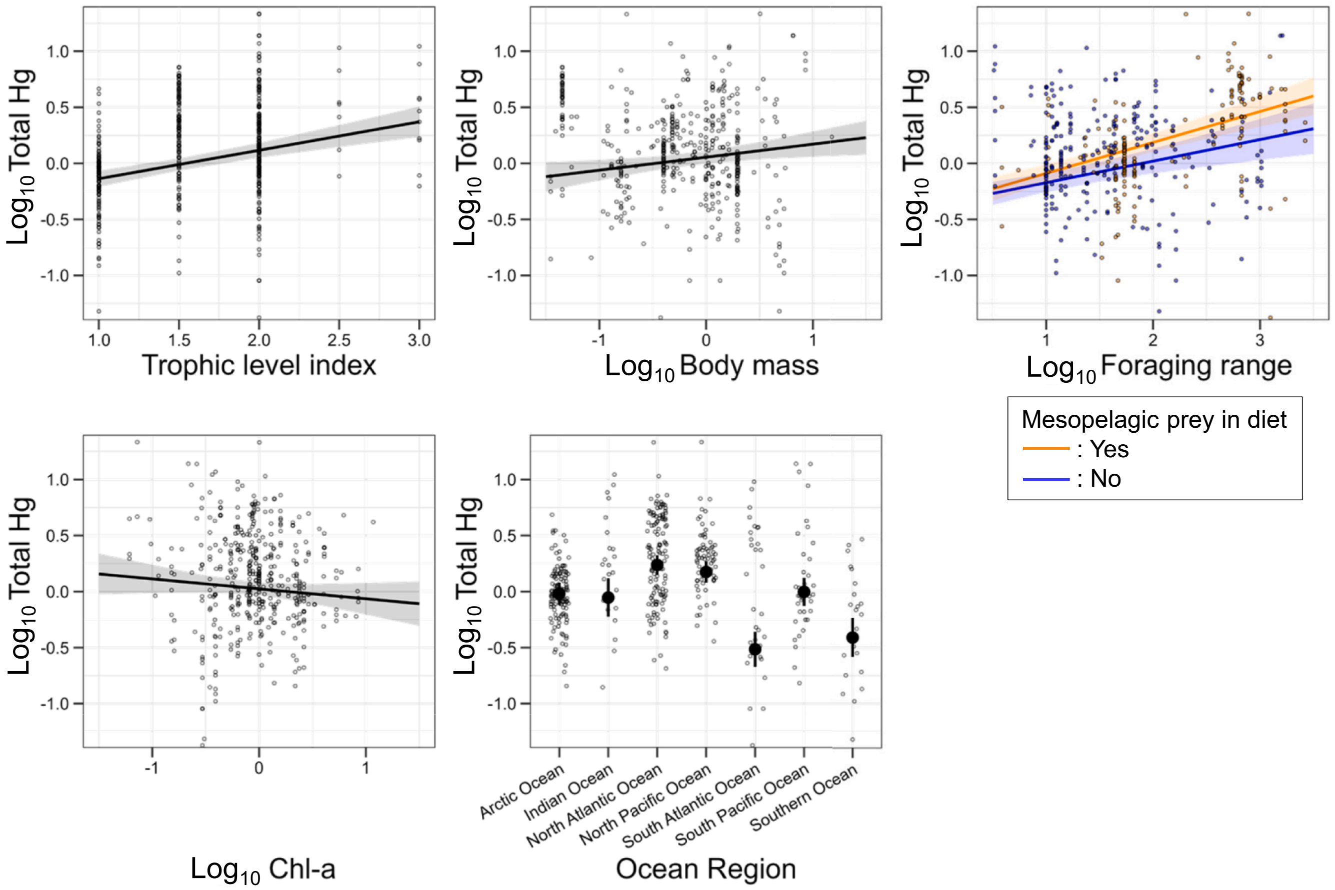

Fig. 4. Effects of biological and spatial variables on variation in total mercury in blood of seabirds, based on a general linear model (GLM). The results are shown for the best model with ΔAIC = 0 (Adjusted r^2 = 0.302). Colored circles or lines indicate predicted values, and error bars or ribbons represent standard errors. To maintain consistent y-axis scales across plots, some extremely high or low values fall outside the axis range.

Table 4
Model coefficients of general linear model (GLM) to explain variation in log$_{10}$-transformed total mercury in blood of seabirds. The coefficients for the lowest AIC model from the GLM analysis (Best GLM1, Table 3) are indicated. Shown are the estimated coefficients (Estimate), standard errors (se), t-values (*t*), and associated p-values (*p*) for each predictor.

Predictor	Estimate	se	*t*	*p*
Intercept (Ocean region: Arctic Ocean)	−0.761	0.103	−7.410	0.000
Log$_{10}$ Body mass	0.116	0.044	2.635	0.009
Log$_{10}$ Chlorophyll-a	−0.089	0.062	−1.429	0.154
Trophic level index	0.254	0.044	5.779	0.000
Log$_{10}$ Foraging range: diet mesopelagic prey N	0.192	0.046	4.148	0.000
Log$_{10}$ Foraging range: diet mesopelagic prey Y	0.276	0.039	7.097	0.000
Ocean region: Indian Ocean	−0.034	0.097	−0.348	0.728
Ocean region: North Atlantic	0.257	0.053	4.813	0.000
Ocean region: North Pacific	0.195	0.068	2.875	0.004
Ocean region: South Atlantic	−0.495	0.092	−5.403	0.000
Ocean region: South Pacific	0.017	0.079	0.210	0.834
Ocean region: Southern Ocean	−0.390	0.097	−4.011	0.000

3.4. Spatial distribution in seabird-model THg

Model selection for the GAMs identified the model, including species, latitude, longitude, and their interaction, as the best-fit model for both datasets. In the model selection process of the GAMs, eight best-fitting models were identified for each dataset: one including all species and the other including only epipelagic prey feeder species (Supplementary Materials 1D, Table S7). All of the best-fitting models included species, latitude, longitude, and their interactions and some also included biological or environmental factors. The simplest model (species, latitude, longitude, and latitude x longitude) had the lowest AIC among the best-fitting models, so we take the simplest one as the most representative overall (all species: r^2 = 0.631, deviance explained = 73.8 %, *GCV* = 0.11454, *n* = 441; epipelagic prey feeders: r^2 = 0.623, deviance explained = 76 %, *GCV* = 0.13005, *n* = 266).

The effects of latitude and longitude differed between the GAM including all species and that including only epipelagic prey feeders (Fig. 5). In the model for all species (Fig. 5A), the predicted values tended to be higher in the mid-latitude regions of both hemispheres as well as in the high-latitude regions of the Northern Hemisphere, while the effect of longitude was not clearly apparent. In contrast, the model for epipelagic prey feeders (Fig. 5B) showed a negative trend with latitude, and a tendency for higher values around longitudes between −180° and − 90°. For all-species model, when we fixed the species variable to a single species and included the latitude–longitude interaction in the prediction, the results showed relatively low Hg concentrations around the equatorial Southern Hemisphere and the Southern Ocean, and relatively high concentrations from north of the equator to the mid-latitudes of the Northern Hemisphere (particularly in the North Atlantic) and in the South Pacific (Fig. 6A). Although the overall spatial pattern was similar between the all-species model and the model for epipelagic prey feeders (Fig. 6B), the latter showed lower predicted Hg

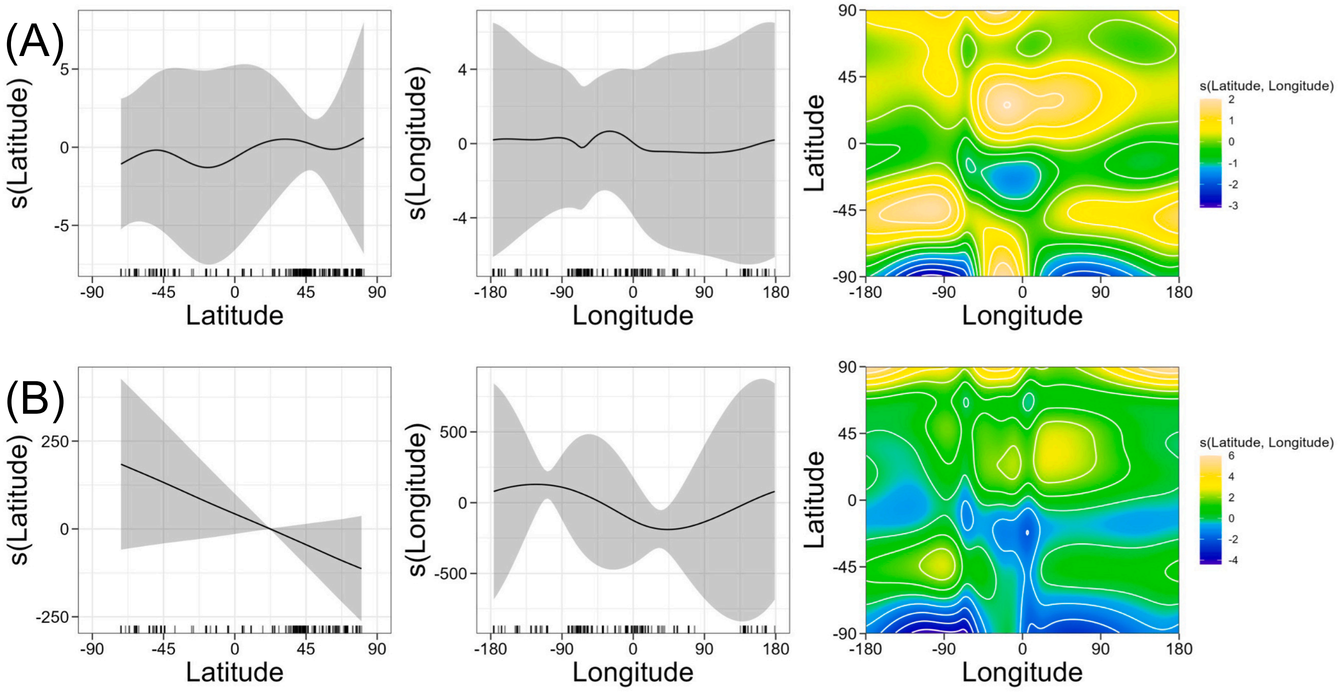

Fig. 5. Effects of latitude, longitude, and their interaction on total mercury (THg) in blood of seabirds, based on a Generalized Additive Model (GAM: blood THg ~ species + s(latitude) + s(longitude) + te(latitude, longitude)). The function s() indicates smooth terms that allow for non-linear relationships between the predictor and response variables.
In the panels, s(Latitude) and s(Longitude) show the individual effects of latitude and longitude, respectively, while s(Latitude, Longitude) (based on a tensor product smooth, te()) shows their spatial interaction. (A) The results of model for all species ($r^2 = 0.631$, Deviance explained = 73.8 %, $GCV = 0.11453$, $n = 441$). (B) The results of model for epipelagic prey feeder species ($r^2 = 0.623$, Deviance explained = 76.0 %, $GCV = 0.13005$, $n = 266$).

concentrations in the North Atlantic, North Pacific, and South Pacific, and higher concentrations in the Arctic.

In the prediction map of ocean-model THg, some sampling locations for our blood THg dataset were categorized as terrestrial areas, and thus ocean-model THg were unavailable for those sites. We assessed the correlation between ocean-model THg and seabird-model one for the remaining sampling locations where both estimates were available ($n = 109$). The THg predictions from the ocean model and the seabird model were uncorrelated when all species were included (Fig. 7A; $r = -0.069$, $p = 0.479$), but showed a weak significant positive correlation when based only on epipelagic prey feeder species (Fig. 7B; $r = 0.233$, $p = 0.015$).

4. Discussion

In total, we compiled 478 blood THg values from 108 seabird species worldwide. To our knowledge, our study provides the first reported blood THg values for the Antipodean albatross (both *antipodensis* and *gibsoni* subspecies), Westland petrel, pelagic cormorant, and the *whenuahouensis* subspecies of South Georgia diving petrel. Our analysis indicates that seabirds feeding at higher trophic levels, consuming mesopelagic prey, and inhabiting low-productivity oceanic regions tend to exhibit higher blood THg levels. We also detected significant differences among ocean regions. The GAM including all species suggested that Hg contamination was relatively higher in the North Atlantic, North Pacific, and south of 40°S in the South Pacific. The model including only epipelagic-feeding species also showed a similar spatial trend, but with comparatively higher levels in the Arctic and lower levels in the North Atlantic and South Pacific. Based on our model, we found a weak but statistically significant positive correlation with ocean-modeled THg at seabird sampling sites.

4.1. Effects of biological and spatial factors on blood THg

Our GLM results showed that species-level biological factors, including body mass, trophic level, and mesopelagic prey consumption, significantly influenced blood THg concentrations, along with spatial factors such as chl-a (mg m^{-3}) and oceanic region (Tables 3 and 4; Fig. 4). To test the robustness of these effects, we also performed PGLMMs, which confirmed the significant influence of both biological and spatial variables even after accounting for species-level random effects (Supplementary Materials 1C). The larger non-phylogenetic random effects relative to phylogenetic effects indicate that species-specific traits better explain variation in Hg concentrations than shared evolutionary history.

Species foraging at higher trophic levels exhibited higher blood THg (Fig. 4). Species attributed to the highest trophic level (index values 2.5 or 3), such as skuas (e.g., *Catharacta* spp.) and large gulls (e.g., *Larus* spp.) that prey on mammals, birds, or carrion, showed consistently elevated blood THg (Fig. 4). This likely reflects the effect of biomagnification of Hg through the food chain (Lavoie et al., 2013). The effect of trophic level or dietary differences on Hg concentrations has been widely reported at both interspecific and intraspecific levels (e.g., Ackerman et al., 2016; Albert et al., 2019; Pollet et al., 2022; Padilha et al., 2023), and our findings are consistent with these previous studies.

Species with heavier body mass also showed higher blood THg levels (Fig. 4). This pattern is consistent with previous studies conducted within specific regions or taxonomic groups (Carravieri et al., 2014). The underlying mechanism may not reflect a direct effect of body mass itself, but rather an indirect effect mediated through diet. Larger-bodied species are generally thought to consume larger prey, which often occupy higher trophic levels (Mancini et al., 2014). Although we included, as an explanatory variable in our analysis, a trophic level index based on the birds' main prey group, this index does not account for prey

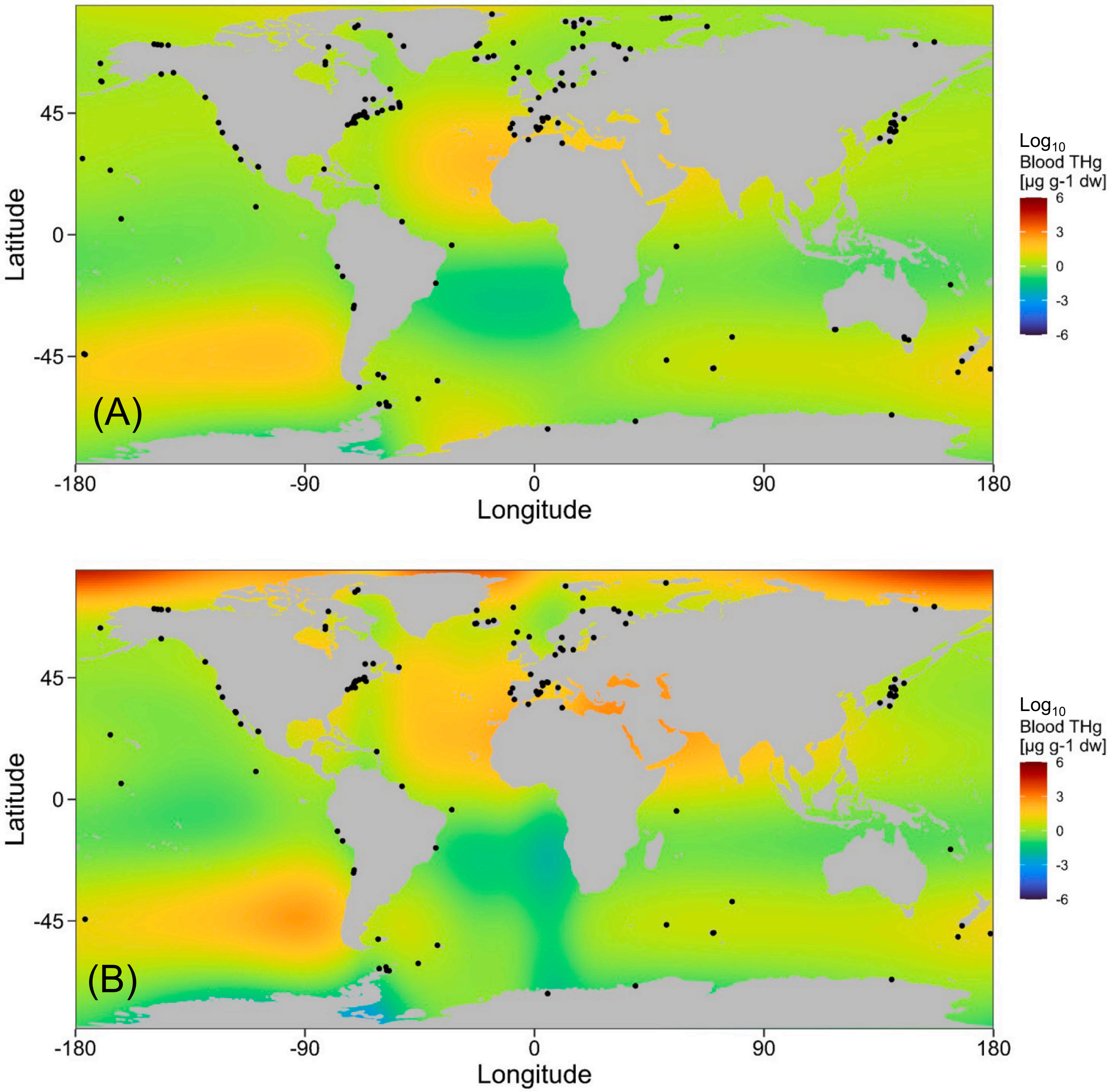

Fig. 6. Extrapolated results of the GAM (seabird blood total mercury ~ species + s(latitude) + s(longitude) + s(latitude, longitude)). Colors indicate spatial differences in total mercury in blood while controlling for species effects. Black dots represent sampling locations. A: Prediction based on the GAM for all species. B: Prediction based on the GAM for epipelagic-prey-feeding species.

size or other detailed foraging characteristics, as it is based on broad dietary categories. Therefore, body mass may function as an additional proxy for trophic position, suggesting variation not fully explained by the variable of trophic level index.

Our results further confirmed that species that consume mesopelagic prey, particularly those with broader foraging ranges including oceanic areas where mesopelagic prey are abundant, exhibited higher blood THg (Fig. 4). The mesopelagic layer over continental slopes and oceanic basins characterized by low light and oxygen conditions, may enhance Hg methylation and reduce degradation, resulting in greater MeHg accumulation than in surface waters (Mason and Fitzgerald, 1993). Indeed, organisms inhabiting the mesopelagic zone have been shown to contain higher Hg concentrations than epipelagic species (Monteiro et al., 1996; Choy et al., 2009). This organic form of Hg readily bioaccumulates into marine organisms such as phytoplankton and efficiently biomagnifies through aquatic food chains (Lavoie et al., 2013; Lehnherr, 2014). Species such as albatrosses, shearwaters, and storm-petrels, which forage over hundreds to thousands of kilometers, are known to feed frequently on mesopelagic prey such as squid and myctophids (Nishizawa et al., 2018; Watanuki and Thiebot, 2018). Previous studies on Procellariidae and Hydrobatidae have also suggested that seabird species or populations that forage in oceanic waters and feed on mesopelagic prey tend to exhibit higher Hg concentrations (Thompson et al., 1998; Anderson et al., 2009; Pollet et al., 2023a). This pattern is

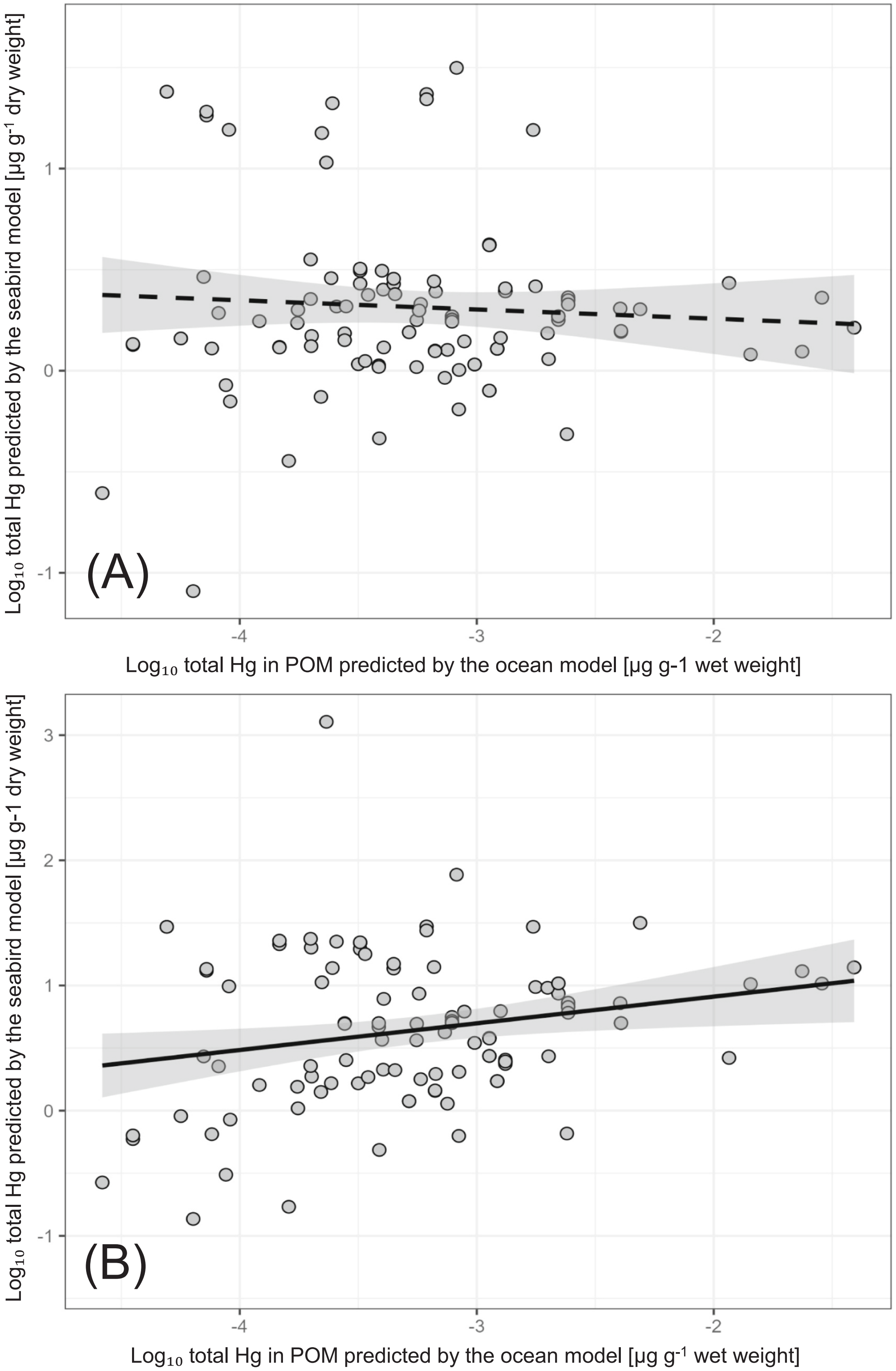

Fig. 7. Comparison between ocean-model total mercury (THg) and those the seabird-model THg (A: prediction by GAM with all species, B: GAM for epipelagic-feeding species). We used ocean-model THg of the 3° × 3° grid directly beneath each sampling site, and seabird-model THg as the average values within a 300 km radius around each site. Regression lines are shown as solid when statistically significant and dashed when not. Shaded areas indicate standard errors. Pearson's correlation results: (A) $r = -0.069$, $p = 0.48$; (B) $r = 0.233$, $p = 0.015$.

consistent with our findings. Meanwhile, even among species classified as not including mesopelagic prey in their diet, those with greater affiliations to oceanic regions appeared to have higher Hg concentrations. Although the reason for this remains unclear, oceanic environments typically have lower productivity and longer food chains than coastal regions (Lalli and Parsons, 1997), which may lead to enhanced biomagnification and increased Hg exposure seabirds foraging in oceanic regions (Ochoa-Acua et al., 2002).

Although chl-a (mg m^{-3}) was a less important predictor than other variables, seabirds inhabiting areas with lower chl-a tended to show higher blood THg (Fig. 4). In general, low-productivity regions are dominated by smaller phytoplankton (e.g., Ko et al., 2022). In low-productivity regions, smaller phytoplankton dominate and form longer food chains (Lalli and Parsons, 1997), which can elevate Hg concentrations in top predators. Their higher surface area-to-volume ratio may further increase MeHg uptake (Thackray and Sunderland, 2019). Consequently, seabirds in low-productivity regions may accumulate more Hg due to both increased MeHg uptake at the base of the food web and biomagnification through a longer trophic pathway.

According to the evaluation of health risks associated with blood THg by species, we found that four species of Diomedeidae, two species of Procellariidae, one species of Hydrobatidae, and one species of Laridae, with high extinction risk by IUCN (more than NT), are exposed to more than moderate health risks from blood THg. At the family level, species in the families Fregatidae, Stercorariidae, and Hydrobatidae were found to be at relatively high risk, with particularly high risk identified in Diomedeidae. Previous regional and global review studies have also pointed out the potential health risks from Hg contamination in these families (Ackerman et al., 2016; Chastel et al., 2022; Evers et al., 2024). Many species in these families consume prey at high trophic levels and/or feed on mesopelagic prey in oceanic regions, exposing them to high Hg exposure (Table 2). By examining ecological factors related to Hg contamination as shown in this study, it is possible to better understand species that are potentially at high health risk from Hg exposure, thereby contributing to improved extinction risk assessments and the development of conservation strategies.

We found that blood THg varied substantially depending on species-specific biological and spatial factors. This raises the question of whether certain species should be prioritized for monitoring marine Hg contamination. For instance, species that exhibit low interannual variation in blood THg levels at a given site may be less susceptible to temporal sampling bias and thus serve as more reliable bioindicators. In this study, no ecological factors explained variation in THg CVs, and we therefore could not identify species that consistently serve as better monitoring indicators. It is important to note that our analysis was limited by a relatively small sample size ($n = 30$, 23 species across 23 sites) and did not incorporate finer aspects of foraging ecology, such as intra-specific dietary flexibility. Therefore, future studies with larger datasets and more refined ecological information will be needed to reassess this question.

4.2. Seabird-model THg prediction across the globe

When discussing spatial variation in Hg contamination based on Hg concentrations in seabirds across different regions, it is important to control species-specific biological traits to avoid potential over- or underestimation. We found that blood THg varied according to species-specific biological traits and environmental factors. We constructed a GAM that incorporated species as a fixed effect, along with relevant biological and environmental factors, and included smooth effects of latitude and longitude. The results indicated that a relatively simple model including species effects and smoothed effects of latitude and longitude had the highest predictive performance. This suggests that the inclusion of species as a fixed effect adequately accounted for variance associated with biological traits, such as trophic level, which were considered in the GLM. Consequently, we were able to successfully extract spatial variations in Hg contamination while effectively controlling interspecific differences in Hg concentrations among seabirds.

Across the world's oceans, Hg concentrations had previously been measured widely in other marine taxa such as fish, sea turtles, and marine mammals (Buck et al., 2019; Rodriguez et al., 2022; Evers et al., 2024). Although several studies have evaluated spatial patterns of Hg exposure within individual groups, very few have attempted to assess such variation across global ocean regions (Buck et al., 2019; Rodriguez et al., 2022; Evers et al., 2024). Given the importance of understanding global Hg pollution and its trend, assessments based on direct biological measures are highly valuable (AMAP, 2021). Despite limitations such as spatial sampling bias, particularly the scarcity of data reflected contamination in the oceanic area, and the constraints of the temporal and spatial resolution that can be inferred, our study provides an important step forward in evaluating global marine Hg pollution using empirical data from seabirds.

Although the predictions from the model for all species (Fig. 6A) and that for epipelagic prey feeders (Fig. 6B) showed relatively similar trends, the latter exhibited lower predicted Hg concentrations in the North and South Pacific and higher concentrations in the Arctic region (Fig. 6B). Given that most seabirds forage on epipelagic prey (Gaston, 2004), the spatial pattern presented in this study is considered to primarily reflect epipelagic Hg contamination. However, for species that may feed on mesopelagic prey, Hg concentrations may reflect intake derived not only from epipelagic layers but also from mesopelagic layers, which Hg is thought to differ significantly from that in surface waters (Wang et al., 2023). Notably, 35 % of the blood THg values used in our model for all species were for the species that may consume mesopelagic prey, suggesting that the predictions may be influenced by Hg contamination in mesopelagic layers. Interestingly, only the seabird-model THg based on epipelagic feeder species showed a weak positive correlation with ocean-model THg in POM in the epipelagic layer, suggesting the importance of considering the vertical layer from which each species accumulates Hg when using seabirds as bioindicators of Hg pollution. In the following paragraphs, unless otherwise noted, we will refer to the predictions from the model based on epipelagic feeder species.

Our estimates demonstrate not only the variation in Hg contamination among different ocean regions but also its variability within each region (Fig. 6). While few studies have estimated global Hg patterns based on top predators, several previous studies used seabirds to suggest regional differences in Hg contamination (Table 1). Comparisons with these studies show both similarities and differences depending on the ocean region and the specific study (Table 1). Our study shows relatively strong agreement with seabird-based research in the Southern Hemisphere using penguins as bioindicators (Carravieri et al., 2016; Gimeno et al., 2024). The spatial pattern of Hg contamination estimated in the central Pacific Ocean is also similar to that observed in wintering streaked shearwaters there (Watanuki et al., 2016) but not those estimated in the North Pacific from red-legged kittiwake and short-tailed shearwater (Watanuki et al., 2015; Fleishman et al., 2019). Some studies in the North Atlantic show consistent results (Pollet et al., 2022; Carravieri et al., 2023), whereas others predict different spatial patterns (Albert et al., 2022, 2024). In the Arctic, our estimate differs from previously reported spatial patterns (AMAP, 2021). The reasons for these discrepancies remain unclear, but the region-specific marine environmental factors, such as ocean currents, sea-ice cover, or chl-a, may influence the region-specific levels of Hg contamination (Tartu et al., 2022). Also, many previous studies estimated Hg exposure during the non-breeding period by analyzing Hg in feathers, which reflect Hg uptake in oceanic regions (Watanuki et al., 2015; Albert et al., 2022, 2024). In contrast, we used blood samples, which mainly reflect Hg uptake around breeding sites during the breeding period. Therefore, the model may not fully capture Hg variation in oceanic areas. Overall, the spatial trends observed in this study are not drastically different from previous studies, but regional differences suggest some divergence in patterns.

The seabird-model THg for epipelagic prey feeder species shows a weak positive correlation with the ocean-model THg (Fig. 7). However, the low correlation coefficient indicate that seabird- and ocean-model THg do not show a consistent spatial trend. The seabird-model THg is based on empirical measurements from organisms and is therefore considered more reliable than values derived from the ocean model. Accordingly, this low degree of agreement may reflect a limitation of the ocean model in capturing actual environmental conditions. We used THg in POM as a representative value for the ocean model. However, it is possible that seabird Hg reflects different chemical forms of Hg, especially MeHg which mainly accumulated in internal tissues and organs of seabirds (e.g., Renedo et al., 2021). Hg concentrations in phytoplankton vary greatly depending on biological traits such as cell size, surface area per volume, and community structure, as well as environmental conditions like light level, nutrients, and water temperature (Chen and Folt, 2005; Zhang et al., 2020; Wang et al., 2023). For example, although MeHg concentrations in seawater were estimated to be high in the Arctic, Antarctic, and equatorial regions, levels in phytoplankton were also estimated to be higher in the mid-latitudes of both hemispheres. Further, in small zooplankton, the equatorial and northern mid-latitude regions were estimated as the most highly contaminated region (Zhang et al., 2020). These findings suggest that Hg concentrations and their spatial distributions are highly different depending on the trophic levels in marine ecosystems. For further validation of seabird-model THg, future research should compare these estimates with Hg concentrations measured across various chemical forms, especially MeHg, and trophic levels in the marine environment.

The comparison presented in this study represents an important step toward improving our understanding of the global spatial distribution of Hg. Several approaches have been used to assess the spatial extent of marine Hg pollution, including direct seawater measurements (Bowman et al., 2020), ocean modeling (Kawai et al., 2020; Wang et al., 2023), and biological indicators (Furness and Camphuysen, 1997). Direct measurements provide site-specific data but are limited by significant logistical and financial constraints, making broad coverage difficult (Bowman et al., 2020). Ocean models estimate the distribution of various forms of Hg across wide oceanic regions by incorporating emission inventories, storage dynamics, physical and chemical circulation, and Hg transformation. However, evaluating the accuracy of these models remains challenging, and most validations rely on limited direct measurement data from specific regions (Kawai et al., 2020; Zhang et al., 2020; Wang et al., 2023). Biological indicators offer a relatively simple alternative for assessing average Hg contamination in each region, although species-specific biases must be carefully considered (Table 1). Each approach has its own strengths and limitations and integrating them may improve the accuracy of Hg distribution estimates. To achieve this, it is essential to compare the outputs of different approaches and identify their consistencies, as demonstrated in our study.

5. Conclusion

Our global meta-analysis indicated that THg levels in seabirds tend to be higher in species feeding at higher trophic levels and their tendency to consume mesopelagic prey in oceanic waters. Additionally, spatial and environmental factors were also found to contribute to this variation. Between 1950 and 2010, global seabird populations are estimated to have declined by 69.7 % (Paleczny et al., 2015), and nearly half of all seabird species are currently classified as Near Threatened or higher on the IUCN Red List (Dias et al., 2019). Marine pollution, including Hg contamination, is considered one of the major threats contributing to these population declines (Paleczny et al., 2015; Dias et al., 2019; Pollet et al., 2023b). Our findings thus provide important insights for identifying conservation priority species and regions from the perspective of Hg exposure. Furthermore, by using seabird-derived data to estimate global spatial contamination of Hg, we found that the model based on species feeding exclusively on epipelagic prey showed a weak correlation with ocean model predictions. The weak correlation instead suggests discrepancies between biological measurements and ocean-model predictions.

Based on these discrepancies, it is expected that future improvements in ocean models and integration of both modeling approaches will further promote our understanding of Hg seascape globally. Our study supports such improved understanding, not only by clarifying the Hg contamination mechanisms in marine ecosystems but also by further illustrating the utility of seabirds as bioindicators to assess the global spatial distribution of Hg pollution.

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CRediT authorship contribution statement

Jumpei Okado: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Bungo Nishizawa:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Johannes H. Fischer:** Writing – review & editing, Project administration, Funding acquisition, Data curation. **Olivia C. Rowley:** Writing – review & editing, Data curation. **Yukihiko Toquenaga:** Writing – review & editing, Funding acquisition. **Yasuaki Niizuma:** Writing – review & editing, Funding acquisition, Data curation. **Chinatsu Nakajima:** Writing – review & editing, Data curation. **Futoshi Ujiie:** Writing – review & editing, Data curation. **Toru Kawai:** Writing – review & editing, Data curation. **Shannon Whelan:** Writing – review & editing, Data curation. **Scott A. Hatch:** Writing – review & editing, Data curation. **Paco Bustamante:** Writing – review & editing, Data curation. **Graeme Elliott:** Writing – review & editing, Data curation. **Graham C. Parker:** Data curation. **Kalinka Rexer-Huber:** Writing – review & editing, Data curation. **Kate Simister:** Writing – review & editing, Data curation. **Grace Tocker:** Data curation. **Kath Walker:** Data curation. **Heiko U. Wittmer:** Writing – review & editing, Data curation. **Igor Debski:** Data curation. **Akiko Shoji:** Writing – review & editing, Validation, Supervision, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization.

Ethical approval

All sampling in Japan was carried out with permission from Ministry of the Environment and the Agency of Cultural Affairs, Akkeshi Town, Tokyo Metropolitan Government, Hokkaido, Aomori Prefecture Government. All sampling in USA was carried out with permission from the Department of the Interior, and the US Fish and Wildlife Service, Migratory Bird Permit Office (USA). All sampling in Aotearoa New Zealand was carried out with permission from Kāi Tahu and the Department of Conservation. All sampling procedures were approved by McGill Animal Care Committee, Animal Experimental Committee of University of Tsukuba and Animal Experimental Committee of Nagoya University, and the animal ethics committee of Victoria University of Wellington, or following standard operation procedures approved by the animal ethics committee of the Department of Conservation.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used ChatGPT for grammar and language checking. After using this tool, the authors reviewed and edited the content as needed and takes full responsibility for the content of the published article.

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Declaration of competing interest

The authors declare no conflicts of interest associated with this manuscript.

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Data availability

The seabird species native to Aotearoa New Zealand sampled in this study are considered *taonga* (treasures) to Kāi Tahu and Ngāti Waiwai (Indigenous peoples of Southern Aotearoa New Zealand). *Rangatiratanga* (sovereignty, chieftainship, and/or self-determination; McAllister et al., 2023) and *kaitiakitanga* (guardianship, practices informed by centuries of experience to achieve intergenerational sustainability; McAllister et al., 2023) over these taonga and the associated data remain with Kāi Tahu and Ngāti Waiwai. SM1 and SM2 contain the means and standard deviation of the data generated through our study, but raw data can only be made available following consultation. The corresponding authors can provide the necessary information to facilitate such consultation.

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