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Assessing mercury contamination in Southern Hemisphere marine ecosystems: The role of penguins as effective bioindicators☆

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ABSTRACT

Mercury (Hg) is a global pollutant known for its significant bioaccumulation and biomagnification capabilities, posing a particular threat to marine environments. Seabirds have been recognized as effective bioindicators of marine pollution, and, among them, penguins present a unique opportunity to serve as a single taxonomic group (*Sphenisciformes*) for monitoring Hg across distinct marine ecosystems in the Southern Hemisphere. In this study, we conducted a comprehensive systematic review of Hg concentrations, and performed a meta-analysis that took into account the various sources of uncertainty associated with Hg contamination in penguins. Beyond intrinsic species-specific factors shaping Hg levels, our results showed that the penguin community effectively reflects spatial patterns of Hg bioavailability. We identified geographic Hg hotspots in Australia, the Indian Ocean, and Tierra del Fuego, as well as coldspots in Perú and the South Atlantic. Furthermore, specific penguin species, namely the Southern Rockhopper (*Eudyptes chrysocome*) and Macaroni penguin (*Eudyptes chrysolophus*), are highlighted as particularly vulnerable to the toxic effects of Hg. Additionally, we identified knowledge gaps in geographic areas such as the Galápagos Islands, South Africa, and the coast of Chile, as well as in species including Fiordland (*Eudyptes pachyrhynchus*), Snares (*Eudyptes robustus*), Erect-crested (*Eudyptes sclateri*), Royal (*Eudyptes schlegeli*), Yellow-eyed (*Megadyptes antipodes*), and Galápagos (*Spheniscus mendiculus*) penguins. Overall, our study contributes to the growing body of literature emphasizing the role of penguins as bioindicators of Hg pollution, but it also highlights areas where further research and data collection are needed for a more comprehensive understanding of Hg contamination in marine ecosystems in the Southern Hemisphere.

1. Introduction

The expansion of human activities (e.g., industrialization, urban development and maritime transport) has led to a drastic increase in the release of pollutants into the environment (Beiras, 2018; Bhardwaj et al., 2018). Oceans act as a terminal sink for most of these pollutants (Driscoll et al., 2013; Zhang et al., 2022), with ultimate and far-reaching consequences for humans and wildlife (Puasa et al., 2021). Within the wide spectrum of toxic substances, mercury (Hg) is a global pollutant of particular concern. Previous studies have reported effects of Hg on animals' physiology and development, endocrine disruption, wing feather asymmetry and neurodevelopmental impairment (Tan et al., 2009; Scheuhammer et al., 2012; Carravieri et al., 2016). Mercury can also alter population dynamics through impacts on individuals' survival and fecundity (Goutte et al., 2014a; Goutte et al., 2014b; Mills et al., 2020). Moreover, Hg can bioaccumulate within individuals, and biomagnifies through the marine food webs, thus becoming an important hazard for long-lived species that occupy higher trophic positions (Carravieri et al., 2016; Seco et al., 2021).

Mercury is introduced into the environment through natural processes (e.g., geothermal activity and volcanism) and anthropogenic activities (e.g., artisanal gold mining and stationary combustion of coal)

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(UNEP, 2019). Mercury emitted to the atmosphere from natural and anthropogenic sources can be spatially redistributed through atmospheric transport and deposited in the environment (Selin, 2009). From there, Hg can volatilize back into the air, or be transported further by ocean circulation reaching distant marine areas often considered pristine such as the Southern Ocean and the Antarctic continent (Becker et al., 2016; Brasso et al., 2015; Mills et al., 2020, 2022). The cycling of Hg is affected, therefore, by ongoing emissions, but also by the re-emissions of Hg emitted, sequestered, and deposited over the last centuries (the so-called legacy Hg; Streets et al., 2019). Importantly, Hg emissions from anthropogenic activities have gradually shifted towards the Southern Hemisphere, with important implications for Hg distribution at the global scale (Streets et al., 2017). Biogeochemical features can also influence the spatial distribution of Hg, in particular, the processes that modify the rate of in situ microbial production of methylmercury (MeHg), the highly toxic and bioavailable form of Hg (Driscoll et al., 2013).

Within the Southern Hemisphere, a latitudinal gradient of Hg and MeHg has been observed in the seawater with higher concentrations in the Antarctic compared to sub-Antarctic and subtropical waters (Cossa et al., 2011; Yue et al., 2023). However, the latitudinal gradient of Hg bioavailability across the Southern Hemisphere biota is the opposite (Brasso et al., 2015; Becker et al., 2016; Cherel et al., 2018; Mills et al., 2020). This paradox remains unresolved, but could be explained by the processes at the basis of the food web (e.g., biodilution associated with highly productive areas) together with the biomagnification rates along the latitudinal gradient (Lavoie et al., 2013; Renedo et al., 2020).

Top and meso-predators such as seabirds can integrate contaminant levels across local to regional marine food webs, and are widely used for pollution assessments and environmental health monitoring (Furness & Camphuysen, 1997; Jerez et al., 2013). Penguins have emerged as reliable and effective bioindicator species for the evaluation and monitoring of Hg contamination in the Southern Hemisphere (see Cusset et al. (2023) for a circumpolar assessment). Furthermore, penguins represent the greatest bird biomass in the Southern Hemisphere (Espejo et al., 2017). They disperse less than flying seabirds, and remain confined to the Southern Hemisphere throughout the annual cycle (including migration), thus integrating Hg contamination over more restricted areas (Brasso et al., 2015; Carravieri et al., 2016; Cherel et al., 2018; Espejo et al., 2017). Because of their annual catastrophic moult, penguins also have less intra-individual differences in Hg feather levels than other seabird groups with protracted moult periods (e.g., Procellariiforms; Brasso et al., 2013; 2015; Bridge, 2006; Carravieri et al., 2014). Finally, penguins have been widely studied and, therefore, we can better understand which life history traits could be shaping their exposure to Hg (e.g. Carravieri et al., 2016; Espejo et al., 2017).

Our study aims to contribute to the growing body of literature emphasizing the role of penguins as bioindicators of Hg pollution in the Southern Hemisphere (Brasso et al., 2015; Carravieri et al., 2016; Cusset et al., 2023). To this aim, we compiled the most comprehensive and updated dataset on Hg concentrations in blood and feathers for all the penguin species with available information through a systematic review of scientific literature (available at DigitalCSIC: https://doi.org/10.20350/digitalCSIC/15722). We further integrated this dataset in a meta-analysis for evaluating spatial patterns in Hg concentrations, and tracking local Hg availability as a fraction of the water-borne Hg that is incorporated into organisms and food webs (Lavoie et al., 2013). This approach allowed us to control for the different sources of uncertainty shaping penguins' Hg body burdens (i.e., species-specific intrinsic traits such as age along with specificities of primary studies included in our review); thus permitting the use of the whole penguin community for large-scale, Hg pollution monitoring. Our results can contribute to the proper evaluation of Hg concentrations among contrasting geographic areas and penguin species. In particular, our assessments allow the identification of geographic Hg hotspots and coldspots, along with particular penguin species and populations most at risk of exposure to Hg. Beyond that, this study builds upon previous works and highlights areas where further research and data collection are needed for a more comprehensive understanding and assessment of Hg contamination in marine ecosystems off the Southern Hemisphere.

2. Methodology

2.1. Literature review

A systematic bibliographic review was conducted using the PRISMA approach and guidelines (Page et al., 2021). Scopus database (https://www.scopus.com) was used to obtain the preliminary list of papers (up to January 2022) to be screened through a broad search that included "penguin" and "pollutants" terms in the title, abstract or the keywords (n = 153). This search was intentionally kept broad to ensure that all papers reporting Hg concentrations in penguins were included in the screening process (Fig. 1). Inaccessible papers (n = 10) and those that do not report pollutant levels in penguins (n = 49) were removed. Additional papers mentioned in some of the articles from the initial list were also included in the screening (n = 5). Of the 99 full-text articles assessed for eligibility, those that do not report Hg concentrations in blood or feathers (n = 76), or do not report arithmetic mean (n = 1) were excluded. A final set of 22 papers reporting 159 Hg concentration records in blood and feather samples for 12 penguin species were used to conduct the meta-analysis (see the database at DigitalCSIC: https://doi.org/10.20350/digitalCSIC/15722 for the complete list of records extracted through the systematic review).

From each paper within the final set, we extracted information on the study area (latitude and longitude), the penguin species, and the reported concentration (arithmetic mean and standard deviation –SD-). The values in blood reported in wet weight (ww) units were converted to dry weight (dw) using a tissue water content of 70% (Thompson & Hamer, 2000). When available, additional information regarding individual intrinsic traits that could affect contaminant loads, such as age or sex, was included in the dataset. To account for Hg biomagnification, we finally added the trophic level of each penguin species obtained from SeaLifeBase (https://www.sealifebase.ca/; accessed in March 2023).

Our Hg dataset included information on Hg concentrations for 30 different locations widely distributed in the Southern Hemisphere (Fig. 2). To account for contrasting baselines and particular physical, biological and environmental features, these locations were geographically clustered following a criterion of geographical proximity. Seven different clusters were created, representing seven different geographic areas: Eastern Antarctica, Australia, Indian Ocean, Perú, Tierra del Fuego, Antarctic Peninsula and South Atlantic.

2.2. Meta-analysis

Penguin feathers integrate individuals' exposure to Hg during the inter-moulting period, except for penguin chick feathers which are also suitable for investigating local contamination (Carravieri et al., 2013). In contrast, blood informs on Hg exposure over a few weeks before the sampling (Albert et al., 2019; Bearhop et al., 2000), typically during the breeding season when individuals are accessible (Renedo et al., 2020). Time-integration frames differed, therefore, between tissues. In addition, seabirds can reduce Hg body burden by mobilizing Hg into their feathers during moulting, depurating 70–90% of the whole-body burden of Hg (Braune, 1987; Honda et al., 1986). These arguments prevent direct comparisons among tissues' Hg concentrations. However, considering multiple tissues simultaneously can provide a more holistic overview of penguin exposure to Hg throughout the annual cycle, with blood and feathers reflecting relatively short and long-term exposure, respectively. Accordingly, the meta-analysis was carried out for each tissue separately.

In meta-analysis, statistical independence is one of the key assumptions when pooling effect sizes (*i.e.*, Hg concentration means) (Higgins

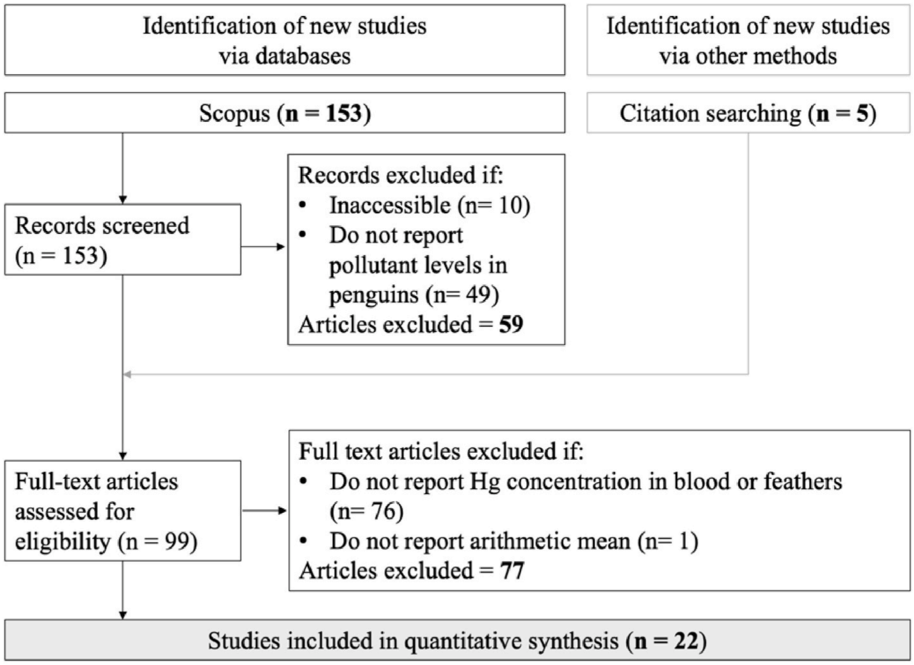

Fig. 1. Flow diagram for the systematic review and selection process used, indicating the number (n) of studies included in this review. The bold numbers are key numerical values associated with the number of studies included in the review.

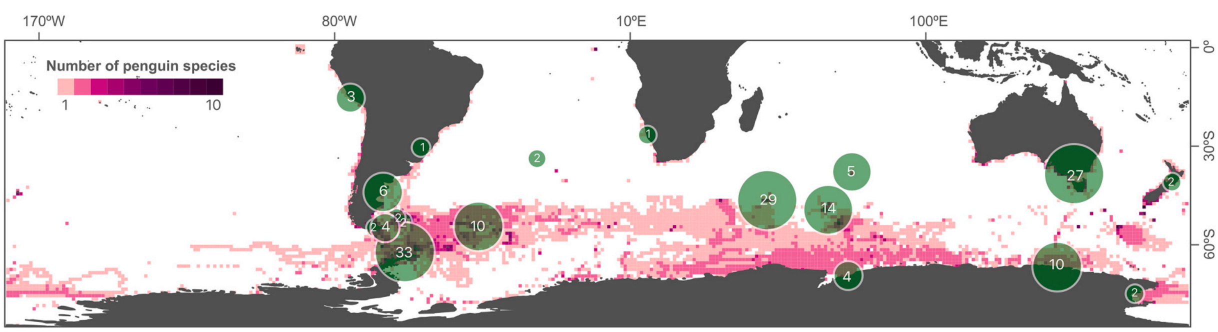

Fig. 2. Distribution of the number of different Hg concentration records mentioned in the papers (database available at DigitalCSIC: https://doi.org/10.20350/digitalCSIC/15722). Name of the clusters: Antarctica (ANT), Australia (AUS), Indian Ocean (IND), Perú (PER), Tierra del Fuego (TDF), Antarctic Peninsula (PANT) and South Atlantic (SATL). The background represents the number of penguin species occurrences by 1 × 1° cells that were available in GBIF (Global Biodiversity Information Facility (https://doi.org/10.15468/dl.urxxj2; accessed in September 2021). This background was used as a proxy for the spatial distribution of the whole penguin community for comparison with the distribution of available Hg records.

et al., 2009). This assumption was violated in our database because the same study can report several effect sizes for different groups (e.g., sex and age-related stage -hereafter stage-: chick, juvenile, adult). To overcome this issue, we accounted for these dependencies through a Hierarchical Three-Level Meta-Analysis Model (Harrer et al., 2021), whereby "penguins" (level 1) were nested within "effect sizes" (level 2), which in turn were nested within "studies" (level 3).

We fitted three different Three-Level Meta-Analysis Models: null, reduced, and full models. For the null models, we used a random-effects model to pool all effect sizes because it was likely that the mean Hg concentrations of each primary study were not deviated only due to sampling error; that is, we anticipated considerable between-study heterogeneity. The penguin age-related stage, geographic area, and species were the random effects in these models. For the reduced models, we pooled effect sizes by geographic area. To this aim, we used mixed-effects models with geographic area as a moderator variable, and penguin stage and species as random effects to account for the variability in the mean Hg concentration due to these factors. In the full models, we pooled effect sizes for each species and geographic area by fitting mixed-effects meta-analysis models in which the penguin stage was a random factor while species nested within the geographic area were included as fixed effects. We did not consider the temporal domain into account in our analyses as Hg variations over time are expected to be relatively limited within this study. Maintaining the penguin stage as a random factor in the statistical models allowed us to consider intra-specific differences due to age-related variability related to bio-accumulation (Renedo et al., 2018) and detoxification (Álvarez-Varas et al., 2018).

To calculate the heterogeneity variance in all models, we used the Restricted Maximum Likelihood Estimator (REML; Viechtbauer, 2005) as it is the most robust method for continuous effect sizes (Langan et al., 2019). Additionally, we used Knapp-Hartung adjustments (Knapp & Hartung, 2003) to calculate the confidence interval around the pooled effect, assuming a t-distribution for the effect size, which is more appropriate for meta-analysis models with random effects (Langan et al., 2019). All models were fitted through the function "rma.mv" from the *metaphor* package (Viechtbauer, 2010) that is implemented in the R software (R Core Team, 2022); version 4.2.2.).

In order to compare the goodness of fit among the three models, we performed Likelihood Ratio Tests (LRT) by using the function "anova.rma" from the *metaphor* package (Viechtbauer, 2010). Particularly, for each tissue sampled, we performed two LRTs, (1) comparing the null model with the reduced model (*i.e.*, segregated by geographic area), and (2) comparing the reduced model with the full one (*i.e.*, considering geographic area and species as nested fixed-effects). Because LRTs are not meaningful when using REML estimation, we refit the models using Maximum Likelihood (ML) estimation to perform the tests. Significant LRTs (*i.e.*, p-values <0.05) suggest that segregation improves the goodness of fit of the model.

We also performed a Test of Moderators (also known as Test of Between-Group Differences) in the reduced and full models to test the statistical association of the groups (geographic area and geographic area - species) with the effect sizes. Significances (*i.e.*, p-values <0.05) suggest different mean Hg concentrations in at least two groups.

We used the "forestplot" function from the *forestplot* R package (Gordon & Lumley, 2021) to create forest plots to visually summarize the results of the meta-analysis models and to display the pooled estimates and confidence intervals for Hg concentrations means in penguin feathers and blood. The Wald test was used to evaluate whether the pooled means of Hg concentrations were significantly different from zero (p-values <0.05). As reference values to assess the overall impact of Hg concentrations in penguin populations, we included in the forest plot the levels of toxicity reported for feathers and blood. Previous studies have identified negative impacts on birds development and survival at Hg concentrations above 5 $\mu g \cdot g^{-1}$ dw in feathers (Evers et al., 2008; Wolfe et al., 1998) and 0.67 $\mu g \cdot g^{-1}$ dw in blood (equivalent to 0.2 $\mu g \cdot g^{-1}$ ww, Ackerman et al., 2016; Chastel et al., 2022). The ww threshold of 0.2 $\mu g \cdot g^{-1}$ ww was also converted to dw using a tissue water content of 70% (Thompson & Hamer, 2000).

3. Results

3.1. Literature review results

We evaluated 22 papers reporting 159 Hg records for 12 out of the 18 world's different penguin species distributed throughout their whole distribution range (Fig. 2). No data are available for Fiordland (*Eudyptes pachyrhynchus*), Snares (*Eudyptes robustus*), Erect-crested (*Eudyptes sclateri*), Royal (*Eudyptes schlegeli*), Yellow-eyed (*Megadyptes antipodes*), and Galápagos (*Spheniscus mendiculus*) penguins. The genus *Pygoscelis* is the one with the largest number of published papers on Hg concentration levels (Fig. 3). When accounting for the number of records on Hg concentration levels, the species with the highest numbers are Gentoo (*Pygoscelis papua*), Adélie (*Pygoscelis adeliae*), and Little penguins (*Eudyptula minor*) (Fig. 3).

The number of records on Hg concentrations also varies spatially (see Fig. 2). Areas such as the Antarctic Peninsula, Crozet Islands and Australia have been extensively studied, with ca. 30 records. Several records are also gathered in the tip of South America, Kerguelen Islands, South Georgia Islands, and eastern Antarctica. In contrast, important gaps of knowledge emerge in relevant areas for penguins such as the Galápagos Islands, South Africa, and the coast of Chile. The full list of records and their associated information is available at DigitalCSIC: https://doi.org/10.20350/digitalCSIC/15722.

3.2. Meta-analysis results

In the case of feathers Hg concentrations, the full model that considered the penguin species as a nested factor within a geographic area shows the greatest goodness of fit (LRT = 72.40; p-value <0.0001, when compared with the reduced model). In the case of blood, the reduced model that considered the geographic area as a moderator variable showed greater goodness of fit than the null model (LRT = 11.53; p-value = 0.021). However, a similar goodness of fit is observed between the reduced model and the full model in the case of blood (LRT = 7.13; p-value = 0.309).

The results of the test of moderators revealed that there are statistically significant differences in the pooled means of Hg concentration between at least two of the subgroups among penguins within geographic areas for feathers (F-statistic = 6.92, p-value <0.001) and among geographic areas for blood samples (F-statistic = 3.07, p-value = 0.004).

In Fig. 4A, the forest plot displays the pooled levels of Hg concentration mean in the feathers of penguins. The areas with the highest

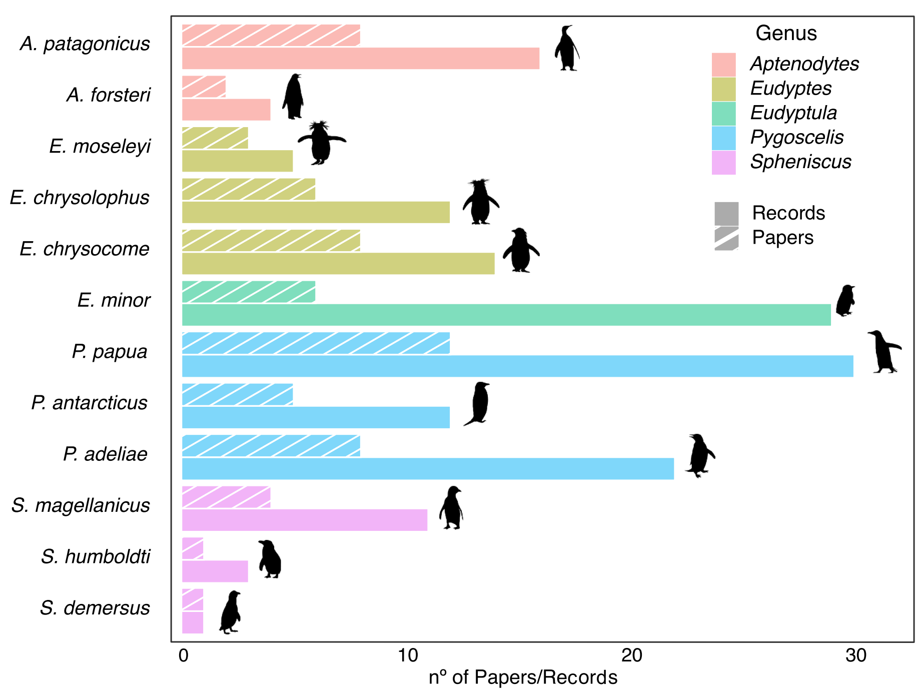

Fig. 3. The bars indicate the number of papers (dashed bars) that report Hg levels and the number of Hg records (solid bars) for the different penguin species.

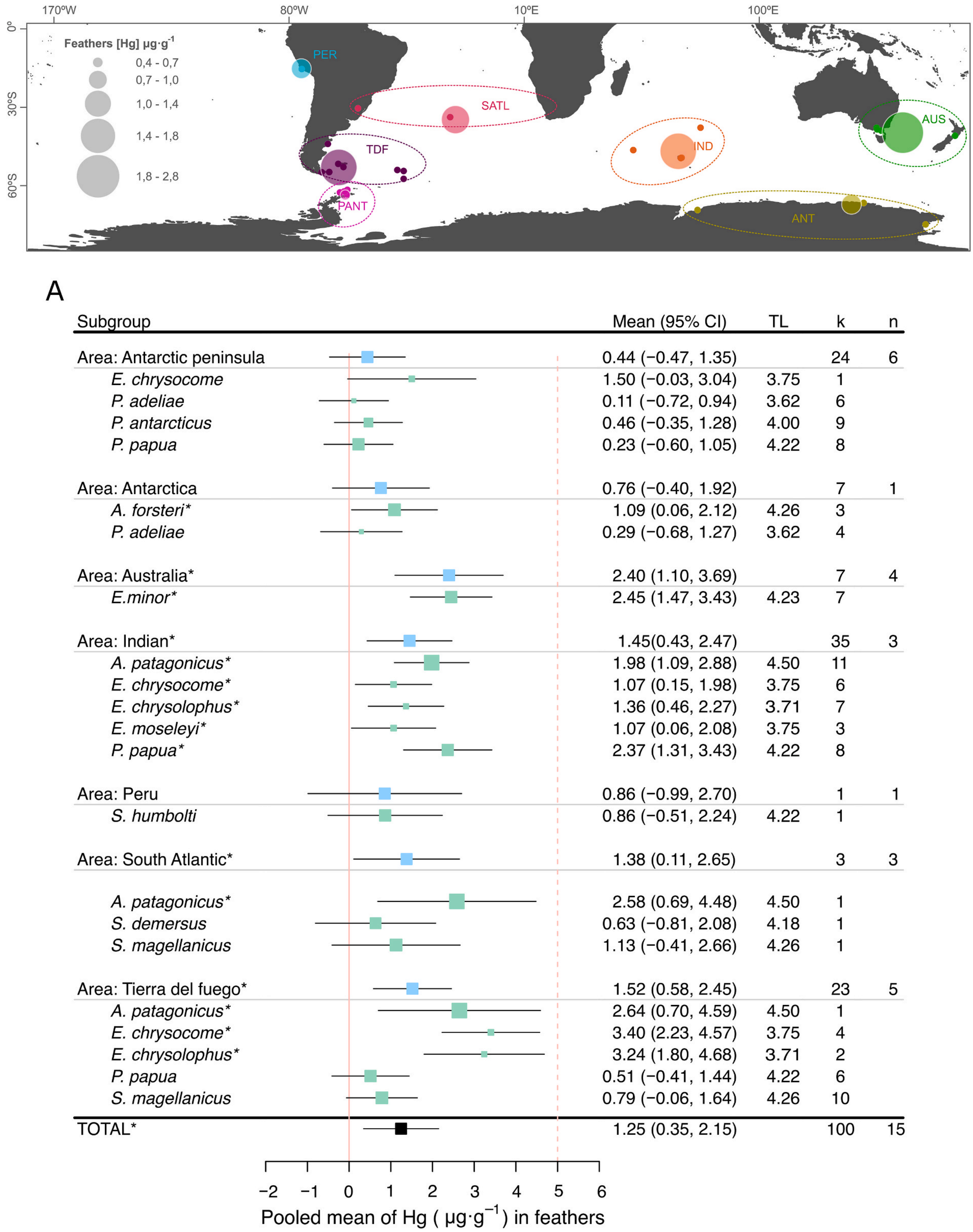

Fig. 4. Results of the meta-analysis for Hg levels ($\mu g \cdot g^{-1}$) in feathers (A) and blood (B). The maps show the results from the reduced model. In both maps, the colours indicate the cluster, the size of the semi-transparent symbol is proportional to the mean value, and the locations of the studies that form the cluster are indicated with points. Name of the clusters: Antarctica (ANT), Australia (AUS), Indian Ocean (IND), Perú (PER), Tierra del Fuego (TDF), Antarctic Peninsula (PANT) and South Atlantic (SATL). The results of the forestplot come from three different models indicated by colours: black = null model, blue = reduced model, and green = full model. The size of the full model symbol is proportional to the trophic level of each penguin species. TL = trophic level, k = number of reports for each species in the corresponding geographic area, and n = number of papers in the corresponding geographic area. The vertical red line indicates the zero and the vertical dashed line indicates the current lowest level in feathers (5 $\mu g \cdot g^{-1}$dw; Wolfe et al., 1998; Evers et al., 2008) and in blood (0.67 $\mu g \cdot g^{-1}$dw; Ackerman et al., 2016) above which observable adverse effects are known. Effect sizes that are statistically different from zero are indicated with an asterisk (*).

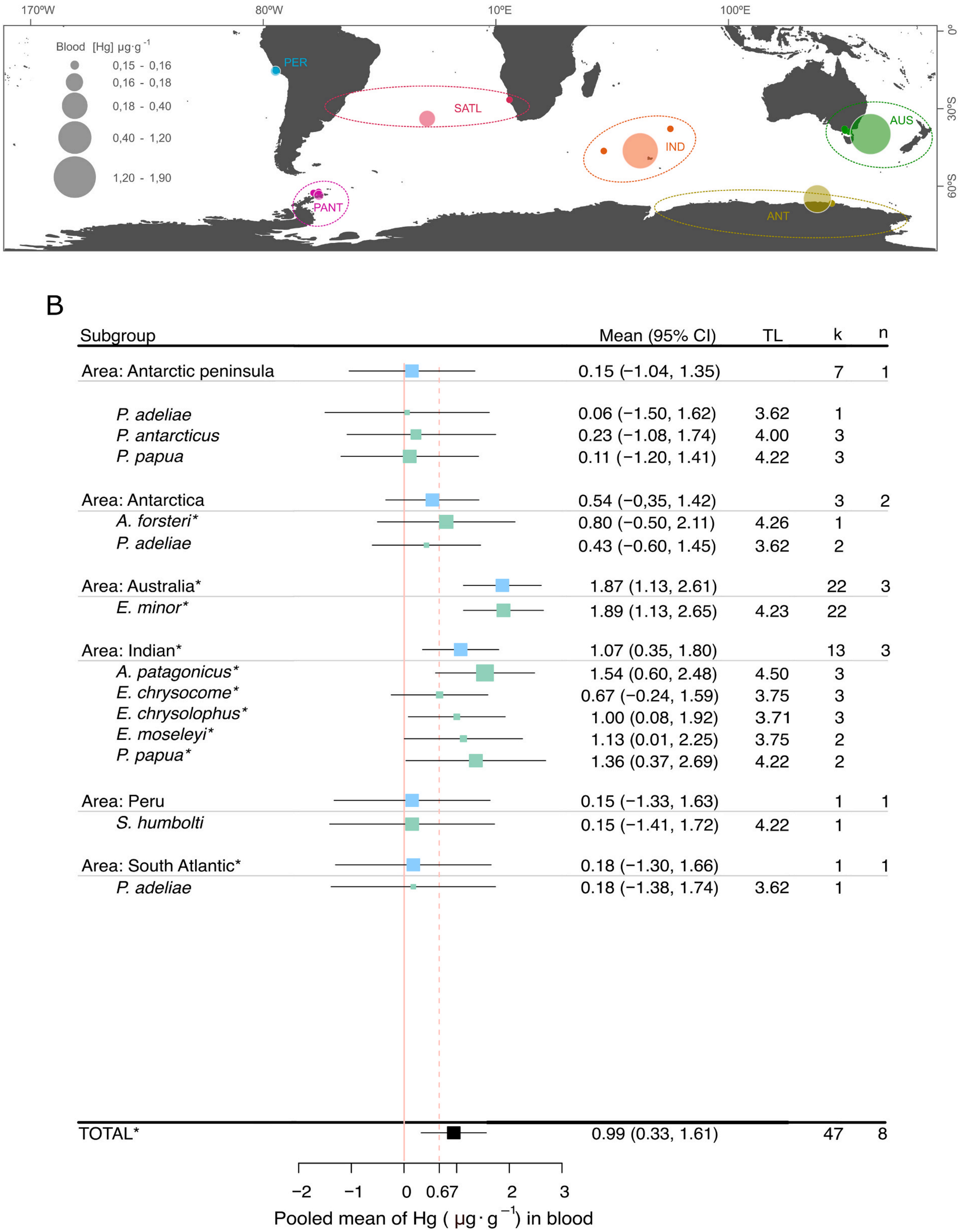

Fig. 4. (*continued*).

values are Australia, Tierra del Fuego, the Indian Ocean, and South Atlantic Ocean. These areas have mean Hg values that are statistically different from zero. Within these areas, we also find the species with the highest values of Hg concentration pooled mean in feathers: Southern Rockhopper (*Eudyptes chrysocome;* Tierra del Fuego), Macaroni (*Eudypes chrysolophus*; Tierra del Fuego), King (*Aptenodytes patagonicus*; Tierra del Fuego and South Atlantic Ocean), Little (Australia) and Gentoo penguin (Indian Ocean). All these species have pooled means that are statistically different from zero. Emperor (*Aptenodytes forsteri*), King (Indian Ocean), Southern Rockhopper (Indian Ocean), and Macaroni penguin (Indian Ocean) also have pooled mean values statistically different from zero. The area with the lowest Hg concentrations is the Antarctic Peninsula, where the species with the lowest Hg values also occurs: the Adélie penguin. Among the penguin species inhabiting the same area, Hg concentrations are generally similar, but with slightly higher Hg levels in species occupying higher trophic levels (TL). The only exceptions for this general pattern are Gentoo and Chinstrap penguin (*Pygoscelis antarcticus*; Antarctic Peninsula), Gentoo penguin (Indian Ocean), and Southern Rockhopper and Macaroni penguin (Tierra del Fuego).

Eight penguin species are present in more than one area. Southern Rockhopper penguins have the highest Hg values at Tierra del Fuego and the lowest at Antarctic Peninsula. Similarly, Adélie and Gentoo penguin from Antarctic Peninsula also show the lowest Hg levels. The highest Hg levels for King and Macaroni penguins are reported for Tierra del Fuego. In contrast, Magellanic (*Spheniscus magellanicus*) and Gentoo penguins from Tierra del Fuego show slightly lower Hg levels than those occurring in the South Atlantic and Indian Ocean regions, respectively. Overall, all penguin species show mean Hg levels below the current observed threshold of toxicity in feathers for seabirds (5 $\mu g \cdot g^{-1}$dw; Wolfe et al., 1998; Evers et al., 2008).

In Fig. 4B, the forest plot displays the pooled levels of Hg concentration mean in the blood of penguins. The areas with the highest values are Australia and the Indian Ocean, with mean Hg values that are statistically different from zero. Within these areas, we also find the species with higher values of Hg concentration pooled mean in blood: Little, Gentoo, King, Northern Rockhopper (*Eudyptes moseleyi*), and Macaroni penguin. All these species have pooled means that are statistically different from zero. The area with the lowest value is the Antarctic Peninsula, and the Adélie penguin has the lowest Hg value. Among the penguin species inhabiting the same area, the Hg levels are generally similar. However, those species with higher trophic levels also show slightly higher Hg values, except for the Gentoo penguin.

The two penguin species present in more than one area are Adélie and Gentoo penguin. Although Adélie penguins have similar values in all areas, slightly higher Hg levels are observed in Antarctica, followed by the South Atlantic Ocean and the Antarctic Peninsula. Hg levels in Gentoo penguins contrast among locations, with higher values of Hg concentration in the Indian Ocean than in Antarctica.

Confidence intervals for all penguin species contain values above the current observed threshold of toxicity in blood (0.67 $\mu g \cdot g^{-1}$dw; Ackerman et al., 2016). The confidence interval in the blood is higher than in feathers, thus pointing to a greater uncertainty. This is because the effect size by subgroup is smaller, as we have fewer reports in blood than in feathers. Only Little, Gentoo (in the Indian Ocean), King, Northern Rockhopper, Macaroni, and Emperor penguin have their pooled mean values above the toxicity threshold in blood.

4. Discussion

We used penguins as bioindicator species to investigate the distribution of Hg across the Southern Hemisphere. Our findings showed variations in Hg levels across the Southern Hemisphere, highlighting certain areas as Hg hotspots like Australia, the Indian Ocean, and Tierra del Fuego, and coldspots in Perú and the South Atlantic. While intrinsic, species-specific factors, such as trophic level, may shape penguins' Hg body concentrations, we argue that penguins' Hg concentration closely track spatial patterns of Hg bioavailability (Becker et al., 2016; Cherel et al., 2018; Mills et al., 2020; Renedo et al., 2020). Our results add to the mounting evidence pointing to penguins as effective bioindicator species to monitor Hg in marine environments (Brasso et al., 2015; Carravieri et al., 2013, 2016; Polito et al., 2016). However, we also shed light on significant knowledge gaps in specific species and geographic regions that should be filled if we aim to properly monitor Hg contamination in the Southern Hemisphere. Our framework could be expanded to other areas (whenever new information become available) and pollutants in future studies and become a useful tool for pollutant assessments and marine environmental health monitoring.

4.1. Hg levels in penguins

Our results show significant variations in Hg concentration values across different areas and penguin species throughout the Southern Hemisphere. In blood samples, reported Hg levels range from 0.01 $\mu g \cdot g^{-1}$ dw in Adélie penguin on the Antarctic peninsula to 1.89 $\mu g \cdot g^{-1}$ dw in Little penguin in Australia. In feathers samples, Hg concentrations are slightly higher, with values ranging from 0.06 $\mu g \cdot g^{-1}$ dw in Adélie penguin at the Antarctic peninsula to 3.37 $\mu g \cdot g^{-1}$ dw in Southern Rockhopper penguin at Tierra del Fuego. Much higher Hg concentrations have been reported for other seabird groups like albatrosses in both blood and feathers (e.g. Tavares et al., 2013; Carravieri et al., 2014; Cherel et al., 2018). For instance, in the Wandering albatross (*Diomedea exulans*) Hg concentrations in feathers reaching up 94.72 $\mu g \cdot g^{-1}$ dw (Bustamante et al., 2016). In contrast, mean Hg concentrations reported for feathers of Brown skua (*Stercorarius* antarcticus) of 1.10 $\mu g \cdot g^{-1}$ dw (Matias et al., 2022) were similar to those observed in some penguin species from the same area. Overall, penguins are comparatively less exposed to Hg than other co-occurring marine top/meso-predators such as giant petrels (Renedo et al., 2020; Manceau et al., 2021; Padilha et al., 2023). However, the exposure to Hg is viewed as a potential threat to this taxa (Ropert-Coudert et al., 2019; Trathan et al., 2015).

4.2. Inter-specific variations and confounding factors

Due to biomagnification processes, intrinsic factors such as trophic level modulate Hg body accumulation in penguins (Bestley et al., 2020; Brasso et al., 2015). For instance, this might explain the higher Hg concentrations reported for Emperor penguins in comparison with co-occurring Adélie penguins. While Adélie penguins usually prey on low trophic level prey (*i.e.*, euphausiids), Emperor penguins preferentially feed on fish, crustaceans, and squid, and hence occupy a higher trophic level (Cherel, 2008). Few examples contrast with this general biomagnification trend. This might be the case for the Southern Rockhopper penguin inhabiting the Antarctic Peninsula and Tierra del Fuego. While occupying lower trophic levels than co-occurring species (like Gentoo, Chinstrap or Magellanic penguins, based on trophic level information sourced from SeaLifeBase), the Southern Rockhopper penguin shows slightly greater Hg mean values in both locations. In part, this could be explained by the time integration period for feathers, and by potential shifts in individuals' diet and trophic level (Brasso et al., 2013, 2015; Polito et al., 2016). Accurate calculation of the trophic level for each specific location and period of integration could bring light into these discrepancies (Brasso et al., 2015). In this regard, it could be very useful the use Compound-specific Stable Isotope Analysis (CSIA), as it provides a good estimate of the trophic position of marine organisms even from spatially variable environments that might have different stable isotope baselines (Quillfeldt et al., 2023). However, this information is lacking in most of the studies, thus preventing its consideration within our analyses.

The trophic habitat where individuals forage can also play a relevant role in shaping penguin Hg concentrations. As an example in the Antarctic Peninsula, Chinstrap penguins feeding on mesopelagic prey had higher Hg concentrations than Adélie and Gentoo penguins that feed on epipelagic prey (Brasso et al., 2015; see also Fig. 4). Species-specific life history traits like longevity and sex (Becker et al., 2002; Carravieri et al., 2014; Tavares et al., 2013), or behavioural and physiological traits (differences in Hg detoxification and moult schedule; Muirhead & Furness, 1988; Tavares et al., 2013) can also influence the Hg body burdens. However, these factors are more important when trying to explain intraspecific variation (Carravieri et al., 2013) and are considered secondary in the influence of species relative exposure to Hg (Polito et al., 2016).

4.3. Spatial patterns

Despite the above-mentioned confounding factors shaping Hg body burdens, Hg concentration patterns are also related with the Hg spatial availability due to the presence of local sources of Hg. Our results spatially agree with previously reported latitudinal gradient for Hg concentrations in biota, with enhanced levels in sub-Antarctic and subtropical waters compared to Antarctic waters (Becker et al., 2016; Cherel et al., 2018; Mills et al., 2020; Renedo et al., 2020). This gradient could be explained by geographic differences in Hg release (e.g., volcanic emissions in Antarctica; Cusset et al., 2023; Schneider et al., 2023), by variations in Hg assimilation efficiency for primary producers that alter Hg availability in organisms between ecosystems, as well as by the different complexity of food webs that may change the biomagnification extend (Lavoie et al., 2013; Renedo et al., 2020). Antarctic ecosystems showed higher productivity compared to sub-tropical ecosystems, allowing Hg dilution at the base of the food web (Renedo et al., 2020; but see Yue et al., 2023). This effect of biodilution associated with highly productive areas could explain the exceptions to the general latitudinal gradient observed for the penguin species inhabiting Perú and the South Atlantic, with lower Hg concentrations in blood than those from the Antarctic Peninsula or Antarctica. Previous studies have observed this biodilution process associated with the Humboldt current for different seabirds that feed on anchovies (Le Croizier et al., 2022), which could also apply to the Humboldt penguin (lower Hg values in Perú) that also have anchovies among their main prey (Herling et al., 2005). These observed Hg coldspots also coincide with areas of predicted lower Hg concentrations (Zhang et al., 2021).

Observed deviations from the general pattern of Hg concentrations in feather samples in the previous section (Inter-specific variations and confounding factors) could also be related to the information reflected by this tissue. Feathers integrate Hg concentrations accumulated by individuals during the inter-moult periods when penguins are no longer central-place foragers. They may show contrasting feeding preferences from the specific region where the sample was taken (Carravieri et al., 2014). This is particularly the case for non-resident penguin species that spread over large marine areas out of the breeding period (Croxall & Davis, 1999; like Southern Rockhopper, Macaroni or Chinstrap penguin). Unfortunately, little is known about the non-breeding distribution of penguin species; thus, preventing from spatial inferences on the exposure to Hg.

Our meta-analyses demonstrate that Hg is spread along the Southern Hemisphere. However, Hg levels are unevenly distributed spatially, and Hg hotspots emerge in Australia, the Indian Ocean, and Tierra del Fuego. These areas coincide with Hg hotspots previously described for penguins (Brasso et al., 2015), but also with those areas of projected enhanced Hg availability (Zhang et al., 2021). According to our results, the populations that could be particularly exposed to Hg were Little (Australia), King (Indian Ocean and Tierra del Fuego), Gentoo (Indian Ocean), Southern Rockhopper (Tierra del Fuego), and Macaroni penguin (Tierra del Fuego). From this list, the Southern Rockhopper and Macaroni penguin are considered vulnerable by the IUCN Red List with a decreasing trend in their populations.

5. Conclusions and future perspectives

This work provides a comprehensive framework where the most up-to-date dataset on Hg level for penguins (available at DigitalCSIC: https://doi.org/10.20350/digitalCSIC/15722) was integrated in a meta-analysis for assessing the spatial patterns of Hg through the Southern Hemisphere. Penguins are excellent for long-term routine monitoring because they present synchronous rather than asynchronous moult of body feathers providing more accurate values (Carravieri et al., 2014). With our study, we add to the growing body of literature emphasizing the role of penguins as bioindicators of Hg pollution, and showcasing the geographical variability of Hg throughout the Southern Hemisphere. Our results confirm the previously described Hg hotspots in Australia, the Indian Ocean, and Tierra del Fuego (Brasso et al., 2015). We also identified coldspots in Perú and the South Atlantic. This comprehensive evaluation of all the published work in penguins' feathers and blood also enables us to gain insight into the information gaps that exist, and may be addressed in the future research. Indeed, we observe a clear geographical bias in the data towards the Antarctica Peninsula, Australia, and Crozet Islands. In contrast, important gaps of knowledge exist in key regions for penguins such as the Galápagos Islands, South Africa, and the coast of Chile; and for key species such as Fiordland, Snares, Erect-crested, Royal, Yellow-eyed, and Galápagos penguins.

Future efforts should prioritize these gaps of knowledge, as well as those penguin species exhibiting Hg levels that may impact their survival and fecundity. We recommend these future studies try to consider CSIA to cope with the isotopic baseline effects when estimating trophic level, so that a direct comparisons can be made at the large scale (Quillfeldt et al., 2022), and among different species from a single locations (Thébault et al., 2021). Moreover, considering the current global change scenario, it would be intriguing to investigate how the threshold of adverse effects might be altered by additional and co-occurring stressors. Indeed, our results only present values over current adverse effect levels of Hg for some of the penguins' populations. Pollution (specifically Hg pollution) is, however, one of the multiple stressors that threaten the penguin community (see Ropert-Coudert et al., 2019 for a comprehensive list of potential stressors), and little is known about how possible joint effects between pollution and other stressors could affect different species (Bestley et al., 2020). Under the current scenario of global environmental change, studying these interactions will be of particular interest as they can lower the threshold of adverse effects in penguins (see Grunst et al., 2023). In such a perspective, selenium levels in penguins should also be considered as this element has protective properties against Hg toxicity (Manceau et al., 2021).

Our study highlights the importance of a comprehensive compilation of available data for assessing global threats and monitoring environmental health. Our results can be used to contribute to the protection of vulnerable species and important habitats, and to the implementation of effective conservation measures focused on highly impacted regions, species, and populations.

CRediT authorship contribution statement

Míriam Gimeno: Data curation, Formal analysis, Writing - original draft, Writing - review & editing. **Laia Rossell:** Data curation, Formal analysis, Writing - original draft, Writing - review & editing. **Laura Julià:** Data curation, Formal analysis, Methodology, Writing - review & editing. **Joan Giménez:** Conceptualization, Supervision, Writing - review & editing. **Carolina Sanpera:** Writing - review & editing. **Marta Coll:** Conceptualization, Funding acquisition, Writing - review & editing. **Paco Bustamante:** Validation, Writing - review & editing. **Francisco Ramírez:** Conceptualization, Funding acquisition, Supervision, Writing - original draft, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Database available at DigitalCSIC: https://doi.org/10.20350/digitalCSIC/15722.

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References

Ackerman, J.T., Eagles-Smith, C.A., Herzog, M.P., Hartman, C.A., Peterson, S.H., Evers, D.C., Jackson, A.K., Elliott, J.E., Vander Pol, S.S., Bryan, C.E., 2016. Avian mercury exposure and toxicological risk across western North America: a synthesis. Sci. Total Environ. 568, 749–769.

Albert, C., Renedo, M., Bustamante, P., Fort, J., 2019. Using blood and feathers to investigate large-scale Hg contamination in Arctic seabirds: a review. Environ. Res. 177, 108588.

Álvarez-Varas, R., Morales-Moraga, D., González-Acuña, D., Klarian, S.A., Vianna, J.A., 2018. Mercury exposure in Humboldt (*Spheniscus humboldti*) and Chinstrap (*Pygoscelis antarcticus*) penguins throughout the Chilean coast and Antarctica. Arch. Environ. Contam. Toxicol. 75, 75–86.

Bearhop, S., Ruxton, G.D., Furness, R.W., 2000. Dynamics of mercury in blood and feathers of great skuas. Environ. Toxicol. Chem. 19, 1638–1643.

Becker, P.H., González-Solís, J., Behrends, B., Croxall, J., 2002. Feather mercury levels in seabirds at South Georgia: influence of trophic position, sex and age. Mar. Ecol. Prog. Ser. 243, 261–269.

Becker, P.H., Goutner, V., Ryan, P.G., González-Solís, J., 2016. Feather mercury concentrations in Southern Ocean seabirds: variation by species, site and time. Environ. Pollut. 216, 253–263.

Beiras, R., 2018. Marine Pollution: Sources, Fate and Effects of Pollutants in Coastal Ecosystems. Elsevier, Amsterdam, Netherlands.

Bestley, S., Ropert-Coudert, Y., Bengtson Nash, S., Brooks, C.M., Cotté, C., Dewar, M., Friedlaender, A.S., Jackson, J.A., Labrousse, S., Lowther, A.D., McMahon, C.R., Phillips, R.A., Pistorius, P., Puskic, P.S., Reis, et al., 2020. Marine ecosystem assessment for the Southern Ocean: birds and marine mammals in a changing climate. Front. Ecol. Evol. 8, 566936.

Bhardwaj, L., Chauhan, A., Ranjan, A., Jindal, T., 2018. Persistent organic pollutants in biotic and abiotic components of antarctic pristine environment. Earth Syst. Environ. 2, 35–54.

Brasso, R.L., Drummond, B.E., Borrett, S.R., Chiaradia, A., Polito, M.J., Rey, A.R., 2013. Unique pattern of molt leads to low intraindividual variation in feather mercury concentrations in penguins: intraindividual variation of mercury in penguin feathers. Environ. Toxicol. Chem. 32, 2331–2334.

Brasso, R.L., Chiaradia, A., Polito, M.J., Raya Rey, A., Emslie, S.D., 2015. A comprehensive assessment of mercury exposure in penguin populations throughout the Southern Hemisphere: using trophic calculations to identify sources of population-level variation. Mar. Pollut. Bull. 97, 408–418.

Braune, B.M., 1987. Comparison of total mercury levels in relation to diet and molt for nine species of marine birds. Arch. Environ. Contam. Toxicol. 16, 217–224.

Bridge, E.S., 2006. Influences of morphology and behavior on wing-molt strategies in seabirds. Mar. Ornithol. 34, 7–19.

Bustamante, P., Carravieri, A., Goutte, A., Barbraud, C., Delord, K., Chastel, O., Weimerskirch, H., Cherel, Y., 2016. High feather mercury concentrations in the wandering albatross are related to sex, breeding status and trophic ecology with no demographic consequences. Environ. Res. 144, 1–10.

Carravieri, A., Bustamante, P., Churlaud, C., Cherel, Y., 2013. Penguins as bioindicators of mercury contamination in the Southern Ocean: birds from the Kerguelen Islands as a case study. Sci. Total Environ. 454–455, 141–148.

Carravieri, A., Bustamante, P., Churlaud, C., Fromant, A., Cherel, Y., 2014. Moulting patterns drive within-individual variations of stable isotopes and mercury in seabird body feathers: implications for monitoring of the marine environment. Mar. Biol. 161, 963–968.

Carravieri, A., Cherel, Y., Jaeger, A., Churlaud, C., Bustamante, P., 2016. Penguins as bioindicators of mercury contamination in the southern Indian Ocean: geographical and temporal trends. Environ. Pollut. 213, 195–205.

Chastel, O., Fort, J., Ackerman, J.T., Albert, C., Angelier, F., Basu, N., Blévin, P., Brault-Favrou, M., Bustnes, J.O., Bustamante, P., Danielsen, J., Descamps, S., Dietz, R., Erikstad, K., et al., 2022. Mercury contamination and potential health risks to Arctic seabirds and shorebirds. Sci. Total Environ. 844, 156944.

Cherel, Y., 2008. Isotopic niches of emperor and Adélie penguins in Adélie land, Antarctica. Mar. Biol. 154, 813–821.

Cherel, Y., Barbraud, C., Lahournat, M., Jaeger, A., Jaquemet, S., Wanless, R.M., Phillips, R.A., Thompson, D.R., Bustamante, P., 2018. Accumulate or eliminate? Seasonal mercury dynamics in albatrosses, the most contaminated family of birds. Environ. Pollut. 241, 124–135.

Cossa, D., Heimbürger, L.-E., Lannuzel, D., Rintoul, S.R., Butler, E.C.V., Bowie, A.R., Averty, B., Watson, R.J., Remenyi, T., 2011. Mercury in the Southern Ocean. Geochem. Cosmochim. Acta 75, 4037–4052.

Croxall, J.P., Davis, L.S., 1999. Penguins: paradoxes and patterns. Mar. Ornithol. 27, 1–12.

Cusset, F., Bustamante, P., Carravieri, A., Bertin, C., Brasso, R., Corsi, I., et al., 2023. Circumpolar assessment of mercury contamination: the Adélie penguin as a bioindicator of Antarctic marine ecosystems. Ecotoxicology 32 (8), 1024–1048.

Driscoll, C.T., Mason, R.P., Chan, H.M., Jacob, D.J., Pirrone, N., 2013. Mercury as a global pollutant: sources, pathways, and effects. Environ. Sci. Technol. 47, 4967–4983.

Espejo, W., Celis, J.E., GonzÃlez-Acuña, D., Banegas, A., Barra, R., Chiang, G., 2017. A global overview of exposure levels and biological effects of trace elements in penguins. In: de Voogt, P. (Ed.), Reviews of Environmental Contamination and Toxicology, vol. 245. Springer, Cham, pp. 1–64.

Evers, D.C., Savoy, L.J., DeSorbo, C.R., Yates, D.E., Hanson, W., Taylor, K.M., Siegel, L.S., Cooley, J.H., Bank, M.S., Major, A., Munney, K., Mower, B.F., Vogel, H.S., Schoch, N., Pokras, M., et al., 2008. Adverse effects from environmental mercury loads on breeding common loons. Ecotoxicology 17, 69–81.

Furness, R., Camphuysen, K., 1997. Seabirds as monitors of the marine environment. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 54, 726–737.

Gordon, M., Lumley, T., 2021. Forestplot: Advanced Forest Plot Using 'grid' Graphics (2.0.1.). R package.

Goutte, A., Barbraud, C., Meillère, A., Carravieri, A., Bustamante, P., Labadie, P., Budzinski, H., Delord, K., Cherel, Y., Weimerskirch, H., Chastel, O., 2014a. Demographic consequences of heavy metals and persistent organic pollutants in a vulnerable long-lived bird, the wandering albatross. Proc. Biol. Soc. 281, 20133313.

Goutte, A., Bustamante, P., Barbraud, C., Delord, K., Weimerskirch, H., Chastel, O., 2014b. Demographic responses to mercury exposure in two closely related Antarctic top predators. Ecology 95, 1075–1086.

Grunst, A.S., Grunst, M.L., Grémillet, D., Kato, A., Bustamante, P., Albert, C., Brisson-Curadeau, É., Clairbaux, M., Cruz-Flores, M., Gentès, S., Perret, S., Ste-Marie, E., Wojczulanis-Jakubas, K., Fort, J., 2023. Mercury contamination challenges the behavioral response of a keystone species to arctic climate change. Environ. Sci. Technol. 57, 2054–2063.

Harrer, M., Cuijpers, P., Furukawa, T.A., Ebert, D.D., 2021. Doing Meta-Analysis with R: A Hands-On Guide, first ed. Chapman and Hall/CRC, New York.

Herling, C., Culik, B.M., Hennicke, J.C., 2005. Diet of the Humboldt penguin (*Spheniscus humboldti*) in northern and southern Chile. Mar. Biol. 147, 13–25.

Higgins, J.P.T., Thompson, S.G., Spiegelhalter, D.J., 2009. A Re-evaluation of random-effects meta-analysis. J. Roy. Stat. Soc. Stat. Soc. 172, 137–159.

Honda, K., Nasu, T., Tatsukawa, R., 1986. Seasonal changes in mercury accumulation in the black-eared kite, *Milvus migrans lineatus*. Environ. Pollut. Ecol. Biol. 42, 325–334.

Jerez, S., Motas, M., Benzal, J., Diaz, J., Barbosa, A., 2013. Monitoring trace elements in antarctic penguin chicks from South shetland Islands, Antarctica. Mar. Pollut. Bull. 69, 67–75.

Knapp, G., Hartung, J., 2003. Improved tests for a random effects meta-regression with a single covariate. Stat. Med. 22, 2693–2710.

Langan, D., Higgins, J.P.T., Jackson, D., Bowden, J., Veroniki, A.A., Kontopantelis, E., Viechtbauer, W., Simmonds, M., 2019. A comparison of heterogeneity variance estimators in simulated random-effects meta-analyses. Res. Synth. Methods 10, 83–98.

Lavoie, R.A., Jardine, T.D., Chumchal, M.M., Kidd, K.A., Campbell, L.M., 2013. Biomagnification of mercury in aquatic food webs: a worldwide meta-analysis. Environ. Sci. Technol. 47, 13385–13394.

Le Croizier, G., Point, D., Renedo, M., Munaron, J.-M., Espinoza, P., Amezcua-Martinez, F., Lanco Bertrand, S., Lorrain, A., 2022. Mercury concentrations, biomagnification and isotopic discrimination factors in two seabird species from the Humboldt Current ecosystem. Mar. Pollut. Bull. 177, 113481.

Manceau, A., Gaillot, A.C., Glatzel, P., Cherel, Y., Bustamante, P., 2021. In vivo formation of HgSe nanoparticles and Hg-tetraselenolate complex from methylmercury in seabird – implications for the Hg-Se antagonism. Environ. Sci. Technol. 55 (3), 1515–1526.

Matias, R.S., Guímaro, H.R., Bustamante, P., Seco, J., Chipev, N., Fragão, J., Tavares, S., Ceia, F.R., Pereira, M.E., Barbosa, A., Xavier, J.C., 2022. Mercury biomagnification in an antarctic food web of the antarctic peninsula. Environ. Pollut. 304, 119199.

Mills, W.F., Bustamante, P., McGill, R.A.R., Anderson, O.R.J., Bearhop, S., Cherel, Y., Votier, S.C., Phillips, R.A., 2020. Mercury exposure in an endangered seabird: long-term changes and relationships with trophic ecology and breeding success. Proc. Biol. Sci. 287, 20202683.

Mills, W.F., Ibañez, A.E., Bustamante, P., Carneiro, A.P.B., Bearhop, S., Cherel, Y., Mariano-Jelicich, R., McGill, R.A.R., Montalti, D., Votier, S.C., Phillips, R.A., 2022. Spatial and sex differences in mercury contamination of skuas in the Southern Ocean. Environ. Pollut. 297, 118841.

Muirhead, S.J., Furness, R.W., 1988. Heavy metal concentrations in the tissues of seabirds from gough Island, South Atlantic ocean. Mar. Pollut. Bull. 19, 278–283.

Padilha, J.A.G., Souza-Kasprzyk, J., Pinzone, M., Bighetti, G.P., Espejo, W., Leite, A., et al., 2023. Mercury exposure in Antarctic seabirds: assessing the influence of trophic position and migration patterns. Chemosphere 340, 139871.

Page, M.J., McKenzie, J.E., Bossuyt, P.M., Boutron, I., Hoffmann, T.C., Mulrow, C.D., Shamseer, L., Tetzlaff, J.M., Akl, E.A., Brennan, S.E., Chou, R., Glanville, J., Grimshaw, J.M., Hróbjartsson, A., Lalu, M.M., et al., 2021. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. PLoS Med. 18, e1003583.

Polito, M.J., Brasso, R.L., Trivelpiece, W.Z., Karnovsky, N., Patterson, W.P., Emslie, S.D., 2016. Differing foraging strategies influence mercury (Hg) exposure in an Antarctic penguin community. Environ. Pollut. 218, 196–206.

Puasa, N.A., Zulkharnain, A., Verasoundarapandian, G., Wong, C.-Y., Zahri, K.N.M., Merican, F., Shaharuddin, N.A., Gomez-Fuentes, C., Ahmad, S.A., 2021. Effects of diesel, heavy metals and plastics pollution on penguins in Antarctica: a review. Animals 11, 2505.

Quillfeldt, P., Bedolla-Guzmán, Y., Libertelli, M.M., Cherel, Y., Massaro, M., Bustamante, P., 2023. Mercury in Ten Storm-Petrel Populations from the Antarctic to the Subtropics. Arch. Environ. Contam. Toxicol. 85, 55–72.

Quillfeldt, P., Cherel, Y., Navarro, J., Phillips, R.A., Masello, J.F., Suazo, C.G., Delord, K., Bustamante, P., 2022. Variation among species and populations, and carry-over effects of winter exposure on mercury accumulation in small petrels. Front. Ecol. Evol. 10, 915199.

R Core Team, 2022. R: A Language and Environment for Statistical Computing (4.2.2.). R Foundation for Statistical Computing, Vienna, Austria.

Renedo, M., Amouroux, D., Pedrero, Z., Bustamante, P., Cherel, Y., 2018. Identification of sources and bioaccumulation pathways of MeHg in subantarctic penguins: a stable isotopic investigation. Sci. Rep. 8, 8865.

Renedo, M., Bustamante, P., Cherel, Y., Pedrero, Z., Tessier, E., Amouroux, D., 2020. A "seabird-eye" on mercury stable isotopes and cycling in the Southern Ocean. Sci. Total Environ. 742, 140499.

Ropert-Coudert, Y., Chiaradia, A., Ainley, D., Barbosa, A., Boersma, P.D., Brasso, R., Dewar, M., Ellenberg, U., García-Borboroglu, P., Emmerson, L., Hickcox, R., Jenouvrier, S., Kato, A., McIntosh, R.R., Lewis, P., et al., 2019. Happy feet in a hostile world? The future of penguins depends on proactive management of current and expected threats. Front. Mar. Sci. 6, 248.

Scheuhammer, A.M., Basu, N., Evers, D.C., Heinz, G., Sandheinrich, M.B., Bank, M.S., 2012. Ecotoxicology of Mercury in Fish and Wildlife: Recent Advances.

Schneider, L., Fisher, J.A., Diéguez, M.C., Fostier, A.H., Guimaraes, J.R.D., Leaner, J.J., Mason, R., 2023. A synthesis of mercury research in the Southern Hemisphere, part 1: Natural processes. Ambio 52, 897–917.

Seco, J., Aparício, S., Brierley, A.S., Bustamante, P., Ceia, F.R., Coelho, J.P., Philips, R.A., Saunders, R.A., Fielding, S., Gregory, S., Matias, R., Pardal, M.A., Pereira, E., Stowasser, G., Tarling, G.A., Xavier, J.C., 2021. Mercury biomagnification in a Southern Ocean food web. Environ. Pollut. 275, 116620.

Selin, N.E., 2009. Global biogeochemical cycling of mercury: a review. Annu. Rev. Environ. Resour. 34, 43–63.

Streets, D.G., Horowitz, H.M., Jacob, D.J., Lu, Z., Levin, L., Ter Schure, A.F.H., Sunderland, E.M., 2017. Total mercury released to the environment by human activities. Environ. Sci. Technol. 51, 5969–5977.

Streets, D.G., Horowitz, H.M., Lu, Z., Levin, L., Thackray, C.P., Sunderland, E.M., 2019. Five hundred years of anthropogenic mercury: spatial and temporal release profiles. Environ. Res. Lett. 14, 084004.

Tan, S.W., Meiller, J.C., Mahaffey, K.R., 2009. The endocrine effects of mercury in humans and wildlife. Crit. Rev. Toxicol. 39, 228–269.

Tavares, S., Xavier, J.C., Phillips, R.A., Pereira, M.E., Pardal, M.A., 2013. Influence of age, sex and breeding status on mercury accumulation patterns in the wandering albatross *Diomedea exulans*. Environ. Pollut. 181, 315–320.

Thébault, J., Bustamante, P., Massaro, M., Taylor, G., Quillfeldt, P., 2021. Influence of species-specific feeding ecology on mercury concentrations in seabirds breeding on the Chatham Islands, New Zealand. Environ. Toxicol. Chem. 40, 454–472.

Thompson, D.R., Hamer, K.C., 2000. Stress in seabirds: causes, consequences and diagnostic value. J. Aquatic Ecosyst. Stress Recovery 7, 91–109.

Trathan, P.N., García-Borboroglu, P., Boersma, D., Bost, C.A., Crawford, R.J., Crossin, G. T., et al., 2015. Pollution, habitat loss, fishing, and climate change as critical threats to penguins. Conserv. Biol. 29, 31–41.

UNEP, 2019. Global Mercury Assessment 2018. *UN Environment Programme. Chemicals And Health Branch*. Chemicals and Health Branch Geneva, Switzerland.

Viechtbauer, W., 2005. Bias and efficiency of meta-analytic variance estimators in the random-effects model. J. Educ. Behav. Stat. 30, 261–293.

Viechtbauer, W., 2010. Conducting meta-analyses in *R* with the **metafor** package. J. Stat. Software 36, 1–48.

Wolfe, M.F., Schwarzbach, S., Sulaiman, R.A., 1998. Effects of mercury on wildlife: a comprehensive review. Environ. Toxicol. Chem. 17, 146–160.

Yue, F., Li, Y., Zhang, Y., Wang, L., Li, D., Wu, P., Liu, H., Lin, L., Li, D., Hu, J., Xie, Z., 2023. Elevated methylmercury in Antarctic surface seawater: the role of phytoplankton mass and sea ice. Sci. Total Environ. 882, 163646.

Zhang, Y., Song, Z., Huang, S., Zhang, P., Peng, Y., Wu, P., Gu, J., Dutkiewicz, S., Zhang, H., Wu, S., Wang, F., Chen, L., Wang, S., Li, P., 2021. Global health effects of future atmospheric mercury emissions. Nat. Commun. 12, 3035.

Zhang, X., Zhang, X., Zhang, Z.-F., Yang, P.-F., Li, Y.-F., Cai, M., Kallenborn, R., 2022. Pesticides in the atmosphere and seawater in a transect study from the Western Pacific to the Southern Ocean: the importance of continental discharges and air-seawater exchange. Water Res. 217, 118439.