Monitoring of mercury in the mesopelagic domain of the Pacific and Atlantic oceans using body feathers of Bulwer's petrel as a bioindicator

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HIGHLIGHTS

- Bulwer's petrels were used as biomonitors of Hg levels in the mesopelagic domain.
- Atlantic colonies showed higher Hg concentrations than those from the Pacific.
- CSIA-AA-derived trophic levels for chicks were similar among colonies.
- Feather Hg levels recorded were lower than those reported in 1992 for the Atlantic.

GRAPHICAL ABSTRACT
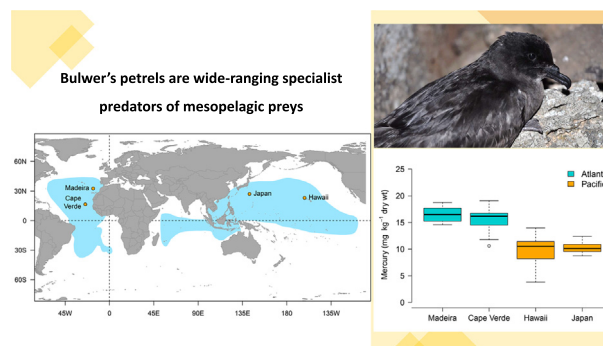
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ABSTRACT

Global mercury pollution has markedly and consistently grown over the past 70 years (although with regional variations in trends) and is a source of major concern. Mercury contamination is particularly prevalent in biota of the mesopelagic layers of the open ocean, but these realms are little studied, and we lack a large scale picture of contamination in living organisms of this region. The Bulwer's petrel *Bulweria bulwerii*, a species of migratory seabird, is a highly specialised predator of mesopelagic fish and squid, and therefore can be used as a bioindicator for the mesopelagic domain. Mercury accumulated by the birds through diet is excreted into feathers during the moulting process in adults and feather growth in chicks, reflecting contamination in the non-breeding and breeding periods, respectively, and hence the influence of different, largely non-overlapping breeding and non-breeding ranges. We studied mercury in feathers and the trophic position in two colonies from the Atlantic Ocean (Portugal and Cape Verde) and two colonies from the Pacific Ocean (Japan and Hawaii). We found significantly lower levels of mercury in adult and chick samples from the Pacific Ocean compared with samples from the Atlantic Ocean. However, we did not detect differences in trophic position of chicks among colonies and oceans, suggesting that differences in mercury measured in feathers reflect levels of environmental contamination, rather than differences in the structure of the trophic chain in different oceans. We conclude that despite a reduction in mercury levels in the Atlantic in recent decades, mesopelagic

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organisms in this ocean remain more heavily contaminated than in the Pacific at tropical and subtropical latitudes. We suggest that Bulwer's petrel is a highly suitable species to monitor the global contamination of mercury in the mesopelagic domain.

1. Introduction

Global mercury pollution has markedly and consistently grown over the past 70 years (although with regional variations in trends) as a result of anthropogenic activities such as gold extraction, industrial production, waste incineration and the use of fossil fuels (Driscoll et al., 2013; Esdaile and Chalker, 2018; Gworek et al., 2016; Lamborg et al., 2014; Streets et al., 2019, 2011). Mercury is widely transported in the atmosphere and is also distributed in marine ecosystems through oceanic circulation (Driscoll et al., 2013). For pelagic ocean zones, the dominant source of mercury is atmospheric deposition (an exception is the Arctic Ocean where coastal erosion is likely the dominant source) (Obrist et al., 2018). This elemental mercury sinks adsorbed to particles and is transformed to methylmercury by biogeochemical processes in low oxygen environments, such as the mesopelagic zone (200–1000 m below the ocean surface) (Choy et al., 2009; Lamborg et al., 2014; Mason and Fitzgerald, 1991; Sunderland et al., 2009). It is in this organic form that it is biomagnified up the food chain, with top predators such as seabirds exhibiting elevated concentrations of mercury (Lavoie et al., 2013). In fact, mesopelagic fauna provide a trophic link between surface and deep waters as a result of their diel vertical migration (Kelly et al., 2019). Consequently, they also transport methylmercury into the epipelagic domain (Madigan et al., 2018; Motta et al., 2019; Thompson et al., 1998).

Top predators, such as pelagic seabirds, particularly those that feed on mesopelagic prey, are highly exposed to persistent and toxic mercury (e.g., Carravieri et al., 2018, 2020; Furtado et al., 2019, 2020; Monteiro and Furness, 1995, 1997; Kim et al., 1996). Because in-situ monitoring of the mesopelagic layer is difficult, bioindicators, as seabirds, are commonly used to monitor these ecosystems. Many biomonitoring efforts report on inter-species comparisons which may introduce other sources of variation, predominantly differences in prey type both at the inter- and intra-species level (e.g., Drevnick et al., 2015; Fleishman et al., 2019; Monteiro and Furness, 1997; Thompson et al., 1998). Some seabirds, such as the Bulwer's petrel (*Bulweria bulwerii*), are specialised predators of mesopelagic prey (Neves et al., 2011; Harrison et al., 1983; Spear et al., 2007; Waap et al., 2017). Their low variability in diet (Spear et al., 2007; Waap et al., 2017) and wide spatial distribution (Dias et al., 2015; Brooke, 2004) makes them ideal candidates to monitor oceanic mercury contamination over multiple ocean basins. The Bulwer's petrel is a small (ca. 100 g), highly pelagic seabird with a large distribution in the tropical and subtropical waters of the world's oceans (Brooke, 2004; Dias et al., 2015; Ramos et al., 2015). In the Pacific Ocean, it breeds on Japan, the Hawaiian Islands, eastern China and French Polynesia, while in the Atlantic it breeds on the Macaronesian archipelagos of the Azores, Madeira, Canaries and Cape Verde (Brooke, 2004).

During the non-breeding season, Bulwer's petrels from Desertas and Cape Verde are mid- to long-distance migrants, moving into tropical deep, open oceanic areas in the Atlantic (Dias et al., 2015; Ramos et al., 2015). Those nesting in Hawaii and Japan migrate to central and eastern tropical Pacific waters and into the Indian Ocean (Brooke, 2004; Harrison, 1990). Outside the breeding season, the wide-ranging movements of birds from colonies from Atlantic and Pacific Ocean (e.g., Dias et al., 2015) mean that populations are sampling at an ocean-basin scale (millions of km²). Mercury values obtained from adult feathers are expected to largely reflect mercury exposure during the non-breeding period, when most body feathers are moulted (ca. mid-September to March) (Furness et al., 1986; Howell, 2012; Monteiro et al., 1996; own unpublished data). On the other hand, during the breeding-season seabirds act as central place foragers, restricting provisioning trips to waters within a range of the colony to be able to regularly feed the chick (Chaurand and Weimerskirch, 1994; Granadeiro et al., 1998; Shoji et al., 2015; Wischnewski et al., 2019). GPS tracking data from Raso, Cape Verde, place the mean maximum displacement from the colony of chick-rearing Bulwer's petrels at 335 ± 159 km (V. H. Paiva, unpublished data). Assuming similar foraging strategies across the four colonies, the chicks of Bulwer's petrels can be seen as biological samplers of a defined area (of tens of thousands of km²) around the breeding colonies.

Apart from geographical differences in mercury contamination, mercury levels in tissue are dependent on trophic position (Lavoie et al., 2013; Monteiro et al., 1998). Recently, compound-specific stable isotope analysis of amino acids (CSIA-AA) has been used to determine trophic position of seabirds robustly (e.g., Gagne et al., 2018; Gatt et al., 2020b; McMahon et al., 2015; Quillfeldt et al., 2017; Quillfeldt and Masello, 2020). By comparing the relative enrichment of ^{15}N in "source" and "trophic" amino acids, typically phenylalanine and glutamic acid respectively, CSIA-AA effectively overcomes the limitations in interpreting bulk isotope ratios in oceanic taxa as a result of a poorly-defined baseline isoscape (Graham et al., 2009). Phenylalanine represents the isotope ratio of primary producers at the base of the food chain, effectively providing the isotopic baseline needed to calculate the trophic position. In contrast, glutamic acid is increasingly enriched with ^{15}N as it undergoes nitrogen fractionation up the food chain (Ohkouchi et al., 2017). Given that Bulwer's petrels are known to be specialist predators of small mesopelagic fishes and squids (Neves et al., 2011; Spear et al., 2007; Waap et al., 2017), we could expect trophic position to be similar between colonies. If trophic positions are similar among individuals from different colonies, then variability in mercury concentrations would reflect geographical variation in mercury contamination at medium to large geographical scales.

Here, we investigate geographical differences in mercury concentration in feathers of adults and chicks of Bulwer's petrels from two Atlantic and two Pacific colonies, which reflect contamination levels in the mesopelagic domain. Furthermore, we quantified CSIA-derived trophic position in chicks to determine whether any differences in mercury exposure may be a result of trophic position. Feathers are the major sink for mercury excretion in birds, where mercury is deposited during feather growth, reflecting accumulation through diet over this period (Monteiro and Furness, 2001). As a result, quantifying mercury in feathers provides temporal and spatial contexts (Hobson, 1999; Monteiro and Furness, 1995). It is known, however, that some mercury is accumulated previous to moult, and the first feathers to be moulted display higher concentrations than the ones moulted later (Gatt et al., 2020a). Avoiding feathers that are moulted earlier (such as the inner primaries) and taking a large number of feathers minimizes and dilutes this problem. Furthermore, this problem does not affect large chicks, for which the contribution of egg mercury is likely very small and virtually all the mercury originates from diet in the well-defined period ranging from hatching to feather growth (Ackerman et al., 2011; Bearhop et al., 2000). We tested whether (a) mercury exposure in adults and chicks was significantly influenced by geographical area, and (b) whether trophic position differed significantly among chicks from different colonies and oceans.

2. Methods

2.1. Study site and sampling procedure

We collected Bulwer's petrels feather samples during the 2018 breeding season from two colonies in the Atlantic Ocean – Deserta Grande (32°30′N 16°30′W) of the Madeiran archipelago, Portugal, and Raso Islet (16°37′N 24°35′W) in Cape Verde and from two colonies in the Pacific Ocean – Nihoa Island (23°03′N; 161°55′W) in Hawaii, USA, and Minami-jima Island (27°02′N; 142°10′E) in Japan (Fig. 1). The colonies sampled have similar breeding phenology (April–October) (Chiba, 2020; Cruz-Flores et al., 2018; Kohno et al., 1986; Nunes and Vicente, 1998; Whittow, 1994). Eight to ten body feathers were collected from incubating adult birds (n = 71 in total, 15–20 individuals per colony) and growing feathers from chicks towards the end of the chick-rearing period (August–October, before fledging) (n = 75 in total, 15–20 individuals per colony) (Table 1). Feathers were clipped, in the superior umbilicus of feather, excluding the calamus, and collected from various locations on the body (dorsal and ventral; below the neck and above the lower extremities) and stored in polyethylene bags.

2.2. Mercury analyses

The feathers were cut into fine pieces to produce a homogeneous sample, and an electronic micro-balance (Sartorius M5P, Sartorius AG, Gottingen, with 0.001 mg precision) was used to prepare between 0.26 mg and 1.02 mg (mean = 0.51 ± 0.14 mg) of sample for mercury determination. We used thermal decomposition atomic absorption spectrometry with gold amalgamation in LECO AMA-254 equipment, to determine the total concentration of mercury in the body feathers (Costley et al., 2000). This procedure does not require sample pre-treatment (e.g., wash), and also allows for a small sample mass to be used. Briefly, feather samples were placed in a nickel boat and covered with aluminium oxide to prevent sample dispersion. Subsequently, the boat enters a combustion tube containing a catalyst where the sample is dried at 120 °C, followed by decomposition at 850 °C. Analyses were performed in triplicate per bird, blanks were analysed at the beginning of each set of samples, and the coefficient of variation between replicates never exceeded 10%. Accuracy and precision were assured by the daily analysis of five readings of a certified reference material (CRM)

lobster hepatopancreas TORT-3 (Lobster hepatopancreas from the National Research Council of Canada; certified mercury concentration: 0.292 ± 0.022 mg kg^{-1} dw). The obtained values (mean ± SD) for the TORT-3 analyses ranged from 75 to 90% (recovery efficiencies of $82.72 \pm 3.38\%$, n = 17), results were corrected using the daily recovery efficiency of CRM. The mass of TORT-3 used for quality control analyses was adjusted to be within the range of total mercury (in ng) present in the samples, with a maximum coefficient of variation of 10%. The limit of detection for this analytical method is 0.01 ng g^{-1} of total mercury. Mercury concentrations in feathers are presented in mg kg^{-1} fresh weight.

2.3. Compound-specific isotope analysis of amino acids

Collected feather samples were homogenized, as in the analysis of mercury, and sent to the Stable Isotope Facility at the University of California, Davis, for CSIA-AA of ^{15}N following calibration techniques detailed in Walsh et al. (2014) and Yarnes and Herszage (2017). Amino acids first underwent acid hydrolysis (6 M HCl, 70 min, 150 °C under a N$_2$ headspace) before derivatization as N-acetyl methyl esters. These derivatives were injected at 260 °C (splitless, 1 min) and separated on a polar gas chromatography column (Agilent DB-35) and combusted at a constant flow rate of 2 mL/min under the following temperature program: 70 °C (hold 2 min); 140 °C (15 °C min^{-1}, hold 4 min); 240 °C (12 °C min^{-1}, hold 5 min); and 255 °C (8 °C min^{-1}, hold 35 min). GC-C-IRMS was performed on a Thermo Trace GC 1310 gas chromatograph linked to a Thermo Scientific Delta V Advantage isotope-ratio mass spectrometer via a GC IsoLink II combustion interface. The combustion reactor is a NiO tube containing CuO and NiO wires maintained at 1000 °C. Water is subsequently removed through a Nafion dryer before the analyte gases are transferred to the IRMS. During ^{15}N analysis, CO$_2$ is removed from the post-combustion carrier stream through the use of a liquid nitrogen trap to prevent isobaric interferences within the ion source. Samples were analysed in duplicate, and triplicate measurements were recorded when average standard deviation exceeded ±1‰. Final quality assessment was based on the accuracy and precision of unbiased quality control materials, which included a calibrated amino acid mixture, UCD AA3, and multiple natural materials (fish skin gelatin reference material, whale baleen reference material and shark muscle reference material).
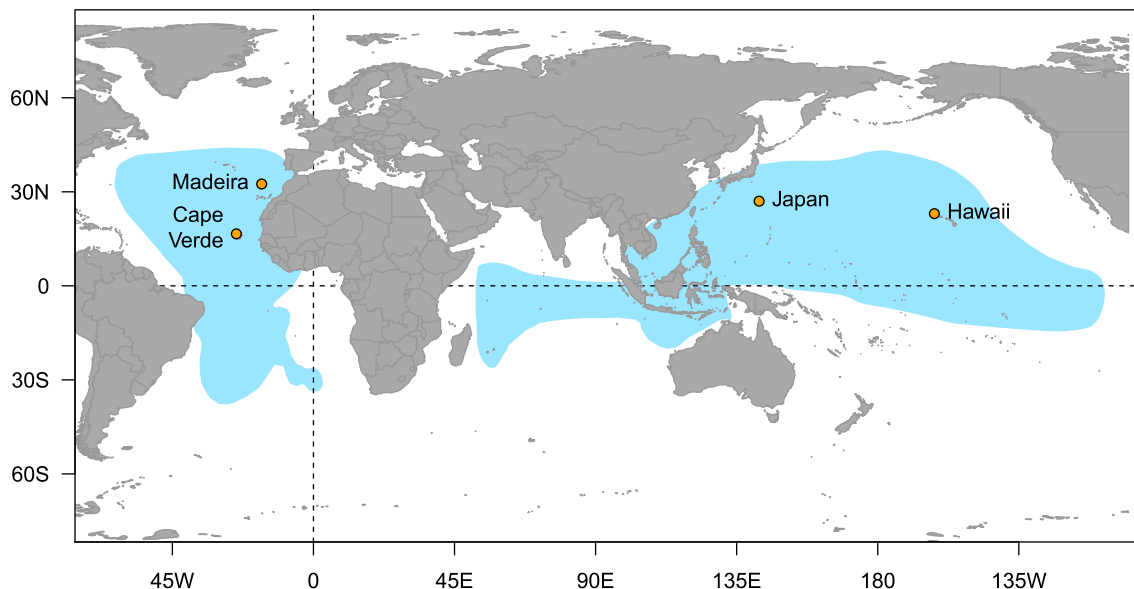

Fig. 1. Location of the four breeding colonies where Bulwer's petrels were sampled, and the species distribution during non-breeding season (blue), adapted from Brooke (2004), Dias et al. (2015) and Ramos et al. (2015). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Mercury concentration in feathers of adults and chicks of Bulwer's petrel (mean ± SD and range, mg kg^{-1} fresh wt).

Age	Ocean	Colony	[Hg] mg kg^{-1}		Number of samples
			Mean ± SD	Range	
Chicks	Atlantic Ocean	Cape Verde	5.11 ± 1.76	2.70–9.96	15
		Madeira	4.38 ± 1.69	2.94–8.25	20
	Pacific Ocean	Japan	2.13 ± 0.38	1.44–3.17	20
		Hawaii	2.90 ± 0.84	1.81–5.21	20
Adults	Atlantic Ocean	Cape Verde	15.65 ± 2.22	10.61–19.09	20
		Madeira	16.49 ± 1.39	14.60–18.76	20
	Pacific Ocean	Japan	10.27 ± 1.11	8.74–12.39	15
		Hawaii	10.00 ± 2.55	3.80–13.97[a]	15

[a] An outlier was removed (21.8 mg kg^{-1}).

2.4. Calculating trophic positions

Trophic position of chicks (Table 2) was calculated from the nitrogen stable isotope values (δ^{15}N) of glutamic acid (Glx) and phenylalanine (Phe). Including multiple trophic discrimination factors (TDF$_{Glx-Phe}$) in the estimation of trophic position, to integrate the span of the trophic web, produces more robust results, calculated as follows:

$$TP = 2 + \frac{Glx - Phe - 3.5 - 3.4}{6.2} \tag{a}$$

where 6.2‰ is the trophic discrimination factor for trophic position at the base of the aquatic food chain ($\Delta_{herbivore}$) (McMahon and McCarthy, 2016), 3.5‰ is the trophic discrimination factor for seabird feathers ($\Delta_{carnivore}$), and 3.4‰ is the difference in δ^{15}N between glutamic acid and phenylalanine in primary producers (β) (McMahon and McCarthy, 2016; Ohkouchi et al., 2017; Quillfeldt and Masello, 2020). To take into account both analytical and ecological variation, the uncertainty in trophic position was calculated by propagation of errors (Ohkouchi et al., 2017):

$$\sigma_{TP}^2 = \left(\frac{1}{\Delta_{carnivore}}\right)^2 \sigma_{\delta15N(Glx)}^2 + \left(\frac{-1}{\Delta_{carnivore}}\right)^2 \sigma_{\delta15N(Phe)}^2$$
$$+ \left(\frac{1}{\Delta_{carnivore}}\right)^2 \sigma_\beta^2 + \left(\frac{-1}{\Delta_{carnivore}}\right)^2 \sigma_{\Delta_{carnivore}}^2$$
$$+ \left\{\frac{-1}{\Delta_{carnivore}^2}\left(\delta^{15}N_{Glx} - \delta^{15}N_{Phe} + \beta - \Delta_{herbivore}\right)\right\}^2 \sigma_{herbivore}^2 \tag{b}$$

where $\sigma_{\Delta carnivore}$ and $\sigma_{\Delta herbivore}$ are estimated at 0.4‰ (McMahon et al., 2015) and 1.4‰ (Chikaraishi et al., 2007) respectively, and σ_β is 0.9‰ (Chikaraishi et al., 2009).

2.5. Statistical analysis

All statistical analyses were carried out with R statistical software (R Core Team, 2020). The means of mercury concentrations are presented with standard deviations. Mercury concentrations in feathers of adults from Hawaii showed a wide range of values, from 3.80 to 23.61 mg kg^{-1}, with the latter value being considered an outlier. We removed this outlier, but note that retaining it does not qualitatively

change any results and statistical conclusions. To compare the mean feather mercury concentrations of adults and chicks among geographical areas, we used ANOVA, followed by Tukey post hoc tests. We used analysis of variance (one-way ANOVA) to compare the trophic position of chicks in the different breeding areas, after checking for data normality. We also use Welch's t-tests for simple comparisons where appropriate.

3. Results

We found significant differences in mercury levels among breeding colonies of Bulwer's petrel for adults (ANOVA: $F_{3,67} = 56.6$, $p < 0.001$) and chicks (ANOVA: $F_{3,71} = 20.79$, $p < 0.001$). Post-hoc Tukey tests indicated that Bulwer's petrels from the Atlantic Ocean had higher feather mercury levels than those from the Pacific Ocean (adults – Atlantic Ocean: 16.07 ± 1.88 mg kg^{-1} and Pacific Ocean: 10.12 ± 1.94 mg kg^{-1}; chicks – Atlantic Ocean: 4.70 ± 1.73 mg kg^{-1} and Pacific Ocean: 2.52 ± 0.75 mg kg^{-1}), with no difference between colonies in the same ocean basin (Atlantic Ocean: ANOVA: $F_{1,73} = 0.25$, $p = 0.619$ and Pacific Ocean: ANOVA: $F_{1,68} = 0.11$, $p = 0.745$).

There were no significant differences in the trophic position of chicks among colonies (Table 2) (ANOVA: $F_{3,20} = 0.81$, $p = 0.50$). Propagated errors associated with trophic position, determined by Eq. (b), were all <0.45 (mean = 0.32), indicating the precision of this method.

Previous studies of mercury in ventral whole feathers of adult Bulwer's Petrels from the Madeiran archipelago, collected from 1992 to 1994, report a concentration of 21.6 ± 0.7 mg kg^{-1} (mean ± SE) (range 12.20–33.80 mg kg^{-1}, $n = 55$) (Monteiro and Furness, 1997). These values are significantly higher than those obtained in this study for the colony of Deserta Grande, Madeira (mean ± SE: 16.49 ± 0.31 mg kg^{-1} (range 14.16–18.76 mg kg^{-1}, $n = 20$)) (Welch's t-test: $t = 6.7$, df = 69, $p < 0.0001$).

4. Discussion

We evaluated the concentration of mercury in Bulwer's petrels' feathers from four colonies across the Atlantic and Pacific Oceans. To our knowledge, this is the first single-species study to assess mercury in birds mostly relying on the mesopelagic domain at the tropics and sub-tropics on a scale of multiple ocean basins.

The diet of Bulwer's Petrel in the Pacific Ocean has been studied in the north-western Hawaiian Islands (Harrison et al., 1983), analysing induced or spontaneous regurgitates, and in the open sea (eastern tropical Pacific Ocean), through the analysis of stomach contents of birds shot for research purposes (Spear et al., 2007). The diet, in the Atlantic Ocean, was studied in the Azores archipelago, analysing induced regurgitates (Neves et al., 2011) and in the Madeiran Archipelago through DNA barcoding, using regurgitations of chicks (Waap et al., 2017). These studies showed that Bulwer's petrels forage almost exclusively on mesopelagic fish (mainly Myctophidae, Gonostomatidae, Phosichthyidae, Sternoptychidae, Centriscidae, Melamphaidae, Macrouridae and

Table 2
CSIA-AA-derived trophic position analysed from body feathers of chicks of Bulwer's petrel.

Ocean	Colony	Trophic position		Number of samples
		Mean ± propagated error	Range	
Atlantic Ocean	Cape Verde	3.37 ± 0.33	3.24–3.58	6
	Madeira	3.35 ± 0.33	3.19–3.47	6
Pacific Ocean	Japan	3.36 ± 0.33	3.22–3.60	6
	Hawaii	3.45 ± 0.30	3.32–3.56	6

Melanonidae) and squid (mainly Ommastrephidae, Histioteuthidae, Mastigoteuthidae, Chiroteuthidae and Cranchiidae) (Neves et al., 2011; Harrison et al., 1983; Spear et al., 2007; Waap et al., 2017). The similarity in trophic position of chicks from different colonies across two oceans reported here strongly suggests that the trophic niche and foraging strategies in Bulwer's petrel are highly conserved across geographies. Moreover, the high, but similar across locations, mercury concentrations in adult Bulwer's petrels from the same oceans reinforce the idea that Bulwer's petrels are specialist predators year-round, with a diet based on mesopelagic preys in both the non-breeding and the breeding seasons, irrespective of colony location. Furthermore, adult Bulwer's petrels from Hawaii, sampled in 2010, appear to occupy a similar trophic position (ca. 3.8) to that of chicks of Bulwer's petrel from Hawaii (ca. 3.5), sampled in this study (Gagne et al., 2018). Together, these results identify the Bulwer's petrel as an ideal monitor of mercury bioavailability in different geographic areas in the oceans. Similarities in mercury exposure in adults from the Japanese and Hawaiian colonies also suggest that they spend the non-breeding period in broadly overlapping oceanic areas, as do Bulwer's petrels from different breeding ranges in the Atlantic (Ramos et al., 2015), or that the mesopelagic preys within the Pacific basin have similar mercury concentrations.

Adults and chicks of Bulwer's petrels from Atlantic colonies had significantly higher (ca. 59% in adults and ca. 86% in chicks) mercury concentrations than those from the Pacific Ocean. Given that trophic differences are not apparent, the most likely explanation for this is that mesopelagic fish and squid in the Atlantic have higher mercury levels as compared to the Pacific, resulting from different bioavailability of methylmercury in mesopelagic zones (e.g., Becker et al., 2016; Carravieri et al., 2014). Such large variation in mercury concentrations of mesopelagic species between the Atlantic and Pacific oceans may arise from a complex interplay of factors, which include among others, variation in atmospheric deposition, variation in productivity and microbial activity, and differences in plankton communities, as different types of phytoplankton display highly distinct bioaccumulation rates (Zhang et al., 2020). Our findings are in accordance with previous investigations reporting higher mercury concentrations in deep water in the mesopelagic domain in the Central South Atlantic (ca. 1.3 ± 0.62 pM in the South Atlantic) than in the central and eastern Pacific (ca. 0.61 ± 0.19 pM in the Central South Pacific and 0.59 ± 0.25 pM in the Eastern Tropical Pacific) (Gill and Fitzgerald, 1988; Bowman et al., 2020).

Mercury concentrations in the North Atlantic waters appear to have decreased during the last several decades, likely due to reduced atmospheric deposition (Bowman et al., 2015; Cossa et al., 2012; Obrist et al., 2018). Such reduction in mercury deposition or mercury concentrations in ocean waters are thought to be driving the declines detected in time series of mercury contamination in Bluefish (*Pomatomus saltatrix*; Cross et al., 2015) and Atlantic bluefin tuna (*Thunnus thynnus*; Lee et al., 2016) in the northwest Atlantic, and in Striped dolphins (*Stenella coeruleoalba*) in the Mediterranean (Borrell et al., 2014). Our results, when compared to those of Monteiro and Furness (1997) for Bulwer's petrels are perfectly in line with the above findings and further support the existence of a decline from 1992 to 2018. We note that our methodological approach was slightly different from the one adopted by Monteiro and Furness (1997), as they used whole feathers while we excluded the calamus. Given that the calamus has lower mercury concentrations than the rachis and the vane (Peterson et al., 2019), we would expect, all other things being equal, that our mercury measurements would be slightly higher than those in the former study (note that the calamus only represents ca. 11% of the feather mass; Peterson et al., 2019). The fact that more recent samples had lower, not higher, mercury concentrations reinforces our conclusions. However, we recognise that measurements in 2 points in time cannot substitute a complete time-series to detect a temporal trend. Data from the Pacific show an increase in mercury bioavailability (Drevnick et al., 2015). However, in many cases the temporal trends in marine biota do not faithfully parallel changes in atmospheric inputs (Wang et al., 2019), due the slow

transport of mercury into lower ocean levels where it is transformed to methylmercury and assimilated by organisms (Driscoll et al., 2013).

Studies on broad spatial and temporal trends in oceanic mercury concentrations often compare data from tuna species (Drevnick et al., 2015; Houssard et al., 2019; Lee et al., 2016; Manhães et al., 2020). However, given that tuna are widely recognised as opportunistic generalist top predators, feeding facultatively on both epipelagic and mesopelagic prey (Duffy et al., 2017; Olafsdottir et al., 2016), their mercury exposure may reflect the confounding effects of environmental contaminant levels, layers in the ocean where they feed (epi- or mesopelagic) and trophic position (Gatt et al., 2020b). Bulwer's petrel feathers could complement the current monitoring in intermediate waters without the difficulties of quantifying and interpreting the influence of trophic position, which seems to be similar in both oceans.

Our observation that chicks bore lower mercury concentration than adults is in agreement with similar comparisons in other seabird taxa (Becker et al., 2002; Tavares et al., 2013). This is attributed to the shorter period of time during which mercury is accumulated in the body through the diet in chicks before they are able to excrete it into growing feathers (Bustamante et al., 2016; Furness et al., 1986; Thompson et al., 1998).

Mercury concentrations in body feathers of adult Bulwer's petrels are higher than those in many other seabirds (e.g., Furtado et al., 2019; Monteiro et al., 1999), comparable to concentrations found in some large albatross species (Thompson et al., 1993). Such high concentrations reflect the Bulwer's petrel's dependency on mesopelagic prey. Mercury concentrations between 5 and 40 mg kg^{-1} in feathers of waterbirds have been reported by some studies to carry negative impacts on reproductive parameters or survival (Scheuhammer et al., 2007; Whitney and Cristol, 2017; Wolfe et al., 1998). However, most research suggests that seabirds exhibit extraordinary resistance to mercury contamination (Carravieri et al., 2018, 2020; Gilmour et al., 2019; Wolfe et al., 1998), with the highest concentrations recorded at 95 mg kg^{-1} in an adult male Wandering Albatross (*Diomedea exulans*) with no obvious impacts to its fitness (Bustamante et al., 2016).

4.1. Conclusions

Our results suggest that, given the similarity in trophic position across the two oceans, and its wide-ranging foraging behaviour, the Bulwer's petrel provides an integrated measure of mercury contamination in the tropical and sub-tropical mesopelagic domain at the scale of multiple ocean basins. Results suggest that birds in the Atlantic Ocean are currently exposed to higher mercury concentrations than those in the Pacific Ocean, reflecting higher contamination in fish and squid of the mesopelagic compartment of the Atlantic Ocean. Results also suggest that mercury levels in the oceanic waters of the tropical/subtropical Atlantic Ocean have declined over the past 2–3 decades, but more data are needed to further confirm this trend. The use of body feathers provides an accessible and non-invasive method for such monitoring. The exceptionally high concentration of mercury in Bulwer's petrels warrants further research to determine potential detrimental effects on behaviour, reproductive success or survival.

CRediT authorship contribution statement

PC and JPG conceptualised the study and acquired funding, RF planned the methodology and drafted the manuscript, RR, KH, VHP,

DM collected the samples. RF, JPG and MCG, compiled and analysed the data. RF, JPG, MCG and PC led the writing - review of the manuscript. PC, JPG and EP supervised the work. All authors contributed critically to revisions. All authors have read the submitted version of the manuscript and approve its submission.

Declaration of competing interest

Acknowledgments

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