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Nutrients and seabird biogeography: Feather elements differ among oceanic basins in the Southern Hemisphere, reflecting bird size, foraging range and nutrient availability in seawater

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Abstract

Aim: Biodiversity hotspots in wide-ranging marine species typically overlap with regions of high productivity, which are often associated with nutrient-rich waters. Here we investigate how element concentrations in feathers vary among highly mobile seabirds in global seabird biodiversity hotspots.

Location: Southern Hemisphere.

Time period: Contemporary.

Major taxa studied: Fifteen species in the order Procellariiformes.

Methods: We collected data on the concentration of 15 elements in feathers for 253 seabirds sampled across Australia and New Zealand and compared the "fingerprint" of micronutrient element profiles to feathers of related seabirds from global hotspots using principal component analysis (PCA), cluster analysis and permutational analysis of variance (PERMANOVA).

Results: Breast feather concentrations of some elements, including aluminium, iron, cobalt, chromium, manganese, nickel, arsenic and cadmium, were tens-to-hundred-fold higher in smaller (<400 g) than larger species (≥400 g). We suggest these results reflect the dominance of pelagic crustaceans in the diet of smaller seabirds, blooms of which are influenced by input of limiting ocean nutrients. Cluster analysis revealed three broad groups of feather elements: large seabirds, and small seabirds in each of the South Pacific and South Atlantic Ocean basins. High concentrations of some elements in feathers match seawater availability and are detectable in lower-trophic feeding seabirds with local movements. Conversely, the element fingerprints of longer-distance, higher-trophic foragers, including albatrosses, do not match availability in seawater at the collection site.

Main conclusions: The feather element concentrations of shorter-range foraging, lower-trophic feeding seabirds vary significantly among ocean basins, reflecting availability in seawater, while longer-range, higher-trophic species do not. We propose that geographically diverse availability of micronutrients, in addition to primary productivity, may play an underrecognized role in seabird biogeography and intra-hemispheric migration, though more research is needed. This study has important implications, considering the role of element availability in supporting biodiversity hotspots for dispersive marine predators and for the designation of protected areas.

KEYWORDS
biogeography, foraging decision, marine predator, marine wildlife, migration, ocean basins, ocean nutrients, seabird range, trace element

1 | INTRODUCTION

Large marine animals, including species of seabirds, cetaceans, marine turtles and tuna, can range hundreds to thousands of kilometres in search of food, often moving between regions of high productivity throughout the year (Burton & Koch, 1999; Camphuysen et al., 2007; Hays & Scott, 2013). Inter-hemispheric migration and movements of marine animals are often related to seasonal sea ice cover and consequent availability of prey (Carey et al., 2014), but long distance intra-hemispheric movements are less well understood. Movement decisions can be plastic within individuals and species (Paiva et al., 2010) and collectively, animals' individual movement decisions determine the location of marine biodiversity hotspots, which are often associated with areas of high productivity (Grecian et al., 2016; Paiva et al., 2010) including regions of upwelling (Kämpf & Chapman, 2016) and seamounts (Boehlert & Genin, 1987; Genin & Dower, 2007). Upwelling and seamounts are associated with nutrient and mineral element-rich waters that support this productivity (Boehlert & Genin, 1987). The southern Pacific Ocean, particularly the region surrounding the Tasman Sea, hosts the world's highest biodiversity of the cosmopolitan tube-nosed seabirds (order Procellariiformes; IUCN, 2021; Jenkins & Van Houtan, 2016). Numerous seabird biodiversity hotspots in the Southern Hemisphere are associated with upwelling and/or seamounts, for example, South Georgia/South Sandwich Islands and Gough Island in the South Atlantic Ocean (Schlitzer et al., 2018). However, this trend is not universal and not all of the Southern Hemisphere's highly productive marine regions support a rich tube-nosed seabird diversity, with factors outside of primary productivity influencing these movement decisions (Davies et al., 2010). Tube-nosed seabirds are unique among birds in that they use olfaction to locate prey, in addition to visual searching, with many species having a foraging distribution that spans several ocean basins (IUCN, 2021). Consequently, they provide a valuable insight into the movement decisions of wide-ranging, dispersive species, including marine predators ranging from tuna to cetaceans.

Dispersive movement decisions can be at odds with the idea that animals seek to conserve energy by minimizing energy loss through long-distance locomotion, and it is likely that another need is driving these decisions. In terrestrial birds, for example, multiple taxa of Central and South American parrots, individuals make daily migrations to “clay licks”, small regions of exposed soil, to engage in geophagy (Brightsmith & Muñoz-Najar, 2004). Though the ingestion of soil and clay offers no energetic benefit, this action benefits the animals by supplementing minerals and elements in their diet (Brightsmith & Muñoz-Najar, 2004), and these movement decisions may be taken to meet the mineral nutritional needs for the birds' physiological functioning. Some mineral elements, for example, chromium (Cr), cobalt (Co), nickel (Ni), copper (Cu), iron (Fe), manganese (Mn) and zinc (Zn), are essential for the physiological functioning of organisms. Other elements, however, including arsenic (As), cadmium (Cd) and lead (Pb), are considered non-essential for living organisms, having no known biological benefit (Bhagavan, 2002; Rainbow, 1999). Depending on the type, speciation and concentration, both essential and non-essential elements can be toxic to organisms (Rainbow, 1999; Reeder et al., 2006).

To maintain homeostasis, animals physiologically regulate essential elements in their tissues, and excess elements are eliminated from the body. In birds, ingested elements are removed from the body via two main pathways: excretion (defecation; Wing et al., 2014) and feather moult (Burger & Gochfeld, 1992). Elements can be excreted directly, without being absorbed because of low bioavailability or after being absorbed if they are excess to physiological need, and some elements are excreted secondarily to metallothionein detoxification (Cd, Zn, small amounts of Cu, Fe and Hg; Andrews et al., 1996; Bhagavan, 2002). Elements that are absorbed from the diet are carried by blood and supplied to developing feathers. Blood vessels atrophy upon completion of feather formation (Burger & Gochfeld, 1992), leaving elements sequestered within the feather. Thus, body feathers closely represent the suite of elements to which the bird is exposed during the time of feather development (Burger & Gochfeld, 1992). The moult of feathers is an important pathway for the excretion of some elements (Cherel et al., 2018; Furness et al., 1986; Stewart et al., 1999). As a result, the examination of feather element concentrations is regularly used as a non-destructive method to assess a bird's exposure to elements (Markowski et al., 2013).

Unlike terrestrial birds, pelagic seabirds cannot access minerals directly from soil outside of breeding (on islands) because of their marine pelagic lifestyle. Many trace elements are rare in seawater, existing at low concentrations of 9–10 to 10–12 mol/L (Lohan & Tagliabue, 2018). Bioactive trace elements, for example, Fe, Co, Cu, Mn and Zn, have depleted concentrations in surface seawater in particular, indicating that they also play an important role in limiting and governing phytoplankton growth in this photic zone (Lohan & Tagliabue, 2018; Moore et al., 2013). However, local hotspots of some micronutrients exist in the ocean; for example, hydrothermal vents trigger massive phytoplankton blooms in the Southern Ocean because of the influx of Fe into this Fe-limited ocean system (Ardyna et al., 2019). Uptake of these elements by phytoplankton makes them available to consumers at higher trophic levels in surface waters, including seabirds. Experimental evidence demonstrates that among terrestrial invertebrates, the addition of micronutrients (including Fe, Mn, Zn, Cu, Ca and Ni) through fertilizer acts synergistically with macronutrients to promote arthropod abundance (Prather et al., 2020), and it is possible that these associations may also occur in marine environments.

The concentrations of some elements, for example, Mn, Co, Cu and Zn, are regulated in the body of seabirds as a normal part of homeostasis (Kim et al., 1998; Lock et al., 1992), while ingested elements that are excess to the birds' physiological requirements are excreted and/or sequestered. We tested whether element concentration in feathers, representing tube-nosed birds' diet during the formation of the feathers, was related to the geography of seabird foraging ranges. If element concentrations in feathers were representative of specific foraging ranges, the “fingerprint” of known element concentrations in different oceans should be comparable to that of tube-nosed taxa sampled in these oceans. If micronutrients have local hotspots, we hypothesize that these hotspots should be associated with species that feed locally in these hotspots, and generally lower in the food-chain than wider-ranging species. This study provides better understanding of the movement decisions of wide-ranging, dispersive species, including seabirds, and the biogeography of marine predators. Considering the impact of climate change on seasonal productivity and associated nutrient cycles and redistribution in the Southern Ocean (Henley et al., 2020; Kim & Kim, 2021), the use of nutrient hotspots by local and wide-ranging species could be affected by these changes, with ecosystem-wide consequences (Mallen-Cooper et al., 2019).

2 | MATERIALS AND METHODS

2.1 | Seabird sampling

Breast feathers (minimum five) were collected from 253 dead tube-nosed seabirds covering 15 species collected in the western South Pacific Ocean/Tasman Sea, a global seabird biodiversity hotspot. Bird feathers are suitable for monitoring environmental availability of elements, including inorganic and organic pollutants (Rutkowska et al., 2018), and breast feathers are usually chosen as they moult regularly and evenly throughout the year, and are representative of whole body loads (Furness et al., 1986; Jaspers et al., 2019; Rutkowska et al., 2018). Petrels moult body feathers asynchronously, and there is often within-individual variation in chemical loads between individual breast feathers (Carravieri et al., 2014). For this reason, sampling a minimum of five breast feathers is the typical method to ascertain an average snapshot of the chemical load for individual birds (Becker et al., 2002, 2016; Furness et al., 1986).

The sampled species spanned a range of sizes, which we have divided into large species (≥400 g) including albatrosses, giant petrels, larger petrels and shearwaters and small species (<400 g) species, including diving petrels, prions and the smaller petrels and shearwaters (Figure 1). Large species included wandering-type albatrosses, *Diomedea exulans* and *Diomedea antipodensis* ($n = 2$), shy-type albatrosses, *Thalassarche cauta* and *Thalassarche steadi* ($n = 11$), black-browed albatross, *Thalassarche melanophris* ($n = 2$), Buller's albatross, *Thalassarche bulleri* ($n = 4$), white-chinned petrel, *Procellaria aequinoctialis* ($n = 10$), Cape petrel, *Daption capense* ($n = 1$), flesh-footed shearwater, *Ardenna carneipes* ($n = 19$) and short-tailed shearwater, *Ardenna tenuirostris* ($n = 39$). Small species included fluttering shearwater, *Puffinus gavia* ($n = 26$), broad-billed prion, *Pachyptila vittata* ($n = 8$), Salvin's prion, *Pachyptila salvini* ($n = 12$), Antarctic prion, *Pachyptila desolata* ($n = 8$), slender-billed prion, *Pachyptila belcheri* ($n = 37$), fairy prion, *Pachyptila turtur* ($n = 55$) and common diving-petrel, *Pelecanoides urinatrix* ($n = 19$).

The seabird carcasses were collected from four sources. Albatrosses and petrels were sourced as Australian fisheries by-catch in the western South Pacific Ocean between 2002 and 2012 and submitted to the Tasmanian Department of Primary Industries, Parks, Water and Environment (Australia). Most prions, fluttering shearwaters and diving petrels were collected dead from beaches following a seabird “wreck” in Auckland and Waikato regions, New Zealand, in August 2016, with a small number having been collected from wildlife hospitals in New Zealand in the preceding 12 months. Other fairy prions were collected dead on eastern Tasmanian beaches (Australia) in 2017. Short-tailed shearwaters were collected dead on eastern Australian beaches in 2013.

Although the movements of these birds during their lives are unknown, their deaths occurred in or near the Tasman Sea region, South Pacific Ocean, demonstrating that this area was inhabited or visited prior to their deaths. Movements of the seabird species were allocated as either “shorter-range” (distribution and movements are largely restricted to the ocean in which their carcass was collected) or “longer-range” (movement spanning more than one ocean) according to IUCN (2021), Onley and Scofield (2007) and Marchant and Higgins (1990) with range maps informed by Birdlife International's bird species distribution maps (BirdLife International and Handbook of the Birds of the World, 2020).

2.2 | Feather processing and element analysis

Feathers were washed using a combination of Milli-Q (MQ) water (>18 MΩ) to remove water-soluble contaminants and acetone to remove organic contaminants following the method detailed in Borghesi et al. (2016). The feathers were visually inspected and cleaned with water to remove skin, sand or other noticeable contamination, and placed in separate 50-ml centrifuge tubes. The tubes were filled with 15 ml water and sonicated in an ultrasonic

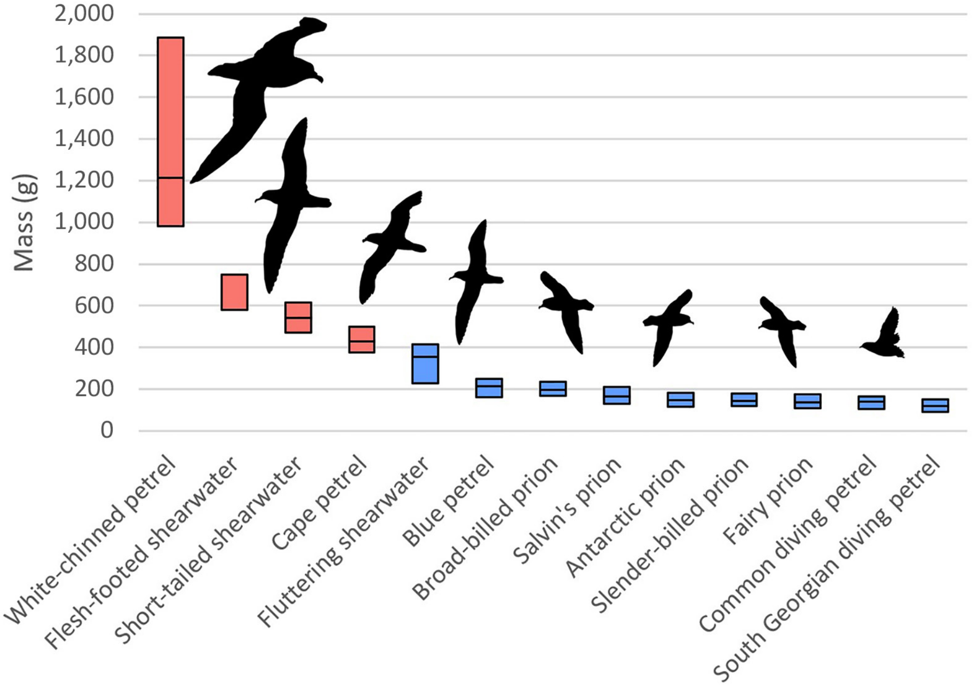

FIGURE 1 Feathers were sampled from seabird species spanning a range of sizes, which were divided into large (≥400 g) and small (<400 g) size categories. The division between large and small was placed at 400 g, where there was a natural division in sizes of petrels sampled. This figure displays the average, upper and lower limits of the mass of the petrels, shearwaters, prions and diving petrels. Masses presented follow the CRC handbook of avian body masses (Dunning, 2007), and Handbook of Australian, New Zealand and Antarctic birds (Marchant & Higgins, 1990) where masses or ranges were not available in Dunning (2007). Albatrosses and giant petrels were all placed in the large size category, with lower limits of mass exceeding 2,000 g, and are not included in this figure.

bath (Soniclean, Adelaide, Australia) for 10 min, ensuring that the feathers stayed submerged in solution, and the used water was discarded. The tubes were then filled with 15 ml acetone and sonicated for 10 min as above, followed by discarding of used acetone. The process of cleaning was repeated at least twice to remove adsorbed contaminants, with a few samples requiring additional washing with acetone to remove visible oil residue. After washing, the feathers were dried at 40 °C overnight.

Approximately 0.1–0.2 g of each feather sample was predigested overnight in 5 ml HNO_3 (70%, trace grade), followed by digestion in a CEM Mars 6 Microwave using the protocol described in Kastury et al. (2021) (ramping up to 150 °C for 10 min and holding at 150 °C for 30 min at 800 psi). The digested samples were made up to 50 ml using MQ water (>18 MΩ), syringe filtered (0.45 μm, cellulose acetate) and stored at 4 °C until analysis using inductively coupled plasma mass spectrometry (ICP-MS) following United States Environmental Protection Agency (USEPA) method 6020A (USEPA, 2007).

Standard Reference Material (SRM) 2976 (mussel tissue, *n* = 10) from the National Institute of Standards & Technology was utilized to confirm the accuracy of digestion. Average ± *SEM* recovery of As was 13.28 ±0.30 mg/kg from a certified total of 13.30 ±1.80 mg/kg (recovery of 99.8%), while recovery of Pb was 1.09 ±0.06 mg/kg from a certified total of 1.19 ±0.18 (recovery of 91.6%). Blanks (*n* = 8) were below limit of detection. Deviation from duplicates (*n* = 13) and continuing calibration verifications (*n* = 38) were within 10% and average Pb recovery (*n* = 14) from spiked samples were within 30% as required by method USEPA 6020A for data validation (USEPA, 2007).

2.3 | Statistical analysis for comparison within groups

We conducted statistical analysis using R studio version 1.1.463 (R Core Team, 2021). To examine the associations between seabird taxa and feather elements, we compared the concentration of each element (dependent variable) among seabirds at the taxonomic levels of species, genera and family; and the median concentration of feather elements per species between small (<400 g) and large (≥400 g) seabird species (independent variables). We tested for normality in the distribution of feather elements using a Shapiro–Wilk normality test. Where the distribution of element concentrations was normal, we used a Welch's *t* test. Where the distribution was non-normal, we used a Mann–Whitney *U*-test for two samples, and a Kruskal–Wallis rank sum test for more than two samples.

2.4 | Statistical analysis for comparison with other studies

We compared the concentrations of Fe, Mn, Zn, Cu and Cd for each species examined in this study with the results from feather element concentrations from 10 tube-nosed seabird species sampled at another seabird biodiversity hotspot: Bird Island, South Georgia (54°00′ S, 38°03′ W) by Anderson et al. (2010). These species included six that overlapped with our study: Antarctic prion (*Pachyptila desolata*), black-browed albatross (*Thalassarche melanophris*), blue petrel (*Halobaena caerulea*), common diving petrel (*Pelecanoides urinatrix*), white-chinned petrel (*Procellaria aequinoctialis*) and wandering albatross (*Diomedea exulans*). Four species examined by Anderson et al. (2010) did not overlap with our study; the small sized South Georgian diving petrel (*Pelecanoides georgicus*) and the large sized grey-headed albatross (*Thalassarche chrysostoma*), northern giant petrel (*Macronectes halli*) and southern giant petrel (*Macronectes giganteus*).

To examine relationships between the groups, birds sampled in the South Atlantic compared to South Pacific, and large compared to small seabirds, we conducted a principal component analysis (PCA) and permutational analysis of variance (PERMANOVA) tests, using the R package “vegan”, to quantify the influence of bird size and ocean upon feather element concentration. We conducted the PCA on mean concentrations of five elements common to both studies and above the limit of detection in feathers for most species: Fe, Mn, Zn, Cu and Cd. We then applied a k-means cluster analysis to the first two principal components, examining 1–10 clusters.

To quantify the relationship between bird size category (small and large) and element (Fe, Mn, Zn, Cu and Cd) concentration in the feathers of seabirds in the South Pacific Ocean only, we performed a one-way PERMANOVA with size category as the independent variable and element concentrations as the dependent variable, treating each sampled bird as an independent sample. To quantify the relationship between bird size category and ocean, we performed a two-way PERMANOVA with an interaction between size category (large or small) and ocean (South Pacific or South Atlantic) as the independent variables and element concentrations (Fe, Mn, Zn, Cu and Cd) as the dependent variable. In these analyses we used the mean concentration of each species from this study and Anderson et al. (2010) as each independent sample.

3 | RESULTS

3.1 | Major elements: Calcium (Ca), potassium (K), magnesium (Mg) and phosphorus (P)

Calcium, K, Mg and P concentrations in breast feathers varied both between and within the 15 examined species (Table 1, Supporting Information Table S1, Figure 2). Median Ca concentration ranged across a threefold increase from 489.14 mg/kg (short-tailed shearwater) to 1,294.08 mg/kg (black-browed albatross). Though the short-tailed shearwater had the lowest median concentration of Ca, the species showed the highest mean concentration at 1,864.01 mg/kg, with three outliers exceeding 10,000 mg/kg of Ca in their feathers, a concentration not seen in other species. The median K feather concentration ranged from 38.65 mg/kg (Cape petrel) to 338.54 mg/kg (short-tailed shearwater); nearly half of the species (7 of 15) had a median of 100–200 mg/kg. Potassium concentrations in the feathers varied less among species and individuals than did Ca concentrations, with the highest K concentration, 1,863.64 mg/kg, found in the breast feathers of a common diving petrel. Median feather Mg concentrations ranged from 381.85 mg/kg (short-tailed shearwater) to 1,216.58 mg/kg (white-chinned petrel). Magnesium was the least variable of the four examined major element concentrations in feathers and the median Mg concentration of most species (9 of 15) was between 850–1,250 mg/kg. The median concentration of P in breast feathers ranged from 49.66 mg/kg (black-browed albatross) to 395.45 mg/kg (slender-billed prion) and varied considerably among species.

3.2 | Trace elements: Iron (Fe), cobalt (Co), chromium (Cr), copper (Cu), manganese (Mn), nickel (Ni) and zinc (Zn)

The mean, median and standard deviation of trace element concentrations in the feathers of the 15 seabird species varied within and between species, with some patterns common to specific seabird groups (Table 1, Supporting Information Table S2, Figure 3). On average, smaller (<400 g) species (fluttering shearwaters, prions and common diving petrels) had significantly higher feather concentrations of Fe, Co, Cr, Mn and Ni than did larger species (≥400 g): albatrosses, white-chinned petrels, Cape petrels, flesh-footed shearwaters and short-tailed shearwaters.

The median concentration of Fe in feathers ranged from 14.76 mg/kg in the largest species (wandering-type albatrosses) to 7,788.12 mg/kg in broad-billed prions, more than a 500-fold increase. Albatrosses, larger shearwaters and white-chinned petrels had median Fe concentrations < 100 mg/kg, while the feather concentration of Fe in the smaller species (fluttering shearwater, prions and common diving petrel) all exceeded 1,000 mg/kg, greater than 10-fold that of the larger species.

The median concentration of Co in feathers ranged from 0 (wandering-type, shy-type and Buller's albatrosses, white-chinned petrels and flesh-footed shearwaters) to 2.91 mg/kg (Salvin's prions). The median concentration of Cr in feathers ranged from 0.51 mg/kg (Buller's albatrosses) to 4.54 mg/kg (Salvin's prions). The median concentration of Cu varied little among species, ranging from 7.12 mg/kg (fairy prion) to 18.65 mg/kg (black-browed albatrosses). The median concentration of Mn in feathers ranged from 0.00 mg/kg (wandering-type albatrosses) to 79.34 mg/kg (Salvin's prions). We found a minimum 10-fold increase in the concentration of Mn in feathers between larger species (maximum median Mn concentration occurred in short-tailed shearwaters at 1.09 mg/kg) and smaller species (minimum median Mn concentration occurred in slender-billed prions at 10.10 mg/kg). The concentrations of Ni and Zn in feathers varied less than those of other trace elements, with median Ni concentration ranging from 0.27 mg/kg (wandering-type albatrosses) to 1.81 mg/kg (Salvin's prions) and median Zn

TABLE 1 Outputs for tests of statistical significance between independent variables (species, genus, family and bird size) and dependent variables (mg/kg concentration of each element in the feather)

Independent variable	Test	Statistical test results for each element							
Major essential elements		Ca		K		Mg		P	
Species	Kruskal–Wallis (d.f. = 14)	28.48*		74.07***		66.41***		70.72***	
Genus	Kruskal–Wallis (d.f. = 7)	19.67**		19.56**		40.24***		33.72***	
Family	Mann–Whitney *U*-test	NS		NS		2781*		832***	
Bird size	Welch *t* test	NS		NS		NS		−3.58**	
Trace essential elements		Al	Fe	Co	Cr	Cu	Mn	Ni	Zn
Species	Kruskal–Wallis (d.f. = 14)	148.55***	158.83***	155.83***	84.11***	103.27***	149.83***	72.91***	51.01***
Genus	Kruskal–Wallis (d.f. = 7)	132.03***	140.72***	140.95***	68.67***	86.04***	130.14***	56.62***	45.71***
Family	Mann–Whitney *U*-test	284***	577***	491***	1399***	NS	432***	1337*	NS
Bird size	Mann–Whitney *U*-test (Al, Fe, Co, Cr, Cu, Mn) & Welch *t* test (Ni, Zn)	0***	0***	0***	3**	NS	0**	−3.67**	3.14**
Non-essential elements		As		Cd		Pb			
Species	Kruskal–Wallis (d.f. = 14)	113.72***		89.02***		60.63***			
Genus	Kruskal–Wallis (d.f. = 7)	95.14***		61.35***		45.93***			
Family	Mann–Whitney *U*-test	601***		1244**		817***			
Bird size	Mann–Whitney *U*-test	0***		NS		10*			

Note: For species, genus and family, we used the data from each individual bird. For bird size, we used the median value for each species. Bird size: see text for small (<400 g) and large (≥400 g) bird species.

Abbreviation: NS, not significant.

*p < .05.; **p < .01.; ***p < .001.

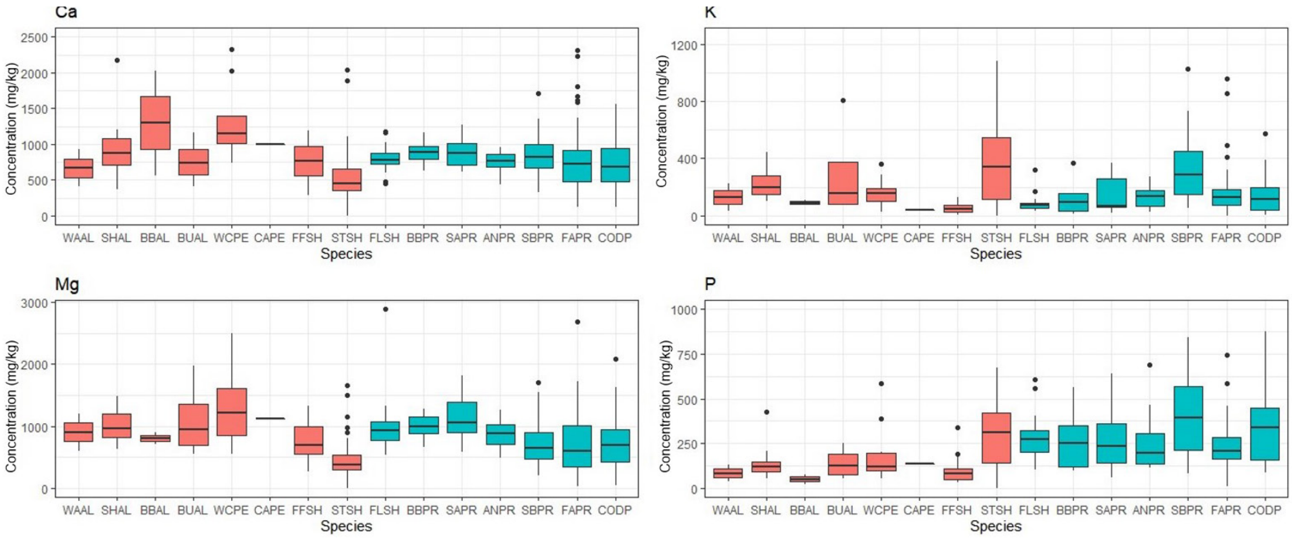

FIGURE 2 Concentrations (mg/kg) of major essential elements Ca, K, Mg and P in the breast feathers of 15 tube-nosed seabird species. Larger species are WAAL = wandering-type albatross (*n* = 2); SHAL = shy albatross (*n* = 11); BBAL = black-browed albatross (*n* = 2); BUAL = Buller's albatross (*n* = 4); WCPE = white-chinned petrel (*n* = 10); CAPE = Cape petrel (*n* = 1); FFSH = flesh-footed shearwater (*n* = 19) and STSH = short-tailed shearwater (*n* = 39). Smaller species are FLSH = fluttering shearwater (*n* = 26); BBPR = broad-billed prion (*n* = 8); SAPR = Salvin's prion (*n* = 12); ANPR = Antarctic prion (*n* = 8); SBPR = slender-billed prion (*n* = 37); FAPR = fairy prion (*n* = 55) and CODP = common diving petrel (*n* = 19). Larger species (≥400 g) are on the left side of graph and coloured pink, smaller species (<400 g) are on the right and blue. See Supporting Information Figure S1 for alternative figure including all outliers.

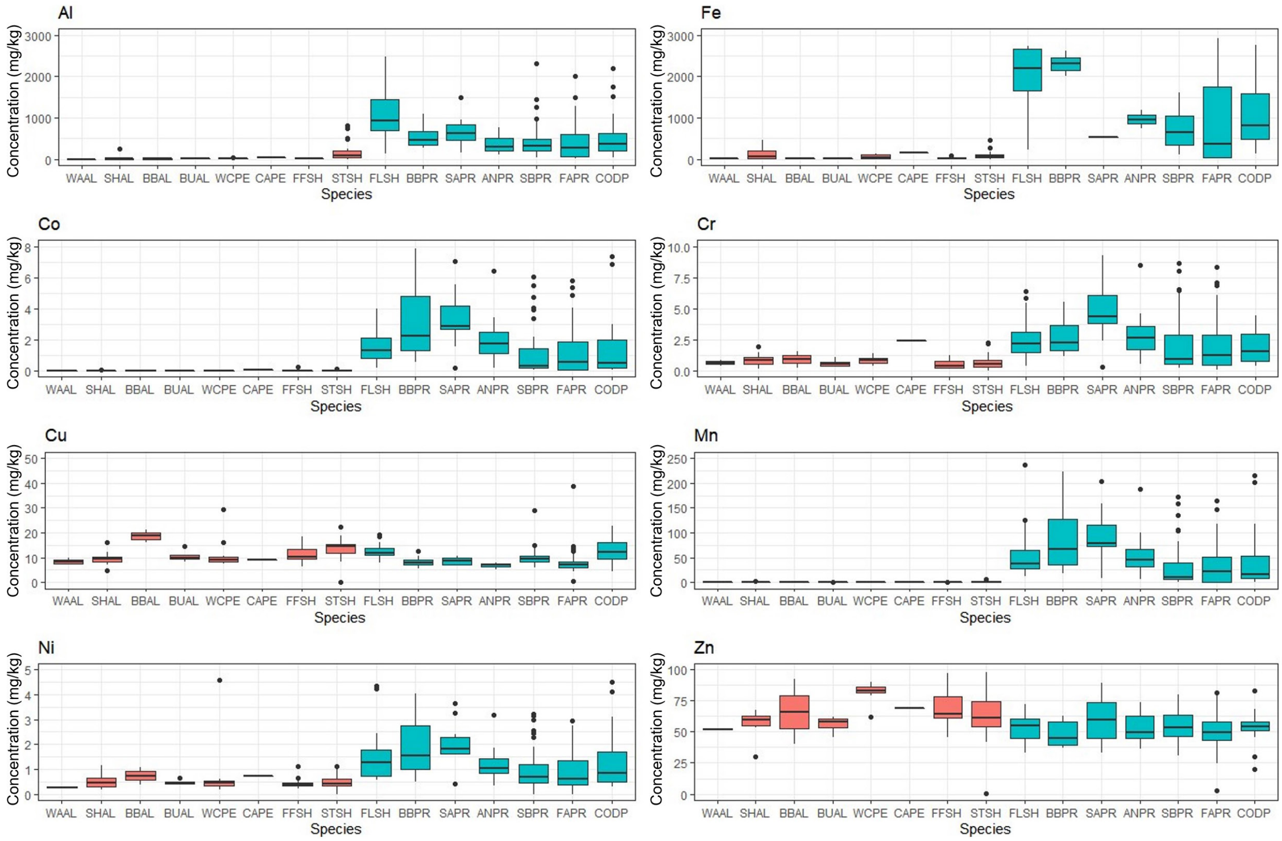

FIGURE 3 Concentrations (mg/kg) of trace essential elements Fe, Co, Cr, Cu, Mn, Ni and Zn in the breast feathers of 15 tube-nosed seabird species. Larger species are WAAL = wandering-type albatross (*n* = 2); SHAL = shy albatross (*n* = 11); BBAL = black-browed albatross (*n* = 2); BUAL = Buller's albatross (*n* = 4); WCPE = white-chinned petrel (*n* = 10); CAPE = Cape petrel (*n* = 1); FFSH = flesh-footed shearwater (*n* = 19) and STSH = short-tailed shearwater (*n* = 39). Smaller species are FLSH = fluttering shearwater (*n* = 26); BBPR = broad-billed prion (*n* = 8); SAPR = Salvin's prion (*n* = 12); ANPR = Antarctic prion (*n* = 8); SBPR = slender-billed prion (*n* = 37); FAPR = fairy prion (*n* = 55) and CODP = common diving petrel (*n* = 19). Larger species (≥400 g) are on the left side of graph and coloured pink, smaller species (<400 g) are on the right and blue. See Supporting Information Figure S2 for alternative figure including all outliers.

concentrations ranging from 49.24 mg/kg (Antarctic prions) to 84.81 mg/kg (white-chinned petrels).

3.3 | Non-essential elements: Aluminium (Al), arsenic (As), cadmium (Cd) and lead (Pb)

The mean, median and standard deviation of the concentrations of the non-essential elements Al, As, Cd and Pb in the feathers of the 15 seabird species varied within and among species (Table 1, Figure 4, Supporting Information Figure S3). Smaller seabird species (<400 g) displayed a pattern of higher concentrations of Al and As. Cadmium also fit this pattern, except for white-chinned petrels, though there was no statistically significant relationship with bird size. We did not find a pattern associated with the concentration of Pb in feathers.

The median concentration of Al in feathers ranged from 5.92 mg/kg (wandering-type albatrosses) to 942.13 mg/kg (fluttering shearwaters). The median concentration of As in feathers ranged from 0.09 mg/kg (Buller's albatrosses) to 0.74 mg/kg (Salvin's prions). The median concentration of Cd in feathers ranged from 0.11 mg/kg (short-tailed shearwaters) to 1.04 mg/kg (Antarctic prions). The median concentration of Pb in feathers ranged from 0.00 mg/kg (wandering-type, shy-type and Buller's albatrosses and white-chinned petrels) to 0.76 mg/kg (Salvin's prions).

3.4 | Statistical analysis for comparison with other studies

Principal component analysis showed that the first principal component (PC1) increased with moderately large increases of Fe (0.65) and Mn (0.65), a modest increase of Cd (0.32) and slight decrease of Zn (−0.19) and Cu (−0.15), explaining 43.8% of the sum of squared distances. The second principal component (PC2) was inversely linked with Cu (−0.72), Zn (−0.64), Fe (−0.19) and Mn (−0.19) and increased marginally with Cd (0.05), and was responsible for 24.6% of sum of squared distances (PC3 = 18.7%, PC4 = 12.9% and PC5 = 0.0%) (Figure 5).

Cluster analysis of PC1 and PC2 revealed that the seabirds were best sorted into four clusters describing 92.8% of variation (between

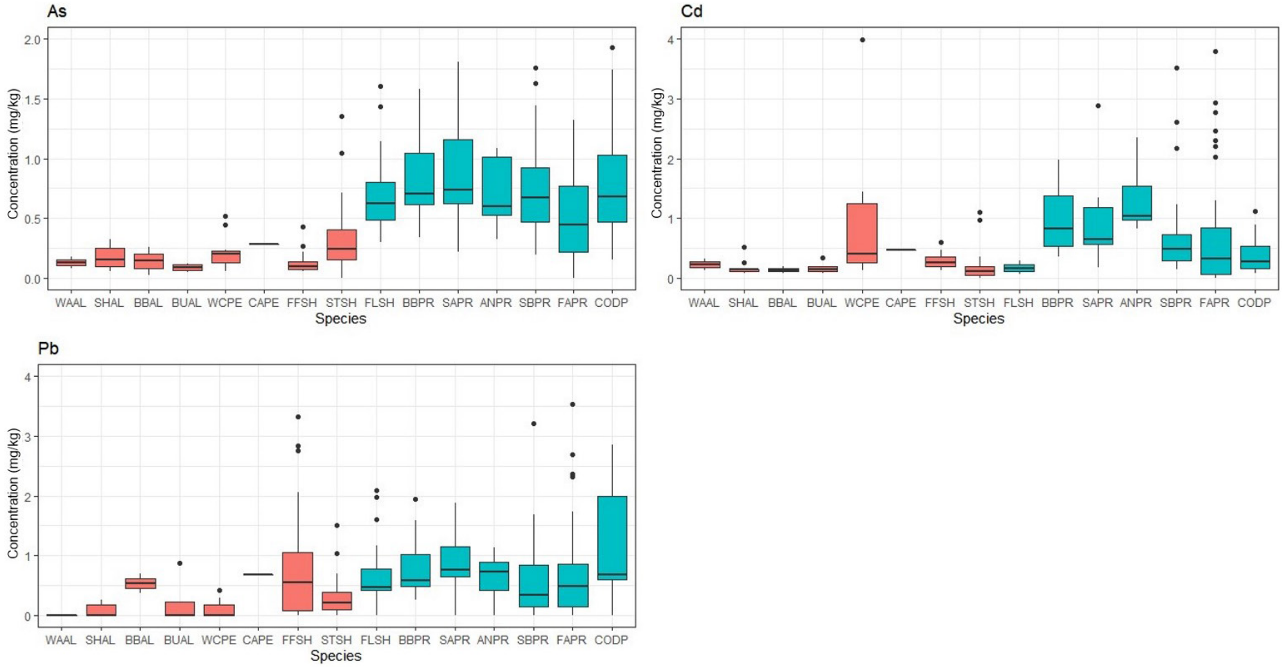

FIGURE 4 Concentrations of non-essential elements Al, As, Cd and Pb in the breast feathers of 15 tube-nosed seabird species. Larger species are WAAL = wandering-type albatross (*n* = 2); SHAL = shy albatross (*n* = 11); BBAL = black-browed albatross (*n* = 2); BUAL = Buller's albatross (*n* = 4); WCPE = white-chinned petrel (*n* = 10); CAPE = Cape petrel (*n* = 1); FFSH = flesh-footed shearwater (*n* = 19) and STSH = short-tailed shearwater (*n* = 39). Smaller species are FLSH = fluttering shearwater (*n* = 26); BBPR = broad-billed prion (*n* = 8); SAPR = Salvin's prion (*n* = 12); ANPR = Antarctic prion (*n* = 8); SBPR = slender-billed prion (*n* = 37); FAPR = fairy prion (*n* = 55) and CODP = common diving petrel (*n* = 19). Larger species (≥400 g) are on the left side of graph and coloured pink, smaller species (<400 g) are on the right and blue. See Supporting Information Figure S3 for alternative figure including all outliers.

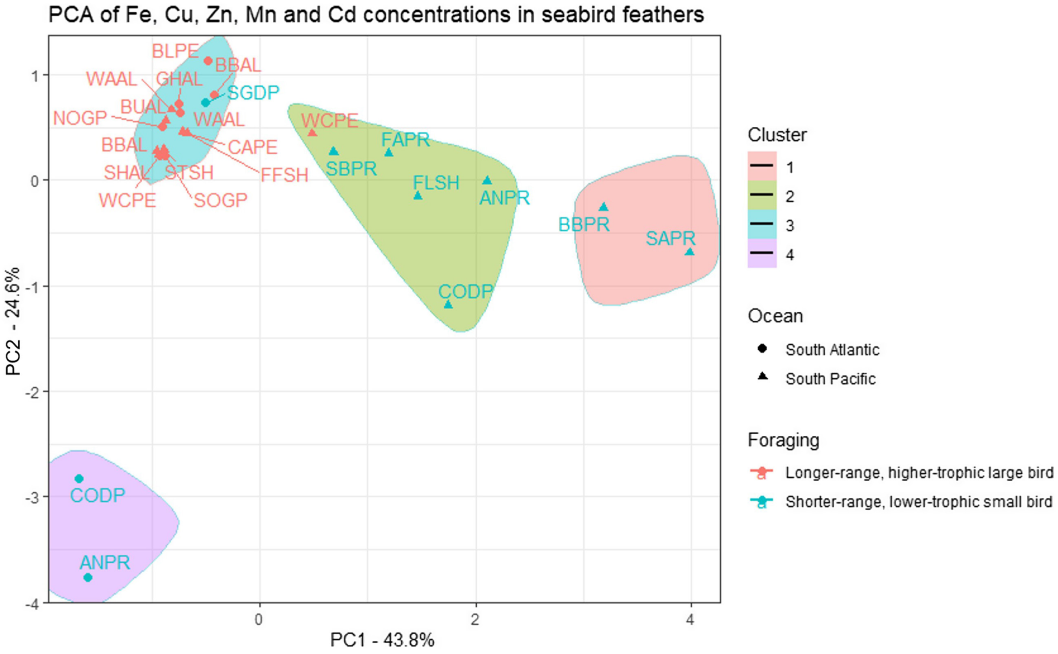

FIGURE 5 Cluster analysis of the first and second principal components (PC1 and PC2) detected four clusters describing Fe, Cu, Zn, Mn and Cd metal concentrations in seabird feathers. These clusters broadly represent three groups: small seabirds of the South Pacific (clusters 1 and 2), small seabirds of the South Atlantic (cluster 4) and large seabirds (cluster 3). WAAL = wandering-type albatross; GHAL = grey-headed albatross; SHAL = shy albatross; BBAL = black-browed albatross; BUAL = Buller's albatross; NOGP = northern giant petrel; SOGP = southern giant petrel; WCPE = white-chinned petrel; CAPE = Cape petrel; BLPE = blue petrel; FFSH = flesh-footed shearwater; STSH = short-tailed shearwater; FLSH = fluttering shearwater; BBPR = broad-billed prion; SAPR = Salvin's prion; ANPR = Antarctic prion; SBPR = slender-billed prion; FAPR = fairy prion; CODP = common diving petrel; SGDP = South Georgian diving petrel. PCA = principal component analysis.

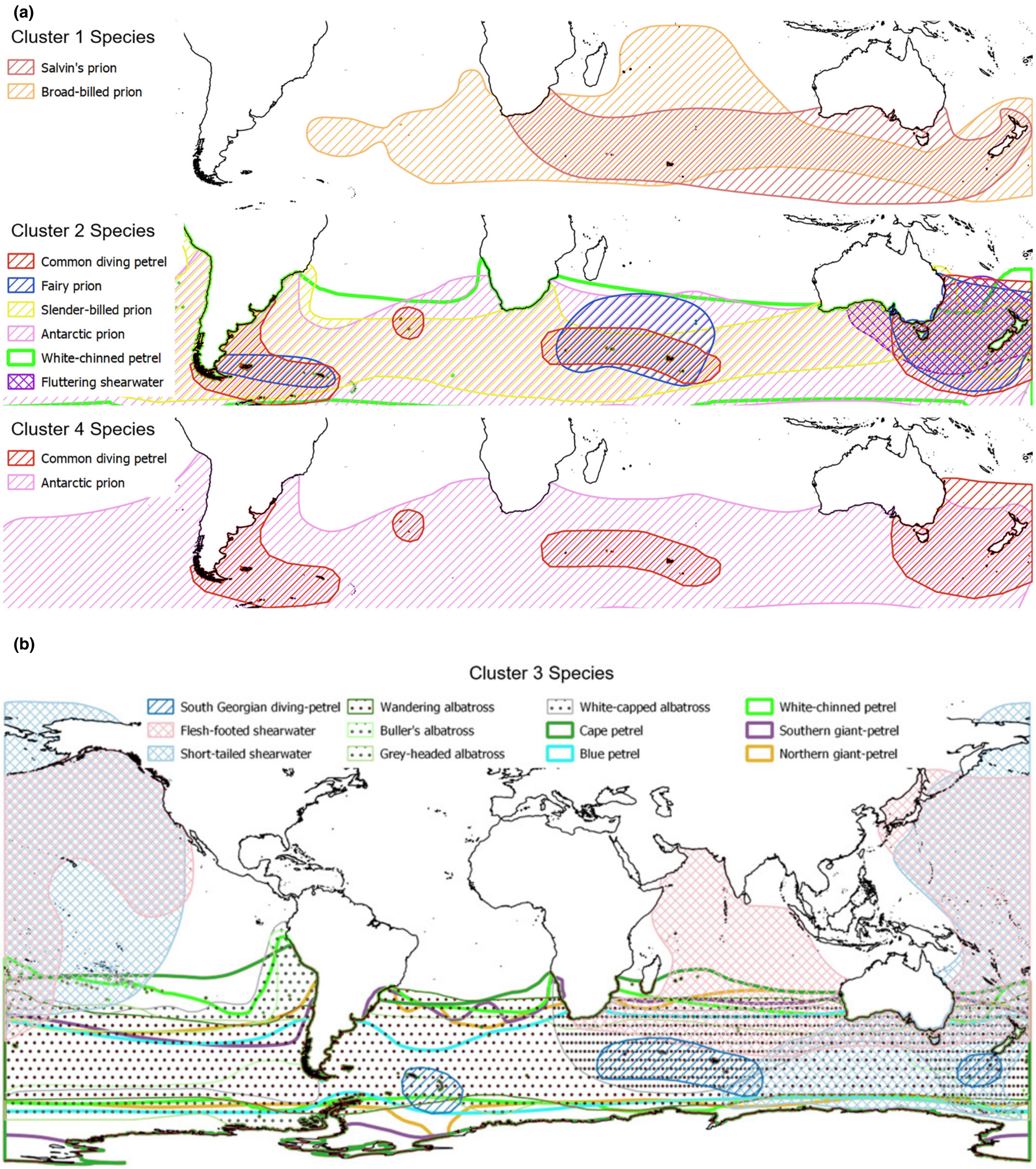

FIGURE 6 (a) Distributions of seabird species sorted into feather element concentration for clusters 1 (small seabirds sampled in South Pacific with a broad bill), 2 (other small seabirds sampled in South Pacific) and 4 (small seabirds sampled in South Atlantic). These distribution ranges show the global distribution of each species, and do not reflect the movements of individuals or specific populations, sourced from Birdlife International's Bird Species Distribution Maps (BirdLife International and Handbook of the Birds of the World, 2020). For a version of this figure overlaid with the location of hydrothermal vents and sea surface currents, see Supporting Information Figure S7a. (b) Distributions of seabird species sorted into Cluster 3 (large seabirds sampled in both South Pacific and Atlantic). These distribution ranges show the global distribution of each species, and do not reflect the movements of individuals or specific populations, sourced from Birdlife International's bird species distribution maps (BirdLife International and Handbook of the Birds of the World, 2020). For a version of this figure overlaid with the location of hydrothermal vents and sea surface currents, see Supporting Information Figure S7b.

SumOfSqs/total SumOfSqs). Cluster 1 contained two small seabirds from the South Pacific [$n = 2$ species, broad-billed prion (BBPR) and Salvin's prion (SAPR)]. Cluster 2 contained five small and one larger seabird from the South Pacific [$n = 6$ species, fairy prion (FAPR), slender-billed prion (SBPR), Antarctic prion (ANPR), fluttering shearwater (FLSH), common diving petrel (CODP) and white-chinned petrel (WCPE)]. Cluster 3 contained all albatrosses, large shearwaters and petrels [excluding South Atlantic WCPE) from both the South Pacific and South Atlantic, and one small seabird, South Georgian diving petrel ($n = 15$ species). Cluster 4 contained two small seabirds from the South Atlantic ($n = 2$ species, CODP and ANPR). Cluster 4 (Figures 5 and 6).

A one-way PERMANOVA showed that there is a statistically significant difference between the feather element concentrations (Fe, Mn, Zn, Cu and Cd) of large and small seabirds in the South Pacific Ocean [d.f. = 1, sum of squares (SumOfSqs) = 24.08, $R^2 = .36$, $F = 138$, $p < .001$; Supporting Information Figures S4 and S5]. A two-way PERMANOVA showed a statistically significant interaction between size category (large or small) and ocean (South Pacific or South Atlantic), and element concentrations in seabird feathers (Fe, Mn, Zn, Cu and Cd) (d.f. = 1, SumOfSqs = 0.73, $R^2 = .12$, $F = 11.367$, $p < .001$).

4 | DISCUSSION

4.1 | Trace element concentration in feathers, seabird size and diet

A major empirical finding of this study is that the breast feather concentrations of Al, Fe, Co, Cr, Mn, Ni, As and Cd were tens to hundreds of times higher in small tube-nosed seabird species (<400 g) than in large tube-nosed seabird species (≥400 g) in the western South Pacific Ocean/Tasman Sea, a global seabird biodiversity hotspot. For example, we observed a 500-fold difference in breast feather Fe concentration between the ~7-kg wandering-type albatrosses (14.76 mg/kg) and the ~0.2-kg broad-billed prions (7,788.12 mg/kg).

Significantly higher concentrations of some trace elements in smaller seabirds than larger species in the western South Pacific Ocean/Tasman Sea have been previously reported. Variation in element concentrations among seabird species was linked to variation in their diets (Anderson et al., 2010; Kim et al., 1998; Muirhead & Furness, 1988). Stewart et al. (1999) examined Zn, Co and Cd concentrations in the tissues of tube-nosed seabirds from the Tasman Sea and nearby region, reporting that element concentrations reflected the importance of crustaceans in the diet, phylogeny, and the duration of the moult cycle. Species in which crustaceans constituted > 33% of the diet, including small seabird species, had significantly lower Cd concentrations in liver tissues than those that consumed mainly or entirely squid and fish (Stewart et al., 1999). Likewise, Anderson et al. (2010) found that Al was generally an order of magnitude higher in crustaceans than fish and that Cd concentrations were approximately 10-fold higher in several squid species and in the planktonic amphipod *Themisto gaudichaudii* than in fish (Anderson et al., 2010; Rainbow, 1989). Rainbow (1989) supported the idea that naturally high concentrations of Cu, Cd and Zn in oceanic amphipod and euphausiid crustaceans were a source of these elements for pelagic seabirds. However, the differences between the element concentrations in liver and kidney tissue of the seabirds examined by Stewart et al. (1999) differed by two- to fivefold, in stark contrast to the tens-to-hundreds of fold increases examined in this study. These large increases in element concentration between seabird liver/kidney tissues and feathers may be due to mineral homeostasis and excretion pathways. Shedding of feathers results in the excretion of elements by birds as part of their normal physiological regulation. Unusually high concentrations in some species show that their diet is likely rich in these elements, which are probably in excess of physiological requirements. Al, Fe, Co, Cr, Mn, Ni and As were not examined by Stewart et al. (1999).

That crustaceans in the diet are a source of high concentrations of some elements sequestered in feathers does not fully explain why small planktivorous seabirds have much greater element concentrations than larger ones. Pelagic crustaceans, including *Euphausia* and *Nyctiphanes* krill and *Thermisto* and *Paraprone* amphipods, comprise a major part of the diet of larger seabirds examined in our study, including black-browed albatrosses (Prince, 1980; Reid et al., 1996), white-chinned petrels (Croxall et al., 1995), short-tailed shearwaters (Montague et al., 1986; Skira, 1986) and Cape petrels (Arnould, 1991; Coria et al., 1997). We propose that these differences in element concentrations between small and large seabirds in the Tasman Sea are due to the duration of dietary exposure to dissolved elements, through crustaceans, in small and large seabirds. Smaller seabirds including the fluttering shearwater, and subspecies of prion and common diving petrel local to the Tasman Sea undertake local foraging movements in the Tasman and adjacent seas (Marchant & Higgins, 1990) and incur longer durations of exposure to dissolved elements in this environment. This exposure differs to that of the dispersive and migratory movements of larger tube-nosed seabird species, such as the albatrosses, white-chinned petrels and *Ardenna* shearwaters, which forage across multiple ocean basins with differing seawater element availability.

4.2 | Small and large seabirds in the South Pacific and South Atlantic: contextualizing the cluster analysis of the "fingerprint" of feather element concentrations

Our cluster analysis detected four clusters describing element concentrations in seabird feathers that can largely be sorted into three broad groups: small seabirds sampled in the South Pacific (clusters 1 and 2), small seabirds sampled in the South Atlantic (cluster 4) and large seabirds sampled across both ocean basins (cluster 3) (Figure 5). This clustering demonstrates a quantitative difference in foraging behaviour that leads to differing "fingerprints" of element concentrations sequestered in the feathers of these groups. The clustering shows that broadly, large seabirds, irrespective of the ocean in which they are sampled, demonstrate a foraging strategy (prey trophic level, horizontal dispersive movements, or both) that differs to that of smaller seabirds. It also shows that smaller seabirds are more likely to have distinct feather-element concentration fingerprints that are local to the region where they were sampled (see Supporting Information Figure S6a–d). It is interesting that there are two clusters of small seabirds sampled in the South Pacific (clusters 1 and 2), although we note that the centroids of these two clusters are close to one another. Cluster 1 contains two species, the broad-billed prion and Salvin's prion, with an unusually broad bill morphology that is specialized for filter feeding and unlike any other seabird species (except perhaps the Antarctic prion, located in cluster 2, but the next closest species to the centroid of cluster 1). It may be that this unusual bill morphology leads to a more specialized diet than in those with a more "typical" bill morphology, and consequently a different element-concentration fingerprint, resulting in two South Pacific small seabird clusters. It is also possible that these two species forage more commonly in the Southern or Indian Oceans than do the others (Figure 6).

We found two exceptions to the large seabird-higher-trophic-widespread movement and small-seabird-lower-trophic-local movement trend. First, the 1.2-kg white-chinned petrel, sampled in the South Pacific (SP-WCPE), among the South Pacific small seabirds, and second, the small South Georgian diving petrel (SGDP) among the large seabird group. The SP-WCPE is located farthest from the centroid of its cluster, and close to the large seabird cluster. Its inclusion in this cluster may reflect that in the South Pacific Ocean basin, the foraging behaviour of the sampled individuals may be more similar to that of smaller seabirds of the South Pacific. Whether this finding is due to birds foraging on lower-trophic prey, local foraging, or both, is not known. The foraging and movement behaviours of white-chinned petrels in the South Pacific Ocean are not as well studied as the behaviours of white-chinned petrels in the South Atlantic; however, genomic work shows genetic differentiation between WCPE populations that breed on islands in the South Pacific compared to South Atlantic (Rexer-Huber et al., 2019), and it is possible that there may also be behavioural differences between the populations. We do not know the reason for the fingerprint of feather element concentrations of the South Georgian diving petrel more closely resembling that of large seabirds than all other small seabirds. Studies of the foraging behaviour of the South Georgian diving petrel at Iles Kerguelen in the South Indian Ocean show a complete trophic segregation compared to the common diving petrel (CODP), with SGDP foraging in offshore waters compared to coastal foraging by common diving petrel (Bocher et al., 2000). If similar foraging/trophic segregation occurs between common diving petrel and South Georgian diving petrel breeding in the South Atlantic, with South Georgian diving petrel making long foraging trips, perhaps this may explain why their feather-element fingerprint is more similar to that of larger seabirds that typically make longer trips than do the smaller seabirds investigated. Furthermore, we acknowledge that there may be interspecific variation among excretion pathways that may influence these patterns that cannot be accounted for in this study, given that these physiological processes are yet to be quantified in seabirds.

4.3 | Trace elements in seawater and seabird biodiversity hotspots

Seabirds feed on a range of vertebrate and invertebrate marine organisms, the food webs of which occur primarily in the photic zone, approximately the surface 200 m of ocean. The surface 200 m of seawater in the foraging range of small seabirds in and adjacent to the Tasman Sea contains higher concentrations of dissolved Fe and Mn than do other tube-nosed seabird biodiversity hotspots, for example those surrounding the South Georgia/South Sandwich Islands and Gough Island in the South Atlantic Ocean (see Schlitzer et al., 2018; Supporting Information Figure S6a,d). Conversely, the surface 200 m of seawater in the Southern and South Atlantic oceans, adjacent to the South Georgia/South Sandwich Islands and Gough Island, contains much higher concentrations of dissolved Cu and Zn than do the regions in and around the Tasman seabird hotspot in the South Pacific Ocean (see Schlitzer et al., 2018; Supporting Information Figure S6a,d). The availability of micronutrients including Fe, Mn, Zn, Cu, in addition to macronutrient availability, are associated with higher arthropod abundance in terrestrial environments (Prather et al., 2020). Should this association occur in marine environments, it may form a basis for hotspots of marine predators congregating to feed on these invertebrates.

The study of elements in the feathers of tube-nosed seabirds at Bird Island, South Georgia, a seabird biodiversity hotspot in the South Atlantic Ocean, found few consistent patterns in element distributions among species, but diet appeared to be highly influential in some instances (Anderson et al., 2010). Anderson et al. (2010) examined 22 elements in seabird prey species at Bird Island, including crustaceans, fish and cephalopods, matching these to the element concentrations in the blood and feathers of sampled seabirds. Though not specifically discussed, except in the context of Cd, their results show higher concentrations of Cu and Zn in the feathers of smaller seabirds (common diving petrel and Antarctic prion) than in the feathers of albatrosses. Notably, these patterns do not match those observed in feathers of small seabirds collected in the Tasman Sea, where instead, feather Fe and Mn were many times higher than they were in larger seabirds. However, this case study of the feather concentrations of Fe, Cu and Mn does match the availability of these trace elements in seawater, therefore available to seabirds, in these two seabird biodiversity hotspots (Figure 7).

In the South Pacific Ocean, phytoplankton are limited by Fe and Cu, and experimental addition of these limiting nutrients boosts productivity (Coale, 1991). Manganese and Fe concentrations are relatively high in waters off New Zealand. Iron is delivered to these waters, and to the Southern Ocean, in sediments and dust from

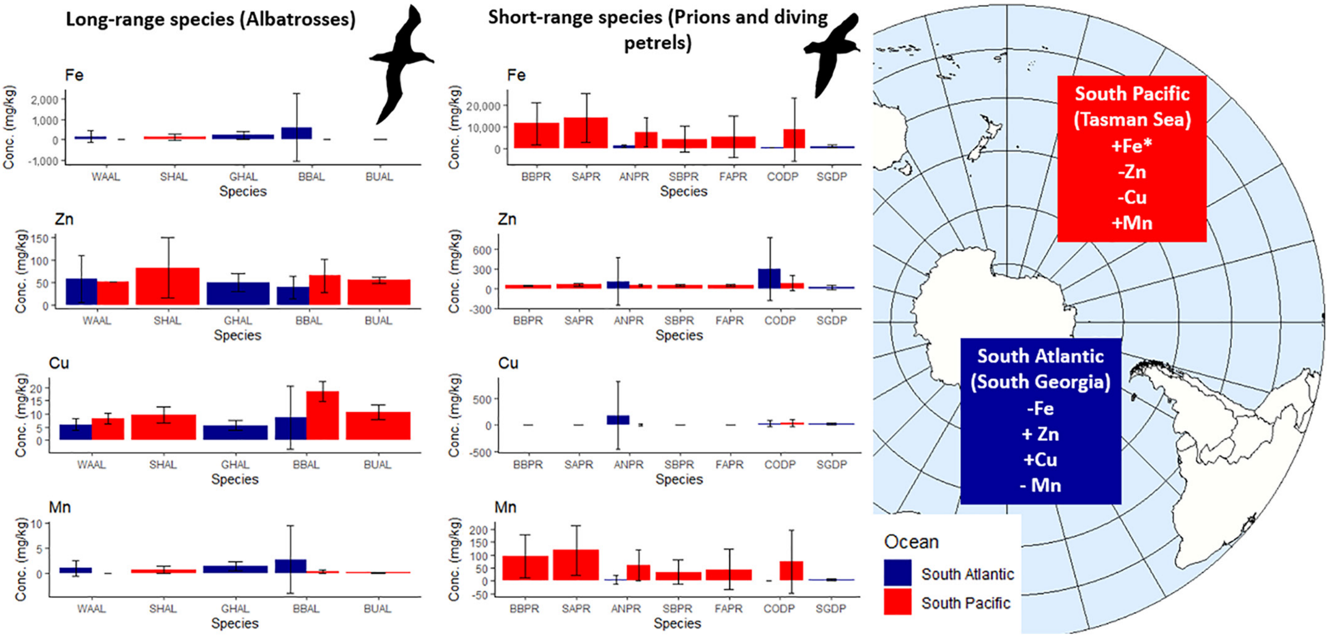

FIGURE 7 Iron (Fe), zinc (Zn), copper (Cu) and manganese (Mn) sequestered in the feathers of long-ranging (albatrosses) and short-ranging (prion and diving petrel) species collected adjacent to the Tasman Sea, South Pacific Ocean (this study) and on South Georgia, South Atlantic Ocean by Anderson et al. (2010). Also shown is the relative availability of these elements dissolved in seawater (up to 200 m depth), with higher (+) and lower (-) availability from sampling voyages in the South Pacific Ocean (GP13, May–Jun 2011) and South Atlantic Ocean (GIPY05_e, Feb–Mar 2008) (Schlitzer et al., 2018). *Higher iron (Fe) occurs near coastal Australia and seamounts. WAAL = wandering-type albatross; SHAL = shy albatross; GHAL = grey-headed albatross, BBAL = black-browed albatross; BUAL = Buller's albatross; WCPE = white-chinned petrel; FFSH = flesh-footed shearwater; STSH = short-tailed shearwater; FLSH = fluttering shearwater; BBPR = broad-billed prion; SAPR = Salvin's prion; ANPR = Antarctic prion; SBPR = slender-billed prion; FAPR = fairy prion; CODP = common diving petrel; SGDP = South Georgian diving petrel.

landmasses (for example, the Australian mainland; Lamy et al., 2014; Li et al., 2008). Manganese concentrations peak along the Tonga-Kermadec ridge in the South Pacific Ocean, possibly because of input from hydrothermal vents (Massoth et al., 2003; Schlitzer et al., 2018; Supporting Information Figure S7a,b). Manganese and Zn enrichment boosts the biomass of various zooplankton species (Coale, 1991). Hydrothermal vents have the potential to trigger massive phytoplankton blooms in the Southern Ocean, potentially as a result of the influx of Fe into this Fe-limited ocean system (Ardyna et al., 2019). Plumes from the inputs of trace elements from hydrothermal events can occur across thousands of kilometres, a process that has been demonstrated for Fe (Resing et al., 2015). The Southern Ocean, containing or adjacent to most seabird biodiversity hotspots, is the largest Fe-limited region of the global ocean and local phytoplankton is sensitive to Fe (Ardyna et al., 2017). However, whether there is a causal link between hydrothermal vents, plankton blooms and the element concentrations detected in seabird feathers in the context of this study is not known, and further investigation is recommended.

In both Stewart et al. (1999) and Anderson et al. (2010), high levels of Cd in feathers and tissues were linked to diet, which likely reflects the availability in Antarctic and sub-Antarctic marine regions. High levels of Cd naturally occur in *Thermisto* amphipods (Rainbow, 1989), and are a likely dietary source for small planktivorous seabird species. This naturally occurring Cd was previously detected at high levels in healthy sub-Antarctic seabirds (Alam & Sadiq, 1993; Jerez et al., 2013; Muirhead & Furness, 1988). Muirhead and Furness (1988) examined Cd concentrations in organ tissue for seabirds on Gough Island, finding the highest detected loads in albatrosses, with the highest mean value of 32 μg/g in wandering albatrosses and 26 μg/g in sooty albatrosses. Although these levels are many times higher than those in terrestrial birds, previous studies suggested that seabirds were not adversely affected, and likely had physiological mechanisms to protect them against these elements (Goutte et al., 2014; Norheim, 1987; Summers et al., 2014).

We propose that the fingerprint of element concentrations observed reflects both the exposure of seabirds to these elements through their diet, and the duration of the exposure due to the seabirds' movements (smaller-range movements for smaller seabirds and longer-range movements for larger seabirds; Figure 8, Supporting Information Figure S7a,b). The feather moult of most species does not typically overlap with breeding, and we can infer that for long-distance travellers, feather development occurs away from the colony, though we do not know specifically where the sampled birds were foraging when their feathers grew, nor can we account for naturally occurring seasonal or annual changes in nutrient variability in the ocean. Element levels in feathers in short-distance foragers reflected ions available in the surface 200 m of seawater near where the birds were sampled (see Schlitzer

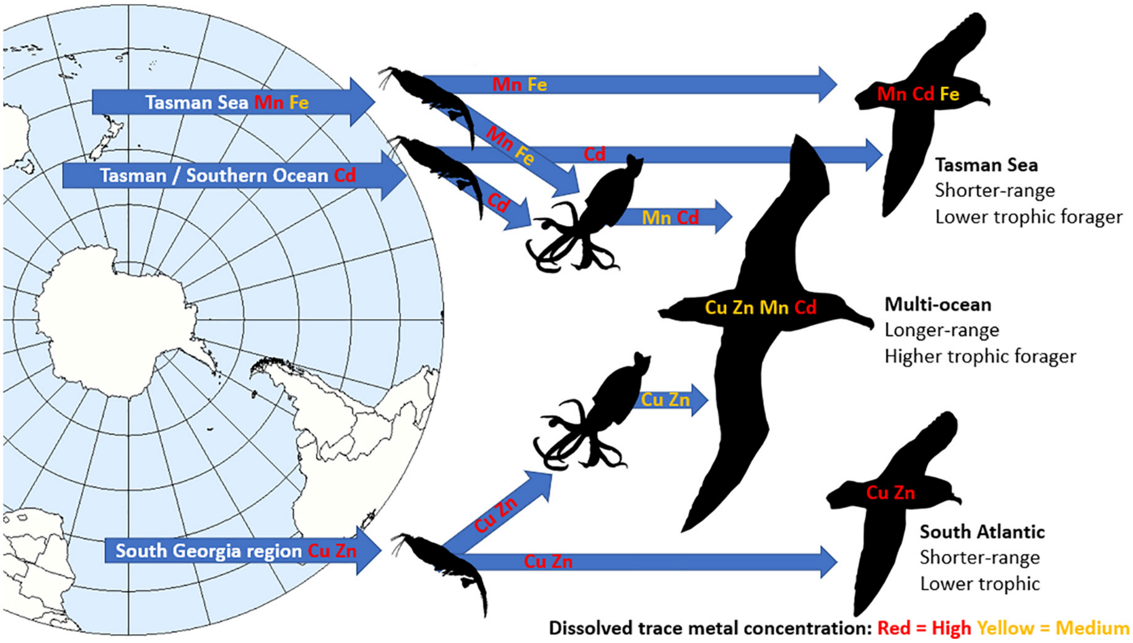

FIGURE 8 Conceptual diagram showing the possible flow of dietary metals between invertebrate prey, lower-trophic (shorter-range) and higher-trophic (longer-range) foraging seabirds that may lead to the observed patterns in feather element concentration.

et al., 2018; Supporting Information Figure S6a–d), matched in corresponding excesses of specific trace elements in the feathers of shorter-range foragers. These observations have important implications for the biogeography of seabird biodiversity hotspots, and beg the question, do highly mobile animals use different locations to meet their mineral nutritional needs, in addition to their energetic needs?

4.4 | Element availability and the biogeography of seabird biodiversity hotspots

Here we propose that the availability of environmentally limited elements, for example Fe, Co, Cr, Mn and Ni, may be a driver in the long-distance foraging movements made by seabirds, and potentially other mobile marine predators. Seabird biodiversity hotspots overlap with regions with high availabilities of specific rare trace elements, for example Fe and Mn in the Tasman Sea, South Pacific and Zn and Cu in the South Atlantic (Jenkins & Van Houtan, 2016; Schlitzer et al., 2018).

To date, research concerning hotspots for marine megafauna biodiversity has focused on productivity, including productivity mosaics driven by bathymetry, biophysical processes, eddies and fronts, and overlap with chlorophyll *a* hotspots (Grecian et al., 2016). In particular, major seabird biodiversity hotspots occur in the South Pacific, South Indian and South Atlantic oceans (Jenkins & Van Houtan, 2016). Though productivity is undoubtedly an important factor in determining marine predator hotspots, many productivity hotspots and seabird biodiversity hotspots do not overlap, suggesting the influence of other factors affecting foraging decisions and horizontal dispersion. Predators selectively forage for balanced dietary nutrient composition to meet physiological demands (Kohl et al., 2015), as has been demonstrated in numerous taxa including invertebrates (Jensen et al., 2012), birds (Thompson et al., 1987) and mammals (Lewis, 1982). Furthermore, selection against high-energy food sources in favour of low-energy but nutrient-dense food has been observed in species including grey squirrels (Lewis, 1982). If seawater element availabilites support biodiversity hotspots for mobile marine predators, this observation has consequences for the allocation of marine protected areas for conservation of long-ranging marine animals (Scott et al., 2012), to balance the diversity of micronutrient availability. However, we note that the evidence presented is correlative, and further research is needed to seek the information required to demonstrate a causal link.

Environmental changes, for example, potential effects of climate change on nutrient cycles and redistribution in the Southern Ocean (Henley et al., 2020; Kim & Kim, 2021), might have an impact on hotspots for seabirds and other mobile marine predators. As Southern Hemisphere seabirds are overrepresented by burrowing species, environmental changes have the potential for cascading effects on broader ecosystem patterns and processes (Mallen-Cooper et al., 2019). Specifically, considering a balance of nutrients available in seawater would benefit the value that marine protected areas provide to wildlife now and as the environment continues to change.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data is available in Supplementary Information.

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BIOSKETCH

This manuscript is a collaboration between four research teams: Commonwealth Scientific and Industrial Research Organisation (CSIRO) Oceans and Atmosphere, Institute for Marine and Antarctic Studies (IMAS), University of Tasmania, focusing on marine research, and University of South Australia's (UniSA) Future Industries Institute and UniSA STEM, focusing on environmental studies.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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