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# Geolocators link marine mercury with levels in wild seabirds throughout their annual cycle: Consequences for trans-ecosystem biotransport<sup>☆</sup>



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## ABSTRACT

Seabirds are widely used as indicators of marine pollution, including mercury (Hg), because they track contaminant levels across space and time. However, many seabirds are migratory, and it is difficult to understand the timing and location of their Hg accumulation. Seabirds may obtain Hg thousands of kilometers away, during their non-breeding period, and deposit that Hg into their terrestrial breeding colonies. We predicted that Hg concentration in rectrices reflects exposure during the previous breeding season, in body feathers reflects non-breeding exposure, and in blood collected during breeding reflects exposure during current breeding. To test this hypothesis, we measured total Hg concentration in these three tissues, which reflect different timepoints during the annual cycle of rhinoceros auklets (*Cerorhinca monocerata*) breeding on both sides of the North Pacific (Middleton Island in Alaska and Teuri Island in Hokkaido), and tracked their wintering movement patterns with biologging devices. We (i) identify the wintering patterns of both populations, (ii) examine Hg levels in different tissues representing exposure at different time periods, (iii) test how environmental Hg exposure during the non-breeding season affects bird contamination, and (iv) assess whether variation in Hg levels during the non-breeding season influences levels accumulated in terrestrial plants. Individuals from both populations followed a figure-eight looping migration pattern. We confirm the existence of a pathway from environmental Hg to plant roots via avian tissues, as Hg concentrations were higher in plants within the auklet colonies than at control sites. Hg concentrations of breast feathers were higher in Alaskan than in Japanese auklets, but Hg concentrations in rectrices and blood were similar. Moreover, we found evidence that tissues with different turnover rates could record local anthropogenic Hg emission rates of areas visited during winter. In conclusion, Hg was transported across thousands of kilometers by seabirds and transferred to local plants.

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## 1. Introduction

Mercury (Hg) is emitted into the atmosphere by natural sources and anthropogenic activities, and, as a potent neurotoxic chemical, poses significant threats to the health of humans, wildlife and

ecosystems (Eagles-Smith et al., 2018; UN Environment, 2019). Global Hg distribution is not uniform and anthropogenic emission rates are particularly high in Asia, relative to Europe or America (UN Environment, 2019). Large-scale atmospheric and oceanic circulation can transport Hg to remote environments; for example, Hg is increasing in the Arctic despite low emission rates within the Arctic Circle (Dietz et al., 2013). High levels of Hg occur as hotspots, such as seabird colonies, where large numbers of seabirds deposit Hg bioaccumulated in their tissues (Blais et al., 2007; Shoji et al., 2019). Although understudied compared to the Arctic and Atlantic Oceans, the large east-west gradient in Hg contamination across the Pacific Ocean suggests that the migratory behavior of seabirds may be linked with spatial variation in Hg concentrations (Sunderland et al., 2009).

Colonial seabirds are widely used as indicators of contaminant trends because they integrate signals across space and time (Monteiro and Furness, 1995; Thompson et al., 1998; Thompson and Furness, 1989). Because seabirds nest in immense colonies, they can create breeding sites with high concentrations of contaminants through the accumulation of feces, feathers, and carcasses (Blais et al., 2005). Contaminant levels are typically measured at breeding sites, where seabirds aggregate in large colonies and deposit marine-derived contaminants on land (Blais et al., 2005; Shoji et al., 2019). However, tissue contaminant levels reflect contaminant load during and preceding tissue growth (Monteiro and Furness, 2001), and different tissues grow at various times in the annual cycle. For example, seabirds typically molt different feather types in discrete time periods throughout the year. Hg in feathers is considered to be a reliable measure of total body burden at the time of feather formation (Monteiro and Furness, 2001) because Hg is sequestered in the sulfhydryl groups of keratins, therefore concentrations reflect the uptake and storage of Hg between molts (Ochoa-Acuña et al., 2002). Indeed, Hg bound in the plumage can account for up to 93% of the accumulated body burden at the time of tissue generation (Braune and Gaskin, 1987). Hence, identifying the source of contaminants and the process of bio-transport is critical for interpreting seabird contamination levels as indicators of ocean health, because the distribution and movement of seabirds likely drives their Hg concentrations. Nonetheless, previous studies have not demonstrated whether the contaminants deposited at colonies are from local (breeding ground) sources concentrated via biomagnification from local dietary sources, or from distant wintering grounds. By using miniature geolocation technology that allows for year-round tracking of seabird

movement, the spatial distribution of seabirds can be linked to their tissue contaminant levels. Coupling modern biologging with traditional biological sampling can therefore reveal where, when, and to what degree seabirds are exposed to environmental contaminants (Ramos et al., 2009).

In this context, the rhinoceros auklet (*Cerorhinca monocerata*) is an apex marine predator whose Hg concentrations can reflect contaminant levels around the breeding colony (Albert et al., 2021). Auklets exhibit large-scale migratory movements that vary between populations and individuals (Hipfner et al., 2020), therefore birds encounter variable Hg exposures across their non-breeding distribution. Auks molt rectrices (tail feathers) after breeding (pre-basic molt) and breast feathers in late winter (pre-alternate molt; Gaston and Dechesne, 2020; Pyle, 2009; Sorensen et al., 2010). Hg concentrations in feathers reflect those in the diet during not only their molting period, but also over a month or longer period prior to molt (Monteiro and Furness 2001). Thus, we assumed that Hg concentrations in rectrices represent exposure mainly during the breeding period (from pre-to post-breeding in the previous year) and concentrations in breast feathers represent exposure during the non-breeding season. Blood Hg concentrations indicate exposure throughout the 70 days prior to sampling (cell turn-over time ~70 days in seabirds; Bearhop et al., 2000). Several studies have reported similar Hg concentrations in auklets despite divergent anthropogenic (human-induced) Hg emission rates across the North Pacific (Table 1). However, no study has simultaneously measured year-round movement, but these movements are likely critical to Hg accumulation.

Here, we test the hypothesis that rhinoceros auklets transport Hg accumulated during the non-breeding period to their terrestrial breeding environment by examining two populations breeding on the east and west coast of the North Pacific, and therefore encountering very different Hg regimes. As birds encounter variable Hg exposure while traveling at sea during winter (throughout this manuscript, we use winter as a synonym for 'non-breeding period'), we also hypothesized that different tissues from a single bird can indicate Hg exposure at multiple times and locations because growing tissues record local environmental contamination levels (as well as accumulation since the previous molt). We measured total Hg concentration in feathers (rectrices and breast) and whole blood of adult rhinoceros auklets at Middleton Island (eastern North Pacific) and Teuri Island (western North Pacific) to better understand the role of environmental contamination levels at distant non-breeding locations in the amount of Hg deposited at

**Table 1**  
Hg levels (mean  $\pm$  SD in  $\mu\text{g g}^{-1}$  dry wt, unless otherwise indicated) in auklets from different regions in the North Pacific.

Location	Rectrix	Body	Blood/Red blood cell	Feces	Liver	n	Source
Middleton Island	2.40 $\pm$ 0.68	6.31 $\pm$ 4.27	3.17 $\pm$ 0.80			11	Present study
Teuri Island	2.44 $\pm$ 0.70	6.25 $\pm$ 4.49	3.25 $\pm$ 0.80			<10 <sup>a</sup>	Present study
Teuri Island			0.86 $\pm$ 0.27 <sup>b</sup>	0.08 $\pm$ 0.10		21	Shoji et al. (2019)
Middleton Island		3.47 $\pm$ 1.63				19	Albert et al. (2021)
		6.89 $\pm$ 2.04 <sup>e</sup>					
Lucy Island					3.55 $\pm$ 1.31	7–9	Elliott and Scheuhammer (1997)
Storm Island					5.39 $\pm$ 1.17	7–9	Elliott and Scheuhammer (1997)
Cleland Island					3.42 $\pm$ 1.21	7–9	Elliott and Scheuhammer (1997)
Destruction Island					5.03 $\pm$ 1.41 <sup>c</sup>	8–9	Blus et al. (1999)
Protection Island					3.63 $\pm$ 1.24 <sup>c</sup>	8–9	Blus et al. (1999)
Triangle Island			1.75 $\pm$ 0.11 (adult) <sup>d</sup>			NA <sup>f</sup>	Hipfner et al. (2011)
			0.41 $\pm$ 0.12 (young) <sup>d</sup>				

<sup>a</sup> Except blood for 9 birds.

<sup>b</sup> Wet weight is given.

<sup>c</sup> Converted to dry weight based on 67% moisture content (Eagle-Smith et al., 2008).

<sup>d</sup> Values of s.e. are given.

<sup>e</sup> Head feathers.

<sup>f</sup> Not available.

breeding colonies. Based on published molt phenology (Gaston and Dechesne, 2020; Pitocchelli et al., 2003; Pyle, 2009; Sorensen et al., 2010; Thompson and Kitaysky, 2004; Thompson et al., 1998) and blood cell turnover, we predicted that Hg concentration in rectrices reflects breeding exposure in the previous year, body feathers reflect non-breeding exposure, and blood collected during breeding reflects breeding exposure in the current year. To test these predictions, we estimated the average level of Hg contamination within a given radius of wintering locations, and tested for individual-level correlations between Hg exposure and tissue contamination. Furthermore, Shoji et al. (2019) found that Hg levels in guano decrease over the breeding season, even though diet trophic position increases (from invertebrates to fish); this suggests that guano does not simply reflect short-term and local diet, but rather reflects much longer timescales and diet on the wintering grounds. We (i) identify the wintering patterns of both populations; (ii) examine Hg levels in different tissues representing exposure at different time periods; (iii) test how environmental Hg exposure during the non-breeding season affects bird contamination, and (iv) assess whether variation in Hg levels during the non-breeding season influences levels accumulated in terrestrial plants.

## 2. Materials and methods

### 2.1. Field procedures

The rhinoceros auklet breeds on islands in the North Pacific from California to Japan and Alaska ( $\sim 33^{\circ}$ – $62^{\circ}$  latitude;  $\sim 135^{\circ}$ – $120^{\circ}$  longitude). Fieldwork was carried out at two colonies on opposite sides of the species' east-west range: Middleton Island, Alaska (hereafter: AK;  $\sim 20,000$  pairs;  $59^{\circ}26'$ ,  $146^{\circ}18'$ ), and Teuri Island, Hokkaido (hereafter: JP;  $\sim 300,000$  pairs;  $44^{\circ}25'$ ,  $-141^{\circ}18'$ ). At each site, we sampled tissues from adult birds during two consecutive breeding seasons (2016–2017) and tracked the overwinter distribution of those same individuals (Table S1). Birds were caught with mist nets at runways within the colony during the chick-rearing period in June–August (AK), or at the nest during the incubation period in May–June (JP). Birds were ringed with a metal band in similar ways at both sites, and a geolocator (GLS) was fitted to an additional custom-made plastic ring (models Mk4083 or Mk3005, Mk3006; Biotrack, C65; Migrate Technology). In the first breeding season (2016), we deployed GLS on 12 auklets at AK and 34 auklets at JP. The following year (2017), we recaptured birds using the same site-specific techniques and retrieved GLS from 11 auklets at AK and 14 at JP. Upon retrieval, we took a blood sample ( $\sim 1$  mL) from the brachial vein using 25–29 G syringes and collected two types of feathers (3 cm tips of the 6th rectrices, 2–3 body feathers, 3 cm tips of the 10th primary feathers were cut off with scissors) for Hg analyses (note: primary feathers were only used for stable isotope analyses to supplement small sample sizes as they reflect same period of rectrices; we minimized the number of feathers taken for ethical purposes, and some rectrix samples had insufficient volume for stable isotope analyses). These tissues were selected to reflect different periods in the annual cycle, therefore representing contaminant levels related to at-sea distribution at different timepoints (rectrices: previous breeding season to early winter; breast feathers: winter; blood: current breeding season, *i.e.*,  $\sim 70$  d prior to sampling). Immediately after collection, both the blood and feather samples were stored in a freezer ( $-10^{\circ}\text{C}$ ).

To quantify transport of auklet-derived marine Hg to terrestrial ecosystems, we collected plant roots during breeding from both the auklet-affected (*i.e.*, center of the colony) and unaffected (*i.e.*, outside of colony) sites in AK and JP ( $n = 80$  roots for each site at each colony respectively). We focused vegetation collection on the dominant plant species at both the auklet-affected and control

sites: salmonberry (*Rubus spectabilis*; AK) and Scandinavian small-reed (*Calamagrostis purpurea*; JP).

### 2.2. Laboratory analyses

Tissue samples from AK were analyzed at the Department of Natural Resource Sciences, McGill University and samples from JP were analyzed at the Department of Environmental Veterinary Sciences, Hokkaido University. Concentrations of total Hg in whole blood, feathers (rectrices, breast), and plant roots were determined using a Direct Thermal Decomposition Hg Analyzer (MA-3000; Nippon Instruments at both labs) in accordance with US EPA Method 7473. Following introduction into the machine, the biological samples were decomposed at  $800^{\circ}\text{C}$ , and the liberated Hg vapor was captured onto a gold trap following which the element was desorbed from the trap and carried to an absorbance cell (253.65 nm) for quantification. Analytical accuracy for Hg was determined through the analysis of reference materials obtained from the Canadian National Research Council (BCR-320 and DOLT-4). Recoveries of all standard reference materials were within the certified range of values (Table S2). The detection limit of the analyzer was at  $0.001$  ng. Concentrations of total Hg are reported in  $\mu\text{g g}^{-1}$  dry weight.

We analyzed the remaining sample of rectrices (after Hg analysis) and primary feathers (not analyzed for Hg) for nitrogen stable isotope ratio ( $\delta^{15}\text{N}$ ). We used the isotope ratio as a proxy for trophic level of AK and JP specific to the feather type. The samples were analyzed using an Isotope Ratio Mass Spectrometer System (Elementar UK, Iso Prime 100, AP-100199) at the Global Facility Center at Hokkaido University (methods in Kato et al. 2018). Final  $\delta$  values are reported in parts per thousand (‰) relative to international standards atmospheric nitrogen ( $\delta^{15}\text{N}$ ).

### 2.3. Spatial data

In total, we retrieved complete migration tracks for 21 individuals (eleven from AK; ten from JP); devices from three additional JP birds failed to record data. Archived light data from the GLS were decompressed and processed using the BASTrack software suite (British Antarctic Survey) and MATLAB R2014b (MathWorks). Location estimates were filtered using speed and equinox filters (following thresholds in Fayet et al., 2016), and data from the breeding season were removed. Spatial data were further processed as in Shoji et al. (2019) to remove outlier location estimates (Fig. S1). We calculated 2-day median positions for all tracks and excluded locations with high standard error ( $SE_{\text{longitude}} > 150$  km,  $SE_{\text{latitude}} > 150$  km) or unrealistic locations (latitude  $< 30^{\circ}\text{N}$  or  $> 80^{\circ}\text{N}$ ). Mean trajectories at each location (AK/JP) were defined by taking year-day average positional fixes (longitude, latitude), on which a 20-day moving average was computed to smooth the trajectory.

### 2.4. Environmental data

Global Hg emission data were obtained from the Arctic Monitoring and Assessment Program website (AMAP;  $0.5^{\circ} \times 0.5^{\circ}$  resolution; <https://www.amap.no/work-area/document/862>; last accessed February 2021). We used the most recent AMAP data (2010; deposited in February 2013) as a proxy for the 2016–17 seasons analyzed here. We limited the analyses to total Hg. As these Hg data are only available on land, we defined neighborhoods of different radii ranging from 500 m to 3000 km to match contamination levels with individual bird location estimates, from a very local to a much broader scale. Note that while this proxy might not be an optimal surrogate for marine Hg, observed atmospheric Hg

concentrations have been stable since 2009 in North America (Zhang et al., 2016) and exhibited very little fluctuation in Japan since 2015 (Marumoto et al., 2019).

## 2.5. Statistical analyses

To test for an association between environmental exposure and contamination levels, we examined relationships between total environmental Hg and Hg levels in the three bird tissues analyzed (rectrices, breast feathers, and blood). Because the timing for when each tissue is replaced (molting for feathers) approximately reflects three different time periods (rectrices: previous breeding season to early winter; breast feathers: winter; blood: late winter to current breeding season), we split these trajectories into three periods that we call *stages* here, which makes it possible to test for a correlation between “local” exposure (the neighborhoods defined above) and contamination levels. Nevertheless, we focus on at-sea locations during the non-breeding period because the GLS did not obtain reliable locations during the breeding season (maximum foraging range of breeding rhinoceros auklets has been reported as 164 km; Kato et al., 2003). As a first approximation, we assumed (based on published molt phenology, Gaston and Dechesne, 2020; Pitocchelli et al., 2003; Pyle, 2009; Sorensen et al., 2010; Thompson and Kitaysky, 2004; Thompson et al., 1998) that Hg levels in rectrices reflect autumn exposure (stage 1: August–October), breast feathers reflect winter exposure (stage 2: February–March), and blood reflects spring exposure (stage 3: March–May for JP birds, May–July for AK birds). Unless otherwise stated, post-hoc comparisons were based on the Dunn test with the Benjamini-Hochberg correction to control false discovery rates, linear regressions were based on the robust MM approach (Yohai et al., 1991), and significance was assessed at the 1% level. All analyses were performed with R (v.4.0.3, R Core Team 2019). The computer code developed in this work is available from GitHub at: [github.com/sarisbro/data/miscel\\_scripts](https://github.com/sarisbro/data/miscel_scripts). Raw data are available upon reasonable request from the lead author (AS).

## 3. Results and discussion

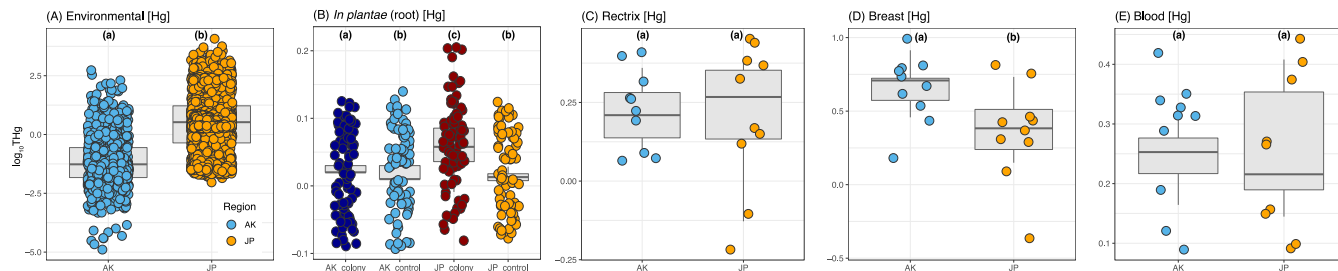
### 3.1. Auklets play a key role in transferring Hg from marine to terrestrial environments

Mean Hg concentrations in breast feathers were higher at both AK and JP, but similar within same feather types at both sites (Table 1), suggesting lower Hg intake near the breeding sites (more coastal) than at wintering grounds (more offshore) at both sites.

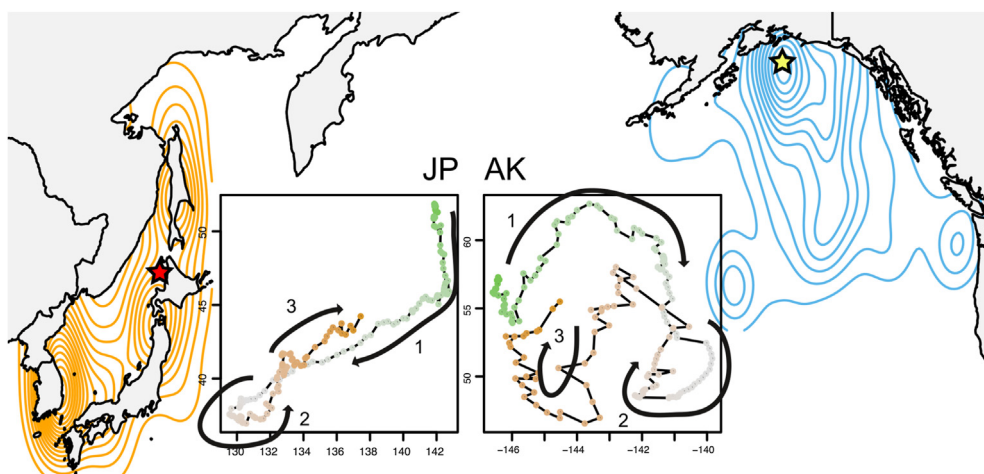
Our results align with Hg concentration reported at our study site and elsewhere (Albert et al., 2021, Table 1). First, we tested whether anthropogenic Hg emissions, Hg concentrations in auklet tissues, and Hg concentrations in plants differ between AK and JP. Environmental Hg contamination levels were higher along the wintering tracks of JP birds, relative to AK birds (Fig. 1A). At both AK and JP, mean Hg concentrations in the roots of terrestrial plants were significantly higher at auklet-affected sites than at control sites (Fig. 1B), presumably due to the disintegration of auklet tissues (guano, feathers, abandoned/inviolate eggs, carcasses) into the soil. Although Hg concentrations within the colony were higher than controls at both sites, the effect size was much greater at JP; background contamination (control) was similar at the two sites. Possible explanations may be that (i) Hg concentrations in plant roots are affected by auklet densities and/or colony size (the auklet colony on Teuri, JP, is 38 times larger than the colony on Middleton, AK; Hipfner et al., 2020), and (ii) rhinoceros auklets have only nested at Middleton Island since 1964 (S. Hatch, personal observation), whereas the Teuri Island auklet colony is likely much older. Furthermore, effects of Hg biomagnification through food chains are likely to be higher than those of bioaccumulation through environmental Hg deposition in given locations (Lavoie et al., 2013). Altogether, these results provide evidence that auklets transport Hg from marine to terrestrial ecosystems at both sites, further supporting the role of auklets as biovectors (Shoji et al., 2019). Among bird tissues, breast feathers contained almost double the contamination levels of rectrices (Fig. 1C–E). Breast feathers often contain higher Hg concentration and are thought to be more representative of body Hg concentrations compared to flight feathers (Furness et al., 1986). Hg concentrations measured in each tissue from rhinoceros auklets at AK and JP colonies are provided in Table S1. The  $\delta^{15}\text{N}$  of AK feathers was higher than JP for both rectrices (AK:  $16.0 \pm 0.8\text{‰}$ ; JP:  $14.7 \pm 0.8\text{‰}$ ,  $n = 10$  per population) and primary feathers (AK:  $16.6 \pm 0.4\text{‰}$ ; JP:  $15.3 \pm 0.8\text{‰}$ ,  $n = 10$  per population); this could indicate that AK birds tend to feed at higher trophic levels throughout the year (or at least during both molting periods) and is consistent with higher Hg in AK breast feathers. However, baseline  $\delta^{15}\text{N}$  may vary between the two sites, thus differences in isotope ratios between the populations do not necessarily reflect differences in trophic position, hence these differences cannot be considered as conclusive.

### 3.2. Wintering movements in three stages

To understand where environmental Hg exposure occurred, we observed wintering movements and distribution of JP and AK



**Fig. 1.** Distributions of Hg concentrations in the local marine environment, plant tissue at the breeding islands, and bird tissues. Jittered distributions of raw data and box plots are shown for Alaska (AK; blue) and Japan (JP; orange) sites. (A) JP birds were exposed to higher environmental Hg than AK birds. Environmental Hg concentrations are from the closest Hg measurement from the AMAP data of each location estimate from the GLS data. Hg concentrations in (B) plant roots of salmon berries (*Rubus spectabilis*) in AK and Scandinavian small-reeds (*Calamagrostis purpurea*) in JP at the auklet-affected sites (colony) and unaffected sites (control); (C) tail feathers (6th rectrices), (D) breast feathers, and (E) blood. Note the different scales for the y-axes across all five panels. All post-hoc comparisons were assessed with the Dunn test, corrected for multiple comparisons with the Benjamini-Hochberg procedure; significance is indicated at the 1% level by letter codes. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)



**Fig. 2.** Non-breeding distribution and typical trajectories of rhinoceros auklets. GLS data were retrieved from birds breeding in Alaska ( $n = 11$ ; blue) and Japan ( $n = 10$ ; orange). Colony locations are indicated with a star (yellow: Middleton Island, AK, red: Teuri Island, JP). Insets: the average trajectories in the latitude/longitude space show how trajectories were split into stages 1–3, for early, mid, and late non-breeding periods, respectively, at both locations. The color gradient is used to indicate relative timing from departure to wintering grounds (green) to return to colony (dark orange).

rhinoceros auklets using miniature loggers that recorded time, location, and activity. The broad pattern of wintering movements was consistent with earlier work on auklets breeding in Japan (Takahashi et al., 2015), where individuals followed a figure-eight pattern reflecting the exploitation of different areas over winter (Fig. 2). Auklets breeding in Alaska exhibited a similar figure-eight pattern, consistently following the same clockwise gyre (Fig. 2). In JP, this migration pattern occurred in three steps: (i) northward migration along the east coast of Sakhalin; (ii) south/southwestern route around the Korean peninsula; and (iii) returning to the colony northwards following the west coast of mainland Japan (Takahashi et al., 2015). Thus, based on the similar figure-eight looping movement at both sites, we split each set of tracks into three stages in order to associate at-sea distribution with specific periods of tissue formation and contamination. These stages correspond to the first 137 (125) days in AK (JP), the next 70 (75) days, and the final 35 (15) days of wintering, based on the dynamics of each mean trajectory (Fig. 2, insets).

### 3.3. Seabirds as tracers of remote environmental Hg concentrations

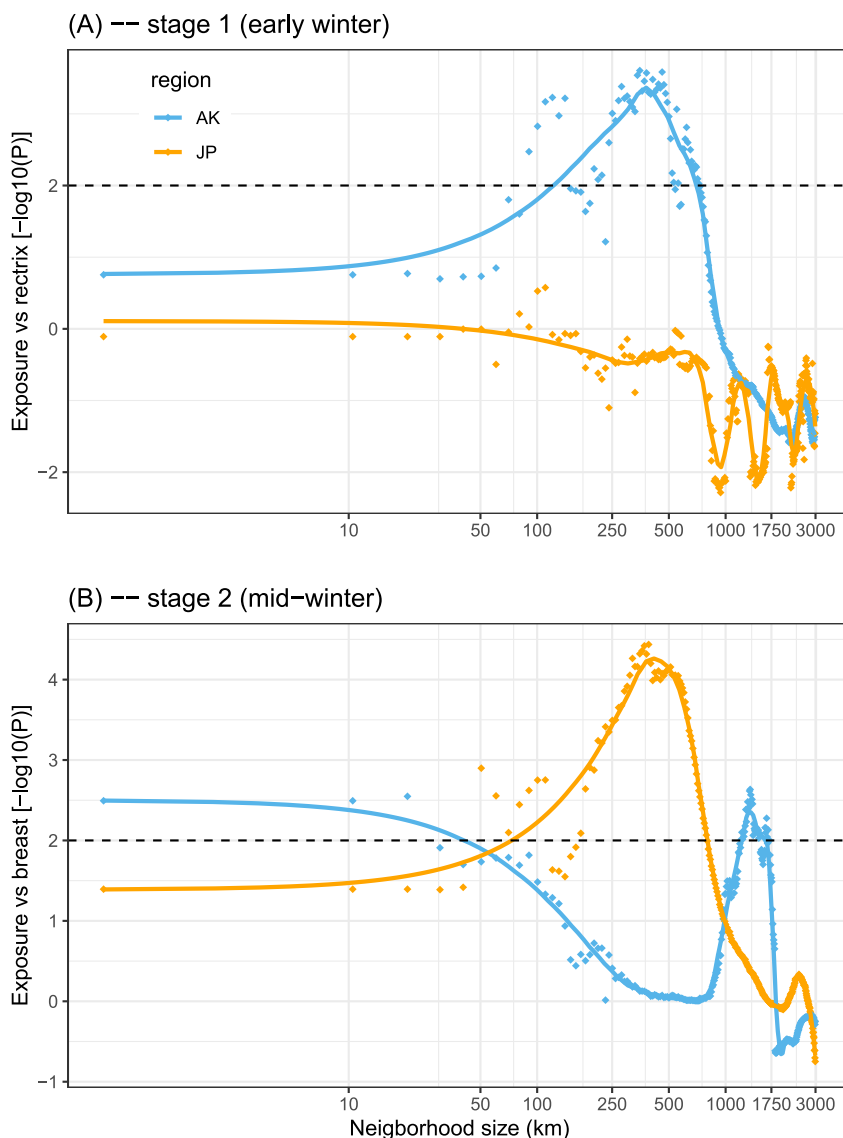
With movement trajectories partitioned into stages, we then tested for correlations between environmental Hg encountered by birds during each stage and their tissue levels. Examples of model fits are shown in Figs. S2–S6, covering the 0.5–3000 km range that we investigated for all three tissues. Each model fit returned a  $P$ -value, which was log-transformed to produce positive numbers for positive correlations ( $-\log_{10}$  transforms) and negative numbers for negative correlations ( $\log_{10}$  transforms; Fig. 3).

Both tissues recorded some Hg exposure during winter (Fig. 3), but not always as expected given current understanding of the species' molt phenology, and with notable differences between AK and JP. Birds recorded local (between 100 and 750 km) exposure levels in their rectrices during early winter (only AK; Fig. 3A), and mid-winter in their breast feathers (between 0.5 and 50 km for AK; 75–750 km for JP; Fig. 3B). The early-winter signal from rectrices is consistent with birds recording environmental Hg exposure near the breeding area/coast for AK birds, while JP birds fly along the western coast of Japan (Fig. 2), which may be less polluted than the US coast. The mid-winter signal from breast feathers is consistent with birds recording environmental Hg exposure in the non-breeding area.

Although there is some evidence that these two tissues are able to record time-stamped local environmental contamination levels, there was high variability. Hg levels in AK birds tended to follow our predictions (based on tissue turnover phenology) more often than JP birds. Hg concentrations in AK bird tissues correlated with environmental contamination at relatively local scales (<750 km) for both rectrices and breast feathers, while the rectrices of JP birds do not appear to carry any trace of environmental contamination at larger scales (up to 3000 km; Fig. 3A). One potential explanation is that timing of molt in JP birds does not follow published phenology. Alternatively, we used terrestrial environmental Hg measurements from 2010 to estimate at-sea contamination, but this study ran from 2016 to 2017. Presumably, local currents and temporal fluctuations would be more important near Asian sources than in Alaska where signals might be averaged across space and time. Future work should (i) investigate regional variation in molt phenology of seabird populations across the North Pacific, and (ii) use environmental Hg measurements that are closer in both space and time to the wintering areas of individual birds. Filling these knowledge gaps is necessary to confidently assess Hg contamination levels of the regions visited by wintering rhinoceros auklets via their tissue contamination levels.

## 4. Conclusions

Our study examined geographic variation in environmental and seabird tissue Hg levels across the North Pacific, and provides a mechanistic link for Hg transfer from distant wintering grounds to summer breeding colonies. We show that Hg in the local environment is incorporated into growing tissues (i.e., feathers, blood) of adult seabirds during both the non-breeding and breeding season; thus, individuals carry Hg from multiple sources, which is then deposited at the breeding grounds and transferred to terrestrial plants. The Hg transferred to terrestrial plants is likely sourced from a combination of breeding (wing feathers, rectrices, blood, partially guano) and non-breeding (body feathers, abandoned/inviolate eggs, partially guano) tissues. By measuring Hg levels in three bird tissues that turn over at different timepoints in the annual cycle, we show the potential for seabirds to be used to estimate Hg distribution in marine environments during winter. We highlight the importance of tissue-specific turnover rates and timing of contaminant uptake, which provide spatiotemporal information



**Fig. 3. Significance of environmental exposure on bird contamination.** Each point in each panel shows the significance of the robust (MM) regression of bird Hg level in a particular tissue vs. average environmental Hg in a neighborhood of a given radius. Results are shown for: (A) rectrices in early winter [stage 1 in Fig. 1], and (B) breast feathers in mid-winter [stage 2]. Significance is shown at the 1% level for positive correlations (horizontal broken lines); positive significance values indicate a positive slope, while negative values indicate a negative slope. In both panels, a LOESS regression was fitted to the data based on a conservative bandwidth to accommodate noise.

about contaminant exposure. These previously untapped seabird indicators of bioavailable Hg concentrations provide a new platform from which to measure and map ocean contaminants, potentially enabling us to cover spatial and temporal measurement gaps.

**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.

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### Credit author statement

AS: Conceptualization, Methodology, Investigation, Data curation, Writing – original draft, Writing-Reviewing and Editing, Funding acquisition. KHE: Methodology, Data curation, Writing-Reviewing and Editing, YW: Data curation, Writing-Reviewing and Editing, NB: Methodology, Investigation, Writing-Reviewing and Editing, Funding acquisition, SW: Investigation, Visualization, Writing-Reviewing and Editing, JC: Investigation, Writing-Reviewing and Editing, SH: Resources and Writing-Reviewing and Editing, HM: Methodology, Investigation, Writing-Reviewing, SMMN: Methodology, Writing-Reviewing, YI: Methodology, Writing-Reviewing, MI: Methodology, Writing-Reviewing, SAB: Software, Investigation, Visualization, Writing – review & editing.

### Appendix A. Supplementary data

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