Seasonal variation of mercury contamination in Arctic seabirds: A pan-Arctic assessment

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HIGHLIGHTS

- Hg concentrations were higher during the non-breeding period.
- Hg concentrations were spatially different between the Atlantic and Pacific.
- Highest Hg seasonal variations appeared in seabirds breeding in the West Atlantic.
- Some populations might be vulnerable to non-breeding Hg exposure.

GRAPHICAL ABSTRACT
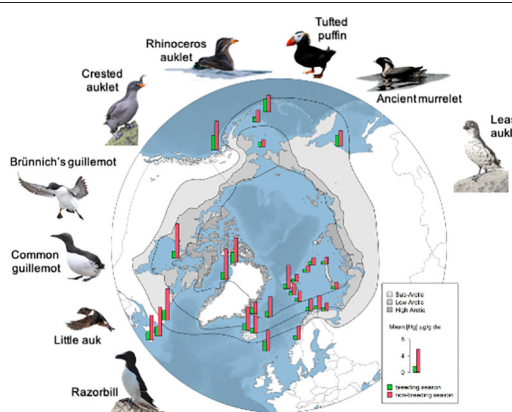
ABSTRACT

Mercury (Hg) is a natural trace element found in high concentrations in top predators, including Arctic seabirds. Most current knowledge about Hg concentrations in Arctic seabirds relates to exposure during the summer breeding period when researchers can easily access seabirds at colonies. However, the few studies focused on winter have shown higher Hg concentrations during the non-breeding period than breeding period in several tissues. Hence, improving knowledge about Hg exposure during the non-breeding period is crucial to understanding the threats and risks encountered by these species year-round. We used feathers of nine migratory alcid species occurring at high latitudes to study bird Hg exposure during both the breeding and non-breeding periods. Overall, Hg concentrations during the non-breeding period were ~3 times higher than during the breeding period. In addition, spatial differences were apparent within and between the Atlantic and Pacific regions. While Hg concentrations during the non-breeding period were ~9 times and ~3 times higher than during the breeding period for the West and East Atlantic respectively, Hg concentrations in the Pacific during the non-breeding period were only ~1.7 times higher than during the breeding period. In addition, individual Hg concentrations during the non-breeding period for most of the seabird colonies were above 5 μg g^{-1} dry weight (dw), which is considered to be the threshold at which deleterious effects are observed, suggesting that some breeding populations might be vulnerable to non-breeding Hg exposure. Since wintering area locations, and migration routes may influence seasonal Hg concentrations, it is crucial to improve our knowledge about spatial ecotoxicology to fully understand the risks associated with Hg contamination in Arctic seabirds.

1. Introduction

Concentrations of mercury (Hg), a naturally-occurring non-essential element, have increased in marine ecosystems over the last decades because of anthropogenic emissions (UNEP, 2013). In its methylated, toxic form (methyl-mercury, MeHg), Hg is considered a pollutant of concern for both wildlife and human health (Braune et al., 2012; Dietz et al., 2013, 2019; Tan et al., 2009; Wolfe et al., 1998), prevalent even in remote areas such as the polar regions (Albert et al., 2019; AMAP, 2018; Johansen et al., 2007; Provencher et al., 2014). Mercury is assimilated by organisms through their diet and biomagnifies through food webs (Morel et al., 1998). The highest concentrations are generally found in top predators, such as seabirds and marine mammals, with the latter often carrying even higher body burdens than seabirds (AMAP, 1998, 2005; Dietz et al., 1996, 2013, 2019). In turn, elevated Hg may be associated with physiological, behavioral or reproductive impacts, such as neurological deficiencies, immune disruption or lowered egg hatchability (Ackerman et al., 2016; Dietz et al., 2019), ultimately having long-term, deleterious effects on seabird population dynamics (Goutte et al., 2014a, 2014b). Spatial differences have been highlighted in numerous marine species with higher Hg concentrations found in the Canadian Arctic compared to the European Arctic (AMAP, 2018), but with large interspecies variation (Albert et al., 2019; AMAP, 2018). However, current knowledge about Hg concentrations in Arctic seabirds is restricted mostly to the breeding period (but see Fleishman et al., 2019; Fort et al., 2014), and little is known about the non-breeding period, which is mostly spent in areas outside the Arctic.

At the end of the breeding period, most Arctic seabirds leave their breeding site and migrate principally to southerly areas where conditions, including environmental Hg contamination, might differ from those encountered at their breeding areas. For example, little auks (or dovekies; *Alle alle*) had higher Hg concentrations during the non-breeding period spent east of Newfoundland than during the breeding period in East Greenland, negatively impacting their subsequent reproduction (Fort et al., 2014). Outside of the Arctic, common guillemots (or common murres, *Uria aalge*) had higher and increasing Hg concentrations while wintering in the North Sea compared to their breeding grounds (Joiris et al., 1997). In this context, to better understand the Hg contamination risk to Arctic seabirds, the concentrations of this element should be studied year-round and at multiple spatial scales.

The alcid family of seabirds (Charadriiformes: Alcidae) comprises the most numerous species in the Arctic, from the High to the sub-Arctic, and shows a circumpolar distribution. Some species are endemic to the Pacific Arctic, such as murrelets (*Brachyramphus*), auklets (Aethiini) and tufted puffins (*Fratercula cirrhata*). Others are endemic to the Atlantic Arctic, such as little auks and razorbills (*Alca torda*), or are common to both regions, such as black guillemots (*Cepphus grylle*), common guillemots and Brünnich's guillemots (or thick-billed murres;

Uria lomvia) (Gaston and Jones, 1998). Alcids feed on zooplankton (e.g. little auks, least auklets), fish (e.g. common guillemots) or both (e.g. Brünnich's guillemot), with diet potentially switching during or between seasons (Gaston and Jones, 1998). In the Arctic, most alcids aggregate in large colonies for reproduction, then migrate to overwinter in open seas, generally farther south.

Alcids undergo two seasonal molts with important implications for their Hg contamination, as approximately 70% to 90% of the Hg body burden is excreted into growing feathers (Agusa et al., 2005; Braune, 1987; Honda et al., 1986). A partial molt (head, cheeks and neck) occurs after the non-breeding period in the spring leading to the nuptial plumage, and a total molt (body, head and wings) occurs after the breeding period, leading to winter plumage. Thus, Hg concentrations in head feathers mostly provide information about non-breeding exposure (from fall to early spring), while concentrations in body and wing feathers mostly provide information about contamination at the breeding sites (from early spring to fall) (Albert et al., 2019; Fort et al., 2014).

Here we focused on nine alcid species distributed around the Arctic, representing different marine foraging niches and ocean systems. More specifically, we used body and head feathers to investigate seasonal, spatial and interspecific variation in Hg contamination. We predicted higher Hg concentrations: i) in head feathers (i.e. non-breeding period) than in body feathers (i.e. breeding period); ii) in the western Atlantic as compared to other regions; and iii) in species feeding at higher trophic levels. We based these predictions on known foraging ecologies (Gaston and Jones, 1998) and previously documented patterns of Hg exposure in the Pacific, and West and East Atlantic. The northern Pacific has higher Hg deposition rates due high emissions from Asia (Selin et al., 2007), but levels in biota are more closely linked to methylation rates by bacteria (Elliott and Elliott, 2016; Wang et al., 2018), which led us to expect high levels in the western Atlantic based on previous work (Albert et al., 2019; AMAP, 2018).

2. Material and methods

2.1. Sample collection

Body feathers and head feathers (hereafter BF and HF, respectively) were collected during the breeding period from ancient murrelets (*Synthliboramphus antiquus*), Brünnich's guillemots, common guillemots, crested auklets (*Aethia cristatella*), least auklets (*Aethia pusilla*), little auks, razorbills, rhinoceros auklets (*Cerorhinca monocerata*) and tufted puffins. Sampling took place at 28 breeding colonies from the North Atlantic to North Pacific and from the sub-Arctic to the High Arctic between 2015 and 2017 during the months of May to August ($n =$ 1331, Fig. 1, Table 1, Table S1). Seabirds were captured during late incubation and chick-rearing with a noose pole, noose carpet, mist-net or by hand, handled for 5–10 min and released after sampling. In the Aleutian Islands and the Sea of Okhotsk, BF and HF were sampled from fresh carcasses.

2.2. Mercury analysis

Prior to chemical analysis, any external contaminants were removed by plunging feathers for 3 min in a 2:1 chloroform:methanol solution in an ultrasonic bath. Feathers were then rinsed twice in a methanol solution and dried at 45 °C for 48 h. Analyses were then performed on a pool of three homogenized feathers reduced to powder with stainless-steel scissors (Carravieri et al., 2014). Total Hg concentrations were measured on a subsample of 0.50–2.00 mg dry powder using an Advanced Mercury Analyzer spectrophotometer (Altec AMA 254) at the Littoral, Environnement et Sociétés laboratory (LIENSs, La Rochelle, France) as described in Chouvelon et al. (2009). Briefly, the samples were combusted under oxygen and the liberated Hg was analyzed by atomic absorption spectrophotometry. For each sample, analyses were repeated two or three times, until the relative standard deviation for the

aliquots was <10%. Subsequently, the mean of the repeated Hg measurements was used for statistical analysis. To ensure the accuracy of measurements, certified reference materials (CRM) were analyzed every 15 samples. These included: lobster Hepatopancreas TORT-3; NRC, Canada; reference values are of $0.292 \pm 0.022 \, \mu g \, g^{-1}$ dry weight (dw) *SD*, mean measured $\pm SD = 0.296 \pm 0.002 \, \mu g \, g^{-1}$ dw, recovery = 101%; and lobster hepatopancreas TORT-2; $0.27 \pm 0.06 \, \mu g \, g^{-1}$ dw *SD*, mean measured $= 0.26 \pm 0.01 \, \mu g \, g^{-1}$ dw *SD*, recovery = 96%. Masses of the CRMs (~10 mg) were adjusted to represent amounts of Hg similar to that in feather samples. In addition, blanks were run prior to the analyses and the detection limit was established at 0.05 ng. All values are given in dry weight unless otherwise noted.

2.3. Statistical analyses

To investigate seasonal Hg variations, we first classified seabird colonies into three regions: the Pacific, the East Atlantic and the West Atlantic (Fig. 1), following previous studies and known differences in the ecology of seabirds across these regions (see Descamps et al., 2019). We used linear mixed models (R package "lme4") (Bates et al., 2015) to examine patterns in Hg seasonality and how that varied among species or region. We considered all species in a first analysis. Subsequently, we examined only the two guillemot species, as these were the only two species sampled in all three regions. In each model, we always included the type of feather (representing the breeding or non-breeding periods), plus the region and the species (1st analysis only) as fixed effects. Colonies and individuals were sampled for one to three breeding periods during the study period (2015–2017). Hence, to address the potential non-independence among Hg concentrations taken within years, within individuals, and within colonies, all three were treated as random effects. The full model followed the form: [Hg] ~ fixed effects (regions + species + type of feathers) + random effects (years + individuals + sampling sites). Hg concentrations were log_e-transformed to meet the parametric assumptions of normality and homoscedasticity of residual distribution, and to avoid impossible predicted values below zero. We used the Akaike Information Criterion (AIC, Burnham and Anderson, 2002) to compare models. As all ΔAIC values between two models differed by more than 2, the model with the lowest AIC was selected. Statistical analyses were performed with R version 3.4.3 (R Core Team, 2017) and maps were created with ArcGIS Pro version 2.5.0 (ESRI, 2019). Means are reported with standard deviation (mean ± SD) unless otherwise noted.

3. Results

Mean Hg concentrations in alcid body and head feathers, by species and by breeding site are summarized in Table 1, illustrated in Fig. S2 (details per year in Table S1), and further summarized by species and region in Table 2 and Fig. S3. The mean Hg concentrations in alcid body and head feathers, by sampling site, are summarized in Fig. 2.

3.1. Hg contamination during the breeding period

Overall, the mean Hg concentration in alcid feathers during the breeding period was $1.20 \pm 0.83 \, \mu g \, g^{-1}$ dw. Regionally, the highest mean Hg concentration across all species during the breeding period was observed in the West Atlantic ($1.70 \pm 0.77 \, \mu g \, g^{-1}$; median = $1.59 \, \mu g \, g^{-1}$; range = 0.41–$6.97 \, \mu g \, g^{-1}$), followed by the Pacific ($1.55 \pm 1.37 \, \mu g \, g^{-1}$; median = $0.95 \, \mu g \, g^{-1}$; range = 0.32–$6.99 \, \mu g \, g^{-1}$) and the East Atlantic ($0.75 \pm 0.26 \, \mu g \, g^{-1}$; median = $0.71 \, \mu g \, g^{-1}$; range = 0.28–$2.29 \, \mu g \, g^{-1}$ – Fig. S4A). The lowest mean species Hg concentration during the breeding period was measured in crested auklets ($1.00 \pm 0.51 \, \mu g \, g^{-1}$) and the highest were observed in rhinoceros auklets ($3.47 \pm 1.63 \, \mu g \, g^{-1}$ – Fig. S5A).
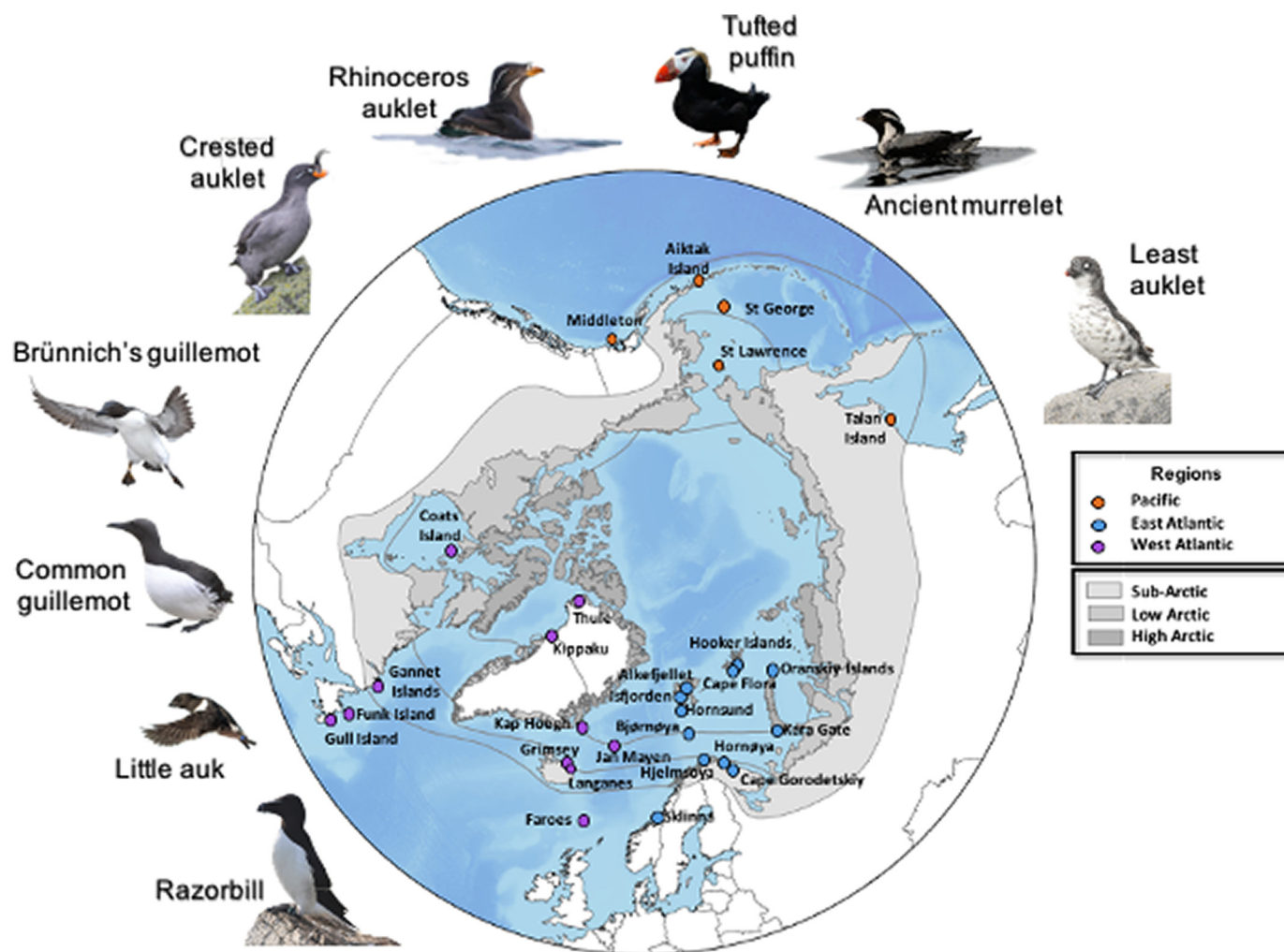
Fig. 1. Location of the sampled breeding colonies of piscivorous and planktivorous alcids and sampling sites. The study sites were divided into three regions: Pacific (orange), East Atlantic (light blue), West Atlantic (purple). Colonies are colored based on the areas they belong to. Sub, Low and High Arctic are represented following the Conservation of Arctic Flora and Fauna delimitations (CAFF, 2001). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Species and region- specific Hg concentrations (mean ± SD; in µg g^{-1} dw) measured in body feathers (BF – representing exposure during the breading period) and head feathers (HF – representing exposure during the non-breeding period). Breeding: non-breeding period Hg concentrations (mean ± SD BF:HF) calculated from individual values. BF:HF ratio are represented in Fig. S6; n = samples size.

Species	Region	Sampling site	GPS Coordinates	n	BF mean ± SD	HF mean ± SD	BF:HF
Ancient murrelet	Pacific	Talan Island	59.18°N, 149.05°E	5	2.64 ± 1.00	3.69 ± 1.18	0.81 ± 0.52
Brünnich's guillemot	Pacific	Saint George	56.59°N, 169.61°W	10	0.90 ± 0.20	3.42 ± 1.10	0.29 ± 0.11
		Saint Lawrence	63.40°N, 170.17°W	40	0.77 ± 0.33	1.43 ± 0.89	0.79 ± 0.49
	East Atlantic	Alkefjellet, Spitsbergen	79.58°N, 18.51°E	32	0.63 ± 0.20	1.70 ± 0.48	0.39 ± 0.14
		Bjørnøya	74.50°N, 18.96°E	48	0.50 ± 0.09	2.91 ± 1.73	0.24 ± 0.15
		Cape Flora, Franz Josef Land	79.95°N, 50.09°E	61	0.74 ± 0.21	1.64 ± 0.35	0.47 ± 0.16
		Cape Gorodetskiy	69.15°N, 35.95°E	19	0.66 ± 0.10	2.06 ± 0.39	0.33 ± 0.07
		Hornøya, N Norway	70.39°N, 31.16°E	59	0.75 ± 0.20	2.45 ± 1.08	0.34 ± 0.13
		Isfjorden, Spitsbergen	78.25°N, 15.51°E	32	1.17 ± 0.37	6.05 ± 1.56	0.21 ± 0.08
		Kara Gate, Novaya Zemlya	71.42°N, 51.95°E	40	0.64 ± 0.20	1.65 ± 0.52	0.41 ± 0.13
		Oranskyi islands, Novaya Zemlya	77.07°N, 67.64°E	34	0.70 ± 0.20	1.79 ± 0.35	0.39 ± 0.10
	West Atlantic	Coats Island	62.47°N, 83.10°W	19	1.63 ± 0.33	8.22 ± 3.27	0.23 ± 0.12
		Gannet Islands	53.94°N, 56.56°W	41	2.39 ± 0.95	9.24 ± 1.73	0.27 ± 0.12
		Grimsey, Iceland	66.54°N, 18.00°W	11	1.52 ± 0.24	5.56 ± 1.04	0.28 ± 0.08
		Jan Mayen	71.03°N, 8.29°W	65	1.63 ± 0.32	5.70 ± 1.77	0.32 ± 0.14
		Kippaku	73.73°N, 56.63°W	20	1.79 ± 0.44	7.38 ± 2.32	0.26 ± 0.07
		Langanes, Iceland	66.18°N, 15.99°W	35	1.38 ± 0.21	4.83 ± 1.14	0.30 ± 0.08
		Thule, NW Greenland	77.47°N, 69.23°W	17	2.62 ± 0.72	8.14 ± 2.73	0.35 ± 0.12
Common guillemot	Pacific	Saint Lawrence	63.40°N, 170.17°W	36	0.59 ± 0.17	1.42 ± 0.63	0.48 ± 0.21
	East Atlantic	Bjørnøya	74.50°N, 18.96°E	48	0.67 ± 0.13	1.95 ± 0.55	0.37 ± 0.12
		Cape Gorodetskiy	69.58°N, 32.94°E	40	0.64 ± 0.14	1.79 ± 0.42	0.37 ± 0.08
		Hjelmsøya, N Norway	71.11°N, 24.73°E	58	0.85 ± 0.20	2.85 ± 0.94	0.32 ± 0.10
		Sklinna	64.74°N, 10.77°E	20	0.94 ± 0.35	3.17 ± 0.90	0.31 ± 0.10
	West Atlantic	Faroes	61.98°N, 6.65°W	8	2.26 ± 1.05	4.91 ± 2.37	0.54 ± 0.26
		Funk Island	49.76°N, 53.18°W	23	2.21 ± 0.39	6.83 ± 1.11	0.33 ± 0.09
		Gannet Islands	53.94°N, 56.56°W	32	2.17 ± 0.51	6.44 ± 1.25	0.35 ± 0.11
		Gull Island	47.95°N, 53.04°W	40	2.04 ± 0.60	5.90 ± 1.47	0.38 ± 0.17
		Jan Mayen	71.03°N, 8.29°W	61	0.98 ± 0.36	3.88 ± 1.65	0.28 ± 0.11
		Langanes, Iceland	66.18°N, 15.99°W	37	1.11 ± 0.39	3.70 ± 0.92	0.31 ± 0.10
Crested auklet	Pacific	Saint Lawrence	63.40°N, 170.17°W	14	1.00 ± 0.51	1.45 ± 0.58	0.75 ± 0.32
Least auklet	Pacific	Saint George	56.59°N, 169.61°W	10	1.58 ± 1.22	2.38 ± 1.29	0.72 ± 0.35
		Saint Lawrence	63.40°N, 170.17°W	20	2.56 ± 1.13	2.75 ± 1.01	0.96 ± 0.31
Little auk	East Atlantic	Bjørnøya	74.50°N, 18.96°E	31	0.82 ± 0.19	2.57 ± 1.12	0.37 ± 0.15
		Hooker Island, Franz Josef Land	80.23°N, 53.02°E	67	0.81 ± 0.21	1.73 ± 0.92	0.57 ± 0.26
		Hornsund, Spitsbergen	76.97°N, 15.78°E	37	0.82 ± 0.35	2.80 ± 1.01	0.34 ± 0.23
		Isfjorden, Spitsbergen	78.25°N, 15.51°E	5	0.90 ± 0.16	2.97 ± 0.70	0.31 ± 0.03
	West Atlantic	Kap Hoegh, E Greenland	70.72°N, 21.55°W	64	1.34 ± 0.44	2.69 ± 0.70	0.52 ± 0.18
		Thule, NW Greenland	77.47°N, 69.23°W	10	2.08 ± 0.52	2.15 ± 0.40	1.00 ± 0.30
Razorbill	East Atlantic	Hornøya, N Norway	70.39°N, 31.16°E	39	0.79 ± 0.31	4.68 ± 1.54	0.20 ± 0.14
	West Atlantic	Gannet Islands	53.94°N, 56.56°W	13	2.89 ± 1.84	4.84 ± 1.55	0.65 ± 0.47
Rhinoceros auklet	Pacific	Middleton	59.44°N, 146.33°W	19	3.47 ± 1.63	6.89 ± 2.04	0.54 ± 0.33
Tufted puffin	Pacific	Aiktak Island	54.18°N, 164.82°W	11	3.12 ± 1.42	4.04 ± 1.35	0.80 ± 0.26

3.2. Hg concentrations during the non-breeding period

Mean alcid Hg concentration in feathers during the non-breeding period was 3.60 ± 2.40 µg g^{-1} dw, three times the mean concentration in the breeding period. The highest mean Hg concentrations during the non-breeding period were observed in the West Atlantic (5.42 ± 2.52 µg g^{-1}; median = 5.21 µg g^{-1}; range = 1.21–15.44 µg g^{-1}) followed by the Pacific (2.64 ± 2.07 µg g^{-1}; median = 2.06 µg g^{-1};

Table 2

Geographical variations in Hg concentrations (mean ± SD - µg g^{-1} dw) measured in body feathers (BF – representing exposure during the breeding period) and head feathers (HF – representing exposure during the non-breeding period). Breeding: non-breeding period Hg concentrations (mean ± SD BF:HF) calculated from individual values; n = samples size.

| Species	Regions	n	BF mean ± SD	HF mean ± SD	BF:HF
Ancient murrelet	Pacific	5	2.64 ± 1.00	3.69 ± 1.18	0.81 ± 0.52
	Pacific	50	0.80 ± 0.31	1.83 ± 1.23	0.69 ± 0.49
Brünnich's guillemot	East Atlantic	325	0.72 ± 0.27	2.45 ± 1.61	0.36 ± 0.16
	West Atlantic	208	1.83 ± 0.67	6.84 ± 2.55	0.29 ± 0.12
	Pacific	36	0.59 ± 0.17	1.42 ± 0.63	0.48 ± 0.21
Common guillemot	East Atlantic	166	0.76 ± 0.23	2.37 ± 0.90	0.34 ± 0.11
	West Atlantic	201	1.60 ± 0.74	5.03 ± 1.88	0.33 ± 0.14
Crested auklet	Pacific	14	1.00 ± 0.51	1.45 ± 0.58	0.75 ± 0.32
Least auklet	Pacific	30	2.24 ± 1.23	2.63 ± 1.10	0.88 ± 0.34
Little auk	East Atlantic	140	0.82 ± 0.24	2.24 ± 1.10	0.46 ± 0.25
	West Atlantic	74	1.44 ± 0.51	2.61 ± 0.69	0.58 ± 0.25
Razorbill	East Atlantic	39	0.79 ± 0.31	4.68 ± 1.54	0.20 ± 0.14
	West Atlantic	13	2.89 ± 1.84	4.84 ± 1.55	0.65 ± 0.47
Rhinoceros auklet	Pacific	19	3.47 ± 1.63	6.89 ± 2.04	0.54 ± 0.33
Tufted puffin	Pacific	11	3.12 ± 1.42	4.04 ± 1.35	0.80 ± 0.26
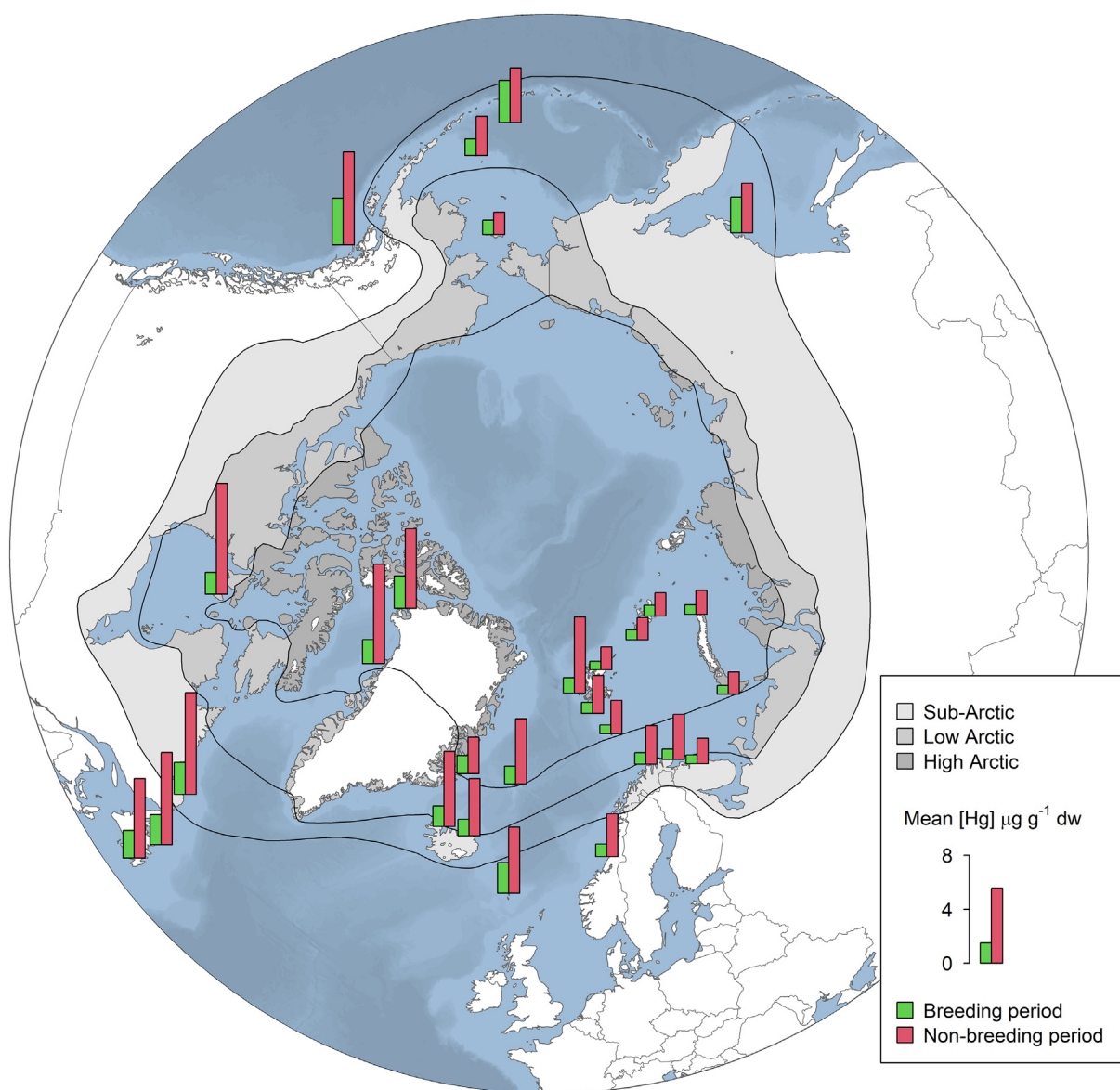
Fig. 2. Hg concentrations during the breeding (body feathers - green) and non-breeding period (head feathers - red) for each study colony. Mean Hg concentrations and *SD* per species and colony are presented in Table 1 and Fig. S2. Sub, Low and High Arctic are represented following the Conservation of Arctic Flora and Fauna delimitations (CAFF, 2001). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

range = 0.26–11.65 µg g^{-1}) and the East Atlantic (2.52 ± 1.46 µg g^{-1}; median = 2.01 µg g^{-1}; range = 0.47–8.77 µg g^{-1} – Fig. S4B). Mirroring the breeding period results, the lowest mean Hg concentration during the non-breeding period was measured in crested auklets (1.45 ± 0.58 µg g^{-1}) while the highest observed was in rhinoceros auklets (6.89 ± 2.04 µg g^{-1} – Fig. S5B).

3.3. Hg seasonality

When testing for seasonal and species variation in Hg concentrations, the best-fit model included the interaction between species and season (AIC model with interaction = 2433.08; AIC model without interaction = 2667.68). This model indicated higher Hg concentrations during the non-breeding period, varying according to species. The largest seasonal differences occurred in Brünnich's guillemots (estimate ± SD = 1.15 ± 0.68 µg g^{-1}), common guillemots (1.12 ± 0.57 µg g^{-1}), little auks (0.82 ± 0.62 µg g^{-1}) and razorbills (1.50 ± 1.22 µg g^{-1}); while no significant seasonal variation in Hg concentrations was found in ancient murrelets (0.36 ± 0.66 µg g^{-1}), crested auklets (0.41 ±

0.69 µg g^{-1}), least auklets (0.23 ± 0.70 µg g^{-1}), rhinoceros auklets (0.75 ± 0.68 µg g^{-1}) and tufted puffins (0.29 ± 0.66 µg g^{-1}). When testing for seasonal differences among regions, the best-fit model included the interaction between season and region (AIC model with interaction = 2643.84; AIC model without interaction = 2815.64). This model indicated higher Hg concentrations during the non-breeding period, varying according to region. The largest seasonal Hg difference was found in the West Atlantic (1.13 ± 0.63 µg g^{-1}) and the East Atlantic (1.13 ± 0.73 µg g^{-1}) followed by the Pacific (0.57 ± 0.73 µg g^{-1}). The frequency of individual (per species and breeding colonies) below or above the toxicity threshold (Eisler, 1987) of 5.00 µg g^{-1} during the non-breeding period is represented in Fig. 3.

We tested for seasonal and spatial differences in Hg concentrations for Brünnich's and common guillemots, the two species sampled in all three regions. For Brünnich's guillemots, the best-fit model included an interaction between the type of feather and the region (AIC model with interaction = 943.16; AIC model without interaction = 1014.28). This indicated that higher Hg concentrations occurred during the non-breeding period with variations being region-specific in this
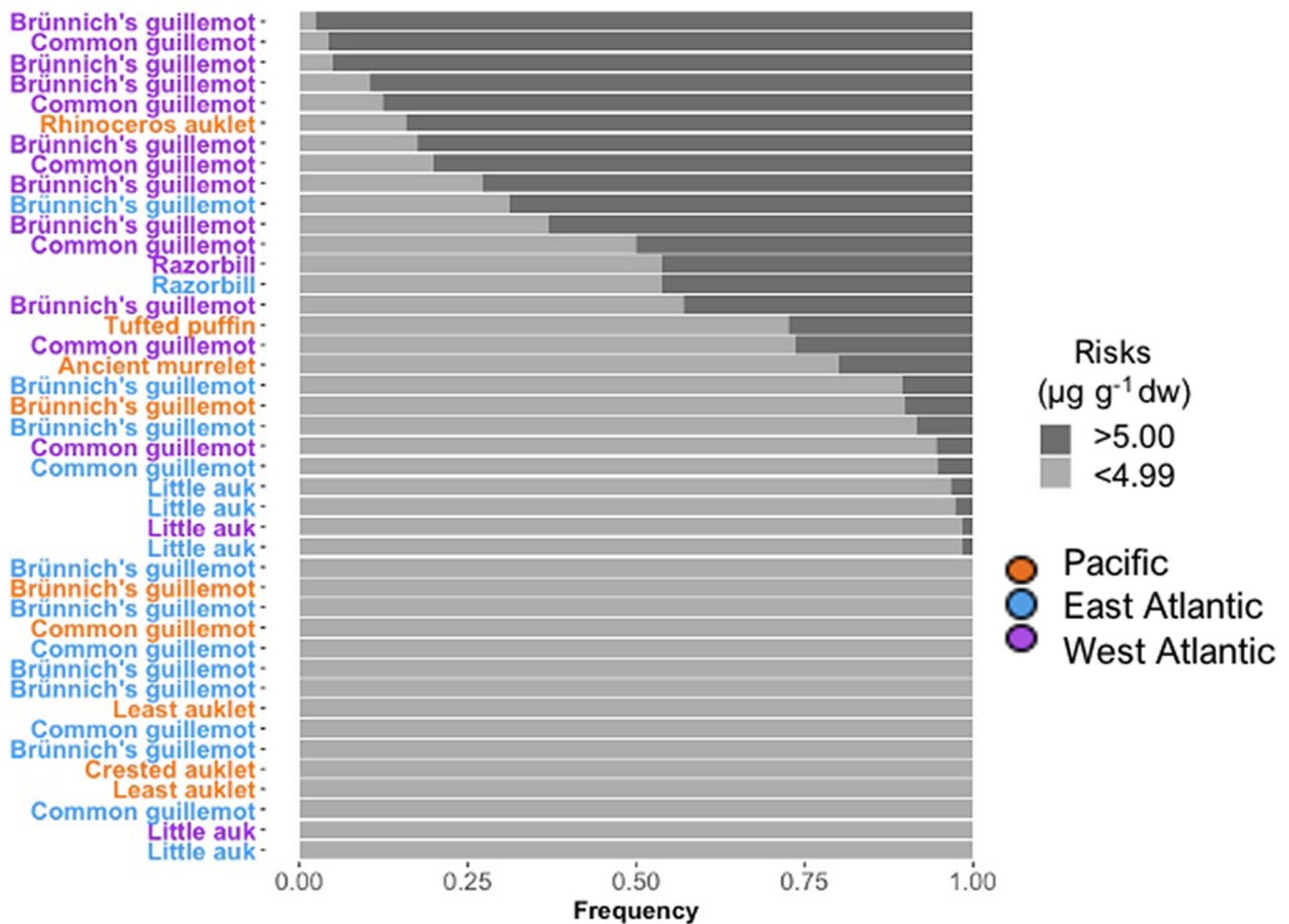
Fig. 3. Frequency of individuals below (light grey) or above (dark grey) the toxicity threshold (Eisler, 1987) of 5.00 µg g^{-1} dw in head feathers (representing exposure during the non-breeding period). The species and breeding colony names are colored by regions (see Fig. 1 - Pacific (orange), East Atlantic (light blue), West Atlantic (purple)). The sample size per species and colony can be found in Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species. The largest seasonal difference in Brünnich's guillemots occurred in the West Atlantic (estimate ± SD = 1.30 ± 0.61 µg g^{-1}), followed by the East Atlantic (1.14 ± 0.76 µg g^{-1}) and the Pacific (0.63 ± 0.60 µg g^{-1}). For common guillemots, similar results were found with contrasting seasonal differences in Hg concentrations across the three regions (AIC model with interaction = 363.37; AIC model without interaction = 379.03), and following the same pattern of largest differences in the West Atlantic (1.12 ± 0.60 µg g^{-1}) and the East Atlantic (1.12 ± 0.55 µg g^{-1}), followed by the smallest differences in the Pacific (0.83 ± 0.51 µg g^{-1}).

4. Discussion

Limited data, from both blood and feather samples previously suggested considerable seasonal variation in seabird Hg concentrations, with higher contamination reported from the non-breeding period when seabirds are often outside of Arctic regions (Fort et al., 2014; Joiris et al., 1997; Lavoie et al., 2014; Takahashi et al., 2020). In our study, we found clear seasonal differences in Hg concentrations for most study sites and species, confirming that higher Hg exposure occurred during the non-breeding period for some species. However, populations of ancient murrelets, crested and least auklets, and tufted puffins from the Pacific, in addition to the little auks from the northwest Atlantic (Thule, Greenland), presented low or no seasonal variation (BF: HF ratio > 0.70) in their Hg concentrations. Non-breeding Hg

contamination can be associated with negative effects during the following breeding season; birds with higher Hg concentrations subsequently had smaller eggs and experienced enhanced contamination during the breeding period (Fort et al., 2014; Lavoie et al., 2014). Further study is needed to assess the importance of effects on breeding driven by Hg contamination, especially for guillemots in the West Atlantic and rhinoceros auklets in the Pacific, as those populations have especially high levels of Hg. Four non-exclusive hypotheses could explain Hg seasonal variation in migratory species: 1) the occurrence of a dietary shift between seasons, 2) different food chain lengths in breeding versus non-breeding areas; 3) contrasting environmental contamination between sites; and/or 4) higher energy requirements (e.g. during storms, increased thermoregulatory costs) and thus enhanced food intakes during the winter period (Burke and Montevecchi, 2018; Dunn et al., 2020; Fort et al., 2009).

4.1. Seasonal and interspecific differences

As food represents the main pathway of Hg exposure for seabirds and other marine predators, their contamination is closely related to their diet and trophic position (Carravieri et al., 2018), with Hg concentrations increasing with trophic level. Therefore, seasonal dietary shifts towards higher trophic level prey or the use of longer food chains during the non-breeding period may lead to higher Hg concentrations (Braune et al., 2014). Nitrogen stable isotope ratios have been widely used to

infer trophic level in Arctic marine systems (e.g. Hobson et al., 2002), including characterization of Hg biomagnification processes (Atwell et al., 1998; Campbell et al., 2005; Pomerleau et al., 2016). However, nitrogen stable isotopes in feathers reflect bird trophic status during the feather growth period only (which lasts a few weeks), while Hg concentrations represent their contamination during the intermolt period (lasting several months). Hence, using nitrogen stable isotopes in feathers to interpret Hg concentrations and their seasonal variations requires a stable diet through the inter-molt period (Bond, 2010). In addition, comparing stable isotope values at large spatial scales requires accurate information about spatial baseline variation (e.g. isoscapes) (Hobson et al., 2012), which is still largely missing for the non-breeding period and the Arctic and subarctic regions. Moreover, the diet of Arctic seabirds is generally well-documented during the breeding period but information about their winter diet is scarce, and only available for five of the nine studied species (Brünnich's and common guillemots, little auks, ancient murrelets, rhinoceros auklets) from a few wintering areas (see references below).

For most populations, higher Hg concentrations were found during the non-breeding period. This contrasts with reported dietary shifts towards lower trophic levels during that period for some species. For example, across their range Brünnich's guillemots feed on both fish and zooplankton during the breeding period (Gaston and Jones, 1998). During the non-breeding period, they forage on lower trophic level prey (mostly invertebrates and fish in the Atlantic and mostly invertebrates in the Pacific, Gaston and Jones, 1998), although differences across sites might occur (Karnovsky et al., 2008; Linnebjerg et al., 2013; Moody and Hobson, 2007). Common guillemots (mostly feeding on fish) and razorbills (feeding on fish during summer and on a mixed diet of fish and zooplankton during winter) are known to have a constant diet or a switch to lower trophic level prey in winter, respectively (e.g. Huettmann et al., 2005; Lilliendahl, 2009; Lorentsen et al., 1999). Again, this contrasts with the higher Hg concentrations measured in the present study during the non-breeding period; we expected that feeding lower in the food web during the winter would result in lower Hg exposure.

A few studies investigated food web structure in the Arctic (e.g., Baffin Bay; Hobson and Welch, 1992; Linnebjerg et al., 2016) and subarctic marine systems (e.g., continental shelf off Newfoundland; Sherwood and Rose, 2005). These findings suggest slightly shortening food chain lengths towards southern locations. Again, this contrast with our finding of higher Hg contamination in birds during the non-breeding period, as they distribute more southerly at that time and we expected higher Hg uptake to result from longer food chains. Thus, our results suggest that other processes, besides diet shifts or differences in food web complexity, could be operating. Alternatively, a larger food intake due to higher energy requirements during the cold season (Burke and Montevecchi, 2018; Fort et al., 2009) and/or less excretion of Hg in winter due to less plumage exchange/formation at this time of the year may explain the higher Hg accumulates measured in feathers grown during the non-breeding period/winter. Therefore, bird movements and distribution, both during summer and winter, are likely the dominant factor in driving seasonal patterns of Hg concentration in Arctic alcids.

4.2. Seasonal and spatial differences

Our results also highlight spatial differences in seabird Hg contamination during the non-breeding period, as reflected by HF measurements. Mean Hg concentrations were higher in seabird populations breeding in the Northwest Atlantic, which are likely overwintering in the Labrador Sea (Linnebjerg et al., 2018; McFarlane Tranquilla et al., 2014), compared to the Northeast Atlantic seabirds, overwintering farther east (Fort et al., 2013a). Such results are concurring with the higher Hg concentrations reported earlier in little auks overwintering off

Newfoundland (Fort et al., 2014) and suggest a Hg hotspot in the Labrador Sea.

In only a few cases, we found low or no seasonal variation in Hg concentrations, suggesting a constant Hg contamination year-round. This occurred almost exclusively in Pacific species and populations (i.e. ancient murrelets, crested, least auklets) as well as in one little auk population breeding in northwest Greenland (Northwest Atlantic). This absence of seasonal variation in the Pacific region could be due to a similar exposure at both their breeding and non-breeding sites, representing long distance and widely dispersed transport of Hg from Asia (Selin et al., 2007). It is unlikely that the similarity is due to a shared resident strategy of birds staying close to the breeding grounds year-round, as many of the Pacific auks at our study sites migrate long distances (Gaston et al., 2017; Takahashi et al., 2020) or remain in the region (Orben et al., 2015). Moreover, some of the Atlantic auks with large seasonal differences have been shown to be relatively resident (e.g. New foundland murres: McFarlane Tranquilla et al., 2014). Further investigations combining migratory movements and Hg contamination in Pacific seabirds are needed to understand seabird vulnerability to Hg in this region (see Fleishman et al., 2019). Northwest Greenland little auk population had higher Hg concentrations compared to other Arctic regions, a pattern also found in some other seabirds and marine top predators (Albert et al., 2019; AMAP, 2011) and might be explained by similar elevated concentrations at both their breeding areas and their non-breeding areas off Newfoundland (Fort et al., 2013a).

Finally, our results show spatial differences in bird Hg contamination and seasonal variation between the Pacific and Atlantic regions. Brünnich's and common guillemots, which are present in both regions, showed smaller seasonal differences and lower non-breeding Hg concentrations in the Pacific than in the Atlantic, suggesting differences in Hg environmental contamination between both regions. The Arctic Ocean is a sink for contaminants such as Hg, with inflows from both atmospheric and oceanic currents, as well as rivers (Sonke et al., 2018). Nevertheless, important outflows of Hg also occur from the Arctic to lower latitudes (AMAP, 2018). Because the Arctic is widely open to the Atlantic with more numerous, complex atmospheric and oceanic fluxes than the Pacific region, oceanic outflows of Hg (e.g. through the Canadian Arctic Archipelagoes and Fram Strait) (see Outridge et al., 2008) could partly explain the higher concentrations in Hg found in species from the Western Atlantic region compared to the Pacific regions of the Arctic. Alternatively, food webs vary among Arctic and sub-Arctic (Murphy et al., 2016), with Chukchi food webs being based on benthic inputs (Whitehouse et al., 2014). Hg levels in Pacific seabirds are closely associated with the base of the food web (Elliott and Elliott, 2016), and variation in food webs among ocean basins may be one cause of lower Hg levels in the Pacific relative to the Atlantic. For example, a recent survey comparing Pacific to Atlantic waters in the Canadian Arctic (where Hg levels are higher in predators in the Pacific) found that variation in Hg in top predators was associated with higher levels of methylation in the Pacific despite lower levels of total Hg (Wang et al., 2018). Clearly, food web processes that affect methylation of Hg are important for explaining region differences, and that study, which linked disparate predator information to a single ship-based transect, might be strengthened by similar pan-Arctic predator information such as that present in our study.

4.3. Inter-individual variability in non-breeding Hg concentrations

In addition to species and population differences, our results showed high inter-individual variability in Hg concentrations during the non-breeding period. Arctic seabirds are central-place foragers, feeding mostly in the vicinity of their colony during the breeding period (Cunningham et al., 2018; Jakubas et al., 2016; Linnebjerg et al., 2015). However, during the non-breeding period, many migrate towards the open seas to spend the winter within or outside the Arctic (McFarlane Tranquilla et al., 2013). Recent tracking studies highlight how

individuals from the same population might engage in contrasting migratory tactics, and thus occupy very different wintering areas (Fort et al., 2013a; Frederiksen et al., 2016; Studholme et al., 2019) where exposure to Hg and other pollutants could be substantially different (Leat et al., 2013; Miller et al., 2020; Watanuki et al., 2015). For instance, Brünnich's guillemots breeding at Coats Island and at the Gannet Islands (Northwest Atlantic) adopt variable individual strategies, with wintering areas ranging from the Labrador Sea to Newfoundland (Frederiksen et al., 2016; McFarlane Tranquilla et al., 2013). This finding is consistent with higher inter-individual variability in Hg concentrations for non-breeding than for the breeding Brünnich's guillemots. In comparison, common guillemots from the same colonies showed lower inter-individual variability in their non-breeding distribution as individuals overwinter close to their breeding colonies off Newfoundland (Fort et al., 2013b; McFarlane Tranquilla et al., 2013). Similarly, this was reflected in our results by lower variability in Hg concentrations for that species. This inter-individual variation in both Hg concentrations and large-scale distribution supports the hypothesis that individual migratory tactics play an important role in Hg exposure and calls for further studies linking individual movements to contamination risks.

4.4. Hg toxicity and risks for non-breeding Arctic seabirds

There is limited information about Hg toxicity thresholds for seabird feathers. Nevertheless, Hg concentrations above 5.00 µg g^{-1} dw in feathers are usually considered to be associated with deleterious health and reproductive effects (Eisler, 1987). In addition, elevated Hg contamination during the non-breeding period can exert carry-over effects on reproductive parameters in the following breeding season (e.g. Fort et al., 2014). Our results demonstrate that some populations of Arctic alcids had Hg values close to or above 5.00 µg g^{-1} dw. In total, 26% of the sampled individuals for which non-breeding Hg was measured exceeded this toxicity threshold. These include rhinoceros auklets breeding in the Gulf of Alaska, and common and Brünnich's guillemot populations breeding in the Northwest Atlantic. This latter region has previously been associated with elevated Hg risk in seabirds. For instance, the investigation of Hg concentrations in the blood of Brünnich's guillemot breeding at Coats Island (Canadian Arctic, Northwest Atlantic) showed that above ~90% of the sampled individuals were associated with at least a moderate risk (Dietz et al., 2019).

Hence, many seabird species and populations might be at high risk of Hg contamination that could negatively impact their reproduction, with potential long-term effects on population dynamics (Goutte et al., 2014a, 2014b). Population trajectories of different Arctic seabird populations vary spatially (e.g. Frederiksen et al., 2016), and the potential role played by environmental pollution on these patterns has been largely overlooked. Therefore, there is a need to include exposure to pollutants, notably during the non-breeding period, in population dynamic studies and conservation programs.

5. Conclusion

The present study is the first to investigate seabird seasonal Hg contamination at a large, pan-Arctic scale. Our results demonstrate that the non-breeding period is critical for Hg contamination of piscivorous and planktivorous seabirds. This period might represent an important risk for these sensitive populations, especially those breeding in the West Atlantic Arctic, and to a lesser extent in the Pacific Arctic and the East Atlantic. This study demonstrates that close monitoring should be pursued to understand both short- and long-term implications of Hg exposure on seabird population dynamics. Our study also shows that higher non-breeding contamination most likely depends on both individual, population, and species-specific migratory strategies determining year-round spatial distributions. We therefore call for further studies linking non-breeding distribution of seabirds and Hg contamination at

the individual and population scales. This would facilitate better understanding of which wintering areas are associated with higher Hg contamination and thus pose higher risks for Arctic seabirds. Further studies including energetic modelling are also required to better understand the role of increased energy requirements on Hg seasonal changes. Therefore, there is a need for more integrative spatial ecotoxicology studies at multiple scales, combining tracking technologies, Hg measurements, dietary investigations, and including a large range of colonies and species.

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.

UAF IACUC protocol #471022, USFWS scientific collection permit #MB70337A, Master Banding permit #23350, and Alaska Department of Fish and Game permits #19-140, 18-131, 17-104, 16-089. The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

Pictures credit: Ancient murrelet: Dr. A. Andreev, Brünnich's guillemot: S. Descamps, little auk, common guillemot and razorbill: C. Albert, crested auklet: A. Will, rhinoceros auklet: tufted puffin: K. Elliott, least auklet: M. Romano.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.142201.

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