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Blood mercury concentrations in four sympatric gull species from South Western France: Insights from stable isotopes and biologging☆

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ABSTRACT

Mercury (Hg) is a toxic trace element widely distributed in the environment, which particularly accumulates in top predators, including seabirds. Among seabirds, large gulls (*Larus* sp) are generalist feeders, foraging in both terrestrial and marine habitats, making them relevant bioindicators of local coastal Hg contamination. In the present study, we reported blood Hg concentrations in adults and chicks of four different gull species breeding on the French Atlantic coast: the European herring gull (*Larus argentatus*), the Lesser black-backed gull (*L. fuscus*), the Great black-backed gull (*L. marinus*) and the Yellow-legged gull (*L. michahellis*). We also investigated the potential role of foraging ecology in shaping Hg contamination across species, using the unique combination of three dietary tracers (carbon, nitrogen and sulfur stable isotopes) and biologging (GPS tracking). A high concentration of Hg was associated with high trophic position and a marine diet in gulls, which was corroborated by birds' space use strategy during foraging trips. Adults of all four species reached Hg concentrations above reported toxicity thresholds. Specifically, adults of Great black-backed gulls had a high trophic marine specialized diet and significantly higher Hg concentrations than the three other species. Blood Hg was 4–7 times higher in adults than in chicks, although chicks of all species received mainly marine and high trophic position prey, which is expected to be the cause of blood Hg concentrations of toxic concern. By using both stable isotopes and GPS tracking, the present study provides compelling insights on the main feeding habits driving Hg contamination in a seabird assemblage feeding in complex coastal environments.

CRediT authorship contribution statement

William Jouanneau: Conceptualization, Investigation, Formal analysis, Writing - Original Draft. **Manrico Sebastiano:** Investigation, Writing - Review & Editing. **David Rozen-Rechels:** Conceptualization, Formal analysis, Writing - Review & Editing. **Stephanie M. Harris:** Formal analysis, Writing - Review & Editing. **Pierre Blévin:** Investigation, Writing - Review & Editing. **Frédéric Angelier:** Investigation, Writing - Review & Editing. **François Brischoux:** Investigation, Writing - Review & Editing. **Julien Gernigon:** Resources, Investigation. **Jean-Christophe Lemesle:** Resources, Investigation. **Frédéric Robin:** Resources, Investigation, Writing - Review & Editing. **Yves Cherel:** Conceptualization, Writing - Review & Editing. **Paco Bustamante:** Resources, Investigation, Writing - Review & Editing. **Olivier Chastel:**

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1. Introduction

Mercury (Hg) is a non-essential trace element released by both natural and anthropogenic processes (Pirrone et al., 2010). Organic Hg (mostly methylmercury; MeHg) is the main bioavailable and toxic form for living organisms (Díez, 2008; Thompson and Furness, 1989). MeHg is incorporated in organisms mainly via ingestion of contaminated food (Eagles-Smith et al., 2018). In birds, accumulation of MeHg has been associated with a wide range of behavioral and physiological detrimental consequences, impacting individual fitness, and ultimately, population dynamics (Tan et al., 2009; Whitney and Cristol, 2017). Due to a relatively long biological half-life in tissues (Stickel et al., 1977), Hg tends to bioaccumulate in organisms over time and biomagnify up trophic food webs, leading long-lived top predators to exhibit elevated Hg concentrations (Atwell et al., 1998; Cherel et al., 2018; Evers et al., 2005). In coastal environments, seabirds are therefore considered as excellent sentinels of the local contamination (Burger and Gochfeld, 2004; Furness and Camphuysen, 1997; Monteiro and Furness, 1995).

Seabirds show a large interspecific variation in foraging strategies (Ceia and Ramos, 2015), leading to varied degrees of Hg exposure among species (Carravieri et al., 2014b; Monteiro et al., 1998; Stewart et al., 1997). Large gulls of the *Larus* genus are omnivorous and opportunistic feeders. *Larus* spp. are known to exploit both marine and terrestrial habitats, and can scavenge from multiple anthropogenic sources including waste dumps, landfill sites and fishing discards, as well as predating upon eggs or chicks (Buckley, 1990; Mudge and Ferns, 1982; Ramos et al., 2009). Assessing Hg concentrations in sympatric *Larus* species with differences in foraging ecology thus enables to have an overview of the local environmental contamination, particularly in complex coastal habitats (Binkowski et al., 2020). Additionally, in seabirds, individual variation in foraging behavior appears to be highly prevalent, with individuals differing in their resource use, habitat selection, and their fidelity to foraging sites (Ceia and Ramos, 2015; Phillips et al., 2017). Such variation in foraging behavior may be consistent over time, and linked to individuals' characteristics, such as their age or sex (Bolnick et al., 2003). As Hg exposure largely varies with feeding strategies and habitat use, this variability shapes intraspecific differences in Hg contamination (Bustamante et al., 2016; Ceia and Ramos, 2015; Stewart et al., 1997), with consequences for individual fitness. Characterizing foraging ecology at the individual level is therefore essential to understand patterns of Hg contamination within and among species.

Tracking devices, including Global Positioning System (GPS) loggers, enable fine scale monitoring of an animal's movements, which facilitates a direct characterization of its habitat use (Burger and Shaffer, 2008). Furthermore, recently developed analytical tools - including hidden Markov models (HMMs) - facilitate behavioral classification of GPS tracking data (Langrock et al., 2012), enabling the identification of the precise locations and habitats in which animals are foraging. The analysis of stable isotopes – used as a proxy for the trophic niche (Newsome et al., 2007) – can also represent an effective tool to define the foraging habitats (carbon: δ^{13}C and sulfur: δ^{34}S) and trophic positions (nitrogen: δ^{15}N) of seabirds (Hobson et al., 1994; Kelly, 2000; Lott et al., 2003). A marine diet is characterized by higher δ^{13}C, δ^{15}N and δ^{34}S values, as opposed to lower levels indicating terrestrial food intakes (Chisholm et al., 1982; Hobson, 1987; MacAvoy et al., 2000; Schoeninger and DeNiro, 1984). More specifically, δ^{34}S is preferentially used to differentiate marine *vs* terrestrial foraging habitats, since it does not present a stepwise enrichment within the food chain, and therefore shows a greater discriminating power than δ^{13}C and δ^{15}N (Hobson, 1999; McCutchan Jr et al., 2003). This characteristic makes δ^{34}S particularly interesting to depict seabirds' use of coastal habitats. Therefore, the use of GPS trackers combined with isotopic measurements enables a holistic overview of birds' feeding strategies with respect to multiple available foraging habitats, as well as a high discriminant power (Bracey et al., 2021; Caron-Beaudoin et al., 2013; Ceia et al., 2018; Mendes et al., 2018).

In France, Hg contamination of seabirds has been largely documented in overseas departments and territories (e.g., French Guiana, Sebastiano et al., 2016; 2017; Scattered Islands, Kojadinovic et al., 2007a; Réunion Island, Kojadinovic et al., 2007b; 2007c) and French Southern and Antarctic Territories (e.g., Blévin et al., 2013; Carravieri et al., 2014a, 2014b; 2016; Goutte et al., 2014a, 2014b; Tartu et al., 2014, 2015a). Although the coasts of metropolitan France host large numbers of breeding seabirds (e.g., 174 000 pairs, Cadiou, 2011), data on Hg concentrations in seabird tissues are scarce and limited to chicks of four gull species (*Larus argentatus*, *Larus fuscus*, *Larus marinus* and *Larus michahellis*) from the Southern Bay of Biscay and the English Channel (Binkowski et al., 2020; Zorrozua et al., 2020). In these studies, high blood Hg concentrations were associated with a diet of marine origin and of high trophic position. Yet, our knowledge on Hg concentrations in other potentially contaminated areas remains very limited.

In the present study, we investigated Hg concentrations in adults and chicks of four gull species from a South Western France colony: Herring gulls *Larus argentatus argenteus*, Lesser black-backed gulls *L. fuscus graellsii*, Great black-backed gulls *L. marinus* and Yellow-legged gulls *L. michahellis*. We were particularly interested to i) describe Hg concentrations of the species during the breeding period; ii) identify the factors driving inter- and intraspecific Hg variations among adults and chicks – in relation to their different feeding habitats inferred from blood δ^{13}C, δ^{15}N and δ^{34}S stable isotopes, and in relation to their individuals characteristics as age and sex; and iii) explore whether fine-scale habitat partitioning using GPS tracking further elucidates the potential variation in adult Hg contamination. Due to the known differences in foraging ecology among the four species, as well as the individual differences within species, we expected a high inter- and intraspecific variation in Hg concentrations. We further predicted that i) individuals feeding at higher trophic positions (indicated by higher δ^{15}N values) or foraging in marine habitats (indicated by both high δ^{13}C and δ^{34}S values, as well as GPS tracking) would exhibit higher Hg concentrations; and that ii) these patterns would persist both between and within species.

2. Materials and methods

2.1. Field methodology

In the breeding seasons of 2016–2019, we sampled gulls breeding in "Lilleau des Niges" National Nature reserve, Ile de Ré, South Western France (46°13′53″ N, 1°30′22″ W; Fig. 1): European herring gulls (EHG, approx. 400 pairs), Lesser black-backed gulls (LBBG, approx. 400 pairs), Great black-backed gulls (GBBG, approx. 200 pairs), and Yellow-legged gull (YLG, approx. 100 pairs). Adult birds were sampled in May (n = 140), and chicks in July (n = 107). All individuals were captured and sampled only once over the four years. Annual sample sizes for adults and chicks of each species can be found in the Supporting Information (SI) Table S1. Adults incubating a full-size clutch (i.e., 2 to 3 eggs) were caught on their nests, using a trap placed over the eggs. Chicks of approximately 1 month of age were caught by hand, within the colony. From an early age, gull chicks are developed enough to explore their environment and do not stay in their nest, therefore we were unable to assign relatedness among chicks and adults. Skull and tarsus were measured using a caliper (±0.1 mm). Wing length was also measured using a ruler (±1 mm), and birds were weighted using a Pesola spring balance (±5 g). Blood samples (2 mL, <1% of the body mass of LBBG, the smallest species in this study) were taken from the brachial vein of adults and chicks using heparinized syringes. Blood was transferred into a 2 mL Eppendorf® tube and immediately stored in a cool box. At the end of each sampling day, whole blood was centrifuged and red blood cells (hereafter "blood") were stored at −20 °C until laboratory analyses.

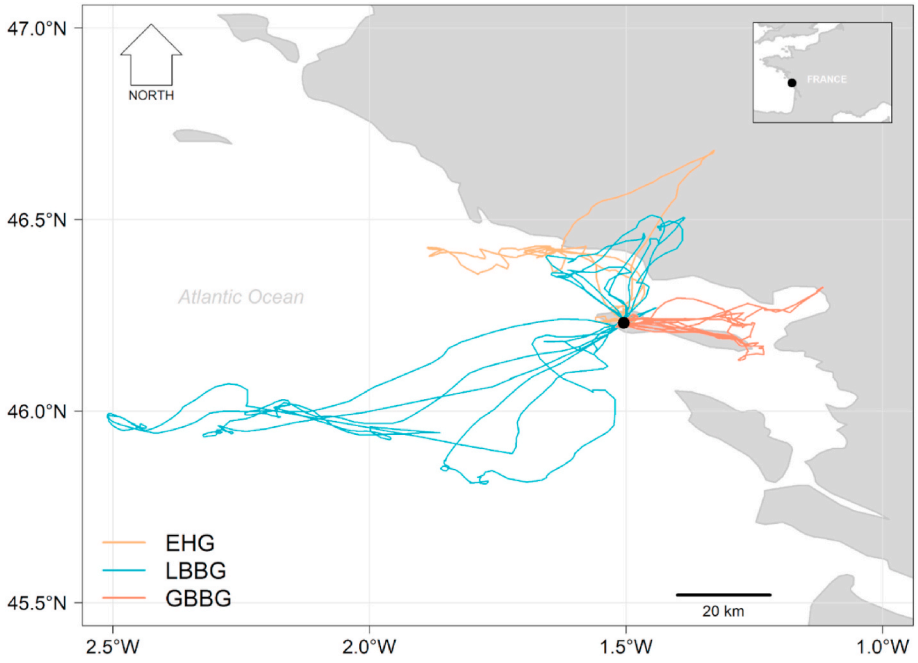

Fig. 1. Map of the Ile de Ré and surroundings, France, visited by the adults of four species of gulls from the "Lilleau des Niges" colony during their breeding period; European herring gulls (EHG), Lesser black-backed gulls (LBBG), Great black-backed gulls (GBBG) and Yellow-legged gulls (YLG). The studied colony is represented by the black point. YLG were not tracked and so are not presented, but were included in analyses of Hg and stable isotopes. Tracks presented here are a random selection of 5 trips per species, see SI Fig. S1 for maps of all tracks per species. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Blood samples were then used to measure Hg and stable isotopes and for molecular sexing.

2.2. Mercury analysis

The analysis of total Hg in lyophilized blood was carried out using an Altec AMA 254 spectrophotometer following Bustamante et al. (2006). Each sample (mass: ~0.5 mg dry weight, dw) was analysed twice and Hg concentrations were then averaged. For each individual, the relative standard deviation was <10%. Accuracy was checked at the beginning and the end of each measurement session using a certified reference material (2016–2018: DOLT-5 dogfish liver - Hg certified concentration (mean ± SD): 0.44 ± 0.18 μg g^{-1} dw; 2019: TORT-3 lobster hepatopancreas - Hg certified concentration: 0.29 ± 0.02 μg g^{-1} dw; obtained from NRC, Canada). Recoveries were respectively 0.422 ± 0.005 and 0.318 ± 0.014 μg g^{-1} dw. Blanks were also run before and after each set of samples. The limit of detection of the AMA was 0.1 ng. Hg concentrations are expressed as μg g^{-1} dw. In several bird species, MeHg represents most of the total Hg in blood (Renedo et al., 2018; Rimmer et al., 2005). Chicks accumulate Hg from hatching, being fed by their parents from local food items. For this reason, they are relevant bioindicators of the local environment contamination (Binkowski et al., 2020; Blévin et al., 2013). By contrast to chicks, using adult gulls as bioindicators of their local environment during breeding is still debated as the half-life of Hg in avian tissues is 1–3 months, and contaminants acquired during migration might still be present in blood (Bearhop et al., 2000; Monteiro and Furness, 2001; Stickel et al., 1977). However, all species used in the present study were on the breeding grounds more than 3 months before sampling, therefore blood Hg should mainly represent local contamination.

2.3. Stable isotope analysis

Sub-samples of blood were weighed (mean ± SD: 0.29 ± 0.06 mg dw for $\delta^{13}C$ and $\delta^{15}N$; 0.71 ± 0.05 mg dw for $\delta^{34}S$) with a microbalance and then packed into tin containers for combustion. Relative abundances of carbon, nitrogen and sulfur isotopes were measured using a continuous flow mass spectrometer (Thermo Scientific Delta V Advantage) coupled with an elemental analyzer (carbon and nitrogen: Thermo Scientific Flash EA 1112; sulfur: Thermo Scientific Flash IRMS EA IsoLink). The delta (δ) notation relative to Vienna PeeDee Belemnite, atmospheric N_2 and Vienna Cañon Diablo troilite for $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ respectively, was used to present isotopic results. Accuracy was checked by replicate measurements of the internal laboratory standard, and analytical precision was <0.10‰ for $\delta^{13}C$, <0.15‰ for $\delta^{15}N$ and <0.20‰ for $\delta^{34}S$ values. The stable isotopes values were computed as $\delta X = \left[\left(\frac{R_{Sample}}{R_{Standard}}\right) - 1\right] x\,1000$, where X stands for ^{13}C, ^{15}N or ^{34}S and R being the ratio $^{13}C/^{12}C$, $^{15}N/^{14}N$ or $^{34}S/^{32}S$. Turnover time for $\delta^{13}C$ and $\delta^{15}N$ in blood is 11–30 days (Barquete et al., 2013; Hobson and Clark, 1992, 1993), therefore stable isotopes values are representative of the breeding period in adults.

2.4. GPS tracking analysis

A subset (n = 43) of the captured adults (18 EHG, 18 LBBG and 7 GBBG, see SI Table S1) were equipped with GPS-UHF loggers (HARRIER, Ecotone®) in 2017 and 2018. Among the 43 GPS equipped birds, 17 EHG, 18 LBBG and 6 GBBG were blood sampled and included in Hg and stable isotopes analyses. The total mass of the logger and the harness (used for attachment) weighted on average 13 g (i.e., <2% of the body mass of LBBG, the smallest species in this study).

GPS loggers were set to record locations every 5 min. For each tracked individual, locations were filtered to the period between the day after blood sampling to the last day before either nest failure or egg hatching had been recorded (Fig. 1 & SI Fig. S1 & Table S2). Foraging sites were identified from GPS tracks by assigning a behavioral state to each location using Hidden Markov Models (hereafter "HMMs", Franke et al., 2004) fitted using the moveHMM R package (Michelot et al., 2016). Additional information on the spatial data treatment and the behavioral classification can be found in the SI. The habitat for each of these locations was assigned as either "pelagic"; "coastal" (i.e., lagoons, estuaries, coastal salt marshes, intertidal flats), or "terrestrial" (all others) based on the CORINE Land Cover dataset (CORINE Land Cover; Feranec et al., 2016). Ratios of pelagic *vs* coastal and marine (i.e., pelagic and coastal) *vs* terrestrial habitats used by each individual were then calculated.

For an overview of the feeding behaviors leading to the observed Hg concentrations in the tracked species, we estimated birds' foraging site

fidelity. As well as giving important insight into the degree of specialization in birds' uses of foraging habitat, this measure of site fidelity served to test whether individuals' foraging behavior in the period after blood sampling was likely to be representative of their behavior prior to blood sampling (see SI). Individual foraging site fidelity was assessed following the randomization procedure of Harris et al. (2020). For each foraging site, the distance to a randomly selected site from the same individual during another trip (within-individual comparison), as well as to a randomly selected site from each other individual of the same species (between-individual comparisons) was measured. The site fidelity index corresponds to the proportion of between-individual sites that were farther from the focal site than the within-individual site. This index is bounded between 0 and 1, with high values representing high site fidelity (an individual forages more closely to its own foraging sites than to the sites of other individuals), and low values representing low site fidelity (an individual forages more closely to the foraging sites of other individuals than to its own foraging sites). Additional information can be found in the SI.

2.5. Molecular sexing

All adults and chicks ($n = 247$) were sexed using blood samples by polymerase chain reaction (PCR) amplification of parts of two highly conserved genes (CHD) of sex chromosomes, following Fridolfsson and Ellegren (1999).

2.6. Statistical analyses

Statistical analyses were performed using R 4.0.0 (R Core Team, 2020). One YLG chick was removed from the dataset due to outliers in $\delta^{13}C$ and $\delta^{34}S$ values. In all species, adults had much higher Hg concentrations than chicks, and therefore chicks and adults were treated separately.

Firstly, relationships between Hg concentrations and diet (inferred by stable isotope values) were investigated. As $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ were positively correlated in adults (Pearson correlation >0.70, $p < 0.001$ for all relationships) and partially correlated in chicks (correlation: C–N = 0.72, $p < 0.001$; S–C = −0.15; S–N = −0.18, both $p > 0.05$), principal components analyses ("FactoMineR" R package, version 2.3; Lê et al., 2008) were performed on the three isotopes to reduce the number of explanatory variables. Principal components (PCs) which explained more than 80% of the total variance were retained. In adults, principal components analysis reduced $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ to one PC (PC_1) explaining 83.6% of the variance and equally influenced by $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ (SI Fig. S2 & Table S3). High PC_1 scores reflected high $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$. In chicks, principal components analyses reduced $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ to two PCs (PC_1 and PC_2) explaining 92.0% of the variance (SI Fig. S2 & Table S3). High PC_1 scores indicated high $\delta^{13}C$ and $\delta^{15}N$ values, and high PC_2 scores indicated high $\delta^{34}S$ values. The isotopic niches, which are essential for an overview of each species' local feeding habits, were investigated, and the foraging ecology of each species were illustrated and described in the SI. Generalized least square (GLS) models were then used to investigate the effects of the selected PCs on Hg ("nlme" R package, version 3.1–151; Pinheiro et al., 2017). For that, using Hg as the response variable, we included as explanatory covariates the selected PCs and the species. Year was not included as a predictor in the models to improve statistical power, and also because four years of sampling was insufficient to evaluate temporal trends in Hg concentration. We used GLS models instead of linear models (LM) due to heteroscedasticity in Hg concentrations among species (see SI for further information). For both adults and chicks, after running GLS models, Tukey post-hoc pairwise comparison tests were performed to quantify the differences in Hg concentrations among species ("emmeans" R package, version 1.7.1–1; Lenth et al., 2021). Although performed on only three variables, PCA enabled the inclusion of ecological information provided by the three stable isotopes rather than exploring the effect of each stable isotopes in independent models (similar conclusions were obtained using both methods, see SI).

Secondly, as Hg levels were found to be highly variable among species, we ran one LM per species to investigate differences between the sexes. With Hg as the response variable, we included the sex as an explanatory variable. This model was not fitted for adults of YLG as only a single female was sampled. In previous studies, chick age has been found to be a key predictor of Hg contamination, as blood Hg strongly fluctuates during chick growth, reaching highest concentrations when feathers stop growing (Spalding et al., 2000). Morphology is commonly used as a proxy of chick age, and we therefore also included the skull length (head and bill) in the LMs for chicks as an additional explanatory variable. Where Hg differed significantly between sexes, an additional LM was built to investigate whether this was linked to sex differences in diet, with the selected PCs fitted as the response and sex as an explanatory variable.

Finally, in GPS-tracked adults, the impact of the use of marine or terrestrial habitats on Hg concentrations was investigated using a GLS model: Hg was fitted as the response variable, and the proportional use of marine *vs* terrestrial habitat and species (to control for the variation among species) were included as explanatory covariates. A similar model was built to investigate the impact of the use of coastal or pelagic habitats on Hg concentrations, including coastal *vs* pelagic habitats and species (to control for the variation among species) as explanatory covariates. Before modelling, two individuals that were tracked but not blood sampled were removed from the dataset.

For all models, a set of candidate models including all possible combinations of the predictors, ranging from the full model (that includes each of the stated variables) to the null model was built. In each case, the best candidate model – i.e., the one with the lowest second-order Akaike's Information Criterion value for small sample size (AICc; "AICcmodavg" R package, version 2.2–2; Mazerolle, 2017), or the most parsimonious model among those with a ΔAICc ≤2 – was retained for inference. Homogeneity and normality of the residuals were visually checked using plots of residuals *vs* fitted values and histograms of the residuals (Zuur et al., 2007). In post-hoc tests, an $\alpha < 0.05$ threshold was used to assess the significance of the tests.

3. Results

3.1. Mercury in relation to feeding habits as inferred by stable isotopes

In chicks, Hg concentrations ranged from 0.27 μg g^{-1} dw in EHG to 3.86 μg g^{-1} dw in GBBG (Table 1). Model selection indicated that PC_1 and species were significant predictors of Hg concentrations, but not PC_2 (SI Table S4). Post-hoc comparison test showed that GBBG had the highest Hg concentrations, followed by YLG that was not significantly different from EHG and LBBG, but LBBG had lower Hg concentrations than EHG (Tables 1 and 2, Fig. 2). Chicks also exhibited a positive relationship between Hg concentration and PC_1 (estimate ± SE = 0.09 ± 0.03, $t = 3.49$, $p < 0.001$; Table 2 & Fig. 3). Sex was not retained as a significant predictor of Hg concentration for any species, but skull size (as a proxy for chick age) was included in the best model for GBBG only (SI Table S5), with Hg significantly increasing with skull size in this species ($F_{1, 26} = 6.51$, $p = 0.017$; estimate ± SE = 0.04 ± 0.02).

In adults, individual blood Hg concentrations ranged from 0.89 μg g^{-1} dw in EHG to 21.5 μg g^{-1} dw in GBBG (Table 1). Model selection showed that PC_1 and species were significant predictors of Hg concentrations in adult gulls (SI Table S4). Post-hoc comparison test indicated that GBBG had the highest Hg concentrations, while lower concentrations were found in YLG, LBBG and EHG (not significantly different among them; Tables 1 and 2, Fig. 2). Adults also showed a significant and positive association between Hg concentration and PC_1 (estimate ± SE = 0.55 ± 0.06, $t = 9.25$, $p < 0.001$; Table 2 & Fig. 3). Sex was retained for GBBG only (SI Table S5), with males having higher Hg concentrations than females in adults of this species ($F_{1, 35} = 19.2$, $p <$ 0.001;

Table 1
Hg concentrations (μg g^{-1} dw) and carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$) and sulfur ($\delta^{34}S$) stable isotope values (‰) measured in blood of adults and chicks of four gull species from the Ile de Ré, France: sample size (*n*), mean ± standard deviation (*SD*), median and range (min-max). For adults, Hg values are presented separately for females (♀) and males (♂).

	n	Hg		$\delta^{13}C$		$\delta^{15}N$		$\delta^{34}S$	
		Mean ± SD	Min/max	Mean ± SD	Min/max	Mean ± SD	Min/max	Mean ± SD	Min/max
Adults									
EHG (*Larus argentatus*)	44	2.29 ± 1.06	0.89/5.01	−19.4 ± 1.93	−22.9/-15.5	12.7 ± 1.82	9.76/16.0	13.1 ± 2.23	8.72/17.0
♀	23	2.05 ± 0.96	0.90/4.31	–					
♂	21	2.55 ± 1.12	0.89/5.01						
LBBG (*Larus fuscus*)	54	3.08 ± 1.31	0.95/6.42	−19.1 ± 1.34	−22.6/-17.6	13.8 ± 1.30	10.9/15.8	15.9 ± 2.37	9.90/18.6
♀	27	2.82 ± 1.03	0.98/4.78	–					
♂	27	3.35 ± 1.52	0.95/6.42						
GBBG (*Larus marinus*)	37	12.5 ± 3.93	6.97/21.5	−16.8 ± 0.83	−19.7/-14.7	16.4 ± 0.41	15.8/17.8	16.9 ± 1.07	14.6/18.7
♀	19	10.3 ± 2.20	6.97/13.8	–					
♂	18	14.9 ± 4.00	7.26/21.5						
YLG (*Larus michahellis*)	5	6.00 ± 2.72	2.25/9.63	−19.4 ± 3.51	−25.2/-16.7	15.1 ± 1.32	12.76/15.91	12.6 ± 4.66	5.87/16.7
♀	1	2.25 ± NA	2.25/2.25	–					
♂	4	6.94 ± 2.00	5.26/9.63						
Chicks									
EHG (*Larus argentatus*)	30	0.68 ± 0.25	0.27/1.19	−18.3 ± 0.66	−19.9/-17.1	13.8 ± 0.75	12.1/15.0	16.8 ± 1.21	14.0/18.7
LBBG (*Larus fuscus*)	37	0.58 ± 0.15	0.35/0.94	−18.3 ± 0.27	−18.8/-17.7	14.5 ± 0.41	13.7/15.2	18.4 ± 0.93	16.7/19.8
GBBG (*Larus marinus*)	28	1.91 ± 0.76	0.81/3.86	−17.1 ± 0.77	−19.33/-16.7	15.6 ± 0.48	14.0/16.6	16.5 ± 1.32	12.8/18.6
YLG (*Larus michahellis*)	11	0.90 ± 0.34	0.48/1.75	−18.0 ± 0.61	−19.37/-17.42	14.9 ± 1.07	12.4/16.1	16.5 ± 1.46	14.07/18.4

Table 2
Outputs of linear models examining the variables affecting Hg concentration in four gull species from the Ile de Ré, France: European herring gulls (EHG), Lesser black-backed gulls (LBBG), Great black-backed gulls (GBBG) and Yellow-legged gulls (YLG). Significant *p*-values are in bold.

Parameter	Estimate	SE	*t*-value	*p*-value
Adults				
PC_1	0.55	0.06	9.25	**<0.001**
EHG - LBBG	0.10	0.19	0.56	0.943
EHG - GBBG	8.56	0.67	12.70	**<0.001**
EHG - YLG	2.65	0.79	3.38	0.089
LBBG - GBBG	8.45	0.66	12.79	**<0.001**
LBBG - YLG	2.55	0.79	3.22	0.099
GBBG - YLG	−5.90	1.02	−5.78	**<0.001**
Chicks				
PC_1	0.09	0.03	3.49	**<0.001**
EHG - LBBG	−0.13	0.05	−2.72	**0.043**
EHG - GBBG	1.01	0.16	6.33	**<0.001**
EHG - YLG	0.11	0.12	0.93	0.792
LBBG - GBBG	1.14	0.15	7.45	**<0.001**
LBBG - YLG	0.24	0.11	2.16	0.189
GBBG - YLG	−0.90	0.18	−5.05	**<0.001**

estimate ± SE = 4.62 ± 1.05). However, sex was not retained as a significant predictor of stable isotopes in GBBG (PC_1; SI Table S6).

3.2. Mercury in relation to habitats use as inferred by GPS tracking

From GPS tracked adults, a total of 1069 foraging trips from 43 individuals were recorded (612 in EHG, 304 in LBBG and 154 in GBBG). The three tracked species showed different patterns of habitat use: GBBG forage predominantly at sea and showed low inter-individual variation (average use of marine habitats ± SD: 0.93 ± 0.05%), while EHG (0.63 ± 0.23%) and LBBG (0.78 ± 0.17%) individuals were more spread on a gradient from strictly terrestrial to strictly marine (Fig. 1 & SI Fig. S3). The use of marine habitats in EHG and GBBG was mainly coastal (proportion of coastal habitats use ± SD: 0.58 ± 0.25 and 0.90 ± 0.07 respectively), while LBBG used pelagic and coastal habitats (proportion of coastal habitats use ± SD: 0.23 ± 0.16; Fig. 1 & SI Fig. S3). Model selection indicated that the proportional use of marine *vs* terrestrial habitats and the species were significant predictors of Hg variations (SI Table S7), Hg concentrations increased with the use of marine habitats in all three species (estimate ± SE = 2.59 ± 0.99, $t = 2.62$, $p = 0.01$; Fig. 4). Conversely, the coastal *vs* pelagic gradient was not a significant predictor of Hg variations in the three gull species. (Table S7). GBBG,

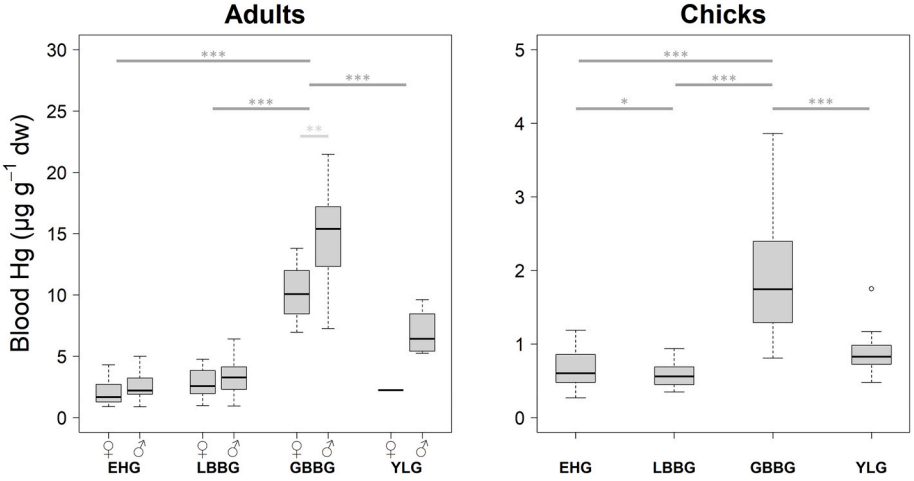

Fig. 2. Blood concentrations of Hg in adults and chicks of four gull species from the Ile de Ré, France; European herring gulls (EHG), Lesser black-backed gulls (LBBG), Great black-backed gulls (GBBG) and Yellow-legged gulls (YLG). For adults (left), Hg values are shown separately for females (♀) and males (♂). Interspecific (dark-grey) and between sex (light grey) statistically significant differences are indicated by the asterisk: *, **, ***; indicating a *p*-value < 0.05, <0.01, and <0.001, respectively. Values are median, 25th and 75th percentiles and range.

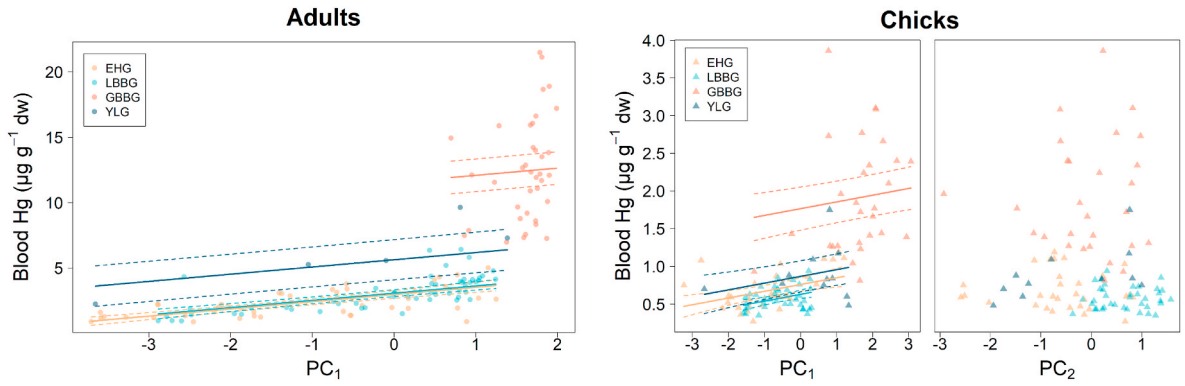

Fig. 3. Relationship between blood Hg concentrations and PC$_1$ (δ^{13}C, δ^{15}N and δ^{34}S values in adults and δ^{13}C, δ^{15}N in chicks) or PC$_2$ (δ^{34}S values in chicks) of four gull species from Ile de Ré, France: European herring gulls (EHG), Lesser black-backed gulls (LBBG), Great black-backed gulls (GBBG) and Yellow-legged gulls (YLG). For each species, the solid line refers to the fitted models obtained and dotted lines represent 95% confident intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

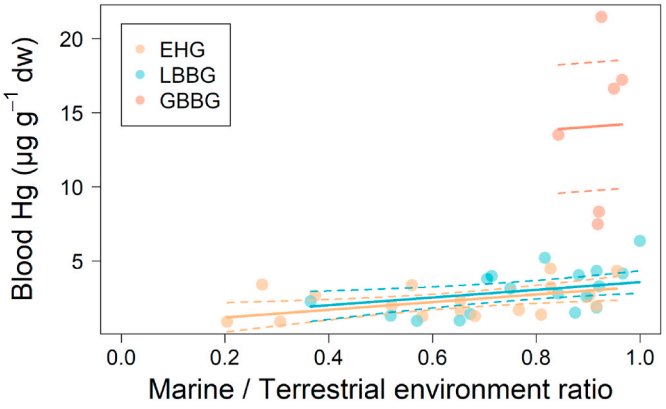

Fig. 4. Relationship between blood Hg concentrations and the proportion of foraging trips in marine (1: exclusively marine) *vs* terrestrial (0: exclusively terrestrial) habitats obtain by GPS tracking in adults of three gull species from Ile de Ré, France; European herring gulls (EHG), Lesser black-backed gulls (LBBG) and Great black-backed gulls (GBBG). For each species, the solid line refers to the fitted models obtained and dotted lines represent 95% confident intervals.

EHG and LBBG exhibited a relatively high fidelity to foraging sites (fidelity index ± SD = 0.71 ± 0.18; 0.59 ± 0.13 and 0.72 ± 0.13 respectively).

4. Discussion

Blood Hg concentrations of four sympatric gull species were investigated in relation to their foraging ecology inferred from stable isotopes δ^{13}C, δ^{15}N and δ^{34}S blood values in adults and chicks, and from GPS tracking of adult birds. High Hg concentrations were related to stable isotopes values representative of a high trophic position food, mainly of marine origin. Foraging movements tracked during breeding corroborated the relationship between Hg and the birds' foraging strategies with relation to terrestrial *vs* marine habitat use. All species showed foraging site fidelity, indicating a degree of specialization in their use of foraging sites, and thus high potential for consistent individual differences in contaminant level to emerge. This led some adult individuals to exceed reported toxicity thresholds in all four species, particularly in GBBG, showing extremely high levels of Hg. These findings are also concerning for chicks, which predominantly receive marine food from their parents, and are therefore likely to accumulate high concentrations of Hg. Together, these results support the use of sympatric species of gulls as bioindicators of contamination in complex coastal habitats.

4.1. Mercury concentrations

LBBG and GBBG chicks had blood Hg concentrations similar to those from the French coast of the English Channel, although EHG chicks had higher Hg concentrations, even compared to the colonies from the Seine estuary, one of the most polluted rivers in Europe (Binkowski et al., 2020; Cossa et al., 2002). Toxicological benchmarks are usually assessed for adult birds, meaning that chicks Hg concentrations can only be compared to published thresholds from adults with caution. However, much lower blood Hg concentrations have been associated with an impaired physiological condition in LBBG chicks (lower metabolism markers, increased oxidative stress and increased anaerobic metabolism; Santos et al., 2020). In the present study, all four species showed similar Hg levels between sexes, likely because sex difference in contaminant exposure is usually visible later in life. However, in GBBG we detected increased levels of Hg with skull size (a proxy of chick age), but this result was not found in other species. Blood Hg is known to increase with the chicks age when most of the feathers have grown (Ackerman et al., 2011). This relationship may be easier to detect in GBBG as they grow larger, thus their among individual variation in size is higher than the other investigated species.

Hg concentrations in adults ranged from similar (EHG and LBBG) to much higher (YLG and GBBG) than in gulls from the Baltic Sea including EHG and GBBG, or Brown skuas (*Stercorarius antarcticus lonnbergi*) from three colonies of the Southern Ocean (Mills et al., 2022; Szumiło-Pilarska et al., 2017). Notably, we found GBBG to have average blood Hg concentrations similar to those of the Wandering albatross (*Diomedea exulans*; Anderson et al., 2009), the highest trophic position seabird in the Southern Ocean (Cherel et al., 2017) and one of the species with the highest known Hg levels worldwide (Blévin et al., 2013; Carravieri et al., 2014a, 2014b; Cherel et al., 2018). Such Hg concentrations are known to significantly impact reproduction, including breeding success in various bird species (Goutte et al., 2015; Tartu et al., 2013, 2014; 2015b; Ackerman et al., 2016). As no physiological endpoints were measured in the present study, it is not possible to directly draw conclusions on the impact of Hg concentrations of this population. Other factors may also contribute to a reduced toxicity of Hg. For instance, selenium – which was not measured in the present study – is an essential trace element which may protect birds against Hg toxicity (Dietz et al., 2000; Manceau et al., 2021). However, Hg is known to affect almost all aspects of avian physiology and life history traits (Sebastiano et al., 2022; Tartu et al., 2015a; Whitney and Cristol, 2017). We therefore emphasize further work to investigate whether the reported high blood Hg concentrations are detrimental to the different species of birds in the region. Similarly to what we observed in GBBG, higher concentrations of Hg in males than in females were previously found in other bird species (Ackerman et al.,

2007; Burgess et al., 2005; La Sala et al., 2011). Interestingly, incubating GBBGs males and females were not found to differ in terms of stable isotopes concentration, suggesting diet is not the main driver of this difference. A possible explanation may be represented by the fact that female gulls deposit Hg into their eggs therefore lowering their circulating contaminants (Lewis et al., 1993).

4.2. Mercury concentrations in relation to foraging ecology

The positive relationship between blood Hg concentrations and $\delta^{13}C$ or $\delta^{15}N$ values observed in gull chicks is in agreement with previous studies on the same four species in the English Channel (Binkowski et al., 2020) and the southern Bay of Biscay (Zorrozua et al., 2020). However, blood $\delta^{34}S$ was not found to be an important driver of Hg contamination at Ile de Ré, contrary to chicks in the English Channel (Binkowski et al., 2020) and Spain (Ramos et al., 2013). In the present study, chick isotopic values were in the highest range values of those of their parents for $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$, meaning that they predominantly received food at a higher trophic position and of marine origin. A diet shift after hatching – reflecting different food requirement before and after hatching – has previously been described in EHG and other species of gulls (Annett and Pierotti, 1989; Bukacińska et al., 1996; Pierotti and Annett, 1987). This specialized chick diet of low marine prey diversity, provided by the parents, may explain why the terrestrial *vs* marine gradient is not a good predictor of Hg variations in chicks.

Isotopic data showed that, similarly to chicks, blood Hg contamination was higher in adult gulls feeding on marine than terrestrial items. This is consistent with previous studies investigating the relationship between Hg and $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ in coastal seabirds and their prey (Gongora et al., 2018; Peterson et al., 2017). These patterns likely reflect the biomagnifying characteristics of Hg along food webs, with longer and more complex food webs in the marine environment (Bełdowska and Falkowska, 2016; Morel et al., 1998), as well as that MeHg is mainly produced in the ocean (Chen et al., 2008). Conversely, some previous studies did not report such relationship in other aquatic birds (Einoder et al., 2018; Soldatini et al., 2020), however, the association between Hg and $\delta^{13}C$ or $\delta^{15}N$ is complex and largely depends on the species or their environments. Different environments likely differ in their $\delta^{15}N$ baseline (Elliott et al., 2021), thus precluding comparing directly consumers' $\delta^{15}N$ values as reflecting their trophic position. This is likely the case of gulls from Ile de Ré, meaning that any blood $\delta^{15}N$ difference at the species or individual level must be interpreted with caution, especially if their $\delta^{13}C$ and $\delta^{34}S$ values indicate foraging in different habitats.

In the present study, EHG, LBBG and YLG showed important inter-individual variations in blood $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values, that characterize populations of generalist species made of specialist individuals (Jaeger et al., 2009). In contrast, GBBG exhibited narrower ranges for all isotopic values, representative of a specialist species. GBBG's isotopic values were in the highest range of those of the other gull species, that characterize a diet based on marine items ($\delta^{34}S$: +15 to +19‰), whereas EHG, LBBG and YLG individuals showed a diet of mixed terrestrial, intertidal and marine sources (Nehlich, 2015; Rees et al., 1978). The very high Hg concentrations found in GBBG are therefore most likely related to its marine diet. These isotopic results are supported by the analyses of foraging trips in EHG, LBBG and GBBG, as the use of a marine habitats was related to higher blood Hg concentrations. In other species of coastal gulls equipped with tracking devices, including the American Herring gull (*Larus smithsonianus*) and the Western gull (*Larus occidentalis*), a similar pattern was recently observed, with individuals mainly foraging in marine environments exhibiting the highest Hg concentrations (Clatterbuck et al., 2021; Thorne et al., 2021). EHG showed higher use of coastal foraging sites but similar Hg concentrations compared to the more pelagic LBBG. The coastal specialists GBBG also presented the highest Hg concentrations, further suggesting that "marine *vs* terrestrial" may represent a better gradient than "coastal *vs* pelagic" to explain Hg variations in gull species. As $\delta^{34}S$ highly discriminates between terrestrial and marine habitats (McCutchan Jr et al., 2003), we further stress the importance of the use of $\delta^{34}S$ as relevant index of foraging habitats.

Nevertheless, Figs. 3 and 4 reveal a weaker relationship between blood Hg and PC_1 in GBBGs. It was however not possible to include the interaction between PC_1 and species in the models to study if this relationship was different among species, due to the relatively different range in PC_1 and Hg values between GBBG and the other species. In chicks, the additive effect of maternal Hg initially transferred in the egg may contribute to blur the relationship in all species.

Surprisingly, the range of Hg concentrations seems to be inversely correlated to the isotopic niche width in adults, i.e., with the foraging habitat diversity. In the specialist GBBG, high fidelity to foraging sites may explain the high inter-individual variation in Hg concentration despite a narrow isotopic niche, i.e., birds feeding on a similar trophic position prey but specialized in areas of different contamination intensities (river estuarine, salt-marshes, intertidal area, open sea, …; Mitchell and Gilmour, 2008), generating individual variation in Hg exposure. EHG and LBBG also exhibited a relatively high fidelity to foraging sites, but the lower range of Hg concentrations compared to GBBG suggests that the foraging areas provided by movement analyses are important to understand the sources of Hg in specialist species.

5. Conclusion

In the present study, we have highlighted the need to refine ecotoxicological studies with stable isotope analyses, as the trophic position (using $\delta^{15}N$ as a proxy) and the feeding habitat ($\delta^{34}S$) were important drivers of blood Hg contamination. We also point out that not only the use of GPS data highly reflects the results on Hg concentrations and habitat selection through isotopic analyses, but it may further provides fundamental insights on inter-individual contamination through habitat fidelity. We argue for the concomitant use of both GPS and the stable isotopes method to characterize the sources of contaminants in seabirds.

Our results also call for a potential toxicological risk in both chicks and adults. As chicks receive high trophic position prey of marine origin from their parents, such diet could lead to Hg concentrations of concern during their development. In adults, GBBG showed particularly high concentrations of Hg due to its almost exclusively marine food. Nonetheless, several adults of all four species might be at risk as they exceeded previously reported Hg toxicity thresholds. It is therefore fundamental to further investigate the potential detrimental effects of Hg exposure on physiological and life-history traits of the studied 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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2022.119619.

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