MESOPELAGIC DIET AS PATHWAY OF HIGH MERCURY LEVELS IN BODY FEATHERS OF THE ENDANGERED BLACK-CAPPED PETREL (DIABLOTIN) *PTERODROMA HASITATA*

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ABSTRACT

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The Diablotin or Black-capped Petrel *Pterodroma hasitata* is an endangered gadfly petrel found in the western North Atlantic, Caribbean Sea, and northern Gulf of Mexico. An estimated ~2000 pairs nest at five known sites on Hispaniola, Greater Antilles, although only 120 nests have been located to date. We collected breast feathers and feces from breeding adults in the Dominican Republic in April 2018 (n = 10) and from non-breeding adults at sea offshore of North Carolina, USA, in May 2019 (n = 10). We measured mercury burden in feathers and used fecal DNA metabarcoding to compare diets. We found higher concentrations of total mercury compared to other *Pterodroma* petrels worldwide, with mean concentrations of 30.3 ± 11.1 ppm dry weight (range: 15.2–53.9; n = 20). Diet was dominated by fish, including a high proportion of mesopelagic groups such as myctophids, as well as fishes of interest to artisanal and commercial Caribbean fisheries. These results confirm earlier suggestions of elevated ingestion of mercury by Black-capped Petrels, likely through the consumption of mesopelagic prey or fishery discards.

Key words: Atlantic, Caribbean, contaminants, diet, mercury, seabirds, trophic ecology

INTRODUCTION

Through anthropogenic emissions into the atmosphere, contaminants have become increasingly prevalent in the marine food web (Lamborg *et al.* 2014). Mercury (Hg), a ubiquitous heavy-metal contaminant, is also naturally present in the marine environment. Human activities, however, have increased natural atmospheric concentrations of Hg by *ca*. 450% since 1450 (Zhang *et al.* 2014, Outridge *et al.* 2018). Anthropogenic Hg now amounts to approximately two thirds of the overall atmospheric Hg (Morel *et al.* 1998), which represents 90% of all Hg inputs into the surface ocean (Mason *et al.* 2012). Although occurring in all ocean basins, marine inputs of anthropogenic Hg are spatially variable, and the extent to which Hg enters a given food web depends on the dynamics of biophysical oceanic transport and processes (Mason *et al.* 2012, Zhang *et al.* 2014). Once Hg enters aquatic ecosystems and their associated food webs, inorganic Hg may be converted to methylmercury (MeHg) by anaerobic microorganisms within the marine water column (Munson *et al.* 2018, Villar *et al.* 2020). MeHg, which is more toxic than inorganic Hg, rapidly assimilates into and biomagnifies through food webs (Driscoll *et al.* 2013). Once metabolized, MeHg can affect the physiology, fitness, and development of apex predators (Evers *et al.* 1998, Tartu *et al.* 2013), resulting in acute and chronic consequences at the population level (Bond *et al.* 2015).

In seabirds, exposure to Hg occurs through the food web and depends on the location of foraging areas (Anderson *et al.* 2009), along with the type, size, and ecology of prey (Becker *et al.* 2016). For example, Hg levels tend to be higher in prey from deeper waters (mesopelagic layer, 200–1000 m depth) compared to shallower waters (epipelagic prey, 0–200 m depth; Ochoa-acuña *et al.* 2002, Choy *et al.* 2009); in general, the former would tend to be less accessible to foraging seabirds. Many mesopelagic fish, however, become accessible through diel vertical migration. By doing so, they connect Hg methylation sites in deep, hypoxic waters to the ocean's surface and, subsequently, to predators that are active there (Robinson *et al.* 2010, Young *et al.* 2015). This transboundary movement of mesopelagic fish thus increases Hg exposure in seabirds that forage in the uppermost meters of the water column (Monteiro *et al.* 1998, Thompson *et al.* 1998b, Seco *et al.* 2020). Once ingested, Hg is metabolized and accumulates in internal organs before being deposited in growing feathers during moult (Furness *et al.* 1986). A fraction of Hg is also excreted through feces (Spalding *et al.* 2000).

Feathers, which essentially contain organic MeHg (Bond & Diamond 2009), have been used as a non-lethal means to monitor Hg in seabirds (Becker *et al.* 2016) because MeHg levels in feathers predictably correlate with levels in body tissues (Agusa *et al.* 2005). However, because feathers reflect contamination to the individual in environments that were occupied prior to the initiation of feather growth, links between diet and Hg levels measured in feathers can be complex (Bond 2010). Diet studies are, nonetheless, necessary to understand pathways of Hg contamination. In seabird species for which diet information is limited or not available, contemporary diet assessments can provide

baseline information independent of the time periods during which Hg levels were measured. Diet may be assessed via several methods including DNA metabarcoding, which is used to identify traces of prey DNA present in seabird feces or regurgitates (Valentini *et al.* 2009, Pompanon *et al.* 2012). Unlike morphological analyses of stomach contents, which can be hindered by the digestion of prey during long foraging trips and be biased towards prey with parts that are difficult to digest such as otoliths and squid beaks, DNA analyses are non-invasive yet robust methods for identifying prey taxa (Pompanon *et al.* 2012, Alonso *et al.* 2014, McInnes *et al.* 2016).

The Black-capped Petrel *Pterodroma hasitata*, also known as the Diablotin, is a mid-size gadfly petrel that breeds in the Caribbean. The species is considered Endangered throughout its range (BirdLife International 2018) and was recently listed as Endangered under the US Endangered Species Act (USFWS 2023). Two phenotypes have been described: a smaller dark form and a larger light form that are genetically distinct (Howell & Patteson 2008, Manly *et al.* 2013). The light form breeds from December to May and the dark form breeds from January to July (Satgé *et al.* 2023a). Black-capped Petrels feed by seizing prey from the ocean surface, sometimes submerging themselves fully beneath the surface (Simons *et al.* 2013, Satgé *et al.* 2023a). Feeding activity is suspected to occur at night or early in the morning. The diet of Black-capped Petrel has not been adequately assessed but is known from stomach analyses to include mesopelagic cephalopods (Haney 1987, Moser & Lee 1992).

The species occurs in waters of the western North Atlantic Ocean, Caribbean Sea, and Gulf of Mexico (Jodice *et al.* 2021, Satgé *et al.* 2023a). Global Hg models suggest a high prevalence of Hg (measured as total Hg) in the mixed layer of each of these three basins (Zhang *et al.* 2014 for all three basins, Satgé *et al.* 2023b for the western North Atlantic only). Since high Hg concentrations have been detected in pelagic seabirds that feed extensively on mesopelagic prey (e.g., Carravieri *et al.* 2014, Furtado *et al.* 2021), we posited that Black-capped Petrels would be exposed to high background concentrations of Hg throughout the annual cycle. The only previous analysis of Hg levels in the Black-capped Petrel (Waling *et al.* 1980, as cited in Simons *et al.* 2013) suggested a mean total Hg concentration of 18.0 ppm (n = 22) in feathers. However, these results were not peer-reviewed, and the methods were never published. Therefore, the objectives of this study were (1) to measure contemporary Hg levels in Black-capped Petrel body feathers and compare these values with other Pterodroma worldwide, and (2) to assess dietary pathways of Hg contamination through an analysis of Black-capped Petrel fecal DNA.

METHODS

Fieldwork

In 2018, we worked at Loma del Toro (18.3°N, 071.7°W), on the Sierra de Bahoruco ridge in the Dominican Republic (Fig. 1). This

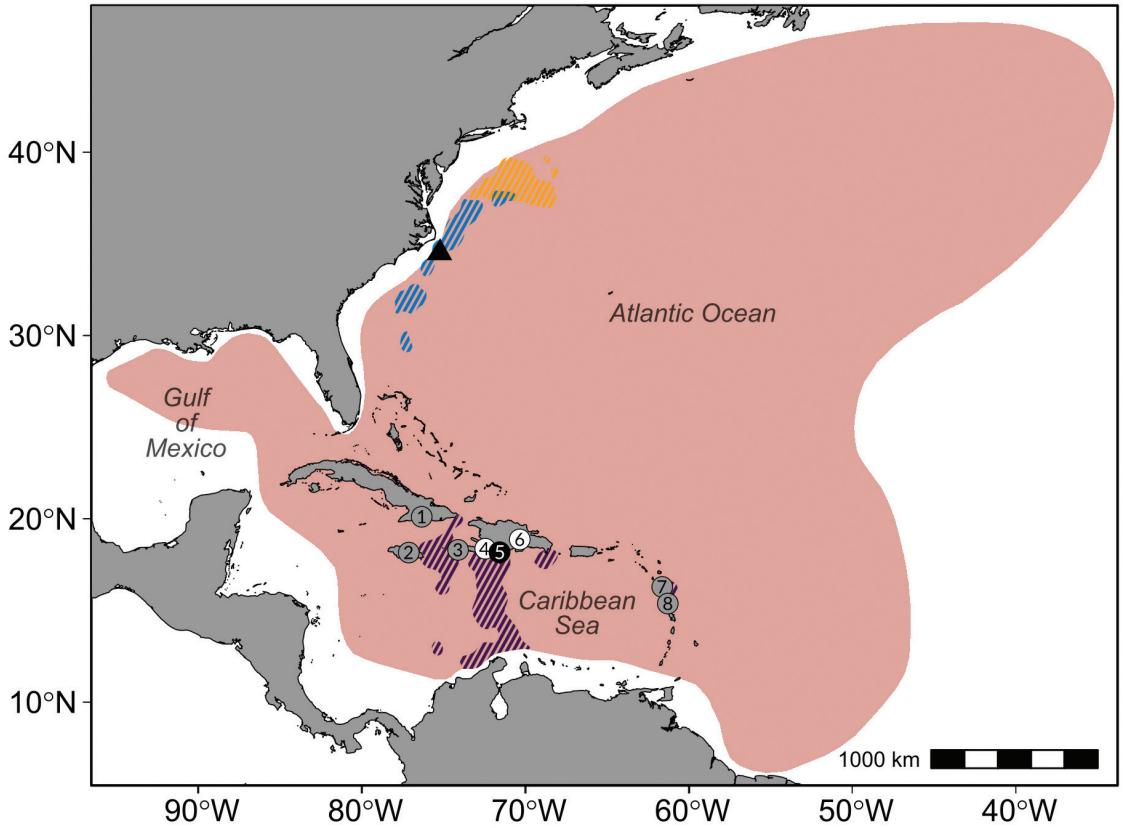

Fig. 1. Map of study area. Circles with numbers indicate breeding colonies; black indicates the study colony, white indicates confirmed breeding, and grey indicates suspected breeding. 1) Sierra Maestra, Cuba; 2) Blue Mountains, Jamaica; 3) Pic Macaya, Haiti; 4) Pic La Visite, Haiti; 5) Morne Vincent, Haiti, and Sierra de Bahoruco, Dominican Republic; 6) Valle Nuevo, Dominican Republic; 7) Guadeloupe; 8) Dominica. The black triangle indicates the capture location at sea. Pink shading represents the species' range (Satgé *et al.* 2023a); blue and yellow hatching represent the core-use areas of the dark and light phenotypes in the western North Atlantic, respectively (Satgé *et al.* 2023b); purple hatching represents the species' core-use area in the Caribbean Sea (Wheeler *et al.* 2021). The basemap was created with package "ggOceanMaps" in R.

site is located *ca*. 30 km inland at an elevation of 2000 m and is characterized by steep slopes and ravines of dense and humid understory vegetation, coupled with ridges dominated by montane forests of Hispaniolan Pine *Pinus occidentalis*. During 13–18 April 2018, we captured chick-rearing adult Black-capped Petrels from nesting burrows as part of a concurrent tracking study (see Satgé *et al.* 2019 for capture methods). From each captured adult, we collected three to four breast feathers. We also collected fresh feathers lost by adults at additional nest sites during early breeding. To avoid sampling both individuals of a pair, we collected only one feather from each sampled nest site. We stored feathers in plastic sample bags until analysis. We did not sample chicks which were still in downy plumage in mid-April.

In 2019, we worked in Gulf Stream waters within a 25-km radius of 34.78°N, 075.33°W (*ca*. 60 km southeast of Cape Hatteras, North Carolina, USA; Fig. 1). Black-capped Petrels commonly forage in this area during the breeding and non-breeding periods (Simons *et al.* 2013, Jodice *et al.* 2015, Satgé *et al.* 2023a; Fig. 1). During 08–14 May 2019, we captured adult Black-capped Petrels as part of a concurrent tracking study (see Satgé *et al.* 2023b for capture methods and a discussion of breeding status). We collected three to four breast feathers from each bird and stored feathers in paper sample envelopes until analysis.

At both locations, after assessing captured petrels for general condition, we measured body mass (±5 g), tarsus length (±0.1 mm), exposed culmen length (±0.1 mm), and bill depth at gonys (±0.1 mm), then banded each with individually numbered metal bands (United States Geological Survey (USGS) Bird Banding Laboratory, Maryland, USA). We photographed the birds' profiles, upper-wings, and under-wings, and we classified each as dark, intermediate, or light forms. We also opportunistically collected feces and regurgitates, which we stored in 70% ethanol until analysis. In 2019, we collected a few drops of blood from one metatarsal vein of each bird for molecular sexing, which was performed at the Centro de Ecologia, Evolução e Alterações Ambientais, University of Lisbon, Portugal, following Fridolfsson & Ellegren (1999) with primers 2550F and 2718R.

Mercury analysis

Mercury analyses took place at the USGS Mercury Research Laboratory (Madison, Wisconsin, USA). We digested one whole-feather sample per individual in 4.5 M nitric acid (HNO_3) at 60 °C for eight hours to extract MeHg (Hammerschmidt & Fitzgerald 2006). Extracts were then treated with ultraviolet light for three to five days to destroy dissolved organic matter and then oxidized with bromine monochloride (BrCl) at 50 °C for five days to convert MeHg to the inorganic form (Hg(II)). We performed a total-Hg analysis according to Method 1631 set out by the US Environmental Protection Agency (USEPA 2002). Briefly, we neutralized aliquots of oxidized samples with hydroxylamine hydrochloride, followed by the addition of stannous chloride to release Hg from the solution in its gaseous Hg(0) form. We purged Hg onto gold traps using ultra-high-purity argon, then desorbed and measured total Hg by cold-vapour atomic fluorescence spectrometry. Certified reference material 407 (a fish homogenate) from the International Atomic Energy Agency was analysed alongside our samples and showed acceptable recoveries (196.2 ± 2.6 ng/g (ppb), 89% recovery, n = 3). In addition, the standard deviation for analytical replicates was 2% and method blanks were less than 0.04 ng/mL (ppb).

We used *t*-tests to compare total Hg levels between phenotypes and years. We did not compare Hg levels between sexes because the sample size of sexed individuals was small (n = 10) and skewed towards males (Table 1). Additionally, we used linear regressions to compare total Hg levels with morphometrics (mass, tarsus length, culmen length, and bill depth). Statistical analyses were done in R (R Core Team 2020). We compared Hg levels in this study with those reported in other *Petrodroma* species. For this, we searched the published literature (including peer-reviewed articles, reports, and theses) on Google Scholar, using the search terms "seabirds AND mercury" and "Pterodroma AND mercury."

Diet analysis

Based on the proven efficacy of the QIAamp Fast DNA Stool Mini Kit (Qiagen; Hilden, Germany; Doyle & Adams 2019), we used it to extract DNA from Black-capped Petrel fecal samples. We performed polymerase chain reaction (PCR) in two stages: the first stage amplified the target amplicon, and the second stage ligated sample-specific adapters to the amplicons. PCR sample preparation was performed in a dedicated clean lab and included the use of both negative controls to monitor for contamination and positive controls (a mock community of fish DNA) to ensure successful amplification of all expected products. We used the universal eukaryotic primers developed by McInnes *et al.* (2017a) to amplify the v7 region of the small subunit rDNA (hereafter 18S), allowing us to theoretically identify all prey to the family or order level. To identify fish prey specifically, we also amplified a fragment of the 12S rRNA gene using the popular MiFish primers (Miya *et al.* 2015) to which we had added TruSeq tails. We visualized PCR products using gel electrophoresis before we diluted and sent them for sequencing at the Hubbard Center for Genome Studies at the University of New Hampshire.

We performed bioinformatics using QIIME 2 v.2021.2 (Bolyen *et al.* 2019). For both the 18S and MiFish amplicons, we trimmed the forward and reverse primers using the *cutadapt* plugin (Martin 2011) before denoising and merging reads using the *DADA2* plugin (Callahan *et al.* 2016). We assigned taxonomy to the 12S amplicons using an iterative Basic Local Alignment Search Tool (BLAST) method, where sequences were compared against a custom reference database created using the *RESCRIPt* plugin (Robeson *et al.* 2021). We then manually checked all species assignments by running the representative sequences against the full GenBank database (National Center for Biotechnology Information; Bethesda, USA). We used the Fishbase (Froese & Pauly 2000) to check that the fishes' ranges overlapped with the foraging areas used by Black-capped Petrels. To assign taxonomy to the 18S sequences, we trained a Naive Bayes classifier using the *feature-classifier* plugin (Pedregosa *et al.* 2011, Bokulich *et al.* 2018) on a QIIME-compatible version of the SILVA rRNA database (v.132, released 10 Apr 2018, 99% clustered, downloaded from https://www.arb-silva.de/download/archive/qiime; Quast *et al*. 2013). Because the 18S gene is relatively conserved across eukaryotes, we did not attempt to assign taxonomy higher than the order level. We excluded non-prey sequences, including those from birds, mammals, parasites, and non-metazoan organisms, and we ignored prey items that represented less than 1% of sequence reads within a sample, as such a low level of DNA sequences typically indicates secondary prey (McInnes *et al.* 2017b). A full description of the methods are available in Appendix 1, available on the website.

TABLE 1
Sex, phenotype, morphometrics, and total mercury (Hg) concentrations in breast feathers of adult Black-capped Petrels *Pterodroma hasitata* collected at nest sites in the Dominican Republic (2018) and at sea off North Carolina, USA (2019)

	Individual ID[a]	Sex	Phenotype[b]	Mass (g)	Tarsus (mm)	Culmen (mm)	Bill depth (mm)	Total Hg concentration (ppm dw)[c]
Dominican Republic (2018)	257[d]	-	-	-	-	-	-	15.28
	258[d]	-	-	-	-	-	-	20.27
	261	-	D	370	39.35	32.15	13.65	21.82
	265	-	D	430	40.75	32.00	13.45	25.56
	264	-	D	410	37.90	33.40	13.15	34.86
	266	-	D	385	37.80	31.50	12.70	35.83
	259[d]	-	-	-	-	-	-	37.35
	262	-	D	450	40.65	33.15	14.35	39.04
	263	-	D	415	40.30	32.31	12.90	39.45
	260[d]	-	-	-	-	-	-	43.04
Offshore North Carolina (2019)	250	F	D	390	38.70	32.50	13.70	15.20
	249	M	D	380	41.70	31.50	14.00	15.87
	253	F	L	390	41.10	36.00	14.10	16.13
	254	M	L	410	40.60	34.60	13.60	23.41
	255	M	L	375	40.20	35.00	14.00	26.96
	248	M	D	380	39.20	34.80	13.60	28.22
	252	F	L	460	41.40	36.00	14.40	32.56
	247	M	D	380	39.00	32.10	14.00	40.52
	256	M	L	420	39.10	35.30	14.30	40.83
	251	M	D	370	39.50	32.60	14.40	53.94

[a] Individual identification (ID) numbers in bold represent individuals for which diet data are available.
[b] D = dark form, L = light form.
[c] Total Hg concentrations were originally measured in ng/g (dw = dry weight).
[d] Dropped feathers collected at nesting sites.

Data availability

Raw sequence reads from prey items and individual Black-capped Petrel metagenomes are available on the Sequence Read Archive (project number PRJNA1083919): https://www.ncbi.nlm.nih.gov/bioproject/1083919

RESULTS

Overall, we obtained 16 samples of known origin from specific individuals and four opportunistic samples. Of the 16 known individuals, 11 were of the dark phenotype and five were of the light phenotype (Table 1). Of the petrels captured at sea, three were female and seven were male. Birds captured at nest sites were not sexed.

Mercury analysis

The mean total Hg concentration was 30.3 ± 11.1 µg/g dry weight (ppm dw; range 15.2–53.9, Table 1). There were no statistically significant differences in total Hg concentrations between the dark (31.8 ± 11.8 ppm) and light phenotypes (28.0 ± 9.3 ppm; *t*-test $t(9.8) = 0.7$, $P = 0.5$) or between the 2018 (29.4 ± 12.8 ppm) and 2019 samples (31.3 ± 9.6 ppm; *t*-test $t(16.7) = -0.37$, $P = 0.7$). Total Hg concentrations were not linearly correlated to mass, tarsus length, culmen length, or bill depth ($R^2 \leq 0.12$, $P \geq 0.2$, and $F \leq 1.6$ for all; see Appendix 2, available on the website).

We located 13 published studies referencing total Hg levels in the feathers of 15 species of *Pterodroma* (Appendix 3, available on the website). Of these, we compared data among 11 studies that assessed total Hg in the body feathers of adults in 10 gadfly species (Table 2). We did not use the remaining two studies because they reported Hg levels in other types of feathers and/or in young birds. The mean concentration of total Hg in Black-capped Petrels from our study ranked third among the species compared, after Grey-faced Petrels *P. gouldi* (36.48 ppm, Lyver *et al.* 2017) and Magenta Petrels *P. magentae* (34.14 ppm, Thébault *et al.* 2021; Fig. 2). The maximum concentration of total Hg detected within an individual petrel from our study ranked second, after a Grey-faced Petrel (64.22 ppm; Lyver *et al.* 2017).

TABLE 2
Synthesis of total mercury concentrations in body feathers of adult *Pterodroma* petrels[a]

Species	Sample type[b]	*n*	Mean	Standard deviation	Min	Max	Years sampled	Study site	Reference
Great-winged Petrel *P. macroptera*	breast	14	15.8	4.4	9.8	27.1	2003–2011	Kerguelen Island	Carravieri *et al.* 2014
	breast	5	28.038	9.984	16.617	39.15	2011	Marion Island	Becker *et al.* 2016
Grey-faced Petrel *P. gouldi*	breast	220	36.48	9.59	18.06	64.22	2006–2012	North Island, New Zealand	Lyver *et al.* 2017
Magenta Petrel *P. magentae*	flank	8	34.14	6.83	27.34	45.69	2015	Chatham Islands	Thébault *et al.* 2021
Soft-plumaged Petrel *P. mollis*	breast	21	10.3	2.30			1983	Gough Island	Thompson *et al.* 1990
	breast	17	9.82	2.32	5.36	13.4	1985	Gough Island	Thompson *et al.* 1993
	breast	19	12.2	4.2	4.7	25.5	2003–2011	Kerguelen Island	Carravieri *et al.* 2014
	breast	10	15.063	3.512	9.180	19.983	2009	Gough Island	Becker *et al.* 2016
	breast	5	7.202	4.977	1.715	11.546	2011	Marion Island	Becker *et al.* 2016
Barau's Petrel *P. baraui*	breast	20	0.96	0.31			2001–2004	Reunion Island	Kojadinovic *et al.* 2007
White-headed Petrel *P. lessonii*	breast	10	12.4	2.00	9.2	17.1	2003–2011	Kerguelen Island	Carravieri *et al.* 2014
	body	1	24.4				1975–1983	New Zealand	Lock *et al.* 1992
Black-capped Petrel *P. hasitata*	unspecified	22	18.0				1980	At sea North Carolina, USA	Simons *et al.* 2013
	breast	10	29.363	12.13	15.196	53.942	2019	At sea North Carolina, USA	This study
	breast	10	31.250	9.14	15.276	43.039	2018	Dominican Republic	This study
Atlantic Petrel *P. incerta*	breast	23	13.9	3.6			1983	Gough Island	Thompson *et al.* 1990
	breast	15	13.5	4.1	3.9	20.1	1985	Gough Island	Thompson *et al.* 1993
	breast	10	20.118	5.006	12.658	27.757	2009	Gough Island	Becker *et al.* 2016
Bonin Petrel *P. hypoleuca*	breast	27	19.700	0.001[c]			N/A	Midway Island	Burger & Gochfeld 2000
	breast	42	9.880	4.710	0.457	16.000	2014–2015	Midway Island	Shaw 2019
Cook's Petrel *P. cookii*	body	1	12.4				1975–1983	New Zealand	Lock *et al.* 1992

[a] Mean, standard deviation, min, and max columns are all measured in µg/g (ppm) dry weight.
[b] As described in the associated reference.
[c] Standard error

Diet analysis

During the 2018 breeding season, we collected seven fecal samples at nesting sites, three fecal samples left outside burrow entrances, one adult regurgitate, and one chick regurgitate (Appendix 4, available on the website). In 2019, we collected two fecal samples from adults captured at sea. We successfully extracted and sequenced DNA from six samples showing DNA amplification for MiFish markers and five for 18S markers: three fecal samples from breeding adults, one regurgitate from a breeding adult, and two fecal samples from adults at sea (only one of which showed amplification for 18S markers; Appendix 4). Fish 18S amplicons were present in all amplified samples (n = 5). DNA from a siphonophore (n = 1), an unidentified cephalopod (n = 1), and a squid (*Teuthida* sp., n = 1) was detected in one sample each (Appendix 1). We detected 12S amplicons in all samples (n = 6). We ignored three fish taxonomic groups that produced less than 50 reads each (< 0.5% of normalized reads).

We were able to identify 88.3% of all fish sequence reads to the family level, 60.5% to the genus level, and 46.1% to the species level (Table 3). For one individual (petrel 262), two samples were analysed: we counted five prey groups in the fecal sample but four

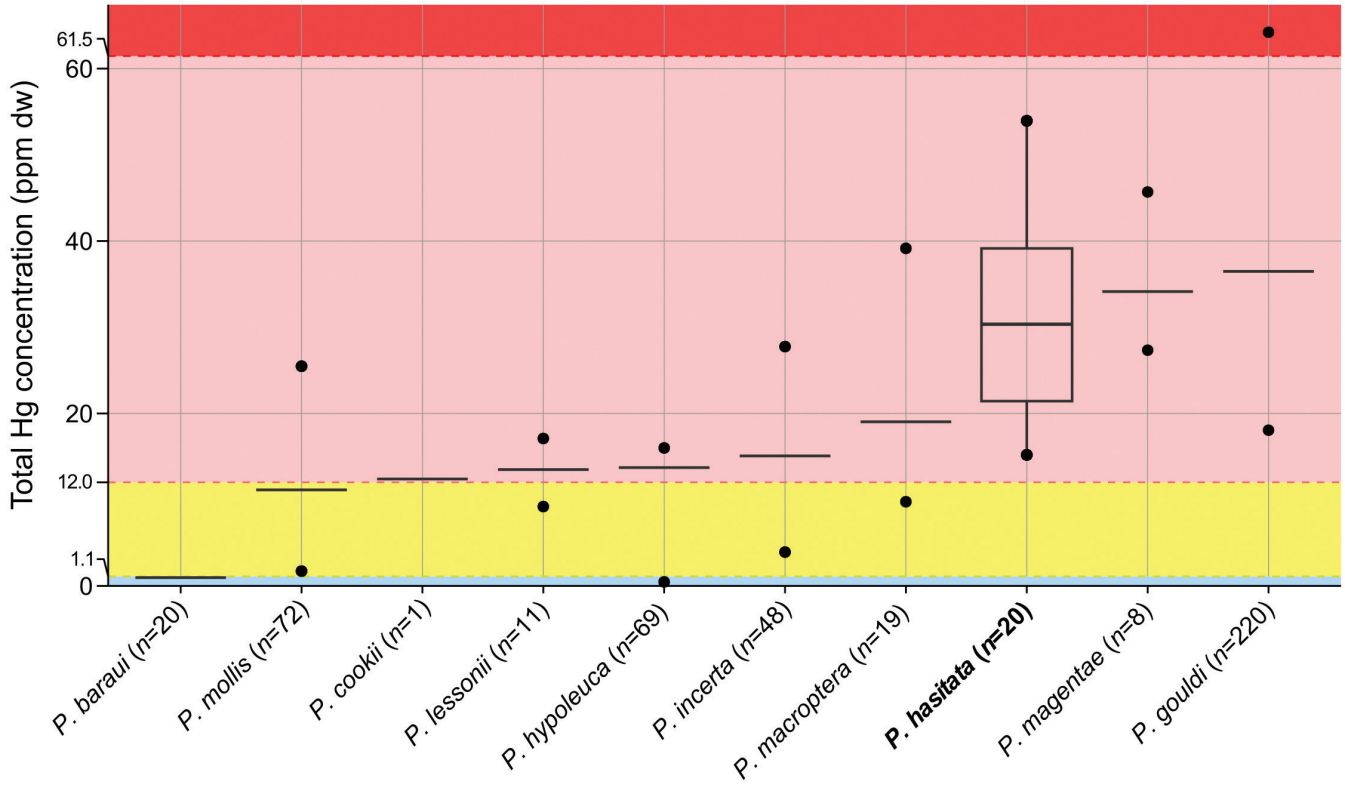

Fig. 2. Total mercury (Hg) concentrations in parts per million dry weight (ppm dw) measured in body feathers of adult *Pterodroma*. Black dots represent minimum and maximum reported total Hg concentrations, as available; in some cases, minimum and maximum concentrations were not reported in the original study. Horizontal bars represent mean concentrations (weighted average). For Black-capped Petrel *P. hasitata* (bold for emphasis), values from this study are represented as a box plot, where the solid line within the box represents the mean and the box edges represent quartiles. Colour shadings represent the risks of adverse Hg effects described in Ackerman *et al.* (2016), adapted to feather-equivalents following Equation 4 in Ackerman *et al.* (2016): blue = below any known effect, yellow = low risk, pink = moderate risk, red = high risk. The total number of individuals sampled for a given species (*n*) is indicated next to each species' name. See Table 2 for details of the dataset.

in the regurgitate; three fish groups were common to both samples (Table 3). The two samples collected at sea counted fewer fish orders (1 and 3 orders) than the four samples collected at nesting sites (2–6 orders; Appendix 5, Fig. 3).

Scombriformes (44.8% of all reads), Anguilliformes (21.7%), Myctophiformes (11.1%), and Caproiformes (7.9%) were the most represented orders in the samples (Appendix 5). Among them, the families Chiasmodontidae (32.5% of all reads), Serrivomeridae (16.7%), and Myctophidae (11.1%) were the most represented. The genera *Serrivomer* sp. (sawpalate; 16.6% of all reads), *Diaphus* sp. (lanternfish; 10.3%), and *Pseudoscopelus* sp. (snaketooth; 9.2%) were the most represented. Fish groups that were found in at-sea samples were not found in nest-site samples. Among the four nest-site samples, eight fish taxonomic groups occurred in one sample, seven groups occurred in two samples, and fish from the genus *Pseudoscopelus* sp. occurred in all four (Appendix 5).

Fish considered to be pelagic were present in all samples. Most DNA sequence reads corresponded to fish groups occurring in mesopelagic to benthic (45.5%), epi- and mesopelagic (25.1% of all sequence reads), and epi- to bathypelagic habitats (16.7%) (Fig. 4). Fish groups that perform diel vertical migrations (mainly Myctophiformes and Stomiiformes) comprised 28.2% of all sequence reads. Most fish groups had a known distribution that included all three ocean basins used by Black-capped Petrels except for Kaup's Arrowtooth Eel *Synaphobranchus kaupii*, which appears limited to the Atlantic, and Polka-dot Ribbonfish *Desmodema polystictum*, which appears limited to the Gulf of Mexico and the northeastern coast of Florida (Froese & Pauly 2023). Three prey groups (Blue Runner *Caranx crysos*, Mackerel Scad *Decapterus macarellus*, and Snapper *Pristipomoides* sp.) are taken in artisanal and commercial fisheries in the Caribbean.

DISCUSSION

Inter- and intraspecific differences in mercury burdens in *Pterodroma* petrels

Due to their high trophic positions, gadfly petrels are very susceptible to Hg bioaccumulation (Monteiro *et al.* 1998, Thébault *et al.* 2021), and they harbour Hg levels among the highest measured in seabirds globally (Thébault *et al.* 2021). In *Pterodroma* species, total Hg concentrations in the contour feathers of adults seem to vary extensively, ranging from 0.96 ±0.31 ppm (mean ± SD) in Barau's Petrel *P. baraui* (Kojadinovic *et al.* 2007) to 36.48 ±9.59 ppm in Grey-faced Petrels (Lyver *et al.* 2017), though most species have means greater than 7.00 ppm (Table 2). Our data indicate that

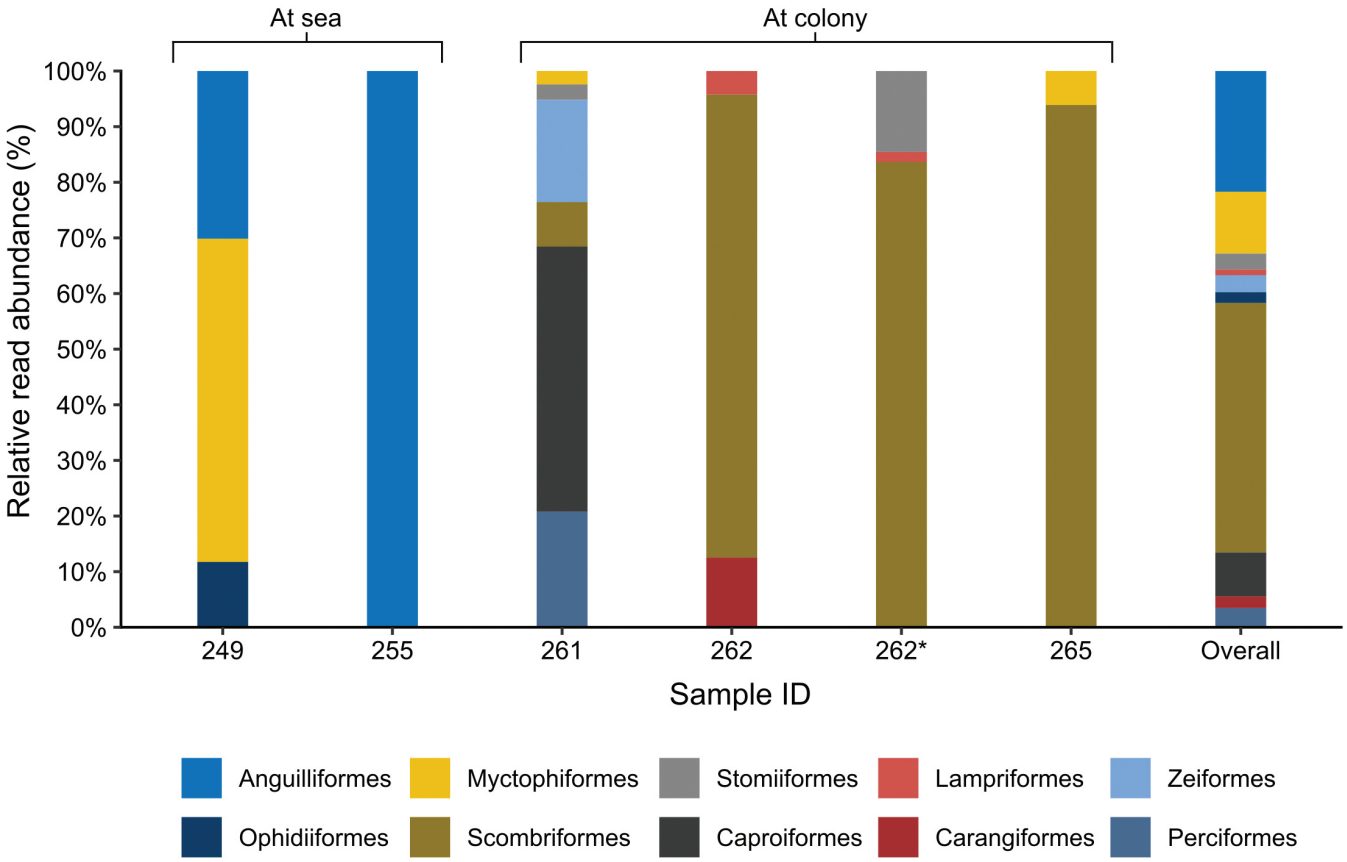

Fig. 3. Relative abundance of prey groups (categorized by taxonomic order) consumed by Black-capped Petrels *Pterodroma hasitata* captured at nest sites in the Dominican Republic in 2018 and at sea off Cape Hatteras, USA, in 2019, as determined using bioinformatic analysis. Percentages represent relative abundance of DNA sequence reads in diet samples. Petrels are identified by individual identification numbers, as in Table 1. Fecal samples were analysed for all individuals; for individual 262, an additional regurgitation sample was analysed (identified with *).

Black-capped Petrel is among those *Pterodroma* species globally that have the highest total Hg concentrations measured in feathers (Table 2, Appendix 3). They have slightly lower concentrations than two larger petrel species breeding in New Zealand, the Grey-faced (Lyver *et al.* 2017) and Magenta (Thébault *et al.* 2021) petrels.

Although mercury data are available for 15 species of *Pterodroma* globally (Appendix 3), few studies have assessed the Hg levels of this group in the North Atlantic. This makes regional comparisons difficult (Pollet *et al.* 2022). One recent study shows lower total Hg levels in the Bermuda Petrel *P. cahow* (a medium-sized petrel breeding and foraging in the western North Atlantic, known locally as the Cahow) than in the Black-capped Petrel (Letizia Campioni pers. comm.). In the Black-capped Petrel, the only previous study showed a mean total Hg concentration of 18.0 ppm (n = 22) in feathers (Waling *et al.* 1980, cited in Simons *et al.* 2013). However, the methods were not published, so the type of feathers used, the age of birds sampled, and the methods used remain unclear. Therefore, it is not possible to assess the reasons for the differences between our work and that of Waling *et al*. (1980).

Additionally, a study of Hg concentrations in Black-capped Petrels indicated a mean total Hg concentration of 26.92 ± 11.35 ppm dw (min = 3.87, max = 58.29, with an outlier at 81.45 ppm dw; Sutherland 2023) in the breast feathers of petrels collected between 1979 and 1989 at sea (offshore Cape Hatteras), in an area similar to our 2019 study area. Our results had a higher mean concentration (30.3 ppm dw) due to a narrower range and a higher minimum concentration (15.2–53.9 ppm dw). Because of the limited sample sizes in both studies and our limited understanding of Black-capped Petrel ecology, it is unclear if the observed differences are due to the characteristics of the samples analysed (e.g., age differences between sampled birds) or a shift in diet to more mesopelagic, Hg-laden prey. These differences may also mirror possible ecological changes since the 1980s, such as an increase of Hg in the marine systems used by Black-capped Petrels. Nevertheless, Sutherland (2023) noted strong variability in total Hg concentrations between breast feathers within individual birds. We acknowledge that we analysed only a single feather per individual in our study, which could result in the reported Hg concentration being different from the individual's actual mean overall body burden. In future studies, the analysis of different feathers as well as other tissues (e.g., blood) could shed light on the Hg body burden within Black-capped Petrels and allow for more robust comparisons of dietary Hg intake.

Black-capped Petrels show variations in phenotype, ranging from a smaller, lighter dark form to a larger, heavier light form, with intermediate phenotypes (Satgé *et al.* 2023a). Based on global Hg distribution models, Satgé *et al.* (2023b) suggest that the different

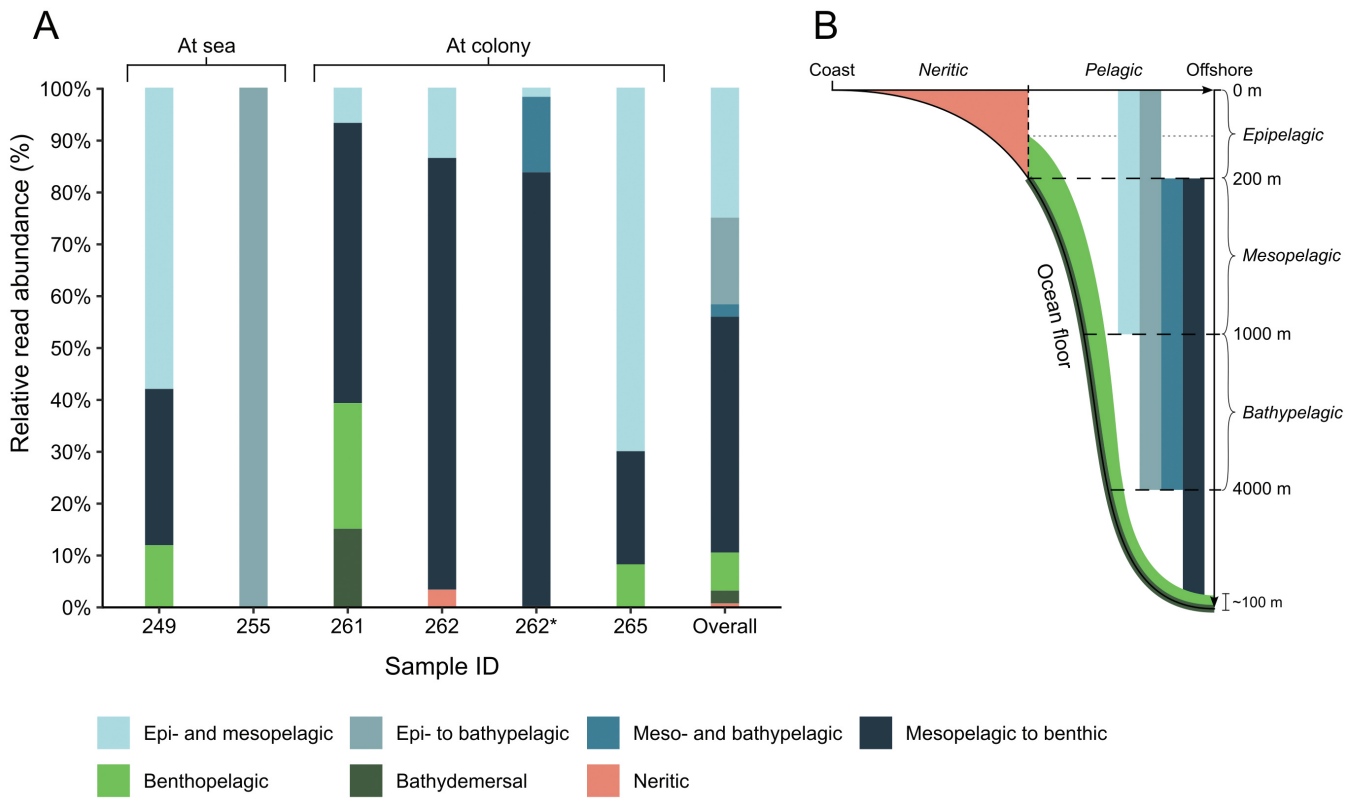

Fig. 4. Relative distribution of habitats of prey consumed by Black-capped Petrels *Pterodroma hasitata* captured at nest sites in the Dominican Republic in 2018 and at sea off Cape Hatteras, USA, in 2019. (A) Percentages represent relative abundance of DNA sequence reads in diet samples. Petrels are identified by individual identification numbers, as in Table 1. Fecal samples were analysed for all individuals; for individual 262, an additional regurgitation sample was analysed (identified with *). Habitat types were collated from fishbase.org (Froese & Pauly 2023). (B) Schematic representation of marine habitat zones. The colours of the habitat zones correspond to habitat colours used in panel (A).

at-sea distributions of dark and light forms can potentially lead to differential exposure to Hg concentrations in the oceanic mixed layer. Both our study and that of Sutherland (2023) failed to detect differences in Hg burden between phenotypes, but caution should be exercised, given disparate sample sizes (n = 11 dark and n = 5 light for our study, n = 42 dark and n = 17 light for Sutherland's). The linkage between Hg presence in the environment, methylation sites, and concentrations in marine food webs is generally poorly understood (Sunderland *et al.* 2009). Although global Hg models may reasonably inform on potential exposure to Hg contamination, they may not adequately capture the fine-scale distributions of the MeHg concentrations that would be relevant to foraging seabirds (Bowman *et al.* 2020).

Diet as a pathway of mercury bioaccumulation

This study is the first to identify main prey items of Black-capped Petrels to the genus or species level. We sampled all individuals opportunistically; therefore, despite its small sample size, we expect our analysis to reasonably describe the species' diet. Unlike previous morphological studies that highlighted cephalopods as a main prey (Haney 1987, Moser & Lee 1992), our results identified cephalopod DNA in only two of five samples and in limited proportions (< 7% of sequenced prey DNA; Appendix 1). Soft and easily digested tissues of cephalopods may be more present in regurgitates (e.g., Campioni *et al.* 2023), but we did not detect cephalopod DNA in our regurgitate sample; however, it is important to note that this result is based on a single sample. Instead, our findings suggest a prevalence of fish in Black-capped Petrel diet, supporting suggestions by Cherel & Bocher (2022) that tropical *Pterodroma* species appear to prey on fish more than their cold-water counterparts. As suggested by Simons *et al.* (2013), the high frequency of occurrence of squid observed in previous studies of Black-capped Petrel diet may have been influenced by the accumulation of squid fragments in stomachs and crops, creating a false impression.

While it is possible that some species can be missed due to mismatched primers, DNA analysis should be less prone to biases caused by issues such as the digestibility of certain prey types. DNA analyses may therefore provide robust methods for identifying prey taxa independently of their frequency of occurrence or accumulation in the digestive system (Pompanon *et al.* 2012, Alonso *et al.* 2014, McInnes *et al.* 2016). However, the accuracy of taxa identification relies on access to and comparison with databases of DNA sequences (e.g., GenBank), which tend to lack comprehensive information on tropical and pelagic marine species. As a result, although all fish DNA sequences in our samples could be identified to the order level, 11.7%, 39.5%, and 54.0% of overall sequence reads could not be identified to a family, genus, or species, respectively. Nevertheless, with the caveat that DNA sequences in low proportions may reflect secondary ingestion (i.e., the prey of a petrel's prey; Sheppard *et al.* 2005), our analysis shows a high taxonomic diversity of the prey consumed by Black-capped Petrels,

with an average of four distinct prey types per sample and a range of one to eight distinct prey types per sample. Our analysis also reveals a high frequency of Scombriformes and epi- to bathypelagic fish. Using relative read abundances of DNA sequences, we can also infer that these deep-water fishes represent a high proportion of ingested biomass (Deagle *et al.* 2019, Clucas *et al.* 2024). These results are consistent with other findings showing that Myctophidae and Stomiidae, two dominant mesopelagic fish families, form a significant part of the diet for both tropical and cold-water petrels (Ainley *et al.* 1992, Spear *et al.* 2007, Alho *et al.* 2022, Cherel & Bocher 2022, Campioni *et al.* 2023).

By engaging in diel vertical migrations, mesopelagic fishes connect the deep ocean and the surface, where they become available to surface predators such as seabirds (Robinson *et al.* 2010). Consequently, these fish play a significant role in the transfer of Hg, which they assimilate as MeHg in the oxygen minimum zone, up through the water column (Chouvelon *et al.* 2012, Blum *et al.* 2013). The diel availability of mesopelagic fish in seabird foraging habitat therefore plays a crucial role in Hg bioaccumulation, with mesopelagic fish species, like myctophids, consistently showing higher Hg concentrations than epipelagic species (Ochoa-acuña *et al.* 2002, Choy *et al.* 2009). Thus, our study appears to support a growing body of literature showing that diet, particularly mesopelagic prey species, is the main uptake route for Hg in pelagic seabirds (e.g., Monteiro *et al.* 1996, Thompson *et al.* 1998b, Seco *et al.* 2020) and results in high levels of Hg bioaccumulation. However, Lavoie *et al.* (2013) suggest that elevated concentrations of MeHg in prey may actually reduce the transfer of Hg to predators.

Besides epi- and mesopelagic prey, approximately 10% of the fish diet of Black-capped Petrels in our study consisted of benthopelagic fish (that inhabit a depth zone around 100 m off the bottom on the continental slope) and bathydemersal fish (that inhabit the bottom at depths > 200 m). The means by which these bottom-dwelling fish become available to Black-capped Petrels remains uncertain, as these fish are not known to undergo diel vertical migrations. It is possible that non-motile larvae and/or juvenile stages are occasionally entrained to the surface in upwelling regimes (Garland *et al.* 2002, Morgan 2014) or are present near the surface during their ontogeny (Badcock & Merrett 1976, Sutton 2013). These juvenile stages may also be the prey of fish targeted by Black-capped Petrels (i.e., secondary prey). Additionally, Black-capped Petrels are known to forage on fish offal (Simons *et al.* 2013) and may feed on discards of the artisanal and commercial fisheries that, in the Caribbean, target the demersal Wenchman *Pristipomoides aquilonaris* (Herrera-Moreno *et al.* 2011, Baremore *et al.* 2021).

Geographic exposure to mercury

Hg concentrations in bird feathers reflect the pool of accumulated and bioavailable Hg at the time of feather growth (Thompson *et al.* 1998a). In particular, body feathers show lower variability of total Hg concentrations among individual feathers than wing or tail feathers, which makes them preferable for Hg studies (Peterson *et al.* 2019). In the Black-capped Petrel, the moulting process has not been studied in detail, but body feathers are assumed to be moulted from chick-rearing until after the breeding season (Howell & Patteson 2008, Satgé *et al.* 2023a). We collected breast feathers in the spring during the breeding season, thus reflecting dietary intake before the last moult (June–August of the previous year). During chick-rearing, Black-capped Petrels breeding in the Dominican Republic regularly commute to the southern Caribbean Sea while also foraging in the western North Atlantic (Jodice *et al.* 2015, Satgé *et al.* 2019). After the breeding season, they appear to leave the Caribbean basin to spend most of the non-breeding period in the western North Atlantic (Jodice *et al.* 2015, Satgé *et al.* 2023b). Therefore, the Hg burdens measured in our study seem to reflect Hg exposure over the few months before feather growth, in both the southern Caribbean Sea and the western North Atlantic. Although movements between these areas and the northern Gulf of Mexico have not been described, connectivity with the northern Gulf of Mexico is also possible (Jodice *et al.* 2021).

Although diet is the main pathway for Hg bioaccumulation in gadfly petrels, the wide extent of their geographic range contributes to varying degrees of exposure, even within oceanic basins. For example, water and fauna of the western North Atlantic (particularly in the Gulf Stream and western North Atlantic Subtropical Gyre) have higher concentrations of Hg than their counterparts in the eastern North Atlantic (Martins *et al.* 2006, Bowman *et al.* 2015, Bowman *et al.* 2020). In the western North Atlantic, Black-capped Petrel and Cahow share similar diets of mesopelagic cephalopods and fish (Campioni *et al.* 2023), but their marine range differs significantly. The Cahow's range encompasses the pelagic waters of the North Atlantic, extending from Bermuda in the south to Newfoundland, Canada, in the north (Brinkley & Sutherland 2020, Raine *et al.* 2021, Campioni *et al.* 2023), while the Black-capped Petrel's marine range extends over three interconnected oceanic basins. These differences in marine range may account for variations in measured Hg concentrations. Indeed, although marine waters within each species' range have high Hg concentrations (Zhang *et al.* 2014), the Black-capped Petrel's range also overlaps with consistent upwelling regimes and anthropogenic activities, potentially resulting in increased Hg exposure. Due to upwelling and freshwater input, global mercury concentration models show relatively high total Hg levels in the mixed layer of the southern Caribbean Sea and the northern Gulf of Mexico, areas regularly occupied by Black-capped Petrels (Zhang *et al.* 2014). In contrast, Hg concentrations are higher in the pelagic waters of the western North Atlantic used by Cahows than in the coastal shelf areas used by Black-capped Petrels (Zhang *et al.* 2020). Nevertheless, in addition to the background availability of Hg in the marine ecosystem, Black-capped Petrels may face localized and discrete exposure to Hg in areas where seabed sediments are disturbed by anthropogenic activity, such as ongoing hydrocarbon production. These areas include the northern Gulf of Mexico (Trefry *et al.* 2007, Liu *et al.* 2009), the Gulf of Venezuela (de Bautista *et al.* 1999, Pirela & Casler 2005, Croquer *et al.* 2016), and to a lesser extent, waters off the Guajira Peninsula, Colombia (Satgé *et al.* 2019).

New insights on marine threats affecting the Black-capped Petrel

Hg exposure in seabirds is a critical concern due to its potentially far-reaching impacts (Zabala *et al.* 2020). MeHg is particularly toxic, and its bioaccumulation can lead to a range of adverse effects, including impaired reproductive success, decreased hatching rates, and weakened immune systems (Evers *et al.* 1998, Tartu *et al.* 2013, Goutte *et al.* 2014). Exposure also can lead to consequences at the population level (Goutte *et al.* 2014, Bond *et al.* 2015). Our results suggest that the Black-capped Petrel may be impacted by high levels of assimilated Hg. Per Ackerman *et al.* (2016), we calculated blood-equivalents of 1.2–2.8 µg/g in the petrels in our

study (Fig. 2); such levels typically result in substantial impairment to health and reproduction (Ackerman *et al.* 2016). Unhatched eggs and burrow desertion in the absence of predation events have been observed occasionally at Black-capped Petrel breeding locations (Rupp 2022, Satgé 2022, Ernst Rupp pers. comm.). Our results suggest that monitoring for Hg contamination in these colonies would therefore be warranted.

Bycatch in commercial fisheries is recognized as a significant direct threat to seabirds worldwide (Dias *et al.* 2019). Great-winged Petrel *P. macroptera* and other *Pterodroma* species have been reported as being captured in longline, trawl, and set-net fisheries (Trebilco *et al.* 2010, Richard *et al.* 2020). Although Black-capped Petrels have not been reported as bycatch in the western North Atlantic as of 2012 (Li *et al.* 2016), they face a high risk of bycatch in the pelagic longline fisheries (Zhou *et al.* 2019) and their foraging range overlaps with longline and other fisheries in the Atlantic and Caribbean basins (Satgé *et al.* 2019, Satgé *et al.* 2023b). Black-capped Petrels are known to forage on fish offal (Simons *et al*. 2013) and may feed on fishery discards. Our results show that chick-rearing Black-capped Petrels occasionally forage on fish targeted by artisanal and commercial Caribbean fisheries. While this does not confirm mortality among Black-capped Petrels due to bycatch, it suggests a need for additional investigations regarding the species' exposure to fisheries, which may occur through foraging facilitation through discards or competition for resources.

CONCLUSIONS

Although small sample sizes prevent us from generalizing our results, our research aligns with a body of studies showing how differences in geographic ranges and foraging habits may affect Hg exposure. Our study provides a baseline for additional research on the Black-capped Petrel exposure to Hg, which could include assessing the origins of Hg contamination, along with its geographic distribution and population effects. Our results also raised several questions about Black-capped Petrel diet that warrant further investigation, such as the notable absence of cephalopods, the apparent increased diversity of fish in the diets of breeding birds, and the availability and accessibility of deep-water prey. Addressing these data gaps would benefit conservation actions designed to conserve this endangered species in the marine environment.

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