



Mercury, legacy and emerging POPs, and endocrine-behavioural linkages: Implications of Arctic change in a diving seabird

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ABSTRACT

Arctic species encounter multiple stressors including climate change and environmental contaminants. Some contaminants may disrupt hormones that govern the behavioural responses of wildlife to climatic variation, and thus the capacity of species to respond to climate change. We investigated correlative interactions between legacy and emerging persistent organic pollutants (POPs), mercury (Hg), hormones and behaviours, in thick-billed murres (*Uria lomvia*) (N = 163) breeding in northern Hudson Bay (2016–2018). The blood profile of the murres was dominated by methylmercury (MeHg), followed by much lower levels of sum (Σ) 35 polychlorinated biphenyls (PCBs), hexachlorobenzene (HCB) and *p,p'*-dichlorodiphenyltrichloroethylene (DDE), polybrominated diphenyl ethers (PBDEs) BDE-47, -99 and BDE-100; all other measured organochlorine pesticides and replacement brominated flame retardants had low concentrations if detected. Inter-annual variations occurred in MeHg, circulating triiodothyronine (T3), thyroxine (T4), and the foraging behaviours of the murres, identified using GPS-accelerometers. Compared to the 50-year mean date (1971–2021) for 50% of sea-ice coverage in Hudson Bay, sea-ice breakup was 1–2 weeks earlier (2016, 2017) or comparable (2018). Indeed, 2017 was the earliest year on record. Consistent with relationships identified individually between MeHg and total T3, and T3 and foraging behaviour, a direct interaction between these three parameters was evident when all possible interactions among measured chemical pollutants, hormones, and behaviours of the murres were considered collectively (path analysis). When murres were likely already stressed due to early sea-ice breakup (2016, 2017), blood MeHg influenced circulating T3 that in turn reduced foraging time underwater. We conclude that when sea-ice breaks up early in the breeding season, Hg may interfere with the ability of murres to adjust their foraging behaviour via T3 in relation to variation in sea-ice.

1. Introduction

Climate change and chemical contamination are a particularly potent combination of environmental stressors in the Arctic, with increasing impacts to Arctic biota and ecosystems (Jenssen, 2006). The Arctic is warming at twice the global average rate, with loss of sea-ice changing Arctic ecosystems (Post et al., 2013), and impacting mercury (Hg) in Arctic food webs, including those of seabirds in Hudson Bay (Morris et al., 2022), through changes in rainfall patterns and sea-ice

melt, among other mechanisms (Chételat et al., 2015, McKinney et al. *in press*). In Arctic seabirds, climate-related ecological shifts include effects on prey availability (Gaston and Elliott, 2014), diet (Amélineau et al., 2019; Divoky et al., 2021), foraging behaviour (Divoky et al., 2021; Gaston et al., 2009) and contaminant exposure (Amélineau et al., 2019). Although seabirds can adjust their behaviour to climate variation (Amélineau et al., 2019; Divoky et al., 2021), some species may not be able to respond sufficiently to adapt to changing conditions. Mandt's black guillemots (*Cephus grylle mandtii*), a species heavily dependent on

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sea-ice (pagophilic), have lower chick growth rates during warm years because the preferred prey (Arctic cod, *Boreogadus saida*) occur primarily in waters below 4 °C (Divoky et al., 2015). However, for little auks (*Alle alle*), decreased sea-ice coverage led to altered diving behaviour, dietary shifts, and increased Hg burdens that adversely affected body condition and growth rates (Amélineau et al., 2019).

There is growing evidence that contaminant concentrations currently measured in Arctic wildlife are disrupting endocrine systems and altering reproductive behaviours (Table 1). Most studies have focused on correlations between contaminant concentrations and

Table 1

Studies that have investigated the relationship between mercury (Hg) and persistent organic pollutants (POPs), behaviour, reproductive success and the endocrine system in polar bird species. This table is representative rather than exhaustive. Contaminants examined include Hg, and organohalogen compounds (OHCs) such as polybrominated diphenyl ethers (PBDEs), per- and poly-fluoroalkyl substances (PFASs), and legacy POPs which include polychlorinated biphenyls (PCBs), organochlorines (OCs). Hormones examined include prolactin (PRL), thyroid hormones (THs), corticosterone (CORT) and luteinizing hormone (LH). Because reproductive hormones are often inter-correlated, relationships with one hormone often imply a relationship with other (potentially unmeasured) hormones; it is not necessary to measure all hormone groups.

Species	Contaminant	Effect	Source
Glaucous gull	PCBs	Decreased nest attentiveness	Bustnes et al. (2005), 2001
Glaucous gull	OCs	Later lay date, reduced second chick size	Bustnes et al. (2003)
Great black-backed gull	PCBs	Later lay date, higher predation rate, Smaller egg size	Helberg et al. (2005)
Glaucous gull	PCBs	Lower THs	Verreault et al. (2004)
Glaucous gull	PCBs	Higher progesterone in males	Verreault et al. (2006)
Glaucous gull	OHCs	Tendency for lower PRL	Verreault et al. (2008)
Glaucous gull	PCBs	Lower nest temperature	Verboven et al. (2009)
Glaucous gull	PCBs/PBDEs	Higher baseline CORT	Verboven et al. (2010)
Black-legged kittiwake	PCBs	Higher baseline CORT (pre-laying)	Verboven et al. (2010)
Black-legged kittiwake	PFAS	Higher TT4	Nøst et al. (2012)
Northern fulmar	PFAS	Higher TT4	Nøst et al. (2012)
Snow petrel	Legacy POPs	Higher baseline CORT	Tartu et al. (2015)
Snow petrel	Hg	Higher baseline PRL	Tartu et al. (2015)
Black-legged kittiwake	Hg	Higher LH and skipped breeding	Tartu et al. (2013)
Black-legged kittiwake	Hg	Skipped breeding	Tartu et al. (2013)
Black-legged kittiwake	Legacy POPs	Increased CORT	Tartu et al. (2014)
Black-legged kittiwake	Hg	Reduced PRL and breeding success	Tartu et al. (2016)
Black-legged kittiwake	OCs	Lower TT3 and reduced metabolic rate	Blévin et al. (2017)
Black-legged kittiwake	PFASs	Higher metabolic rate	Blévin et al. (2017)
Glaucous gull	OCs	Lower THs	Melnes et al. (2017)
Glaucous gull	PFAS	Higher FT3	Melnes et al. (2017)
Black-legged kittiwake	OCs	Lower temperature incubation and hatching success	Blévin et al. (2018)
Black-legged kittiwake	PFAS	Higher baseline PRL and nest attendance	Blévin et al. (2020)
Black-legged kittiwake	PCBs	Decreased egg-turning behaviour	Blévin et al. (2020)

behaviours, such as nest attentiveness, lay date and chick feeding rates (Table 1). It is often assumed that changes in these behaviours are associated with fitness. However, there is growing awareness that rather than being directly associated linearly with the behaviours themselves, fitness can be associated with plasticity of these behaviours, which can be linked to hormone systems (Charmantier and Blondel, 2003; Reed et al., 2011). That is, flexibility in behaviour is regulated by hormones that allow individuals to deal with environmental modifications, such as varying sea-ice conditions as a result of climate change. Thyroid hormones (TH), specifically triiodothyronine (T3) and thyroxine (T4), are involved in the regulation of whole animal oxygen consumption rate, tissue oxygen consumption and thermoregulation (McNabb, 2000; Elliott et al., 2013). Since metabolic rate limits dive duration in any breath-hold diver, T3 may also mediate the duration of diving when seabirds forage (Elliott et al., 2015a). Therefore, T3 may be a physiological mechanism for organisms to adjust their behavioural to sea-ice availability, via increased time spent foraging underwater (Elliott et al., 2015a).

Modification of circulating thyroid and glucocorticoid hormones were reportedly associated with the exposure of Arctic biota to environmental contaminants, including Hg and organochlorines (Table 1) (Dietz et al., 2019). Circulating T3 was negatively associated with polychlorinated biphenyls (PCBs) and polybrominated diphenyl ethers (PBDEs) (Svendensen et al., 2018), and similarly, T3 and metabolic rate were negatively associated with chlordanes but not Hg (Blévin et al., 2017), in adult black-legged kittiwakes (*Rissa tridactyla*). In glaucous gulls (*Larus hyperboreus*), THs were negatively associated with concentrations of PCBs (Verreault et al., 2004); moreover, PCBs, *p*, *p'*-dichlorodiphenyltrichloroethane (DDT), chlordane and metabolites, were negatively associated with basal metabolic rate (Verreault et al., 2007). Environmental contaminants have also modified corticosterone (CORT), a hormone that triggers physiological and behavioural adjustments in response to stress (Angelier and Wingfield, 2013). Previous studies reported a negative association between Hg and baseline CORT that was correlated with the late arrival at breeding colonies of eider ducks (*Somateria mollissima borealis*) (Provencher et al., 2016). In snow petrels (*Pagodroma nivea*), high POP concentrations were positively related to stress-induced CORT levels, indicating a higher adrenocortical response to acute stress in the most contaminated birds (Tartu et al., 2015).

The thick-billed murre (*Uria lomvia*) is a deep-diving, long-lived seabird that is widely distributed in the Arctic. It relies heavily on sea-ice when foraging and is sensitive to changes in environmental conditions such as temperature and sea-ice conditions (Irons et al., 2008). For the past three decades, sea-ice breakup has occurred increasingly earlier in Hudson Bay (Gagnon and Gough, 2005), affecting several behavioural traits of the murre breeding at Coats Island in Hudson Bay. Melting sea-ice has advanced more rapidly than murre are able to respond, creating a mismatch between chick-rearing and the time of peak food availability that has adversely affected adult body mass and growth rates in relation to the decline in summer ice cover (Gaston et al., 2005, 2009).

In this study, our overall objective was to examine the interactive effects of sea-ice conditions and contaminants on the physiology and behaviour of thick-billed murre, by: 1) determining their exposure to Hg, PCBs, organochlorine (OC) pesticides, PBDEs and other brominated flame retardants (BFRs); 2) characterizing circulating THs and CORT, as well as 3) foraging behaviours, in breeding thick-billed murre. We hypothesized that because of the relatively high Hg concentrations compared to the other measured contaminants, Hg will disrupt behavioural plasticity in response to changes in ice conditions by altering hormone levels. To evaluate potential endocrine disruption, we first determined possible relationships between hormones (i.e., circulating THs, CORT) and measured contaminants (i.e., Hg, PCBs, OC pesticides, PBDEs and other BFRs), and then broadened that approach to investigate all potential relationships among the measured circulating

contaminants (i.e., Hg, PCBs, OC pesticides, PBDEs and other BFRs), circulating hormones (i.e., T3, T4, CORT), and foraging behaviours (e.g., flying, swimming, diving) of the murres. We predicted that high circulating Hg concentrations would impair thyroid and corticosterone levels of the birds, and in turn, this would decrease their foraging plasticity.

2. Materials and methods

Sea-ice Conditions: We used a previous methodology (Gaston et al., 2005, 2009) to assess and classify annual sea-ice conditions. For each year of our study (2016–2018), we determined the date when Hudson Bay had 50% sea-ice coverage remaining, and compared that date to the 50-year average date, i.e., the first week of July (1971–2021; Canadian Ice Service), to classify the annual start of sea-ice melting and sea-ice conditions, henceforth referred to as sea-ice breakup.

Field data collection: All bird handling protocols in this research were approved by the Animal Care Committee of McGill University and conducted with appropriate permits from Environment and Climate Change Canada (Banding Permit 10,892, Scientific Permit NUN-SCI-16-03) and the Government of Nunavut (Nunavut Wildlife Research Permits, 2016–036, 2017–025, and 2018–021). Adult breeding thick-billed murres were sampled during incubation (2016, 2018) and chick rearing (2017, 2018) at a colony of 30,000 individuals on Coats Island, Canada (62°56'52.20"N, 82°01'03.70"W) over three years (2016–2018). Blood samples were collected from 163 adults (2016: n = 38 (♀ = 13, ♂ = 25); 2017: n = 61 (♀ = 26, ♂ = 31, Unknown = 4); 2018: n = 64 (♀ = 10, ♂ = 54)) to assess circulating free (F) and total (T) triiodothyronine (T3), thyroxine (T4), CORT, PCBs, OC pesticides, PBDEs and other BFRs in blood plasma; red blood cells were used to determine Hg levels and to genetically sex the individual birds. Blood (4 mL; 1 mL before and 3 mL after each foraging trip) was collected from the alar vein within 3 min post-capture, using 3 mL heparinized syringes with a 25-gauge needle. The samples were stored in heparinized vacutainers on ice and centrifuged (2000 g) for 10 min within ~3 h of collection. The resulting plasma and red blood cells were aliquotted for each bird, and immediately transferred to a dry shipper (–150 °C) for field storage and transportation to the National Wildlife Research Center (NWRC, Ottawa, Ontario), where they were maintained at –80 °C until laboratory analysis.

Behaviours: GPS-accelerometers (18 g, AxyTrek, TechnoSmart Europe) were deployed on the same individual birds (N = 163) by attaching the device to the dorsal feathers using tesa tape (TESA 4651, Hamburg, Germany). The loggers were programmed to record GPS locations every 1–3 min, depth measurements at 1 s intervals, and tri-axial acceleration at 25 Hz for 1–5 days. We retrieved the devices when recapturing the individual bird, obtaining complete foraging trips for a

total of 105 birds (2016: n = 15, 2017: n = 31, 2018: n = 59). Sample sizes further varied as a function of having birds with complete foraging behaviours and sufficient blood samples to measure all targeted endocrine and contaminant parameters (Table 2). First, we classified the GPS-accelerometer data for all individuals into four behavioural categories (i.e., diving, flying, swimming, and on colony) using hidden Markov models (HMM, *momentuHMM*) (McClintock and Michelot, 2018) with wing beat frequency, pitch, diving, and distance from colony as predictor variables in the HMM (Patterson et al., 2019); a detailed description of this analysis is provided in the Supplementary Material. For each bird, we then calculated the proportion of time it spent performing each behaviour, for each day of deployment (e.g., total time diving/total time of deployment*24), as well as its mean diving depth and mean number of dives per day of deployment. Further details are provided in the Supplementary Material.

Hormone analyses: Plasma FT3, TT3, FT4, TT4, and CORT, were analyzed using commercially available enzyme immunoassay (EIA) kits following the manufacturer’s instructions (TH: Diagnostics Biochem Canada Inc.; CORT: Enzo Life Sciences Inc.). Concentrations of T3 and T4 were quantified using standard curves constructed from serial dilutions of the calibration standard. The method detection limits for the 2016 and 2017 samples were 0.15 pg/mL, 0.08 ng/mL, 0.50 pg/mL and 3.00 ng/mL for FT3, TT3, FT4 and TT4, respectively, while for the 2018 samples, the limits were 0.30 pg/mL (2016: 0.15 pg/mL), 0.08 ng/mL, 0.50 pg/mL and 3.00 ng/mL for FT3, TT3, FT4 and TT4, respectively. Analytical accuracy and precision were assessed using a standard reference material (SRM; human serum-based matrix samples obtained from the Diagnostics Biochem Canada Inc.) and by analyzing duplicate samples. CORT levels were quantified using a standard curve with a detection limit of 27.0 pg/mL (range: 32–20,000 pg/mL). Thyroid hormone analyses were conducted by Laboratory Services at NWRC, and CORT analyses at McGill University. Concentrations are expressed in ng/mL (TT3 and TT4) and pg/mL (FT3, FT4 and CORT).

Contaminant Analysis: For Hg analyses, red blood cells were freeze-dried, weighed into nickel combustion boats and analyzed for total mercury (THg) using a Direct Mercury Analyzer (DMA-80) equipped with an autosampler (details provided in the Supplementary Information (SI)). The detection limits were 0.020 ng for 2016 samples and 0.032 ng for 2017 and 2018 samples. Methylmercury (MeHg) was determined in a subsample of murres (n = 21; 2017: n = 10, 2018: n = 11) that we considered to accurately represent the range of THg concentration values. The mean MeHg concentration corresponded to 91.3% of the mean THg concentration measured in the murres. We used this estimate to calculate MeHg concentrations for all birds (n = 146). All Hg analyses were conducted by Laboratory Services at NWRC. THg and MeHg concentrations are reported in µg/g (dry weight) and were

Table 2

Circulating concentrations of total mercury (THg), methylmercury (MeHg), ∑35PCB (i.e., CB-17/18, –28/31, –33, –44, –49, –52, –70, –74, –87, –95, –99, –101, –105, –110, –118, –128, –138, –149, –151, –153, –156, –158, –170, –171, –177, –180, –183, –187, –194, –195, –205, –206, –208 and –209), *p,p'*-DDE, HCB, and ∑3PBDEs (i.e., BDE-47, -99, –100), as well as free (F) and total (T) triiodothyronine (T3) and thyroxine (T4) and corticosterone (CORT), in thick-billed murres sampled in 2016, 2017 and 2018. n: sample size; DR: detection rate (%); Mean: arithmetic mean; SE: standard error; Min: minimum; Max: maximum. Concentrations are expressed in ng/mL (TT3 and TT4), pg/mL (FT3, FT4 and CORT), µg/g dw (THg and MeHg), ng/g ww (BFRs) and µg/g ww (OC pesticides and PCBs).

	2016						2017						2018					
	n	DR	Mean	SE	Min	Max	n	DR	Mean	SE	Min	Max	n	DR	Mean	SE	Min	Max
THg	38	100	1.68	0.05	1.1	2.74	48	78	1.37	0.04	0.81	2.28	60	93	1.99	0.07	1.03	4.38
MeHg	38	100	1.54	0.05	1	2.5	48	78	1.23	0.04	0.69	2.01	60	93	1.82	0.06	0.94	4
∑35PCB	28	100	0.01	0.001	0.001	0.02	–	–	–	–	–	–	–	–	–	–	–	–
<i>p,p'</i> -DDE	28	100	0.004	0.0003	0.0007	0.01	–	–	–	–	–	–	–	–	–	–	–	–
HCB	28	100	0.004	0.0002	0.003	0.01	–	–	–	–	–	–	–	–	–	–	–	–
∑3PBDE	28	50	0.08	0.02	0	0.46	35	14	0.03	0.01	0	0.36	30	13	0.02	0.01	0	0.15
FT3	34	–	2.09	0.11	1.03	4.12	42	–	2.84	0.24	0.22	7.46	62	–	0.82	0.05	0.26	1.94
TT3	30	–	0.8	0.06	0.33	1.69	40	–	0.8	0.06	0.29	2.14	54	–	3.41	0.21	0.07	7.72
FT4	36	–	9.38	1.69	3.16	66.9	50	–	11.85	0.69	3.25	26.85	58	–	8.27	0.28	4.62	13.45
TT4	36	–	8.1	0.99	0.55	23.65	50	–	16.57	1.27	1.08	43.3	53	–	16.13	0.9	5.06	33.8
CORT	33	–	117.06	10.8	17.17	228.06	33	–	217.56	41.7	0.8	767.08	NA	–	–	–	–	–

measured in all three years of the study.

Concentrations of PCBs, OC pesticides, BFRs and PBDEs were determined in plasma from a subsample of birds ($n = 28$ in 2016 only) by Laboratory Services at NWRC. Plasma concentrations were screened for 35 PCB congeners, i.e., CB-17/18, -28/31, -33, -44, -49, -52, -70, -74, -87, -95, -99, -101, -105, -110, -118, -128, -138, -149, -151, -153, -156, -158, -170, -171, -177, -180, -183, -187, -194, -195, -199, -205, -206, -208, and -209. In addition, plasma concentrations were determined for the following 20 OC pesticides: 1,2,4,5-tetrachlorobenzene, 1,2,3,4-tetrachlorobenzene, pentachlorobenzene, hexachlorobenzene (HCB), α -, β - and γ -hexachlorocyclohexane, octachlorostyrene, heptachlor epoxide, oxy-chlordane, *trans*- and *cis*-chlordane, *trans*- and *cis*-nonachlor, *p,p'*-DDT, *p,p'*-DDE, *p,p'*-DDD, dieldrin, photomirex, and mirex. Plasma concentrations were also determined for 22 BFRs, including polybrominated diphenyl ethers (PBDEs) BDE-17, -28, -47, -49, -66, -85, -99, -100, -138, -153, -183, -190, -209, and BDE-154/BB-153, as well as 1,2-bis-(2,4,6-tribromophenoxy) ethane (BTBPE), hexabromobenzene (HBB), Dechlorane Plus (*syn*-DCC-CO and *anti*-DCC-CO; formerly DP), tetrabromoethylcyclohexane (α -DBE-DBCH, β -DBE-DBCH/BDE15), hexabromocyclododecane (HBCDD), and brominated biphenyl (BB101). Briefly, plasma samples were extracted and cleaned following previously described methods (Chen et al., 2012; Lazar et al., 1992) with some modifications, then analyzed by gas chromatography with a mass selective detector (Agilent Technologies) (details in SI) (Braune et al., 2019).

For quality assurance, the NIST Standard Reference Material® 1947 (Lake Michigan fish tissue) was analyzed with each batch of samples. The detection limits (MDL) were $\leq 0.0037 \mu\text{g/g ww}$ for PCBs; $\leq 0.012 \mu\text{g/g ww}$ for OC pesticides; $\leq 0.47 \text{ ng/g ww}$ for BFRs excluding PBDEs; $\leq 0.77 \text{ ng/g ww}$ for PBDEs. The reporting limits (MRL) were $\leq 0.011 \mu\text{g/g ww}$ for PCBs; $\leq 0.004 \mu\text{g/g ww}$ for OC pesticides; $\leq 1.40 \text{ ng/g ww}$ for BFRs excluding PBDEs; and $\leq 0.232 \text{ ng/g ww}$ for PBDEs. Results are recovery and blank corrected. Concentrations of PCBs and OC pesticides are expressed in $\mu\text{g/g wet weight (ww)}$, and BFRs and PBDEs in ng/g ww .

Statistical analyses: The Shapiro-Wilk test and visual plots from the *performance* package were used to assess the normality of residuals (Lüdecke et al., 2021). One-way analysis of variance (ANOVA) tests were used to examine inter-annual differences in THg and MeHg concentrations, and Kruskal-Wallis and Wilcoxon signed rank tests to examine possible inter-annual differences in each hormone and foraging behaviour. A Kruskal-Wallis test was also used to identify possible differences among MeHg, PCBs, OC pesticides, BFRs and PBDEs, available for 2016 only. Given the very low circulating concentrations of PCB congeners, OC pesticides, BFRs and PBDEs, measured in the murrelets (Table 2; Table S1), only MeHg concentrations were used in the linear and generalized models. Linear models (LM) were used to examine whether TH and CORT concentrations changed as a function of MeHg concentrations, and whether foraging behaviours (i.e., diving, swimming, flying and diving depth) changed as a function of measured hormone levels using the *lme4* (Bates et al., 2015) and *lmerTest* package (Kuznetsova et al., 2017). We fitted an independent model for each of the circulating hormones for each year sampled. Data for THg, MeHg, and hormones (TT3, FT3 and FT4) levels were log-transformed for the hormone models, while THg, MeHg and all foraging behaviours were log-transformed for the foraging analyses. Generalized linear models (GLM) with a poisson distribution were used to evaluate the relationships between measured hormone levels and the number of dives per day of deployment. These models included hormone level, year, the interaction between hormone level and year as well as duration of deployment as an offset (Zuur et al., 2009). We fitted an independent model for each of the circulating hormones sampled. Finally, we ran a path analysis using the *lavaan* package (Rosseel et al., 2021) to identify possible causal relationships among the measured contaminants (i.e., MeHg, 35 PCB congeners, HCB, *p,p'*-DDE, BDE-47, -99, -100), circulating hormones

(TT3, TT4, CORT) and foraging behaviours of the birds (i.e., total time diving, flying, swimming, number of dives and diving depth). Models were then repeated with THg substituted for MeHg. All statistical analyses were conducted in R (v.4.0.2, R Development Core) (R Core Team, 2020) and significance was considered at $p \leq 0.05$.

3. Results

3.1. Sea-ice conditions

Compared to the 50-year average when there was 50% sea-ice coverage remaining in Hudson Bay (i.e., the first week of July), sea-ice breakup was earlier in 2016 (June 25th), the earliest on record in 2017 (June 18th), but consistent with the 50-year average in 2018 (July 2nd).

3.2. Circulating contaminants

PCBs were detected in 100% of the murrelets sampled in 2016; the most commonly measured circulating PCB congeners were CB-28/31, -74, -105, -118, -138, -153, -187, and 35 PCB congeners accounted for $>99\%$ of the sum (Σ) PCB concentrations. The $\Sigma 35\text{PCB}$ concentrations ranged from 0.0006 to 0.02 $\mu\text{g/g ww}$ (Table S2). Concentrations of OC pesticides primarily consisted of HCB (100%; $0.004 \pm 0.0002 \text{ ng/g ww}$) and *p,p'*-DDE (100%; $0.004 \pm 0.0003 \text{ ng/g ww}$), with all of the remaining measured OC pesticides not detected or having low detection rates and concentrations (Table S2). In contrast, only 24% of the murrelets had detectable and very low concentrations of $\Sigma 3\text{PBDEs}$ (0.05–0.46 ng/g ww) consisting of BDE-47, -99, -100, with extremely low or no detectable circulating concentrations of BDE-153 or replacement BFRs (Table 2; Table S2). THg, detected in 78–100% of the birds each year, consisted primarily of MeHg (91.3%). In 2016, MeHg was significantly higher than the concentrations of measured PCBs, OC pesticides, PBDE congeners or other BFRs ($\chi^2 = 64.18$; $p < 0.0001$). There were significant inter-annual differences in MeHg ($F_{2,143} = 38.8$, $p < 0.0001$) and THg ($F_{2,143} = 36.11$, $p < 0.0001$), with the lowest concentrations occurring in 2017 and the highest concentrations in 2018 (Table 2).

3.3. Annual variation in hormones

Circulating concentrations of THs and CORT measured in the breeding murrelets are presented in Table 2, and their range of TT3 concentrations (0.07–7.72 ng/mL) is consistent with that in previous murrelets also incubating eggs on Coats Island (0.04–9.6 ng/mL) (Elliott et al., 2015b). Circulating TT3 concentrations were similar in 2016 and 2017 ($\chi^2 = 0.24$, $p = 0.63$) but were higher in 2018 (vs. 2016: $\chi^2 = 47.85$, $p < 0.001$; 2017: $\chi^2 = 55.94$, $p < 0.001$). Circulating FT3 was highest in 2017 (vs. 2016: $\chi^2 = 6.31$, $p = 0.01$; 2018: $\chi^2 = 51.30$, $p < 0.001$) and lowest in 2018 (vs. 2016: $\chi^2 = 56.77$, $p < 0.001$). Similarly, FT4 levels were higher in 2017 (vs. 2016: $\chi^2 = 16.01$, $p = 0.01$; 2018: $\chi^2 = 20.15$, $p < 0.001$) but comparable between 2016 and 2018 ($\chi^2 = 1.62$, $p = 0.20$). Circulating TT4 was lower in 2016 than 2017 ($\chi^2 = 18.85$, $p < 0.001$) and 2018 ($\chi^2 = 24.91$, $p < 0.001$), but similar between 2017 and 2018 ($\chi^2 = 0.004$, $p = 0.95$). CORT was statistically similar in 2016 and 2017 ($\chi^2 = 0.22$, $p = 0.64$); CORT was not measured in 2018.

3.4. Relationships between mercury and hormones

Circulating MeHg was correlated with circulating TT3 in 2016 and 2017, but not in 2018. In 2016, TT3 levels increased with MeHg concentrations ($\beta \pm \text{SE} = 1.05 \pm 0.37$, $p = 0.008$) (Fig. 1A). In contrast, in 2017, TT3 levels decreased with MeHg concentrations ($\beta \pm \text{SE} = -0.87 \pm 0.29$, $p = 0.005$) (Fig. 1B), but the relationship was not significant in 2018 ($\beta \pm \text{SE} = -0.23 \pm 0.45$, $p = 0.61$) (Fig. 1C). Similarly, FT3 levels were negatively correlated with MeHg in 2017 ($\beta \pm \text{SE} = -1.00 \pm 0.45$, $p = 0.03$) but not in 2016 ($\beta \pm \text{SE} = 0.16 \pm 0.38$, $p = 0.67$) or 2018 ($\beta \pm$

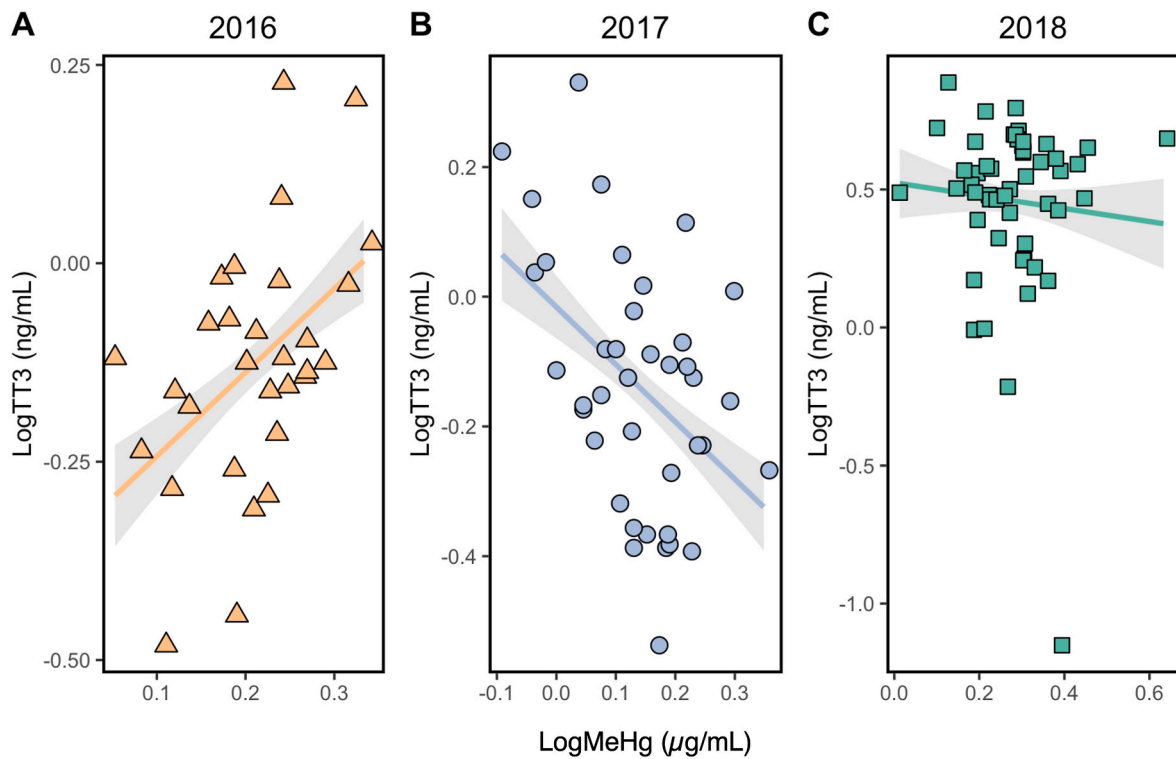


Fig. 1. TT3 levels as a function of MeHg concentrations in the thick-billed murres in A) 2016 (n = 30), B) 2017 (n = 39) and C) 2018 (n = 51). Lines indicate model predictions and the shaded areas represent the standard errors.

SE = -0.21 ± 0.27 , $p = 0.44$) (Table S3).

3.5. Annual variation in foraging behaviours

When foraging, murres spent an average of 2.3 ± 0.1 h diving each day, performed 4.54 ± 0.18 dives per day, and dove to a mean depth of 26.85 ± 1.40 m (Table 3). The proportion of time spent diving significantly differed among years (2016 vs 2017: $\chi^2 = 11.34$, $p < 0.001$; 2016 vs 2018: $\chi^2 = 10.71$, $p < 0.001$; 2017 vs 2018: $\chi^2 = 5.47$, $p = 0.02$), with the birds spending the least time underwater in 2016 (1.54 ± 0.15 h/day) and the most time underwater in 2017 (2.88 ± 0.15 h/day). The murres performed significantly fewer dives per day in 2016 (3.29 ± 0.37 dives/day) than 2018 (4.68 ± 0.23 dives/day) ($\chi^2 = 5.90$, $p = 0.02$), but daily diving rates were similar in 2016 and 2017 ($\chi^2 = 3.40$, $p = 0.06$) and in 2017 and 2018 ($\chi^2 = 2.67$, $p = 0.10$). The murres foraged in shallower waters in 2016 (18.20 ± 2.70 m), deeper waters in 2017 (35.85 ± 3.08 m), and at an intermediate depth in 2018 (24.4 ± 1.3 m): the mean depth that birds dove to was significantly shallower in 2016 than 2017 ($\chi^2 = 11.34$, $p < 0.001$) and deeper in 2017 than 2018 ($\chi^2 = 14.05$, $p < 0.001$), but similar between 2016 and 2018 ($\chi^2 = 2.74$, $p = 0.09$) (Table 3).

Table 3

Summary of the foraging behaviours recorded for the murres from 2016 to 2018. Diving: proportion of time diving (hr/d); Flying: proportion of time flying (hr/d); Swimming: proportion of time swimming (hr/d); Diving depth: average diving depth (m); dives: total number of dives per deployment; n: sample size; Mean: mean; SE: standard error about the mean; Min: minimum; Max: maximum; and p: p value of the Wilcoxon test (2016: difference between 2016 and 2017; 2017: difference between 2017 and 2018; and 2018: difference between 2016 and 2018). Significant relationships are identified in bold font.

	2016						2017						2018					
	n	Mean	SE	Min	Max	p	n	Mean	SE	Min	Max	p	n	Mean	SE	Min	Max	p
Diving	16	1.54	0.15	0.03	2.59	0.001	31	2.88	0.23	0.84	5.14	0.02	59	2.23	0.09	1.05	3.65	0.001
Flying	16	1.16	0.19	0.33	3.77	0.002	31	1.99	0.16	0.22	3.77	0.0002	59	1.31	0.07	0.37	2.91	0.09
Swimming	16	8.80	0.91	4.75	18.63	0.36	31	7.70	0.57	3.64	19.32	0.07	59	8.13	0.29	3.20	14.71	0.91
Diving depth	9	18.19	2.69	8.89	36.47	0.001	31	35.85	3.08	13.09	80.02	0.0002	59	23.43	1.30	9.10	53.72	0.10
Number of Dives	9	3.29	0.37	2.92	5.84	0.06	31	4.63	0.35	1.60	8.66	0.10	59	4.68	0.23	2.04	8.49	0.02

3.6. Relationship between hormones and foraging behaviours

Circulating TT3 was associated with foraging behaviours of the murres. Higher levels of TT3 were associated with a lower proportion of time spent diving in 2016 ($\beta \pm SE = -1.25 \pm 0.24$, $p = 0.0004$) and 2017 ($\beta \pm SE = -0.35 \pm 0.14$, $p = 0.024$), but not in 2018 ($\beta \pm SE = 0.00005 \pm 0.01$, $p = 0.99$) (Fig. 2). When two statistical outliers were removed, this relationship was no longer significant in 2016 ($\beta \pm SE = -0.30 \pm 0.17$, $p = 0.13$), potentially because of the small sample size (n = 11). However, given that the effect size and slope were similar with and without these two outliers, we considered this relationship between TT3 and time spent diving to be representative in 2016 and 2017. As with TT3, FT3 was significantly correlated with the proportion of time that the murres spent diving, but only in 2017 ($\beta \pm SE = -0.35 \pm 0.14$, $p = 0.02$). There were no other significant associations between measured circulating hormones and the proportion of time spent diving, flying or swimming, or with the number or depth of the dives (Table S4).

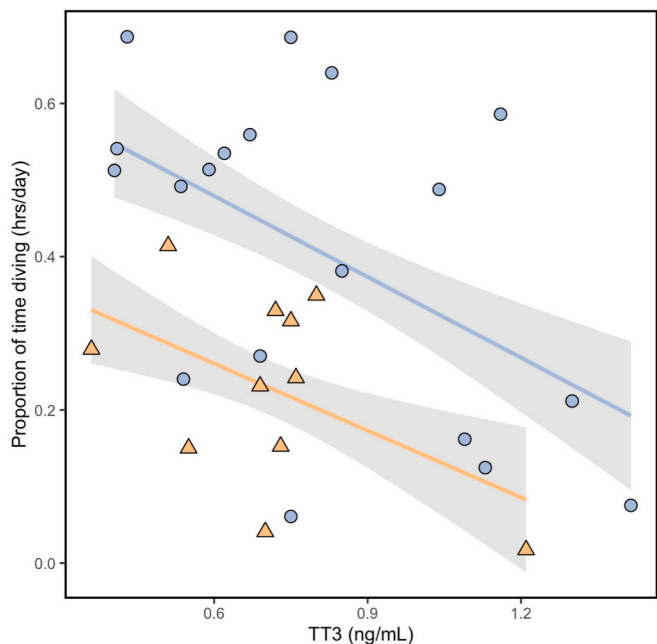


Fig. 2. Time spent diving declined with increasing TT3 for thick-billed murres at Coats Island in 2016 (n = 12; orange triangles) and in 2017 (n = 19; blue circles) but not in 2018 (data not shown). Lines indicate model predictions and the shaded areas represent standard errors. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.7. Path analysis: Relationships among contaminants, Hormones and foraging behaviours

Of all of the measured contaminants having possible causal effects on THs and/or CORT, only MeHg had a significant direct effect on circulating TT3, but not TT4 or CORT (Fig. 3). In turn, of all the measured hormones, only circulating TT3 concentrations had a significant direct behavioural effect, and only on the proportion of time spent diving by the birds. The significant direct relationships with MeHg, TT3 and time spent diving, were evident in 2016 and 2017, but not 2018 (Fig. 3), reflecting the pattern of results of the previous linear models: MeHg was significantly correlated with TT3 in 2016 and 2017 but not 2018, and TT3 was significantly correlated with time spent diving by the birds in 2016 and 2017 but not 2018. When the models were repeated with THg, the results were consistent with those reported here for MeHg; we report only the MeHg results because of the known toxicity of MeHg.

4. Discussion

In the present study, 50% of sea-ice coverage across Hudson Bay, henceforth referred to as sea-ice breakup, occurred 1–2 weeks earlier in 2016 and 2017, but occurred during the first week of 2018, the same as the 50-year mean date for Hudson Bay. Indeed, 2017 was the earliest year on record. Circulating Hg in breeding thick-billed murres exceeded concentrations of $\sum 35$ PCBs, *p,p'*-DDE, HCB, and $\sum 3$ PBDEs in 2016, and all other measured OC pesticides and BFRs were largely undetected or had very low concentrations. Across the three years of study (2016–2018), inter-annual differences were evident in sea-ice coverage (i.e., sea-ice breakup) available for foraging by the murres that concurrently experienced annual differences in their diving behaviours.

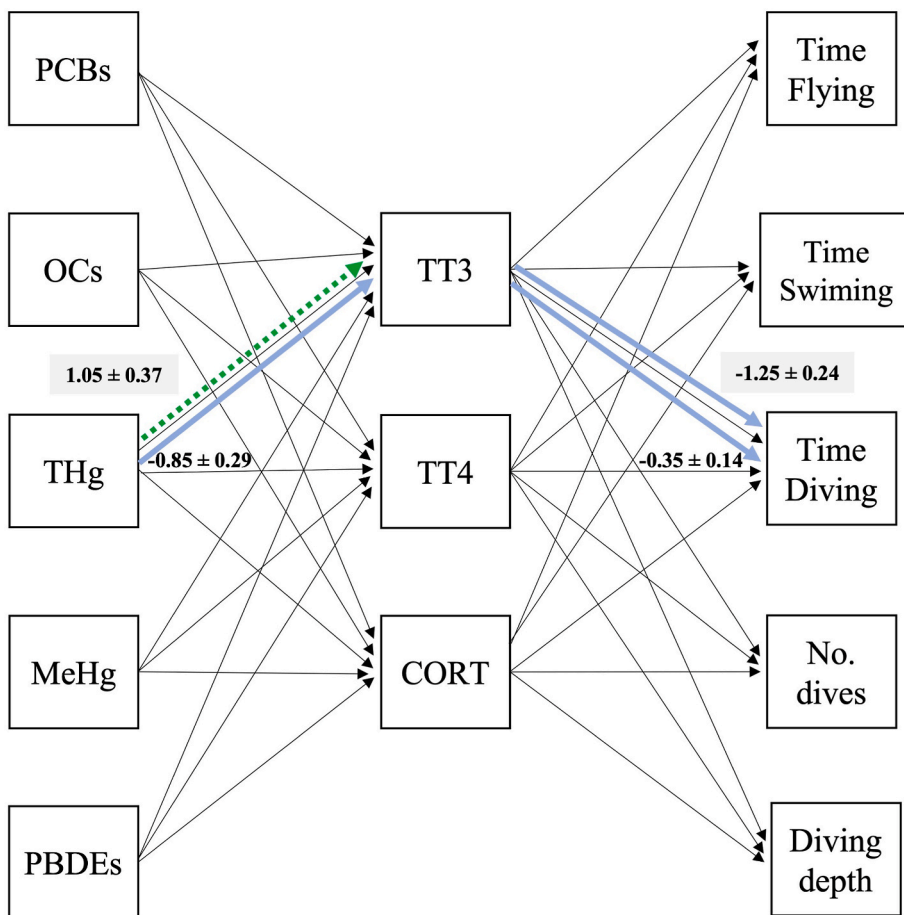


Fig. 3. Path analysis showing interactions among the most frequently detected measured contaminant groups, hormones, and behaviours evaluated in breeding thick-billed murres in 2016, 2017 and 2018. Significant interactions occurred in 2016 and 2017, but not 2018, and are shown with colored arrows only; positive interactions are indicated with a dashed line and negative interactions with a solid line. Path estimates ($\beta \pm SE$) are given for each significant path for 2016 (gray squares) and 2017 (white squares). Interactions shown for five types of chemical contaminants (PCBs, OC pesticides, MeHg, PBDEs and other BFRs); thyroid (TT3 and TT4) and corticosterone (CORT) hormones; and five foraging behaviours (time spent flying, swimming and diving, number [No.] of dives and diving depth).

The birds also exhibited strong inter-annual patterns in circulating THs, particularly TT3, and circulating Hg, with relationships varying annually among Hg, TT3 and foraging behaviours. Based on the statistical outcomes of the path analysis identifying possible relationships among all parameters measured in the birds (i.e., environmental pollutants, hormones, foraging behaviours), it appears that the birds' uptake of MeHg was influencing circulating TT3, that in turn was influencing the amount of time diving underwater when foraging; these interrelated patterns occurred in 2016 and 2017, when sea-ice break-up was earlier than the 50-year average for Hudson Bay. Thus, relationships between MeHg, hormones and foraging were only apparent when birds were already stressed by climate change.

The contaminant profile of the present murres was dominated by circulating MeHg, followed by Σ 35PCBs, *p,p'*-DDE, HCB, at very low levels, and then BDE-47, BDE-100 and BDE-99. All of the other contaminants measured in the blood of these murres had low detection rates and very low concentrations. The profile and low levels of POPs in the murres is consistent with previous results for other Arctic birds (Braune et al., 2019; Letcher et al., 2010; Rig  t et al., 2019), and in part, reflects the sampling of the murres after egg-laying was completed (i.e., maternal transfer). Nevertheless, circulating THg concentrations ($5.82 \pm 2 \mu\text{g/g ww}$) in the present murres were much higher than previously reported for this species ($0.12 \pm 0.01 \mu\text{g/g ww}$) (Ackerman et al., 2016), and indeed were similar to or exceeded the estimated lethal concentration of MeHg for this species (LC_{50} : $1.2 \mu\text{g/g ww}$ blood equivalent) (Ackerman et al., 2016; Braune et al., 2012) in each year of the present study (discussed later). The uniformly low OC pesticide blood concentrations in the present thick-billed murres is consistent with the temporal decline of OC pesticides reported in other seabirds breeding in the Canadian Arctic (Braune et al., 2015). The plasma concentrations of *p,p'*-DDE ($0.004 \pm 0.0003 \text{ ng/g ww}$) and HCB ($0.004 \pm 0.0002 \text{ ng/g ww}$), the only measurable OC pesticides in the present murres, were considerably lower than those reported in the plasma of ivory gulls (*Pagophila eburnea*) (*p,p'*-DDE: $303 \pm 38.9 \text{ ng/g ww}$; HCB: $7.94 \pm 0.56 \text{ ng/g ww}$) (Lucia et al., 2017) or whole blood of black-legged kittiwakes (*p,p'*-DDE: $3.74 \pm 2.27 \text{ ng/g ww}$; HCB: $2.22 \pm 0.89 \text{ ng/g ww}$) (Goutte et al., 2015) in the Norwegian Arctic. The differences in circulating *p,p'*-DDE and HCB levels among the three species reflect their breeding status when sampled: the murres had completed egg laying whereas the ivory gulls and kittiwakes were sampled prior to egg laying. BFR concentrations were also low (Σ 3PBDE: $0.11 \pm 0.03 \text{ ng/g ww}$) in the present murres, but similar to concentrations in other Arctic seabirds including the northern fulmar (*Fulmarus glacialis*) ($0.17 \pm 0.22 \text{ ng/g ww}$) and the black-legged kittiwake ($0.09 \pm 0.04 \text{ ng/g ww}$) (N  st et al., 2012). Based on a large body of evidence, we strongly suspect that the very low concentrations of *p,p'*-DDE and HCB (Letcher et al., 2010), or PBDEs and replacement BFRs (Guigueno and Fernie, 2017), were unlikely to influence circulating hormones or behaviour of the murres.

4.1. Inter-annual variation in hormones: environmental variables and contaminants

Variations in environmental factors (e.g., habitat, weather, food) are known to influence circulating THs and CORT in wildlife so as to elicit appropriate physiological (e.g., thermoregulation, metabolism) and behavioural responses. Kokubun et al. (2018) reported that thick-billed murres from the southeastern Bering Sea had higher circulating CORT in cold years than in warm years that they concluded reflected greater nutritional stress. In our study, we suggest that the earlier sea-ice breakup in 2016 and 2017, presumably reflecting warmer conditions than average, may partially explain the similarity in CORT of the present murres between these two years; CORT was not measured in 2018 when the break up of sea-ice occurred during the first week of July, the norm for the past 50 years in Hudson Bay.

Exposure to environmental contaminants at sufficient concentrations can also disrupt endocrine systems essential for adaptation to

environmental variation, including the thyroid system (McNabb, 2007; N  st et al., 2012; Tan et al., 2009). Mean blood MeHg in the present murres in 2016 ($0.59 \mu\text{g/g ww}$), 2017 ($0.46 \mu\text{g/g ww}$) and 2018 ($0.67 \mu\text{g/g ww}$), exceeded the threshold for sub-lethal adverse effects of Hg in birds (e.g., 400 ppb ww or $0.4 \mu\text{g/g ww}$) (Wada et al., 2009), and as stated above, was substantially lower than the estimated lethal concentration of MeHg for murres (LC_{50} : $1.2 \mu\text{g/g ww}$ blood equivalent) (Ackerman et al., 2016; Braune et al., 2012). In the present murres, blood MeHg concentrations were correlated with circulating TT3 in 2016, 2017, but not 2018, consistent with the findings of an earlier study in which circulating THs were suppressed in tree swallows (*Tachycineta bicolor*) having elevated blood Hg concentrations ($354 \pm 22 \text{ ppb ww}$) (Wada et al., 2009). The lack of correlation with MeHg and CORT in the murres is consistent with some (Tartu et al., 2016, 2015; Wada et al., 2009) but not all studies (Franceschini et al., 2009; Herring et al., 2012; Provencher et al., 2016) with free-ranging birds.

The correlations of blood MeHg and circulating TT3 in the present thick-billed murres provides further evidence that Hg may be associated with thyroid function in birds, but other environmental factors may have also influenced their TH concentrations. In the present study, circulating TT3 was similar in 2016 and 2017, but significantly lower in 2018; circulating TT3 was associated with blood MeHg in 2016 and 2017, but not 2018. In 2016 and 2017, 50% of sea-ice coverage of Hudson Bay had melted earlier in the breeding season than the 50-year average, arguably resulting in less optimal foraging habitat for murres that are strongly pagophilic (associated with sea-ice). In contrast, sea-ice breakup in the 2018 breeding season was consistent with the long-term average, potentially providing more optimal sea-ice conditions for the birds that foraged closer to the breeding colony (K. Elliott, unpubl. data) than in the previous two years of study. Further research is needed to better inform on the interactive/synergistic effects of reduced habitat quality, Hg, and thyroid function in Arctic seabirds and other biota in conjunction with variations in climate.

4.2. Foraging behaviours and thyroid hormones

Annual differences in foraging behaviours were also observed in the present study. In years when sea-ice breakup was earlier (2016, 2017), the foraging behaviour of the murres was considerably different, spending less (2016) or more (2017) time underwater, performing fewer dives per day (2016), or performing shallower (2016) or deeper (2017) dives, than under sea-ice conditions in 2018 that were consistent with the long-term average for Hudson Bay. The murres spent more time underwater and performed deeper dives when the sea-ice broke up earlier (2017) than the long-term average for Hudson Bay. Arctic cod (*Boreogadus saida*), a species that requires cold sea temperatures and was a main prey species of murres (Gaston and Elliott, 2014; Braune et al., 2014), has declined in the diet of murres at Hudson Bay, as was recently predicted to be linked with variation in sea-ice cover and temperatures (Huserbr  ten et al., 2019). For black guillemots, dive duration and diving depth increased in relation to sea-surface temperature and Arctic cod availability (Divoky et al., 2021), while in little auks, diving depth increased, but time underwater decreased, with sea-ice loss (Am  lineau et al., 2019). We hypothesize that with the earlier ice breakup observed in 2017 in our study, and concurrent warmer sea temperatures with suspected reduced availability of Arctic cod, resulted in murres modifying their diving and foraging behaviors to capture Arctic cod and other prey; the availability of Arctic cod governs dive duration (i.e., underwater search time) in thick-billed murres (Elliott et al., 2008).

Foraging behaviours, notably diving behaviours, and circulating T3 were associated in the present murres. In 2016 and 2017, the time spent underwater by the murres was negatively correlated with circulating TT3 concentrations: birds with higher TT3 levels spent less time diving underwater (Fig. 2). T3 appears to be an important influence on the duration and depth of diving by birds, and extending time underwater is key to increasing foraging time in diving animals, such as murres, that

exclusively capture prey at depth. Circulating T3 is associated with resting metabolic rate that facilitates thermoregulation (Elliott et al., 2013; McNabb, 2007; Welcker et al., 2013). In warm waters, high T3 concentrations may reduce dive duration by increasing oxygen consumption during dives (i.e., metabolic rate) (Elliott et al., 2015a), reflecting the observed association of higher TT3 and reduced dive duration in 2016 and 2017 when sea-ice breakup occurred earlier and sea temperatures were warmer. In comparatively colder waters, such as may have occurred with the more typical recession of sea-ice in 2018, higher circulating T3 levels (such as occurred in 2018) may increase dive duration by improving thermoregulation, consistent with the lack of T3-diving relationship in 2018 (McNabb, 2007). Since T3 has an important role in diving metabolic homeostasis, regulating and maintaining diving rates, there is potential for environmental contaminants to further influence these parameters via modifications of T3. Young Galliforme birds demonstrated changes in thyroid function that were consistent with changes in their resting metabolic rate and growth when exposed to an organophosphate FR (Guigueno et al., 2019). Future studies should consider including resting metabolic rate and oxygen consumption to further explore the relationships between MeHg, T3 and dive duration in Arctic seabirds.

4.3. Contaminants, thyroid hormones, foraging/diving behaviours: collective considerations

Environmental factors (e.g., varying climate, habitat quality, prey availability, exposure to contaminants) influence endocrine systems, physiology, and behaviours of wildlife in a complex network of interactions. For the present thick-billed murres, out of ~20 possible interactions investigated among MeHg, hormones and foraging behaviours, only MeHg influenced circulating TT3, and in turn, TT3 influenced the extent of time the birds searched underwater when diving; these interactions only occurred when sea-ice broke up 1–2 weeks earlier (2016, 2017), and not in more typical ice conditions (2018) of the past 50 years in Hudson Bay. That the MeHg-TT3 interactions were opposing in direction (2016, 2017) suggests the likely influence of additional physiological (e.g., metabolism), ecological (e.g., shifts in diet) and/or environmental (e.g., weather) parameters in this complex ecosystem that were not included in the model, and warrants further research. In the somewhat stressful year (2016), Hg could lead to increased T3 levels by interfering with TSH at the level of the brain. In the more stressful year (2017), systems could be nearer to physiological exhaustion, and Hg could lead to decreased T3. The MeHg-TT3-behaviour (i.e., diving duration) interactions in the path analysis are consistent with the Hg-TT3 and TT3-diving time relationships discussed previously, and collectively highlight the influence of varying sea-ice availability on the physiology and behaviour of pagophilic species like thick-billed murres. When sea-ice breaks up early reducing the availability of sea-ice for foraging (e.g. 2016, 2017), blood MeHg may influence circulating TT3, altering underwater diving time, and conceivably successful foraging for fish, consistent with TT3 increasing metabolism and shortening dive duration as previously observed in this species (Elliott et al., 2015a). The murres' ability to modify dive duration is a key component of plasticity associated with foraging behaviour, and our results may suggest one possible mechanism involved in the adaptability of this pagophilic Arctic seabird to varying climate and sea-ice conditions.

5. Conclusion

Our study explored the ability of thick-billed murres to respond to climate change in relation to environmental contaminants. In 2016 and 2017, sea-ice break-up was markedly earlier in Hudson Bay, and murres concurrently exhibited inter-annual differences in, and direct interactions with circulating MeHg, T3, and their foraging behaviours. When murres were likely already stressed by the early sea-ice breakup

(2016, 2017), MeHg influenced circulating T3 that in turn reduced foraging time underwater. We conclude that when sea-ice breaks up early in the breeding season, Hg may interfere with the ability of murres to adjust their foraging behaviour via modifying T3, in relation to the variations in sea-ice from which the birds forage.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.envres.2022.113190>.

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