General and Comparative Endocrinology 337 (2023) 114261

Contents lists available at ScienceDirect

General and Comparative Endocrinology

journal homepage: www.elsevier.com/locate/ygcen

Research paper

Do foraging ecology and contaminants interactively predict parenting hormone levels in common eider?

Reyd A. Smith [a,*], Jérôme Fort [b], Pierre Legagneux [c,d], Olivier Chastel [d], Mark L. Mallory [e], Paco Bustamante [b,f], Jóhannis Danielsen [g], Sveinn A. Hanssen [h], Jón Einar Jónsson [i], Ellen Magnúsdóttir [i], Børge Moe [j], Charline Parenteau [d], Kyle J.L. Parkinson [a], Glen J. Parsons [k], Grigori Tertitski [l], Oliver P. Love [a]

[a] University of Windsor, Windsor, Ontario N9B 3P4, Canada
[b] Littoral, Environnement et Sociétés (LIENSs), UMR 7266 CNRS – La Rochelle Université, 17000 La Rochelle, France
[c] Université Laval, Département de Biologie and Centre d'Études Nordiques, Québec City, Québec G1V 0A6, Canada
[d] Centre d'Études Biologiques de Chizé, UMR 7372 CNRS-La Rochelle Université, 79360 Villiers-en-Bois, France
[e] Acadia University, Wolfville, Nova Scotia B4P 2R6, Canada
[f] Institut Universitaire de France (IUF), 1 rue Descartes, 75005 Paris, France
[g] Faroe Marine Research Institute, Tórshavn FO-110, Faroe Islands
[h] Norwegian Institute for Nature Research, Sognsveien 68, N-0855 Oslo, Norway
[i] University of Iceland's Research Centre at Snæfellsnes, Hafnargata 3, 340, Stykkishólmur, Iceland
[j] Norwegian Institute for Nature Research, PB 5685 Torgarden, N-7485 Trondheim, Norway
[k] Nova Scotia Department of Natural Resources and Renewables, Kentville, Nova Scotia B4N 4E5, Canada
[l] Institute of Geography of the Russian Academy of Sciences, Moscow 119017, Russian Federation

ARTICLE INFO

Keywords:
Stable isotopes
Carbon-13
Nitrogen-15
Mercury
Seabird
Arctic

ABSTRACT

Global climate change is causing abiotic shifts such as higher air and ocean temperatures, and disappearing sea ice in Arctic ecosystems. These changes influence Arctic-breeding seabird foraging ecology by altering prey availability and selection, affecting individual body condition, reproductive success, and exposure to contaminants such as mercury (Hg). The cumulative effects of alterations to foraging ecology and Hg exposure may interactively alter the secretion of key reproductive hormones such as prolactin (PRL), important for parental attachment to eggs and offspring and overall reproductive success. However, more research is needed to investigate the relationships between these potential links. Using data collected from 106 incubating female common eiders (*Somateria mollissima)* at six Arctic and sub-Arctic colonies, we examined whether the relationship between individual foraging ecology (assessed using δ^{13}C, δ^{15}N) and total Hg (THg) exposure predicted PRL levels. We found a significant, complex interaction between δ^{13}C, δ^{15}N and THg on PRL, suggesting that individuals cumulatively foraging at lower trophic levels, in phytoplankton-dominant environments, and with the highest THg levels had the most constant significant relationship PRL levels. Cumulatively, these three interactive variables resulted in lowered PRL. Overall, results demonstrate the potential downstream and cumulative implications of environmentally induced changes in foraging ecology, in combination with THg exposure, on hormones known to influence reproductive success in seabirds. These findings are notable in the context of continuing environmental and food web changes in Arctic systems, which may make seabird populations more susceptible to ongoing stressors.

1. Introduction

Increasing anthropogenic activity has resulted in rapid and wide-ranging abiotic shifts in marine systems associated with climate change, including rising air and ocean temperatures (Screen and Simmonds, 2010; Najafi et al., 2015), changes in ocean circulation and salinity (Timmermans et al., 2011; Zika et al., 2018), and dramatic changes in sea ice abundance and distribution within polar systems

* Corresponding author at: Department of Biology, Carleton University, 1125 Colonel by Drive, Ottawa, Ontario K1S 5B6 Canada.
E-mail address: reydsmith@cmail.carleton.ca (R.A. Smith).

https://doi.org/10.1016/j.ygcen.2023.114261
Received 15 November 2022; Received in revised form 6 March 2023; Accepted 7 March 2023
Available online 10 March 2023

(Johannessen et al., 2004; Hoegh-Guldberg and Bruno, 2010). Arctic regions disproportionately exhibit these simultaneous, cumulative effects (IPCC, 2019; AMAP, 2021), resulting in impacts on food web relationships (Vasseur and McCann, 2005; Frederiksen et al., 2006; Parmesan, 2006; Pecuchet et al., 2020). Alterations in the abundance and distribution of lower trophic level organisms (i.e., primary producers) have been evident, with organisms such as phytoplankton displaying advanced phenology and higher abundance relative to sea ice algae (Frederiksen et al., 2006; Renaut et al., 2018; Lewis et al., 2020). Additionally, changes in higher trophic level foraging ecology have been associated with climate change, as prey disruptions further disturb the relationships among food webs (Moline et al., 2008; Watt et al., 2016). Thus, bottom-up and top-down trophic level alterations can result in modifications to individual and species foraging ecology and, in some cases, sizeable population declines (Legagneux et al., 2012; Perkins et al., 2018; Durant et al., 2019). Seabirds are particularly susceptible to adverse outcomes resulting from changes in both directions of trophic alterations, which can influence body condition and, importantly, downstream reproductive success (Baird, 1990; Hamer et al., 1993; Suryan et al., 2006; Perkins et al., 2018; Hovinen et al., 2019). Additionally, changing predator–prey dynamics and spatio-temporal prey abundance can alter, either positively or negatively, individual seabird exposure to environmental contaminants such as mercury (Hg) through changes in prey selection and foraging locale (Bearhop et al., 2000; Braune et al., 2014; Fort et al., 2016, Tartu et al., 2022).

Arctic marine systems are contaminated with Hg via northward transportation of Hg through air and ocean circulation as well as through Arctic rivers (Macdonald et al., 2000; Sonke et al., 2018; DiMento et al., 2019), and the melting of the cryosphere which releases stored Hg from years of higher contaminant output back into the system (Rydberg et al., 2010; Schuster et al., 2018; Hawkings et al., 2021). These factors have all cumulatively resulted in spatiotemporally heterogeneous environmental Hg levels in Arctic regions that influence organism Hg levels by factors including spatio-temporal location and foraging ecology (Braune et al., 2005; 2015; Leu et al., 2011; de la Vega et al., 2019; Albert et al., 2021b). Individuals foraging at higher trophic levels, usually determined using nitrogen stable isotope analysis (δ^{15}N, in relation to ^{15}N to^{14}N ratios), are often correlated with elevated Hg levels resulting from the methylmercury (MeHg) biomagnification process, although individual variation outside of this correlation often exists (Atwell et al., 1998; Bearhop et al., 2000; DiMento et al., 2019). Moreover, the influence of Arctic marine primary producers on the diets of higher order predators, often determined using ratios of carbon isotopes (^{12}C - phytoplankton enriched, ^{13}C - ice algae enriched; δ^{13}C), can offer insight into potential Hg sources based on foraging location and sea ice abundance (Hobson and Welch, 1992; Hobson et al., 1995; McMahon et al., 2006).

MeHg is a biologically converted form of Hg that affects endocrine functioning, behaviour, and reproductive success in birds at even low, sub-lethal levels (Wiener et al., 2003; Whitney and Cristol, 2017; Evers, 2018, Chastel et al., 2022). While the Hg levels in most seabirds (95%) are considered lower risk, there have been recent calls to examine the potential impact of Hg in a cumulative stressor framework to help address Article 22 of the Minimata Convention (https://www.mercuryconvention.org/sites/default/files/documents/information_document/4_INF12_MonitoringGuidance.English.pdf). Article 22 calls for an evaluation of the effectiveness of the convention, in which Arctic seabirds serve as indicators for assessing environmental contamination (Chastel et al., 2022). Avian reproduction can be affected by Hg exposure through its endocrine-disrupting properties that can influence female breeding behaviour (Tan et al., 2009; Ackerman et al., 2016; Whitney and Cristol, 2017, Chastel et al., 2022). For example, in the beginning stages of reproduction, sub-lethal Hg has been correlated with a decreased likelihood to breed, attributed to the effect of Hg on luteinizing hormone (LH) and the subsequent release of sex hormones (i.e., estrogen; Tartu et al., 2013; 2014). Importantly, exposure to Hg has been linked to a decrease in prolactin (PRL), a pituitary hormone key for parental care behaviours (El Halawani et al., 1984; Tartu et al., 2015; Angelier et al., 2016; Tartu et al., 2016). However, no link between Hg and PRL has been observed in other studies, indicating a potentially complex relationship and role of PRL in avian incubation (Gilmour et al., 2019; Blévin et al., 2020).

In birds, PRL secretion commences after the parent physically touches their eggs and increases following the cessation of laying and the onset of incubation behaviour (Buntin, 1996; Sockman et al., 2000). In common eider (*Somateria mollissima*, hereafter eider), PRL increases at the onset of incubation and remains at a consistent level during incubation, followed by a steep increase immediately before hatching (Criscuolo et al., 2002). Additionally, the role of PRL in clutch size determination has been previously proposed, with increased PRL signalling for a decrease in LH that stops the laying period in anticipation of incubation (Sockman et al., 2000). Disruption of PRL secretion during incubation has been proposed as a likely mechanistic link that results in lowered quality of incubation behaviour via decreased incubation attentiveness (Angelier and Chastel, 2009; Angelier et al., 2009). Incubating females in worsened body condition may have lower PRL levels, thus reducing incubation quality and increasing predation risk (Criscuolo et al., 2002). Overall, the cumulative and interactive effects of prey consumption and Hg accumulation on PRL can influence key reproductive traits such as incubation behaviour and reproductive success. These linkages are important to examine, especially given the accelerating rate of environmental shifts in Arctic marine systems.

A recent study from our group indicated that eider colonies highly varied in multidimensional niche dynamics: migratory colonies had higher δ^{15}N and Hg but lower δ^{13}C, and sea-ice cover positively correlated with δ^{15}N, δ^{13}C and Hg (Smith et al., 2021). The study also found that individual eiders with lower δ^{13}C and higher trophic positions had higher Hg (Smith et al., 2021). In the current study, we built from these results to examine the interactive effects of foraging ecology, inferred with stable isotope analysis (Kelly, 2000), and Hg on PRL levels of incubating female common eiders. Eiders are long-lived, colonial-nesting marine ducks with dispersed breeding populations across the circumpolar and sub-Arctic. As such, they are exposed to diverse environmental conditions, which influence variation in their foraging ecology and Hg exposure (Albert et al., 2021a; Smith et al., 2021). Eider prey includes a diversity of benthic invertebrates (e.g., urchins and mussels) and pelagic macroinvertebrates (e.g., amphipods; Sénéchal et al., 2011). Eiders forage extensively in the pre-breeding period in various ice conditions depending on the timing of spring melt to obtain an appropriate body condition needed to breed (Jean-Gagnon et al., 2018). Importantly, female eiders undergo a 24–26 day uniparental incubation fast, relying solely on their endogenous stores to fuel the incubation period (Hanssen et al., 2002; Bottitta et al., 2003; Sénéchal et al., 2011). During this fasting period, contaminants including Hg increase in the blood due to the mobilization of endogenous lipid and protein stores (Wayland et al., 2005; Bustnes et al., 2010; McPartland et al., 2020). These levels can go over the threshold known to be negatively correlated with PRL secretion in other seabird species (Tartu et al., 2015; 2016). Consequently, in combination with reduced body condition, elevated blood levels of Hg may interfere with hormones such as PRL, with the potential for downstream influences on incubation behaviour and reproductive success (Tartu et al., 2016). However, intricate relationships between these and other physiological aspects have been demonstrated previously in the literature. In common eiders, complex and integrated relationships have been shown between clutch size, body condition/mass, incubation duration, PRL and the primary glucocorticoid in birds, corticosterone (CORT) (Erikstad et al., 1993; Criscuolo et al., 2006). Clutch size and body condition were positively related, while body condition can be negatively correlated with incubation duration, but positively correlated with incubation attentiveness (Erikstad et al., 1993; Erikstad and Tveraa, 1995). Meanwhile, body mass was positively linked to PRL levels, while baseline levels of CORT were negatively

correlated with plasma PRL, altogether leading to reductions in overall reproductive success (Criscuolo et al., 2002; 2005; 2006). These relationships provide a background for examining the effects of foraging ecology and Hg on PRL in female eiders.

Our overall hypothesis was that the combined effects of foraging ecology and Hg contamination would affect PRL levels in incubating eiders. Specifically, we predicted that lower levels of PRL would be correlated with lower δ^{15}N (lower trophic level foraging, lesser quality prey), higher δ^{13}C (sea ice algae-based foraging, more restrictive foraging environment), and elevated Hg levels. Examining these relationships will allow for a more extensive determination of the indirect mechanisms by which climate change affects at-risk Arctic seabird populations.

2. Methods

2.1. Sample collection and physiological analysis

Seven Arctic and sub-Arctic breeding colonies were monitored in 2018 (Fig. 1, Table 2, N = 136). Incubating eiders were captured on their nests using noose poles, bownets, or dogs (John's Island location only; Milton et al., 2016). A 200–1,000 μL blood sample was collected from each female's tarsal vein, jugular vein (Grindøya and Kongsfjorden), or brachial vein (Iceland) using a 23G thin-wall, 1-inch needle attached to a heparinized 1 mL syringe (10 mL syringe - Grindøya and Kongsfjorden). Samples were centrifuged within 8–12 h of collection at approximately 10,000 rpm for 10 min to obtain red blood cells (RBC) for stable isotope (isotope-ratio mass-spectrometer) and total Hg (THg; Advanced Mercury Analyser; see Smith et al., 2021 for further details on these methods and results). Plasma was collected from the centrifuged whole blood, frozen for storage in the field, and later sent for PRL analysis to the Centre d'Etudes Biologiques de Chizé (CEBC), France. Plasma samples were analyzed for PRL using radioimmunoassay (RIA) following the procedure detailed in Cherel et al. (1994) and validated in common eiders in previous studies (Criscuolo et al., 2002). The analysis consisted of duplicates with colonies split into two runs: John's Island, Iceland and Tern Island in one run (intra-assay variation = 12.01%), and Grindøya, Faroe Islands, Kongsfjorden, and Solovetskiy Islands in a second run (intra-assay variation = 9.28%). Inter-assay variation between the two runs was 14.75%, calculated from a sample run in both assays in 6 replicates. PRL was measured in 10 μL, and the lowest detectable limit was 0.45 ng/mL.

As specific individual incubation stage was unable to be determined at many sites or hens, we could not correct the potential effect of incubation fasting on THg or δ^{15}N levels (Hobson et al., 1993; Wayland et al., 2005; Smith et al., 2021). However, using RBCs to determine isotopic and THg values minimized this effect as δ^{15}N enrichment is lesser in blood cells than in plasma (Cherel et al., 2005). Further, as PRL levels are consistent throughout incubation stages in eiders prior to hatching (Criscuolo et al., 2002), we were able to conduct inter-colony and individual comparisons of PRL without correction for individual or colony incubation stage.

2.2. Statistical analysis

To examine whether PRL levels varied between colonies, we first ran an ANOVA followed by a posthoc Tukey's Honest Significant Difference (HSD) test using the R package car v.3.0-10 (Fox and Weisberg, 2019). We then used compact letter display, in combination with the R package ggplot2 v.3.3.6, to visually determine significance at an alpha level of 0.05 between the seven colonies using the R package multcompView v.0.1-8 (Graves et al., 2015; Wickham, 2016). Following this, we calculated AICc values for 12 potential models to determine the most parsimonious model using the R package AICcmodavg v.2.3-1 (Mazerolle, 2020). The model with the lowest AICc also had a significantly higher log-likelihood value, thus, was a better fit than the other models (Table 1). We then used a general linear mixed model (GLMM) with a normal distribution to determine the interactive effect of δ^{15}N, δ^{13}C and THg levels on PRL secretion. The dependent variable was PRL, with δ^{15}N, δ^{13}C and THg values included as fixed independent variables in all single, two- and three-way interactions. Additionally, we included female body mass (g) and clutch size as fixed independent variables in a two-way interaction. All independent variables were standardized and centred for comparison to remove misrepresentation of effects and

Fig. 1. Locations of the seven pan-Arctic and subarctic common eider colonies used in this study (stars). Colonies are numbered by descending median colony PRL levels (1 = highest, 7 = lowest). Map provided by naturalearthdata.com.

Table 1
Results of model selection on plasma PRL levels of 106 female common eiders from 6 breeding colonies. The number of parameters (k), corrected Akaike information criterion (AICc), change in AICc (ΔAICc), AICc weight, and log-likelihood are provided for each competing model. Colony was included as a random variable in all models, however, when clutch size was included as a random variable it is denoted with [R].

Model	k	AICc	ΔAICc	AICc Weight	Log-likelihood
THg*δ^{15}N*δ^{13}C + Mass*Clutch	**13**	**1106.61**	**0.00**	**0.80**	**−538.33**
THg*δ^{15}N*δ^{13}C + Mass + Clutch	12	1109.70	3.09	0.17	−541.17
THg*δ^{15}N + THg*δ^{13}C + δ^{15}N*δ^{13}C + Mass*Clutch	12	1113.91	7.30	0.02	−543.28
THg*δ^{15}N*δ^{13}C + Mass + Clutch[R]	12	1115.73	9.12	0.01	−544.19
THg*δ^{13}C + δ^{15}N + Mass + Clutch	9	1123.24	16.63	0.00	−551.68
δ^{13}C*δ^{15}N + Mass + Clutch	8	1126.41	19.80	0.00	−554.46
THg + δ^{15}N + δ^{13}C + Mass + Clutch	8	1126.57	19.96	0.00	−554.54
δ^{15}N + Mass + Clutch	6	1136.47	29.86	0.00	−561.81
δ^{13}C + Mass + Clutch	6	1139.02	32.40	0.00	−563.08
THg + Mass + Clutch	6	1139.53	32.91	0.00	−563.34
THg*δ^{15}N*δ^{13}C + Mass	11	1173.26	66.64	0.00	−574.30
THg*δ^{15}N*δ^{13}C + Clutch	11	1191.18	84.57	0.00	−583.28
THg*δ^{15}N*δ^{13}C	10	1457.05	350.44	0.00	−717.64

increase the interpretability of coefficients (Schielzeth, 2010). We included breeding colony in the model as a random variable to control for inter-colony PRL variation, with the objective being to examine individual variation. All statistical analyses were conducted in RStudio version 2022.07.2 (RStudio Team, 2022). All model assumptions were met by visually inspecting histograms to confirm a normal data distribution, quantile–quantile plots, and residual plots from the model outputs. We also confirmed the absence of multicollinearity between all variables using correlation coefficients and variance inflation factors (VIF), which were below 0.36 and 3.90 (3-way interaction), respectively. In interpretations of three-way interactions, the interaction among two factors (A * B) differs along with levels of a third factor (C). To assist with the visualization of these complex relationships, significant interactions were graphed using the R package Interactions v.1.1.3 (Long, 2019). This package calculated Johnson-Neyman intervals and simple slopes analysis to determine the significant slopes within the three-way interaction.

3. Results

Median PRL levels were variable among eider colonies, ranging from 245.18 ng/mL (Tern Island) to 348.99 ng/mL (Kongsfjorden), with the median PRL for all eiders at 287.60 ng/mL (Table 2, Fig. 2). At the individual eider level, the lowest (142.72 ng/mL) and highest (489.20 ng/mL) values were found at the Kongsfjorden colony. Mean colony PRL levels significantly varied between colonies, with the Kongsfjorden colony having significantly higher mean PRL levels than every colony except for Grindøya (Fig. 2). Conversely, Tern Island had significantly lower mean PRL levels than all colonies but Faroe Islands (Fig. 2). Although we report the PRL values for the John's Island colony, researchers at this location did not collect body mass measurements. Therefore, this colony was omitted from the statistical model ($n = 18$) and any individuals that did not have body mass and/or clutch size data ($n = 12$, total individuals omitted = 30), with a remaining sample size of 106 individuals for the GLMM.

The GLMM showed that δ^{15}N ($t_{80} = 2.289$, $p = 0.025$; Table 3) as well as the three-way interaction between δ^{15}N, δ^{13}C and THg were significant ($t_{95} = 2.089$, $p = 0.039$; Table 3). Johnson-Neyman intervals and simple slopes analysis determined that 6/9 of the slopes in the three-way interaction were significantly different from zero. In particular, 3/3 slopes were significant at THg + 1 standard deviation (SD), 2/3 were significant at mean THg levels, and 1/3 were significant THg −1 SD (Fig. 3). At higher levels of THg (+1 SD), all levels of δ13C values (-1 SD, mean, and +1 SD) resulted in significant positive relationships between δ15N and PRL (Fig. 3). At mean THg levels, mean and low δ13C values (-1 SD) also resulted in significant positive relationships between δ15N and PRL (Fig. 3). At low THg levels (-1 SD), only low δ^{13}C values (-1 SD) resulted in significant positive relationship between δ15N and PRL (Fig. 3). However, there was no significant relationship between female body mass, clutch size, or a two-way interaction of those variables with PRL (Table 3).

4. Discussion

We examined the interactive effects of individual foraging ecology and THg contamination on PRL levels in incubating female common eiders across six colonies at a pan-Arctic scale. We predicted an effect of the interaction between δ^{15}N, δ^{13}C and THg on PRL levels, given the potential effect of these variables on female body condition and hormone regulation. Consistent with our prediction, individuals at lower trophic levels (lower δ^{15}N) showed the lowest PRL levels, most commonly in combination with individuals at higher THg levels and those foraging in predominantly phytoplankton-based environments (lower δ^{13}C). Our findings suggest a potential cumulative, interactive effect of foraging ecology and elevated THg exposure on PRL levels in wild eider colonies.

4.1. Interactive relationship between foraging ecology and PRL levels

We found a significant positive relationship between δ^{15}N and PRL levels. Pre-breeding eiders foraging at lower trophic levels may potentially have a relatively lower body condition going into and then throughout incubation. PRL and incubating body condition have been linked in previous studies, where lower-condition females showed reduced PRL levels (Criscuolo et al., 2002). Although body mass did not correlate with PRL, there is nonetheless potential for the indirect linkages between trophic level (i.e., δ^{15}N) and body condition to influence PRL secretion (see section 4.3). Changes in food web structure are apparent with continuing climate change and are likely to vary spatio-temporally between colonies with differing prey availability (see section 1; Smith et al., 2021). These effects are important for a species such as eiders since a lower body condition beginning in the pre-breeding

Table 2
Locations of common eider colonies used in this study, sample size, month samples were obtained, colony coordinates as well as median and range of PRL levels.

Location	n	Sampling month	Latitude	Longitude	Female mass (g)	Median PRL (ng/mL)
Breiðafjörður, Iceland	21	June	65.078	−22.736	1780 ± 111.6	310.21 ± 57.02
Grindøya, Norway	17	June	69.633	18.844	2050 ± 168.3	336.50 ± 48.13
John's Island, Canada	18	July	43.645	−66.041	N/A	277.68 ± 49.58
Kirkjubøhólmur, Faroe Islands	16	July	61.950	−6.799	1400 ± 223.9	264.75 ± 41.13
Kongsfjorden, Norway	16	June	78.918	11.910	1525 ± 210.7	348.99 ± 82.29
Solovetskiy Islands, Russia	24	June	65.048	35.774	1800 ± 105.4	280.04 ± 49.38
Tern Island, Canada	24	June	69.547	−80.812	1660 ± 213.7	245.18 ± 44.65

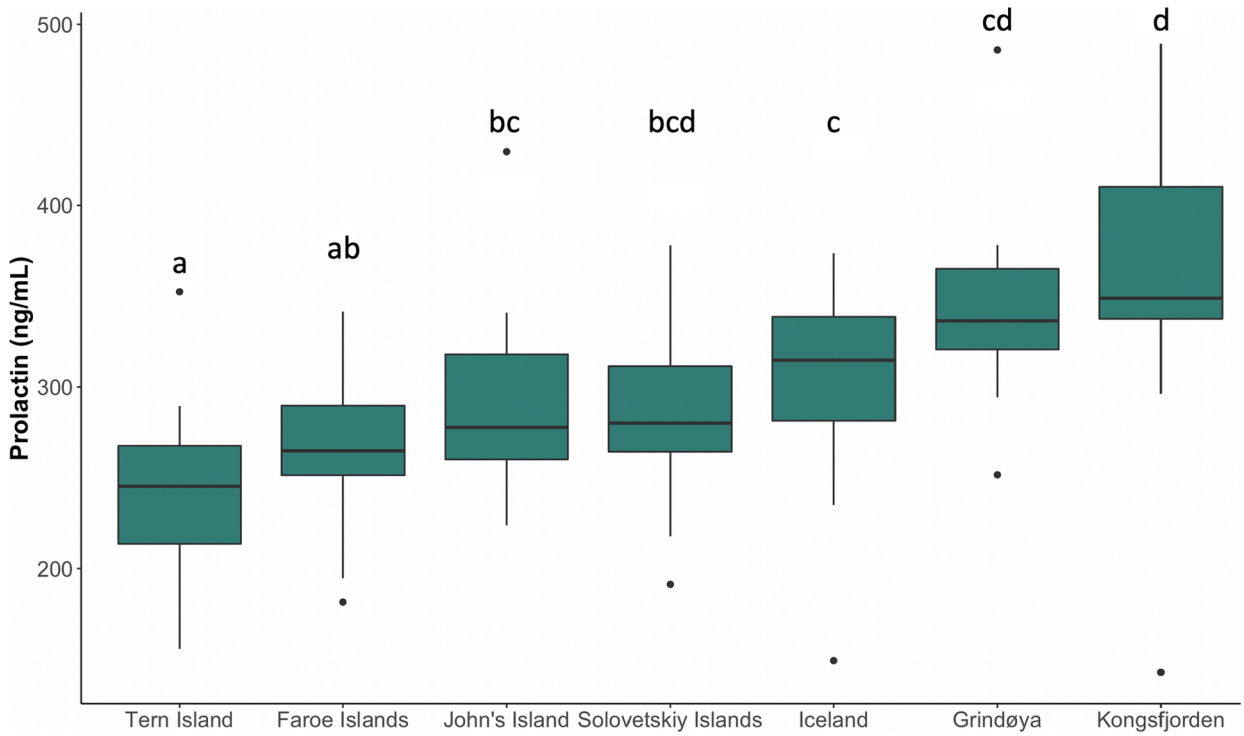

Fig. 2. Boxplot depicting whether the mean PRL levels at each common eider colony vary significantly. Significance was determined using a one-way ANOVA at an alpha of 0.05 and a posthoc Tukey test using the R package car v.3.0–10. Letters above each colony show whether a colony significantly differs from the others, where the absence of shared letters indicates significant difference in mean PRL levels between locations.

Table 3
Results of a general linear mixed effects model examining the interactive effects of THg (μg/g dry weight), δ^{15}N and δ^{13}C (‰) as well as an interaction between body mass (g) and clutch size on prolactin (PRL) levels (ng/mL). The breeding colony (n = 6) of the 106 female arctic-breeding common eiders throughout Canada and Eurasia was a random variable in the model, with the John's Island eiders and 12 additional individuals from other colonies removed from the model due to the absence of morphometrics (significant p-values are bolded).

	Estimate	Standard Error	df	t-value	p-value
Intercept	306.746	19.540	4.526	15.599	**<0.001**
Body Mass	−9.472	7.375	93.941	−1.284	0.202
Clutch Size	4.628	6.389	94.890	0.724	0.471
Mass*Clutch	−0.36	6.872	92.220	−0.053	0.958
THg	−7.108	9.509	93.910	−0.747	0.457
δ^{13}C	−17.543	11.313	77.172	−1.551	0.125
δ^{15}N	25.427	11.107	80.279	2.289	**0.025**
THg*δ^{13}C	7.484	8.609	94.777	0.869	0.387
THg*δ^{15}N	6.437	5.918	94.889	1.088	0.280
δ^{15}N*δ^{13}C	−13.376	10.882	92.772	−1.229	0.222
THg*δ^{15}N*δ^{13}C	14.138	6.767	94.561	2.089	**0.039**

stage could reduce the amount of PRL during incubation, with potential implications on nest attentiveness and overall breeding success (Erikstad et al., 1993; Criscuolo et al., 2002). Eiders forage primarily on amphipods and bivalves, which have demonstrated sensitivity to warming ocean temperatures (Węsławski et al., 2011; Dalpadado et al., 2016; Vinarski et al., 2021). Based on our current results, changes in eider trophic niches due to ecosystem shifts (likely to vary widely and depend on spatio-temporal prey availability) may have downstream impacts on body condition and PRL levels. For example, individuals that consume a greater abundance of lower trophic level prey could have comparatively lower body condition with expected negative impacts on PRL levels. This prey may include bivalves, which have lower energy returns due to a low ratio of flesh content to shell size compared to shell-less macroinvertebrates (Hamilton et al., 1999; Schummer et al., 2008). In colonies where trophic niches shift to a greater abundance of higher trophic level prey, such as arthropods, the reverse effect is possible where higher trophic level prey may improve reproductive output, as seen in blue-footed boobies (González-Medina et al., 2018). Interestingly, the colonies with the lowest median PRL levels (Faroe Islands, Tern Island) were also identified previously as having the lowest median δ^{15}N out of the colonies studied (Smith et al., 2021), indicating that their lower PRL values may be linked with their utilization of lower trophic level prey such as bivalves. Despite these potential patterns, the eventual outcome of prey abundance shifts on eider hormonal mechanisms at the heart of successful incubation outcomes remains to be seen as climate change effects increase annually. However, our work provides a valuable baseline to examine subsequent future changes.

We also detected a significant relationship between δ^{13}C and PRL levels in combination with δ^{15}N and THg. Along with the food web changes described with δ^{15}N above, the most consistently detected relationship was associated with phytoplankton-based foraging (low δ^{13}C) and PRL levels in our three-way interaction. Due to the increasing effects of climate change, phytoplankton blooms are expected to become more intense and occur earlier in the year (Kahru et al., 2011; Ardyna and Arrigo, 2020). Phytoplankton blooms are also increasingly apparent when sea ice is still present, even in the benthos, due to increased light transmission with thinning ice (Arrigo et al., 2012; Horvat et al., 2017; Shiozaki et al., 2022). In eiders, phytoplankton blooms in the Baltic Sea have been linked to a reduction in nesting eiders (Larsson et al., 2014). In this study, the relationship was suggested to be connected to an impact of the phytoplankton bloom on blue mussel (*Mytilus edulis*) availability (either through toxic or non-toxic pathways), followed by a subsequent reduction in eider body condition that impacted their breeding propensity (Larsson et al., 2014). Our results showing a consistently significant effect of low δ^{13}C in our three-way model on PRL may be related to phytoplankton-based environments resulting in less prey availability (such as blue mussels), either quality or quantity, that affects eider body condition and subsequently PRL.

Conversely, we also detected a significant relationship between sea

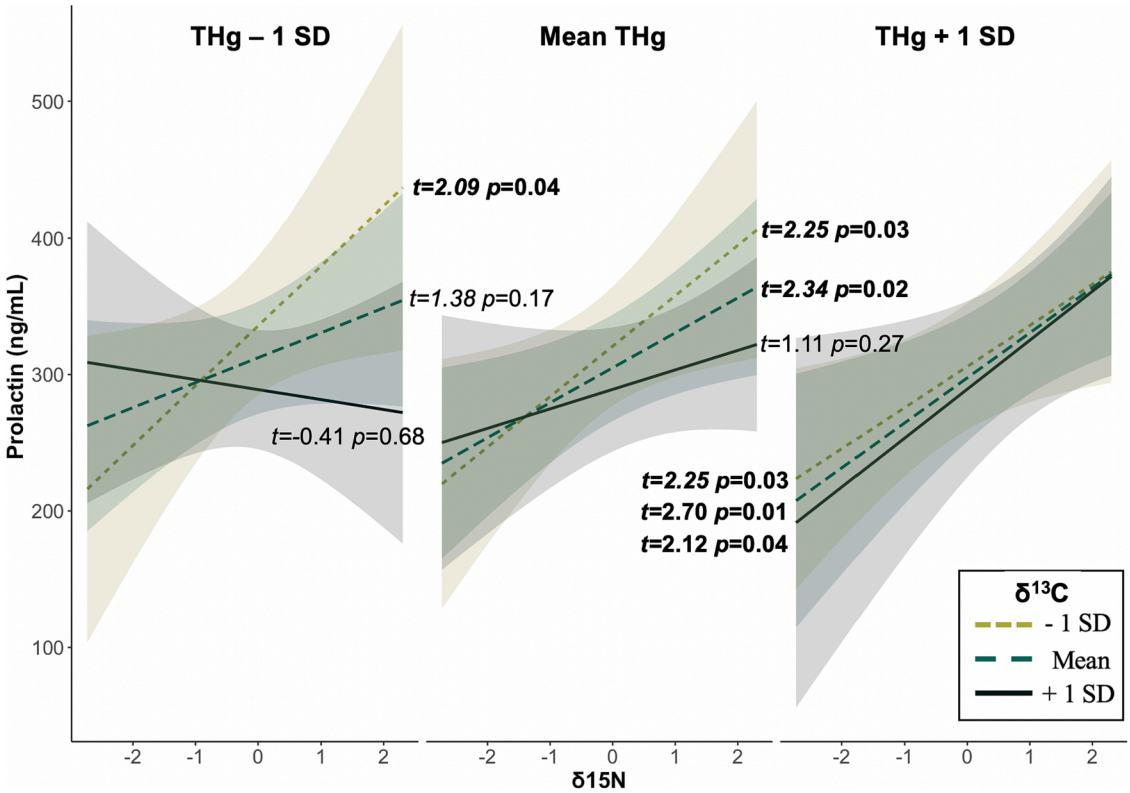

Fig. 3. Interactive effect of δ^{15}N, δ^{13}C and THg (visualized using standard deviation from the mean; SD) on PRL levels in 106 incubating common eiders combined from six pan Arctic breeding colonies. The model used for this analysis included eider colony as a random variable. Values for δ^{15}N, δ^{13}C and THg are without units as they are derived from standardized model output for simplicity using the R package Interactions version 1.1.3. Shaded areas represent a 95% confidence interval for each slope. Slopes that are significantly different from zero, as determined by Johnson-Neyman simple slopes analysis, are bolded.

ice algae-based foraging (high δ^{13}C) and PRL levels in our three-way interaction, only in high THg individuals. The relationship between high δ^{13}C and PRL, along with elevated THg, may be due to constraints in foraging areas with higher sea ice cover, as seen previously in eiders that rely on access to open water to reach benthic and pelagic areas (Jean-Gagnon et al., 2018). As such, constraints in prey availability, combined with a high proportion of ice cover, could result in lower energetic stores (i.e., body condition) available to eiders during incubation, with possible downstream impacts on PRL levels.

Overall, the relationships we have detected between foraging ecology (based on isotopic niche) and PRL provide an initial look into how pre-breeding prey selection may indirectly influence key reproductive hormones in eiders. Future studies may benefit from integrating research into whether pre-breeding prey availability and quality may influence incubating PRL.

4.2. Importance of THg levels in relation to incubating PRL

The interactive relationship between δ^{13}C and δ^{15}N with PRL, as described in section 4.1, was most often significant in combination with high THg. The importance of THg in this relationship could potentially relate to the endocrine-disrupting properties of THg (Zhu et al., 2000; Tan et al., 2009). In addition, negative relationships between THg and body condition, as seen in previous studies (Provencher et al., 2016; but see Carravieri et al., 2022), may have also played a role in the effect of THg on PRL in combination with δ^{13}C and δ^{15}N. Importantly, our findings support concern over THg as an important component of cumulative stressors systems in the Arctic, where the combination of stressors such as contaminants, climate change and food web dynamics are expected to have cumulative impacts on birds (Chastel et al., 2022; Esparza et al., 2022; Smith et al., 2022). Overall, we found that THg played an important interactive role along with foraging ecology on PRL levels. However, whether this is related to the direct effects of THg on PRL, or indirectly mediated by foraging ecology or other intermediate physiological parameters is unclear and requires further study.

4.3. Other physiological and external factors with a potential influence on PRL

We were able to examine the relationship between body mass and PRL levels in this study. However, while previous studies successfully used this metric to determine eider body condition (Descamps et al., 2011), this measure of female condition may have been an incomplete look into the relationship between body condition and PRL in incubating eiders. Body condition, often measured as body mass divided by total head length (Jamieson et al., 2006) or scaled mass index (Peig and Green, 2009), may provide a more in-depth look into female quality at the time of sampling, rather than only body mass which does not adjust for overall body size. Additionally, individual body mass declines as eiders progressively use their endogenous resources during their incubation fast (Criscuolo et al., 2002; Hanssen et al., 2002). We were unable to control the incubation stage or body size in this study, but this would be ideal for future research on this topic.

It is worth highlighting that the primary glucocorticoid hormone in birds, corticosterone (CORT), is an important factor in eider pre-incubation body condition, where higher baseline CORT corresponds to more intensive foraging in eiders (Hennin et al., 2015; 2018). Baseline CORT may play an essential regulating role in the relationship we have detected between PRL and foraging ecology during pre-breeding periods. For example, during pre-breeding foraging, females with higher baseline CORT may result in downstream elevated PRL levels during incubation due to more intensive foraging, leading to higher body conditions at the start of incubation (Criscuolo et al., 2002; Angelier et al., 2016). Additionally, elevated baseline CORT has also been linked

to a greater need for resources during incubation, as seen in incubating macaroni penguins (*Eudyptes chrysolophus*; Crossin et al., 2012). Eiders, which fast during one single incubation bout, have demonstrated a negative relationship between CORT and PRL during incubation periods in previous studies that regulates incubation behaviour (Criscuolo et al., 2005; 2006). The same pattern has been seen in birds that forage during incubation, with stressed individuals leaving more often on foraging trips (Angelier and Chastel, 2009; Angelier et al., 2009). In addition, elevated CORT levels may negatively affect female immunity and mass loss during incubation, as seen in previous common eider studies (Bourgeon and Raclot, 2006; Bourgeon et al., 2009). Higher energetic stress could have foraging ecology-mediated links to PRL levels. While high CORT levels may be initially beneficial during the pre-breeding period, these elevated may be detrimental to PRL during incubation, especially in fasting female eiders. Further implications may also arise from the added effects of elevated stress-induced CORT, especially as predator–prey relationships and climate conditions shift in Arctic systems.

Many eider colonies are facing increasing predation pressure from polar bears (*Ursus maritimus)*, arctic foxes (*Vulpes lagopus*) and *Larus* sp. gulls (Smith et al., 2012; Hanssen et al., 2013; Prop et al., 2015; Jagielski et al., 2021). Eiders must also contend with elevated thermal environments that can influence female incubation behaviour, especially when combined with Hg exposure (Smith et al., 2022). Interestingly, studies on eiders in the Baltic Sea have determined that those with elevated PRL and higher body condition may have higher nest predation risk (Mohring et al., 2021). However, the correlation between PRL and elevated predation risk was speculated to be attributed to an absence of low-quality individuals with reduced PRL levels at nesting sites with higher predation risk (Mohring et al., 2021). In general, lower PRL may result in a greater risk for egg predation due to lowered incubation consistency. In comparison, higher PRL, thus greater incubation consistency, may lead to higher female predation risk. However, further research is needed to establish these links. Ultimately, the cumulative stressors eiders are now more often exposed to both pre-breeding and during incubation have the potential to greatly decrease nesting success with a 'perfect storm' of stressors influencing reproductive parameters via PRL secretion. In this study, we were unable to examine the links between PRL levels and eider breeding behaviour, predation, or nest success. However, examining these metrics, along with foraging ecology and contaminant loads, would provide holistic context to the implications of these stressors on avian reproductive success.

5. Conclusion

The interactive effects of foraging ecology and THg exposure on PRL levels were examined in incubating female common eiders. Our results show that individuals with high THg that were interactively foraging at lower trophic levels (low δ^{15}N) and in areas with greater phytoplankton abundance (low δ^{13}C) had the most significant relationships resulting in lowered PRL levels. Overall, this complex interactive system, based on foraging ecology and Hg exposure, may have downstream implications for reproductive success through hormone alteration and, therefore, population demography. These effects may be strengthened within the context of continually changing environmental conditions on a global scale. However, further studies are required to fully understand these complex relationships and their reproductive and demographic consequences in a changing Arctic.

CRediT authorship contribution statement

Reyd A. Smith: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Jérôme Fort:** Conceptualization, Investigation, Resources, Writing – review & editing. **Pierre Legagneux:** Methodology, Resources, Writing – review & editing. **Olivier Chastel:** Methodology, Resources, Writing – review & editing. **Mark L. Mallory:** Investigation, Resources, Writing – review & editing. **Paco Bustamante:** Investigation, Resources, Writing – review & editing. **Jóhannis Danielsen:** Investigation, Resources, Writing – review & editing. **Sveinn A. Hanssen:** Investigation, Resources, Writing – review & editing. **Jón Einar Jónsson:** Investigation, Resources, Writing – review & editing. **Ellen Magnúsdóttir:** Investigation, Resources, Writing – review & editing. **Børge Moe:** Investigation, Resources, Writing – review & editing. **Charline Parenteau:** Methodology, Resources, Writing – review & editing. **Kyle J.L. Parkinson:** Conceptualization, Investigation, Writing – review & editing. **Glen J. Parsons:** Investigation, Resources, Writing – review & editing. **Grigori Tertitski:** Investigation, Resources, Writing – review & editing. **Oliver P. Love:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Supervision, Writing – review & editing.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

Acknowledgments

Thank you to the Isotopic Spectrometry Facility at LIENSs (La Rochelle University - CNRS, La Rochelle) and the Service d'Analyses Biologiques at CEBC for their help with sample analysis. We also thank Environment and Climate Change Canada (ECCC), the Natural Sciences and Engineering Research Council of Canada, Canada Research Chairs Program, the Nunavut Wildlife Management Board, Northern Scientific Training Program, Polar Continental Shelf Project, POLAR Canada, the Canadian Network of Centres of Excellence (ArcticNet), the Government of Ontario, the University of Windsor and the Arctic Institute of North America for logistical support, research and/or personal funding. The IUF (Institut Universitaire de France) is acknowledged for its support to P. Bustamante as a Senior Member. This work also contributes to the ARCTOX initiative (https://arctox.cnrs.fr) and the ARCTIC-STRESSORS project (ANR-20-CE34-0006-01).

References

Ackerman, J.T., Eagles-Smith, C.A., Herzog, M.P., Hartman, C.A., Peterson, S.H., Evers, D.C., Jackson, A.K., Elliott, J.E., Vander Pol, S.S., Bryan, C.E., 2016. Avian mercury exposure and toxicological risk across western North America: a synthesis. Sci. Total Environ. 568, 749–769.

Albert, C., Bråthen, V.S., Descamps, S., Anker-Nilssen, T., Cherenkov, A., Christensen-Dalsgaard, S., Danielsen, J., Erikstad, K.E., Gavrilo, M., Hanssen, S.A., Helgason, H. H., 2021a. Inter-annual variation in winter distribution affects individual seabird contamination with mercury. Mar. Ecol. Prog. Ser. 676, 243–254.

Albert, C., Helgason, H.H., Brault-Favrou, M., Robertson, G.J., Descamps, S., Amélineau, F., Danielsen, J., Dietz, R., Elliott, K., Erikstad, K.E., Eulaers, I., 2021b. Seasonal variation of mercury contamination in Arctic seabirds: a pan-arctic assessment. Sci. Total Environ. 750, 142201.

Amap, 2021. Arctic Climate Change Update 2021: Key Trends and Impacts. Summary for Policy-makers. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway.

Angelier, F., Chastel, O., 2009. Stress, prolactin and parental investment in birds: a review. Gen. Comp. Endocrinol. 163, 142–148.

Angelier, F., Clément-Chastel, C., Welcker, J., Gabrielsen, G.W., Chastel, O., 2009. How does corticosterone affect parental behaviour and reproductive success? A study of prolactin in black-legged kittiwakes. Funct. Ecol. 23 (4), 784–793.

Angelier, F., Wingfield, J.C., Tartu, S., Chastel, O., 2016. Does prolactin mediate parental and life-history decisions in response to environmental conditions in birds? A review. Horm. Behav. 77, 18–29.

Ardyna, M., Arrigo, K.R., 2020. Phytoplankton dynamics in a changing Arctic Ocean. Nat. Clim. Chang. 10 (10), 892–903.

Arrigo, K.R., Perovich, D.K., Pickart, R.S., Brown, Z.W., van Dijken, G.L., Lowry, K.E., Mills, M.M., Palmer, M.A., Balch, W.M., Bahr, F., Bates, N.R., Benitez-Nelson, C.,

Bowler, B., Brownlee, E., Ehn, J.K., Frey, K.E., Garley, R., Laney, S.R., Lubelczyk, L., Mathis, J., Matsuoka, A., Mitchell, B.G., Moore, G.W.K., Ortega-Retuerta, E., Pal, S., Polashenski, C.M., Reynolds, R.A., Schieber, B., Sosik, H.M., Stephens, M., Swift, J. H., 2012. Massive phytoplankton blooms under Arctic sea ice. Science 336 (6087), 1408.

Atwell, L., Hobson, K.A., Welch, H.E., 1998. Biomagnification and bioaccumulation of mercury in an arctic marine food web: insights from stable nitrogen isotope analysis. Can. J. Fish. Aquat. Sci. 55 (5), 1114–1121.

Baird, P.H., 1990. Influence of abiotic factors and prey distribution on diet and reproductive success of three seabird species in Alaska. Ornis Scand. 21 (3), 224–235.

Bearhop, S., Phillips, R.A., Thompson, D.R., Waldron, S., Furness, R.W., 2000. Variability in mercury concentrations of great skuas Catharacta skua: the influence of colony, diet and trophic status inferred from stable isotope signatures. Mar. Ecol. Prog. Ser. 195, 261–268.

Blévin, P., Shaffer, S.A., Bustamante, P., Angelier, F., Picard, B., Herzke, D., Moe, B., Gabrielsen, G.W., Bustnes, J.O., Chastel, O., 2020. Contaminants, prolactin and parental care in an Arctic seabird: contrasted associations of perfluoroalkyl substances and organochlorine compounds with egg-turning behavior. Gen. Comp. Endocrinol. 291, 113420.

Bottitta, G.E., Nol, E., Gilchrist, H.G., 2003. Effects of experimental manipulation of incubation length on behavior and body mass of common eiders in the Canadian Arctic. Waterbirds 26 (1), 100–107.

Bourgeon, S., Le Maho, Y., Raclot, T., 2009. Proximate and ultimate mechanisms underlying immunosuppression during the incubation fast in female eiders: roles of triiodothyronine and corticosterone. Gen. Comp. Endocrinol. 163 (1–2), 77–82.

Bourgeon, S., Raclot, T., 2006. Corticosterone selectively decreases humoral immunity in female eiders during incubation. J. Exp. Biol. 209 (24), 4957–4965.

Braune, B., Chételat, J., Amyot, M., Brown, T., Clayden, M., Evans, M., Fisk, A., Gaden, A., Girard, C., Hare, A., Kirk, J., 2015. Mercury in the marine environment of the Canadian Arctic: review of recent findings. Sci. Total Environ. 509, 67–90.

Braune, B.M., Outridge, P.M., Fisk, A.T., Muir, D.C.G., Helm, P.A., Hobbs, K., Hoekstra, P.F., Kuzyk, Z.A., Kwan, M., Letcher, R.J., Lockhart, W.L., 2005. Persistent organic pollutants and mercury in marine biota of the Canadian Arctic: an overview of spatial and temporal trends. Sci. Total Environ. 351, 4–56.

Braune, B.M., Gaston, A.J., Hobson, K.A., Gilchrist, H.G., Mallory, M.L., 2014. Changes in food web structure alter trends of mercury uptake at two seabird colonies in the Canadian Arctic. Environ. Sci. Technol. 48 (22), 13246–13252.

Buntin, J.D., 1996. Neural and hormonal control of parental behavior in birds. Adv. Study Behav. 25, 161–213.

Bustnes, J.O., Moe, B., Herzke, D., Hanssen, S.A., Nordstad, T., Sagerup, K., Gabrielsen, G.W., Borgå, K., 2010. Strongly increasing blood concentrations of lipid-soluble organochlorines in high arctic common eiders during incubation fast. Chemosphere 79 (3), 320–325.

Carravieri, A., Vincze, O., Bustamante, P., Ackerman, J.T., Adams, E.M., Angelier, F., Chastel, O., Cherel, Y., Gilg, O., Golubova, E., Kitaysky, A., Luff, K., Seewagen, C.L., Strøm, H., Will, A.P., Yannic, G., Giraudeau, M., Fort, J., 2022. Quantitative meta-analysis reveals no association between mercury contamination and body condition in birds. Biol. Rev. 97 (4), 1253–1271.

Chastel, O., Fort, J., Ackerman, J.T., Albert, C., Angelier, F., Basu, N., Blévin, P., Brault-Favrou, M., Bustnes, J.O., Bustamante, P., Danielsen, J., Descamps, S., Dietz, R., Erikstad, K.E., Eulaers, I., Ezhov, A., Fleishman, A.B., Gabrielsen, G.W., Gavrilo, M., Gilchrist, G., Gilg, O., Gislason, S., Golubova, E., Goutte, A., Grémillet, D., Hallgrimsson, G.T., Hansen, E.S., Hanssen, S.A., Hatch, S., Huffeldt, N.P., Jakubas, D., Jónsson, J.E., Kitaysky, A.S., Kolbeinsson, Y., Krasnov, Y., Letcher, R.J., Linnebjerg, J.F., Mallory, M., Merkel, F.R., Moe, B., Montevecchi, W.J., Mosbech, A., Olsen, B., Orben, R.A., Provencher, J.F., Ragnarsdottir, S.B., Reiertsen, T.K., Rojek, N., Romano, M., Søndergaard, J., Strøm, H., Takahashi, A., Tartu, S., Thórarinsson, T.L., Thiebot, J.B., Will, A.P., Wilson, S., Wojczulanis-Jakubas, K., Yannic, G., 2022. Mercury contamination and potential health risks to Arctic seabirds and shorebirds. Sci. Total Environ. 844 (2022), 156944.

Cherel, Y., Mauget, R., Lacroix, A., Gilles, J., 1994. Seasonal and fasting-related changes in circulating gonadal steroids and prolactin in king penguins, *Aptenodytes patagonicus*. Physiol. Zool. 67 (5), 1154–1173.

Cherel, Y., Hobson, K.A., Bailleul, F., Groscolas, R., 2005. Nutrition, physiology, and stable isotopes: new information from fasting and molting penguins. Ecology 86 (11), 2881–2888.

Criscuolo, F., Chastel, O., Gabrielsen, G.W., Lacroix, A., Le Maho, Y., 2002. Factors affecting plasma concentrations of prolactin in the common eider *Somateria mollissima*. Gen. Comp. Endocrinol. 125 (3), 399–409.

Criscuolo, F., Chastel, O., Bertile, F., Gabrielsen, G.W., Maho, Y.L., Raclot, T., 2005. Corticosterone alone does not trigger a short term behavioural shift in incubating female common eiders *Somateria mollissima*, but does modify long term reproductive success. J. Avian Biol. 36 (4), 306–312.

Criscuolo, F., Bertile, F., Durant, J.M., Raclot, T., Gabrielsen, G.W., Massemin, S., Chastel, O., 2006. Body mass and clutch size may modulate prolactin and corticosterone levels in eiders. Physiol. Biochem. Zool. 79 (3), 514–521.

Crossin, G.T., Trathan, P.N., Phillips, R.A., Gorman, K.B., Dawson, A., Sakamoto, K.Q., Williams, T.D., 2012. Corticosterone predicts foraging behavior and parental care in macaroni penguins. Am. Nat. 180 (1), E31–E41.

Dalpadado, P., Hop, H., Rønning, J., Pavlov, V., Sperfeld, E., Buchholz, F., Rey, A., Wold, A., 2016. Distribution and abundance of euphausiids and pelagic amphipods in Kongsfjorden, Isfjorden and Rijpfjorden (Svalbard) and changes in their relative importance as key prey in a warming marine ecosystem. Polar Biol. 39 (10), 1765–1784.

De La Vega, C., Jeffreys, R.M., Tuerena, R., Ganeshram, R., Mahaffey, C., 2019. Temporal and spatial trends in marine carbon isotopes in the Arctic Ocean and implications for food web studies. Glob. Chang. Biol. 25 (12), 4116–4130.

Descamps, S., Bêty, J., Love, O.P., Gilchrist, H.G., 2011. Individual optimization of reproduction in a long-lived migratory bird: a test of the condition-dependent model of laying date and clutch size. Funct. Ecol. 25 (3), 671–681.

DiMento, B.P., Mason, R.P., Brooks, S., Moore, C., 2019. The impact of sea ice on the air-sea exchange of mercury in the Arctic Ocean. Deep Sea Res. Part I 144, 28–38.

Durant, J.M., Molinero, J.C., Ottersen, G., Reygondeau, G., Stige, L.C., Langangen, Ø., 2019. Contrasting effects of rising temperatures on trophic interactions in marine ecosystems. Sci. Rep. 9 (1), 1–9.

El Halawani, M.E., Burke, W.H., Millam, J.R., Fehrer, S.C., Hargis, B.M., 1984. Regulation of prolactin and its role in gallinaceous bird reproduction. J. Exp. Zool. 232 (3), 521–529.

Erikstad, K.E., Bustnes, J.O., Moum, T., 1993. Clutch-size determination in precocial birds: a study of the common eider. Auk 110 (3), 623–628.

Erikstad, K.E., Tveraa, T., 1995. Does the cost of incubation set limits to clutch size in common eiders *Somateria mollissima*? Oecologia 103 (3), 270–274.

Esparza, I., Elliott, K.H., Choy, E.S., Braune, B.M., Letcher, R.J., Patterson, A., Fernie, K. J., 2022. Mercury, legacy and emerging POPs, and endocrine-behavioural linkages: implications of Arctic change in a diving seabird. Environ. Res. 212, 113190.

Evers, D., 2018. The effects of methylmercury on wildlife: a comprehensive review and approach for interpretation. Encyclopedia Anthropocene 5, 181–194.

Fort, J., Grémillet, D., Traisnel, G., Amélineau, F., Bustamante, P., 2016. Does temporal variation of mercury levels in Arctic seabirds reflect changes in global environmental contamination, or a modification of Arctic marine food web functioning? Environ. Pollut. 211, 382–388.

Fox, J., Weisberg, S., 2019. An R Companion to Applied Regression, Third edition. Sage, Thousand Oaks CA.

Frederiksen, M., Edwards, M., Richardson, A.J., Halliday, N.C., Wanless, S., 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. J. Anim. Ecol. 75 (6), 1259–1268.

Gilmour, M.E., Lavers, J.L., Lamborg, C., Chastel, O., Kania, S.A., Shaffer, S.A., 2019. Mercury as an indicator of foraging ecology but not the breeding hormone prolactin in seabirds. Ecol. Ind. 103, 248–259.

González-Medina, E., Castillo-Guerrero, J.A., Herzka, S.Z., Fernández, G., 2018. High quality diet improves lipid metabolic profile and breeding performance in the blue-footed booby, a long-lived seabird. PLoS One 13 (2), e0193136.

Graves, S., Piepho, H.P., Selzer, M.L. 2015. Package 'multcompView'. Visualizations of paired comparisons.

Hamer, K.C., Monaghan, P., Uttley, J.D., Walton, P., Burns, M.D., 1993. The influence of food supply on the breeding ecology of kittiwakes *Rissa tridactyla* in Shetland. Ibis 135 (3), 255–263.

Hamilton, D.J., Nudds, T.D., Neate, J., 1999. Size-selective predation of blue mussels (*Mytilus edulis*) by common eiders (*Somateria mollissima*) under controlled field conditions. Auk 116 (2), 403–416.

Hanssen, S., Engebretsen, H., Erikstad, K., 2002. Incubation start and egg size in relation to body reserves in the common eider. Behav. Ecol. Sociobiol. 52 (4), 282–288.

Hanssen, S.A., Moe, B., Bårdsen, B.-J., Hanssen, F., Gabrielsen, G.W., 2013. A natural anti-predation experiment: predator control and reduced sea ice increases colony size in a long-lived duck. Ecol. Evol. 3, 3554–3564. https://doi.org/10.1002/ece3.735.

Hawkings, J.R., Linhoff, B.S., Wadham, J.L., Stibal, M., Lamborg, C.H., Carling, G.T., Lamarche-Gagnon, G., Kohler, T.J., Ward, R., Hendry, K.R., Falteisek, L., Kellerman, A.M., Cameron, K.A., Hatton, J.E., Tingey, S., Holt, A.D., Vinšová, P., Hofer, S., Bulínová, M., Vètrovský, T., Meire, L., Spencer, R.G.M., 2021. Large subglacial source of mercury from the southwestern margin of the Greenland Ice Sheet. Nat. Geosci. 14 (7), 496–502.

Hennin, H.L., Legagneux, P., Bêty, J., Williams, T.D., Gilchrist, H.G., Baker, T.M., Love, O.P., 2015. Pre-breeding energetic management in a mixed-strategy breeder. Oecologia 177 (1), 235–243.

Hennin, H.L., Dey, C.J., Bêty, J., Gilchrist, H.G., Legagneux, P., Williams, T.D., Love, O. P., Portugal, S., 2018. Higher rates of prebreeding condition gain positively impacts clutch size: a mechanistic test of the condition-dependent individual optimization model. Funct. Ecol. 32 (8), 2019–2028.

Hobson, K.A., Alisauskas, R.T., Clark, R.G., 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. Condor 95 (2), 388–394.

Hobson, K.A., Ambrose Jr, W.G., Renaud, P.E., 1995. Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from δ^{13}C and δ^{15}N analysis. Mar. Ecol. Prog. Ser. 128, 1–10.

Hobson, K.A., Welch, H.E., 1992. Determination of trophic relationships within a high Arctic marine food web using δ^{13}C and δ^{15}N analysis. Mar. Ecol. Prog. Ser. 84 (1), 9–18.

Hoegh-Guldberg, O., Bruno, J.F., 2010. The impact of climate change on the world's marine ecosystems. Science 328 (5985), 1523–1528.

Horvat, C., Jones, D.R., Iams, S., Schroeder, D., Flocco, D., Feltham, D., 2017. The frequency and extent of sub-ice phytoplankton blooms in the Arctic Ocean. Sci. Adv. 3 (3), e1601191.

Hovinen, J.E., Tarroux, A., Ramírez, F., Forero, M., Descamps, S., 2019. Relationships between isotopic ratios, body condition and breeding success in a High Arctic seabird community. Mar. Ecol. Prog. Ser. 613, 183–195.

IPCC 2019: Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems [P.R. Shukla, J. Skea, E. Calvo Buendia, V. Masson-Delmotte, H.-O. Pörtner, D. C. Roberts, P. Zhai, R. Slade, S.

Connors, R. van Diemen, M. Ferrat, E. Haughey, S. Luz, S. Neogi, M. Pathak, J. Petzold, J. Portugal Pereira, P. Vyas, E. Huntley, K. Kissick, M. Belkacemi, J. Malley, (eds.)].

Jagielski, P.M., Dey, C.J., Gilchrist, H.G., Richardson, E.S., Love, O.P., Semeniuk, C.A., 2021. Polar bears are inefficient predators of seabird eggs. R. Soc. Open Sci. 8 (4), 210391.

Jamieson, S.E., Gilchrist, H.G., Merkel, F.R., Falk, K., Diamond, A.W., 2006. An evaluation of methods used to estimate carcass composition of common eiders *Somateria mollissima*. Wildl. Biol. 12 (2), 219–226.

Jean-Gagnon, F., Legagneux, P., Gilchrist, G., Bélanger, S., Love, O.P., Bêty, J., 2018. The impact of sea ice conditions on breeding decisions is modulated by body condition in an arctic partial capital breeder. Oecologia 186 (1), 1–10.

Johannessen, O.M., Bengtsson, L., Miles, M.W., Kuzmina, S.I., Semenov, V.A., Alekseev, G.V., Nagurnyi, A.P., Zakharov, V.F., Bobylev, L.P., Pettersson, L.H., Hasselmann, K., 2004. Arctic climate change: observed and modelled temperature and sea-ice variability. Tellus A: Dyn. Meteorol. Oceanogr. 56 (4), 28–341.

Kahru, M., Brotas, V., Manzano-Sarabia, M., Mitchell, B.G., 2011. Are phytoplankton blooms occurring earlier in the Arctic? Glob. Chang. Biol. 17 (4), 1733–1739.

Kelly, J.F., 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Can. J. Zool. 78 (1), 1–27.

Larsson, K., Hajdu, S., Kilpi, M., Larsson, R., Leito, A., Lyngs, P., 2014. Effects of an extensive *Prymnesium polylepis* bloom on breeding eiders in the Baltic Sea. J. Sea Res. 88, 21–28.

Legagneux, P., Gauthier, G., Berteaux, D., Bêty, J., Cadieux, M.-C., Bilodeau, F., Bolduc, E., McKinnon, L., Tarroux, A., Therrien, J.-F., Morissette, L., Krebs, C.J., 2012. Disentangling trophic relationships in a High Arctic tundra ecosystem through food web modeling. Ecology 93 (7), 1707–1716.

Leu, E., Søreide, J.E., Hessen, D.O., Falk-Petersen, S., Berge, J., 2011. Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: timing, quantity, and quality. Prog. Oceanogr. 90 (1–4), 18–32.

Lewis, K.M., van Dijken, G.L., Arrigo, K.R., 2020. Changes in phytoplankton concentration now drive increased Arctic Ocean primary production. Science 369 (6500), 198–202.

Long, J.A. 2019. Interactions: Comprehensive, User-Friendly Toolkit for Probing Interactions. R package version 1.1.0, https://cran.r-project.org/package=interactions.

Macdonald, R.W., Barrie, L.A., Bidleman, T.F., Diamond, M.L., Gregor, D.J., Semkin, R.G., Strachan, W.M.J., Li, Y.F., Wania, F., Alaee, M., Alexeeva, L.B., 2000. Contaminants in the Canadian Arctic: 5 years of progress in understanding sources, occurrence and pathways. Sci. Total Environ. 254 (2–3), 93–234.

Mazerolle, M.J. 2020. Model Selection and Multimodel Inference Based on (Q)AIC(c). R package version 2.3-1, https://cran.r-project.org/web/packages/AICcmodavg/index.html.

McMahon, K.W., Ambrose Jr, W.G., Johnson, B.J., Sun, M.Y., Lopez, G.R., Clough, L.M., Carroll, M.L., 2006. Benthic community response to ice algae and phytoplankton in Ny-Ålesund, Svalbard. Mar. Ecol. Prog. Ser. 310, 1–14.

McPartland, M., Garbus, S.E., Lierhagen, S., Sonne, C., Krøkje, Å., 2020. Lead isotopic signatures in blood from incubating common eiders (*Somateria mollissima*) in the central Baltic Sea. Environ. Int. 142, 105874.

Milton, G.R., Iverson, S.A., Smith, P.A., Tomlik, M.D., Parsons, G.J., Mallory, M.L., 2016. Sex-specific survival of adult common eiders in Nova Scotia, Canada. J. Wildlife Manage. 80 (8), 1427–1436.

Mohring, B., Angelier, F., Jaatinen, K., Parenteau, C., Öst, M., 2021. Parental investment under predation threat in incubating common eiders (*Somateria mollissima*): a hormonal perspective. Front. Ecol. Evol. 474 (9), 637561.

Moline, M.A., Karnovsky, N.J., Brown, Z., Divoky, G.J., Frazer, T.K., Jacoby, C.A., Torres, J.J., Fraser, W.R., 2008. High latitude changes in ice dynamics and their impact on polar marine ecosystems. Ann. N. Y. Acad. Sci. 1134, 267–319.

Najafi, M.R., Zwiers, F.W., Gillett, N.P., 2015. Attribution of Arctic temperature change to greenhouse-gas and aerosol influences. Nat. Clim. Chang. 5 (3), 246–249.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37, 637–669.

Pecuchet, L., Blanchet, M.A., Frainer, A., Husson, B., Jørgensen, L.L., Kortsch, S., Primicerio, R., 2020. Novel feeding interactions amplify the impact of species redistribution on an Arctic food web. Glob. Chang. Biol. 26 (9), 4894–4906.

Peig, J., Green, A.J., 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118 (12), 1883–1891.

Perkins, A., Ratcliffe, N., Suddaby, D., Ribbands, B., Smith, C., Ellis, P., Meek, E., Bolton, M., Dunn, J., 2018. Combined bottom-up and top-down pressures drive catastrophic population declines of Arctic skuas in Scotland. J. Anim. Ecol. 87 (6), 1573–1586.

Prop, J., Aars, J., BÃ¥rdsen, B.J., Hanssen, S.A., Bech, C., Bourgeon, S., de Fouw, J., Gabrielsen, G.W., Lang, J., Noreen, E., Oudman, T., Sittler, B., Stempniewicz, L., Tombre, I., Wolters, E., Moe, B., 2015. Climate change and the increasing impact of polar bears on bird populations. Front. Ecol. Evol. 3.

Provencher, J.F., Forbes, M.R., Hennin, H.L., Love, O.P., Braune, B.M., Mallory, M.L., Gilchrist, H.G., 2016. Implications of mercury and lead concentrations on breeding physiology and phenology in an Arctic bird. Environ. Pollut. 218, 1014–1022.

Renaut, S., Devred, E., Babin, M., 2018. Northward expansion and intensification of phytoplankton growth during the early ice-free season in Arctic. Geophys. Res. Lett. 45 (19), 10590–10598.

RStudio Team, 2022. RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA http://www.rstudio.com/.

Rydberg, J., Klaminder, J., Rosén, P., Bindler, R., 2010. Climate driven release of carbon and mercury from permafrost mires increases mercury loading to sub-arctic lakes. Sci. Total Environ. 408 (20), 4778–4783.

Schielzeth, H., 2010. Simple means to improve the interpretability of regression coefficients. Methods Ecol. Evol. 1 (2), 103–113.

Schummer, M.L., Petrie, S.A., Bailey, R.C., 2008. Dietary overlap of sympatric diving ducks during winter on northeastern Lake Ontario. Auk 125 (2), 425–433.

Schuster, P.F., Schaefer, K.M., Aiken, G.R., Antweiler, R.C., Dewild, J.F., Gryziec, J.D., Gusmeroli, A., Hugelius, G., Jafarov, E., Krabbenhoft, D.P., Liu, L., Herman-Mercer, N., Mu, C., Roth, D.A., Schaefer, T., Striegl, R.G., Wickland, K.P., Zhang, T., 2018. Permafrost stores a globally significant amount of mercury. Geophys. Res. Lett. 45 (3), 1463–1471.

Screen, J.A., Simmonds, I., 2010. Increasing fall-winter energy loss from the Arctic Ocean and its role in Arctic temperature amplification. Geophys. Res. Lett. 37 (16), L16707.

Sénéchal, É., Bêty, J., Gilchrist, H.G., Hobson, K.A., Jamieson, S.E., 2011. Do purely capital layers exist among flying birds? Evidence of exogenous contribution to arctic-nesting common eider eggs. Oecologia 165 (3), 593–604.

Shiozaki, T., Fujiwara, A., Sugie, K., Nishino, S., Makabe, A., Harada, N., 2022. Bottom-associated phytoplankton bloom and its expansion in the Arctic Ocean. Glob. Chang. Biol. 28 (24), 7286–7295.

Smith, P.A., Tulp, I., Schekkerman, H., Gilchrist, H.G., Forbes, M.R., 2012. Shorebird incubation behaviour and its influence on the risk of nest predation. Anim. Behav. 84 (4), 835–842.

Smith, R.A., Yurkowski, D.J., Parkinson, K.J., Fort, J., Hennin, H.L., Gilchrist, H.G., Hobson, K.A., Mallory, M.L., Bustamante, P., Danielsen, J., Garbus, S.E., Hanssen, S.A., Jónsson, J.E., Latty, C.J., Magnúsdóttir, E., Moe, B., Parsons, G.J., Sonne, C., Tertitski, G., Love., O.P., 2021. Environmental and life-history factors influence inter-colony multidimensional niche metrics of a breeding Arctic marine bird. Sci. Total Environ. 796, 148935.

Smith, R.A., Albonaimi, S.S., Hennin, H.L., Gilchrist, H.G., Fort, J., Parkinson, K.J., Provencher, J.F., Love, O.P., 2022. Exposure to cumulative stressors affects the laying phenology and incubation behaviour of an Arctic-breeding marine bird. Sci. Total Environ. 807, 150882.

Sockman, K.W., Schwabl, H., Sharp, P.J., 2000. The role of prolactin in the regulation of clutch size and onset of incubation behavior in the American kestrel. Horm. Behav. 38 (3), 168–176.

Sonke, J.E., Teisserenc, R., Heimbürger-Boavida, L.E., Petrova, M.V., Marusczak, N., Le Dantec, T., Chupakov, A.V., Li, C., Thackray, C.P., Sunderland, E.M., Tananaev, N., 2018. Eurasian river spring flood observations support net Arctic Ocean mercury export to the atmosphere and Atlantic Ocean. Proc. Natl. Acad. Sci. 115 (50), E11586–E11594.

Suryan, R.M., Irons, D.B., Brown, E.D., Jodice, P.G., Roby, D.D., 2006. Site-specific effects on productivity of an upper trophic-level marine predator: bottom-up, top-down, and mismatch effects on reproduction in a colonial seabird. Prog. Oceanogr. 68 (2–4), 303–328.

Tan, S.W., Meiller, J.C., Mahaffey, K.R., 2009. The endocrine effects of mercury in humans and wildlife. Crit. Rev. Toxicol. 39 (3), 228–269.

Tartu, S., Goutte, A., Bustamante, P., Angelier, F., Moe, B., Clément-Chastel, C., Bech, C., Gabrielsen, G.W., Bustnes, J.O., Chastel, O., 2013. To breed or not to breed: endocrine response to mercury contamination by an Arctic seabird. Biol. Lett. 9 (4), 20130317.

Tartu, S., Bustamante, P., Goutte, A., Cherel, Y., Weimerskirch, H., Bustnes, J.O., Chastel, O., 2014. Age-related mercury contamination and relationship with luteinizing hormone in a long-lived Antarctic bird. PLoS One 9 (7), e103642.

Tartu, S., Angelier, F., Wingfield, J.C., Bustamante, P., Labadie, P., Budzinski, H., Weimerskirch, H., Bustnes, J.O., Chastel, O., 2015. Corticosterone, prolactin and egg neglect behavior in relation to mercury and legacy POPs in a long-lived Antarctic bird. Sci. Total Environ. 505, 180–188.

Tartu, S., Bustamante, P., Angelier, F., Lendvai, Á.Z., Moe, B., Blévin, P., Bech, C., Gabrielsen, G.W., Bustnes, J.O., Chastel, O., Hörak, P., 2016. Mercury exposure, stress and prolactin secretion in an Arctic seabird: an experimental study. Funct. Ecol. 30 (4), 596–604.

Tartu, S., Blévin, P., Bustamante, P., Angelier, F., Bech, C., Bustnes, J.O., Chierici, M., Fransson, A., Gabrielsen, G.W., Goutte, A., Moe, B., Sauser, C., Sire, J., Barbraud, C., Chastel, O., 2022. A U-Turn for mercury concentrations over 20 years: how do environmental conditions affect exposure in arctic seabirds? Environ. Sci. Tech. 56, 2443–2454.

Timmermans, M.L., Proshutinsky, A., Krishfield, R.A., Perovich, D.K., Richter-Menge, J.A., Stanton, T.P., Toole, J.M., 2011. Surface freshening in the Arctic Ocean's Eurasian Basin: an apparent consequence of recent change in the wind-driven circulation. J. Geophys. Res. Oceans 116 (C8), C00D03.

Vasseur, D.A., McCann, K.S., 2005. A mechanistic approach for modeling temperature-dependent consumer-resource dynamics. Am. Nat. 166 (2), 184–198.

Vinarski, M.V., Bolotov, I.N., Aksenova, O.V., Babushkin, E.S., Bespalaya, Y.V., Makhrov, A.A., Nekhaev, I.O., Vikhrev, I.V., 2021. Freshwater Mollusca of the Circumpolar Arctic: a review on their taxonomy, diversity and biogeography. Hydrobiologia 848 (12), 2891–2918.

Watt, C.A., Orr, J., Ferguson, S.H., 2016. A shift in foraging behaviour of beluga whales Delphinapterus leucas from the threatened Cumberland Sound population may reflect a changing Arctic food web. Endanger. Species Res. 31, 259–270.

Wayland, M., Gilchrist, H.G., Neugebauer, E., 2005. Concentrations of cadmium, mercury and selenium in common eider ducks in the eastern Canadian arctic: influence of reproductive stage. Sci. Total Environ. 351, 323–332.

Węsławski, J.M., Kendall, M.A., Włodarska-Kowalczuk, M., Iken, K., Kędra, M., Legezynska, J., Sejr, M.K., 2011. Climate change effects on Arctic fjord and coastal

macrobenthic diversity—observations and predictions. Mar. Biodivers. 41 (1), 71–85.
Whitney, M.C., Cristol, D.A., 2017. Impacts of sublethal mercury exposure on birds: a detailed review. Rev. Environ. Contam. Toxicol. 244, 113–163.
Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York https://ggplot2.tidyverse.org.
Wiener, J.G., Krabbenhoft, D.P., Heinz, G.H., Scheuhammer, A.M., 2003. Ecotoxicology of mercury. Handb. Ecotoxicol. 2, 409–463.
Zhu, X., Kusaka, Y., Sato, K., Zhang, Q., 2000. The endocrine disruptive effects of mercury. Environ. Health Prev. Med. 4 (4), 174–183.
Zika, J.D., Skliris, N., Blaker, A.T., Marsh, R., Nurser, A.G., Josey, S.A., 2018. Improved estimates of water cycle change from ocean salinity: the key role of ocean warming. Environ. Res. Lett. 13 (7), 074036x.

Further reading

Chastel, O., Lacroix, A., Weimerskirch, H., Gabrielsen, G.W., 2005. Modulation of prolactin but not corticosterone responses to stress in relation to parental effort in a long-lived bird. Horm. Behav. 47 (4), 459–466.