Multiple stressors: evaluating the effect of pollution, climate change and oceanographic processes in Tropical and Arctic seabirds

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A female brown booby nesting at Bona Island, Panama

A thick-billed murre with a GPS/accelerometer biologger

Preface

This Master's project was supervised by Dr. Kyle Elliott from Macdonald campus of McGill University and Dr. Héctor Guzmán from the Smithsonian Tropical Research Institute.

The purpose of the thesis is to explore the impact of multiple stressors on seabird performance by describing the effect of co-occurring natural stressors in a tropical species and the effect of anthropogenic stressors in an Arctic species.

This thesis is divided into two chapters. The first chapter looks at the effects of upwelling and other highly correlated oceanographic variables on the egg/chick survival probability of the brown booby (*Sula leucogster*), a widely distributed seabird in the Tropics. The second chapter looks at the impact of chemical contamination on the thick-billed murres' (*Uria lomvia*) ability to adapt to changes in ice availability in the Canadian Arctic. This chapter will be submitted to the journal *Environmental Research*.

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Abstract

Wildlife and ecosystems are currently exposed to multiple stressors that affect ecological patterns at both individual and ecosystem levels. Multiple natural and anthropogenic stressors often occur simultaneously and interact in complex ways which are not yet fully understood. For the past three decades, researchers have been trying to understand and predict the effect of the interactions between stressors. However, with new stressors constantly emerging and the effects of other stressors intensifying, understanding the effects of co-occurring stressors is still a priority for risk assessment, and the identification of conservation and mitigation measures. Here, we used two seabird species as indicators to help assess the effects of co-occurring natural and anthropogenic stressors threatening marine ecosystems on two different systems, the Tropics and the Arctic.

In the first chapter of this thesis, I studied the brown booby (*Sula leucogaster*), a widely distributed seabird in the Tropics to assess the effects of co-occurring natural stressors, specifically upwelling and highly correlated oceanographic conditions (sea-surface temperature, precipitation, chlorophyll-a concentration, wind speed and wind direction) on reproductive success. I used productivity data from 61 nests from the brown booby colony at Bona Island in the Gulf of Panama, as well as remote-sensing environmental features. Chick survival probability was positively associated with chlorophyll-α concentration and negatively associated with (chlorophyll-α)^2 and laying date. This study provides evidence that upwelling has a strong effect over tropical seabirds reproduction and that seabirds in the Tropics follow seasonal pulses similar to those observed in species in polar and temperate regions. Nonetheless, my findings need to be complemented with more years of monitoring or information on other tropical species to properly assess how upwelling and oceanographic conditions are impacting tropical seabirds' reproductive success.

In the second chapter, I studied the thick-billed murre (*Uria lomvia*), a pagophilic (ice-associated) deep-diving seabird, to investigate the effects of chemical contamination on behavioural plasticity in response to changes in ice availability in the Canadian Arctic. I used data on contaminants (Hg, PCB congeners, OC pesticides, BFRs and PBDEs) and hormone concentrations (thyroid and stress hormones) in blood, as well as foraging behaviours (time spent diving, swimming and flying, diving depth and number of dives) collected over three breeding seasons (2016-2018) at Coats Island in Hudson Bay. Circulating concentrations of PCB congeners, OC pesticides, BFRs and PBDEs were extremely low, therefore, I only investigated the potential relationships between circulating mercury, thyroid and corticosterone levels and foraging behaviours. Methylmercury concentrations were correlated with blood plasma total T3 levels in thick-billed murres, indicating potential thyroid function disruption. Thyroid function was disrupted in 2016 and 2017, both years with early-ice melting, but not 2018, a year with late-melting conditions. Moreover, total T3 was correlated negatively with total time spent underwater during the same years, which is unsurprising as total T3 increases metabolism and thus shortens dive duration. In summary, in warm years, methylmercury may disrupt total T3 levels and thus interfere with how the murres can adjust to changing ice levels by altering their diving behaviour. Thus, our study demonstrates how the indirect effects of contaminants on behaviour may affect the way species cope with climate change.

Resumé

La faune et les écosystèmes sont actuellement exposés à de multiples facteurs de stress qui affectent les tendances écologiques au niveau individuel et écosystémique. De multiples facteurs de stress naturels et anthropiques se produisent souvent simultanément et interagissent de manières complexes qui ne sont pas encore entièrement comprises. Au cours des trois dernières décennies, les chercheurs ont tenté de comprendre et de prédire l'effet des interactions entre les facteurs de stress. Cependant, avec l'émergence constante de nouveaux facteurs de stress et l'intensification des effets d'autres facteurs de stress, la compréhension des effets des facteurs de stress concomitants est toujours une priorité pour l'évaluation des risques et l'identification de mesures de conservation et d'atténuation. Ici, nous avons utilisé deux espèces d'oiseaux marins comme indicateurs pour aider à évaluer les effets des facteurs de stress naturels et anthropiques concomitants menaçant les écosystèmes marins sur deux systèmes différents, les tropiques et l'Arctique.

Dans le premier chapitre de cette thèse, j'ai étudié le Fou brun (*Sula leucogaster*), un oiseau marin largement répandu dans les tropiques pour évaluer les effets de facteurs de stress naturels, en particulier la remontée des eaux et les conditions océanographiques fortement corrélées (température de surface de la mer, précipitations, concentration en chlorophylle-a, vitesse et direction du vent) sur le succès reproducteur. J'ai utilisé les données de productivité de 61 nids de la colonie de Fous bruns de l'île de Bona dans le golfe du Panama, ainsi que des caractéristiques environnementales de télédétection. J'ai trouvé que la probabilité de survie des poussins était positivement associée à la concentration de chlorophylle-α et négativement associée avec (chlorophylle-α)^2 et à la date de ponte. Cette étude fournit des preuves que la remontée des eaux a un effet important sur la reproduction des oiseaux marins tropicaux et que les oiseaux marins des tropiques suivent des impulsions saisonnières similaires à celles enregistrées chez les espèces des régions polaires et tempérées. Néanmoins, mes conclusions doivent être complétées par plus d'années de surveillance ou d'informations sur d'autres espèces tropicales pour évaluer correctement l'impact des remontées d'eau et des conditions océanographiques sur le succès de reproduction des oiseaux marins tropicaux.

Dans le deuxième chapitre, j'ai étudié le Guillemot de Brünnich (*Uria lomvia*), un oiseau marin pagophile (associé à la glace) qui plonge en profondeur, pour étudier les effets de la contamination chimique sur la plasticité comportementale en réponse aux changements de disponibilité de la glace dans l'Arctique canadien. J'ai utilisé des données sur les contaminants (Hg, congénères de PCB, pesticides OC, BFR et PBDE) et les concentrations d'hormones (FT3, TT3, FT4, TT4 et CORT) sur le sang, ainsi que les comportements de recherche de nourriture (temps passé à plonger, nager et voler, plonger profondeur et nombre de plongées) recueillies au cours de trois saisons de reproduction (2016-2018) sur l'île Coats dans la baie d'Hudson. Les concentrations de congénères de PCB, de pesticides OC, de RFB et de PBDE étaient extrêmement faibles. Par conséquent, j'ai seulement étudié les relations potentielles entre les niveaux de mercure, de thyroïde et de corticostérone et les comportements de recherche de nourriture. J'ai découvert que les concentrations de méthylmercure étaient corrélées avec les taux plasmatiques de T3 total chez les Guillemots de Brünnich, indiquant une perturbation potentielle de la fonction thyroïdienne. La fonction thyroïdienne a été perturbée en 2016 et 2017, deux années avec une débâcle précoce, mais pas en 2018, une année avec des conditions de glace moyennes. De plus, le T3 total était négativement corrélé avec le temps total passé sous l'eau au cours des mêmes années, ce qui n'est pas surprenant car le T3 total augmente le métabolisme et raccourcit ainsi la durée de la plongée. En résumé, pendant les années chaudes, le méthylmercure peut perturber les niveaux totaux de T3 et ainsi interférer avec la façon dont les Guillemots peuvent s'adapter aux changements des niveaux de glace en modifiant leur comportement de plongée. Ainsi, notre étude démontre comment les effets indirects des contaminants sur le comportement peuvent affecter la façon dont les espèces font face au changement climatique.

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Contribution of coauthors

Given that my original research project changed with the COVID-19 outbreak, I used existing data for both of my chapters. The data were previously collected by Dr. Héctor Guzmán (chapter 1) and Dr. Kyle Elliott, Dr. Kim Fernie and Allison Patterson (chapter 2). I designed and analyzed the first chapter with the help of Dr. Héctor Guzmán and Dr. Kyle Elliott. Co-authors of chapter 2 (Dr. Kyle Elliott, Dr. Kim Fernie, Dr. Birgit Braune and Robert Letcher, Allison Patterson) designed the field component of the study, collected the blood samples and ran the chemical analyses. Dr. Kim Fernie and Dr. Emily Choy, also coauthors of the second chapter, helped with important feedback. I completed the statistical analyses and wrote both chapters with help from coauthors.

Introduction

Wildlife around the globe is currently exposed to natural and anthropogenic stressors that influence their physiology, behaviour and fitness. Given the range of human activities and the propagation of their effects, most likely all wildlife populations are currently exposed to multiple anthropogenic stressors occurring simultaneously (Breitburg et al. 1998). Therefore, for the past three decades ecologists have been trying to understand the effects of co-occurring stressors, both natural and anthropogenic, on wildlife and the environment (Breitburg et al. 1998; Piggott et al. 2015). However, these interactions can be complex (Orr et al. 2020), and as new stressors continue to appear (e.g., 'emerging' chemical contaminants) or to intensify (e.g., climate change), understanding the potential effects of multiple stressors remain a priority to predict ecological change (Holmstrup et al. 2010 & Piggot et al. 2015).

The use of indicator species can help assessments of the impact of natural and anthropogenic stressors at a larger scale. Indicator species are living organisms that are easily monitored and whose status reflects or predicts the condition(s) of their environment (Burger 2006; Siddig et al. 2016). Indicator species are often used to assess a number of stressors and are useful in ecosystem-based management (Burger 2006). For example, arable weed species can act as indicators of biodiversity in agro-ecosystems (Albrecht 2003) while raptors are commonly use as indicators of pesticide contamination (Burger 2006). In marine environments, seabirds are often used as indicators of marine ecosystem function, as they offer a unique insight into ecosystem status and change (Piatt et al. 2007). Colonial seabirds are highly visible animals that gather annually in large numbers, making them easy to sample. Moreover, they forage over large areas and at high trophic levels, integrating information over large marine spatial scales and multiple trophic scales, while detecting changes at lower trophic levels (Furness and Camphuysen 1997; Elliott and Elliott 2013). Therefore, seabirds are ideal models to study the effects of multiple stressors in Tropical and Arctic marine environments.

The general objective of this thesis is to broaden knowledge of the effects of co-occurring natural and anthropogenic stressors on marine ecosystems using two widely distributed seabird species, the brown booby (*Sula leucogaster*) and the thick-billed murre (*Uria lomvia*). The first chapter aims to assess the effects of upwelling and other oceanographic conditions on reproductive success of tropical seabirds. Seabirds in temperate and polar regions are known to breed during seasonal pulses, however this has been much less explored in tropical species. Here, I explore whether tropical seabirds in seasonal environments like the Gulf of Panama experience changes in its reproductive success caused by natural stressors. In the Gulf of Panama upwelling occurs seasonally from January to May, coinciding with the brown booby's early breeding season, specifically when chick rearing has started for early breeders. I hypothesize that chick survival probability will be higher in offspring exposed to upwelling conditions, thus chicks born early in the breeding season will have higher chances of survival.

The second chapter aims to address how co-occurring anthropogenic stressors affect seabirds in the Arctic. Through the analysis of three years of GPS-accelerometer data, circulating thyroid and corticosterone hormone concentrations, as well as mercury (Hg), polychlorinated biphenyls (PCBs), organochlorines (OCs), brominated flame retardants (BFRs) and polybrominated diphenyl ethers (PBDEs) concentrations in the blood, I evaluate whether chemical contamination is affecting the ability of thick-billed murres to adapt to changes in the sea-ice availability. I hypothesize that high contamination levels will disrupt behavioural plasticity in response to changes in ice availability by altering hormone levels. Through this study I aim to increase knowledge of chemical contamination and climate change, a particularly potent combination in the Arctic (Jenssen 2006).

Literature Review

Wildlife and ecosystems are currently affected at different temporal and ecological scales by a variety of stressors (Breitburg et al. 1998; Jackson et al. 2021). A stressor can be define as any natural or anthropogenic pressure that causes a quantifiable environmental change, both positive or negative (Boyd and Hutchins 2012). Natural stressors include hypoxia, suboptimal salinity and alterations in nutrient flow (Orr et al. 2020); while anthropogenic stressors include human disturbances such as habitat loss, climate change and chemical contamination (Dirzo et al. 2014; Urban 2015). More often than not, multiple stressors occur simultaneously, interacting in complex ways that can result in combined effects that go beyond antagonistic or synergistic effects (Piggott et al. 2015; Folt et al. 1999). The multiple stressors approach have been commonly used by ecotoxicologists to assess the combined effects of multiple chemical contaminants on individual organisms or populations for almost a century (Bliss 1939; Orr et al. 2020). However, for the past three decades multiple stressor research has now expanded to more diverse stressor combinations (Orr et al. 2020). Despite these efforts, multiple stressors studies are still relatively scarce and given the complexity of the interactions among stressors, predicting, understanding and reducing the effects of co-occuring stressors are among the most important challenges facing conservation biology (Breitburg et al. 1998; Jackson et al. 2021).

Natural stressors

Ecosystems are dynamic environments, where the behaviour, physiology and fitness (e.g., reproductive success and survival) of individuals vary according to changes in the conditions that surround them (Archard et al. 2012; Killen et al. 2013; Love et al. 2013; MacLeod et al. 2018). Environmental factors can become stressors if their condition is insufficient or excessive in comparison with the needs of organisms or ecosystem processes (Boyd and Hutchins 2012; Freedman 2015). As a consequence, natural stressors can have an effect on responses, from individual behavioural traits to entire ecosystem processes (Freedman 2015). Because individuals may exhibit genetically based differences in their tolerance to specific stressors, the way each individual respond to a natural stressor might vary, and therefore influences the evolutionary dynamic of populations and species (Badyaev

2005). Moreover, the response to natural stressors may vary depending of the magnitude of the event, but also may differ among species, as well as at a temporal and special scale (Breitburg et al. 1998; Freedman 2015).

Natural stressors encompass a wide variety of environmental factors, which have been classify by Freedman (2015) into four categories: climatic, chemical, wildfire, physical and biological stressors. Climatic stressors are associated with extremes environmental conditions like temperature, solar radiations, wind, humidity, and the combination of these factors. These factors become stressors if they are insufficient or excessive and therefore, compromise the necessities of organisms or the ecosystem. Under extreme conditions, climatic stressors can cause great damage, such as disturbance by a hurricane, an ice storm, or an extreme precipitation event. Chemical stressors involve environments in which the availability of certain substances is high enough to cause toxicity or alter an organisms behaviour, physiology or fitness (Holmstrup et al. 2010). These stressors can include gases like sulphur dioxide that can be released naturally in volcanic eruptions, and bio-toxins which are produced by organisms like phytoplankton. Physical stressors are associated with disturbances that occurs through a short-term exposure to kinetic energy intense enough to damage organisms and ecosystems. For example, volcanic eruptions, tsunamis and ice souring. Finally, biological stressors are related to interactions among organisms, like herbivory, predation and parasitism (Freedman 2015).

As climate change continues to intensify, environmental factors like floods, droughts and red tides have become natural stressors of even greater concern with severe consequences over wildlife and the ecosystem. For example, the intensification of natural climatic variations, like flooding and droughts, have caused a shift in the animal composition in the Amazon Basin (Bodmer et al. 2018). Changes in animal composition could potentially alter ecosystem dynamics, specifically the community structure and composition as well as resource availability for local people (Bodmer et al. 2018). Similarly, red tides have increased in frequency, duration and extension, becoming a natural chemical stressor threatening wildlife, as well as human health, fishing and tourism (Zohdi and Abbaspour 2019). For example, red tides cause direct poisoning of aquatic animals like fish, crabs and benthic invertebrates by absorption of toxins and oxygen depletion by decomposition of dead flora and fauna (Pierce and Henry 2008; Zohdi and Abbaspour 2019; Gravinese et al. 2020).

In marine ecosystems, multiple climatic stressors, like low pH, dissolved oxygen and temperature, occur simultaneously during seasonal upwelling, affecting species performance and interactions (Menge and Menge 2013). Nonetheless, these co-occurring stressors are usually studied in isolation and few studies have examined the effects of these stressors through a multiple stressors approach (Murie and Bourdeau 2021).

Upwelling

Upwelling is an oceanographic process where coastal or equatorial winds transport surface water offshore, causing them to be replaced by cold and nutrient-rich waters from depth (Wang et al. 2015). These conditions can last for several weeks or months controlled by the Coriolis force (i.e. rotational effects), as well as through geostrophic balance, a state of equilibrium between the Coriolis force and the horizontal pressure-gradient force (Kämpf and Chapman 2016). In more detail, the oceanic circulation that takes place during upwelling consists of wind-driven currents (upwelling jets) parallel to the coast, which move near-bottom water shoreward and upward into the euphotic zone (the upper 200 m of the ocean; NOAA 2017). Through this dynamic process, upwelling jets transport cold water to the surface along with nutrients and organic matter, triggering phytoplankton blooms that support high levels of productivity (Kämpf and Chapman 2016). The combination of these physical and biological conditions make upwelling regions some of the most productive and biodiverse in the world (Largier 2020).

The timing, duration and intensity of coastal upwelling are known to have a critical role in coastal marine ecosystems (Aravena et al. 2014; Bakun et al. 2015). For example, cold conditions are associated with the development of large zooplankton and phytoplankton communities (Rykaczewski and Checkley 2008), as well as an increase in fish availability like anchovy and sardine (Ward et al. 2006; Gomez et al. 2012). These changes in primary productivity can have a direct impact across higher trophic levels (Thompson et al. 2012). In the case of seabirds, variability in climatic upwelling-associated conditions can negatively impact reproductive success, population dynamics and foraging behaviour (Sydeman et al. 2006; Wolf et al. 2010; Lieber et al. 2021). For example, in the California Current Ecosystem, poor upwelling conditions and anomalously warm sea-surface temperature decreased the Cassin's auklet (*Ptychoramphus aleuticus*) hatching success, potentially due to a mismatch in food availability and the timing of breeding (Sydeman et al. 2006). Whereas, seabird's abundance and species richness decreased with sea-surface temperature and salinity, and increased with chlorophyll-α concentration along the Eastern South Pacific Ocean (Serratosa et al. 2020). Moreover, climate change is expected to cause upwelling events to become less frequent, stronger and longer in duration (Iles et al. 2012). In this context, it is important to understand how seabirds respond naturally to upwelling, as well as how they are responding to these modifications, and the potential implications of upwelling on their reproductive success.

Anthropogenic stressors

In addition to natural stressors, global diversity and the ecosystem processes are increasingly impacted by anthropogenic stressors (Dirzo et al. 2014; Urban 2015). The intensification of human activities like agriculture, industrialization and ship traffic have led to two general environmental concerns: 1) the human impact on the environment and ecosystems through alterations in carbon storage, element cycling and climate, and 2) changes in biota and communities caused mainly by the introduction of exotic invasive species, habitat loss and climate change (Chapin et al. 2001). Given the wide range of human activities and its widespread effects, most likely all wildlife populations are currently threatened by anthropogenic stressors (Breitburg et al. 1998). For example, a meta-analysis by Haddad and colleagues (2015) showed that habitat fragmentation reduced biodiversity by 13 to 75% over the past 35 years, and impaired key ecosystem functions by decreasing biomass and altering nutrient cycles. However, other studies have also shown that wildlife can show a high degree of behavioral plasticity to anthropogenic disturbance. For example, in another meta-analysis, Gaynor and colleagues (2018) showed that mammals (n = 141 species) around the world are shifting their hours of activity by becoming more nocturnal. This shift in activity might benefit wildlife by reducing human encounters, however, it could also have negative ecological consequences, including changes in trophic cascades and interspecific interactions, which could potentially have implications for the entire ecosystem community.

Climate change in the Arctic

One of the places where these anthropogenic stressors have been heavily affecting wildlife is the Arctic. This ecosystem is warming at twice the global rate (Post et al. 2013), leading to an annual increase in air temperature of 2.7°C and precipitation of 6.2% since the 1970's (Box et al. 2019). These two factors are the main physical drivers of major changes in various components of the Arctic system, including a decrease in snow cover and an increase in summer tundra greenness, fire risk and river water discharge (Box et al. 2019). Environmental changes can affect wildlife in a variety of ways. For example, a reduction in sea-ice cover is known to reduce suitable habitat for pagophilic (ice-associated) species like the polar bear (*Ursus maritimus*) (Amstrup et al. 2010), while opening new habitats for open-water species, like the killer whale (*Orcinus orca*) (Higdon et al. 2012) and the blue whale (*Balaenoptera musculus*) (Moore et al. 2011). Moreover, the combination of multiple Arctic climate stressor, like permafrost thaw and temperature rise, can lead to earlier and shorter flowering periods and a mismatch between flowering and pollinators with possible subsequent cascading effect through the ecosystem (Høye et al. 2013; Schmidt et al. 2016).

Lower trophic levels often respond more quickly to these environmental changes than higher trophic levels (Franceschini et al. 2009). In the case of Arctic seabirds, climate-related ecological shifts include effects on phenology (Gaston et al. 2005; Moe et al. 2009), prey availability (Gaston and Elliott 2014a; Kortsch et al. 2015) and diet (Grémillet et al. 2015; Amélineau et al. 2019; Divoky et al. 2021), as well as reproduction and foraging behaviour (Gaston et al. 2009b; Shultz et al. 2009; Grémillet et al. 2015; Amélineau et al. 2019; Divoky et al. 2021). Despite seabirds' effort to adjust to the numerous environmental modifications linked to climate change, seabirds might not be able to respond fast enough to keep pace with rapid change. For example, seabirds match chick rearing with phytoplankton bloom which occurs right after the ice departs (Laidre et al. 2008). Yet, climate change can cause ice to melt more rapidly than seabirds are able to respond, creating a mismatch between the time when seabirds rear their offspring and the time of peak food availability, leading to unsustainable levels of energy expenditure (Gaston et al. 2009b). Moreover, diet switching and changes in foraging behaviour have been associated with a reduction in prey quality and greater foraging efforts, modifications that could potentially increase the cost of reproduction and decrease adult survival (Divoky et al. 2021).

Chemical contaminants

In addition to climate change, wildlife in the Arctic are also threatened by chemical contamination, where concentrations of contaminants like mercury (Hg) are particularly high. Chemical contaminants are carried into the Arctic from southern latitudes via ocean currents and rivers and through long-range atmospheric transport (Braune et al. 2005; de Wit et al. 2006). Many lipophilic compounds (i.e., Hg and POPs), bioaccumulate and biomagnify through marine food webs (Dietz et al. 2019), causing marine apex predators such as seals, whales and seabirds to be particularly vulnerable to toxic contamination (Letcher et al. 2010).

Mercury (Hg) is a trace metal found naturally in the environment. However, emissions from anthropogenic sources as well as permafrost thaw have led to an increase in Hg levels (Rydberg et al. 2010; Driscoll et al. 2013; Schaefer et al. 2020). In its organic form, Hg is a potent neurotoxic that can have various deleterious effects on organisms (Dietz et al. 2013). The effects of Hg have been extensively documented in seabirds (Dietz et al. 2013; Ackerman et al. 2016), showing that high Hg concentrations can negatively affect reproduction, survival and growth (Dietz et al. 2019). For example, in thick-billed murres and Arctic terns (*Sterna paradisaea*), eggs injected with methylmercury (MeHg) had reduced egg hatchability and survival at higher doses (Braune et al. 2012). Moreover, in black-legged kittiwakes (*Rissa tridactyla*), individuals with higher Hg concentrations in blood were more likely to avoid breeding (Tartu et al. 2013). Increasing contamination concentrations in marine wildlife, among other reasons, led to the adoption of the Minamata Convention on Mercury, an international agreement to reduce Hg production and use (UNEP 2013).

Persistent organic pollutants (POPs) can also have effects on reproduction, survival, bioenergetics and behaviour (Letcher et al. 2010; Dietz et al. 2019). For example, in glaucous gulls (*Larus hyperboreus*) in the Norwegian Arctic, survival was negatively associated with

OCs in the blood, with females being more sensitive to contamination (Erikstad et al. 2013). In males from the same species, negative associations were found between basal metabolic rate (BMR) and plasma concentrations of ΣPCBs, suggesting potential altered function of the basal metabolism (Verreault et al. 2007). The harmful effect on humans and wildlife of many POPs, largely comprised of chlorinated, brominated and/or fluorinated organohalogenated compounds (OHCs), has been long recognized (Letcher et al. 2010). As a consequence the Stockholm Convention on Persistent Organic Pollutants (UNEP 2005) was created to reduce or eliminate the production, use, and/or release of some POPs. During the past two decades, the concentration of many of these POPs has decline in Arctic marine biota. However, every year thousands of new chemicals are produced; for example, flame retardants (FRs), including polybrominated diphenyl ethers (PBDEs) among others. These new contaminants can also affect key reproductive traits like incubation. For example, in glaucous gulls, high plasma concentrations of ΣPBDEs were negatively correlated to mean nest temperature, potentially causing suboptimal thermic conditions for embryo development and affecting development in offspring from highly contaminated parents (Verboven et al. 2009). Therefore, there is a continuous need for efficient monitoring of both legacy and emerging contaminants as the total exposure of Arctic biota to chemical contaminants will likely increase during the next decade (Elliott and Elliott 2013).

In marine ecosystems, seabirds have been widely used as indicators to assess the impact of natural and anthropogenic stressors. Seabirds are conspicuous animals, sensitive to environmental changes (e.g., food availability and contamination), and are therefore suitable as sentinel organisms (Furness and Camphuysen 1997). Although other marine organisms like pinnipeds and cetaceans are also useful sentinels, seabirds have particular advantages. Seabirds return every year to breed in large colonies, making them easy to sample, obtain big sample sizes and study at a long term. In addition, they often forage over large areas at high trophic levels, allowing scientists to assess the effect of stressors at lower trophic levels (Elliott and Elliott 2013).

Brown booby

The brown booby (*Sula leucogaster*), is a potential indicator species to assess environmental change in the Tropics. First, the brown booby is a long-lived seabird widely distributed in pantropical oceans, where the species is abundant, having a global breeding population of ~500,000 individuals (Partners in Flight 2021). This facilitates the collection of big sample sizes while assessing environmental change at large scales. Second, the booby is a colonial philopatric species with asynchronous breeding and long breeding seasons (incubation: 42 ± 3 days; brood care: 5 months) (Nelson 1978). As birds return annually to a central place (i.e. colony) this makes them easy to sample while making possible collection of information over longer periods of time. Third, brown boobies are sensitive to changes in environmental conditions, such as sea-surface temperature, chlorophyll concentration and El Niño events. Variations in these environmental conditions are known to change the brown booby's population density (Woodworth et al. 2021), reproduction (Mellink 2000) and foraging behaviour (Castillo-Guerrero et al. 2016; Gilmour et al. 2018), making the brown booby a good species to assess the effect of natural stressors.

Previous studies, have used brown boobies as an indicator of environmental changes (Castro Tavares et al. 2016b; Woodworth et al. 2021), but also anthropogenic stressors like chemical contamination (Ceyca et al. 2016) and plastic pollution (Lavers et al. 2013; Castro Tavares et al. 2016a; Grant et al. 2018). For example, population trends for the species have been monitored for the past four decades to assess habitat disturbance and natural stressors (e.g., marine heatwaves and sea-surface temperature) along the Great Barrier Reef (Woodworth et al. 2021). Moreover, given that brown boobies are known to use marine debris (e.g., fishing gear and plastic) as nest material, the frequency of debris in brown booby nests have also been used as a potential indicator of the abundance of marine pollution by plastic debris at a local scale (Lavers et al. 2013; Castro Tavares et al. 2016a; Grant et al. 2018).

Thick-billed murre

The thick-billed murre is a long-lived seabird widely distributed in the Arctic that has been commonly used as indicator species across the Arctic (Gaston et al. 2003; Bond et al.

2013; Braune et al. 2014; Brisson-Curadeau and Elliott 2019). This species is a deep-diving wing-propelled swimmer that can forage at depths of up to 200 m in waters below 8°C (Elliott et al. 2007, 2008), and is associated with areas of seasonal and sometimes extensive sea-ice cover (Gaston and Hipfner 2000). Thick-billed murres nest on cliffs in large colonies composed of up to 1.5 million individuals (Brown et al. 1975). They have biparental care, laying one egg, which is incubated for ~33 days and have 15-30 days of brood care before the father takes the single offspring to sea for 30-50 days (Gaston and Hipfner 2000).

Due to its strong ice affinity, this species is particularly sensitive to changes in temperature and sea-ice availability. Previous studies have shown a population decline in relation to shifts in sea-surface temperature (Irons et al. 2008). Moreover, murres advanced their date of egg-laying presumably as a consequence of earlier clearance of ice over the past few decades (Gaston et al. 2009b). However, although murres adjust to the environmental changes by breeding earlier, these advances (~one week over the past 30 years) is insufficient to match the timing of ice clearing (~one month over the past 30 years), leading to a mismatch in chick rearing and food availability (Gaston et al. 2009b). Ice cover loss has also led to shifts in diet, decreasing the proportion of Arctic cod (*Boreogadus said*), the murres' preferred prey and increasing the proportion of capelin (*Mallotus villosus*) (Gaston and Elliott 2014a).

Notes on this chapter

This chapter corresponds to a manuscript with the same title in which I am first author. This manuscript has been written in collaboration with Hector Guzmán from the Smithsonian Tropical Research Institute and Kyle Elliott from McGill University.

CHAPTER 1: Upwelling links reproductive success and phenology in a tropical seabird

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ABSTRACT

For organisms living in seasonal environments, timing of breeding is key. Temperate and Arctic seabird species follow seasonal pulses, matching their breeding events with ocean productivity peaks. However, seasonality has been much less explored in tropical seabirds. Here, we explored the effects of seasonal variation in oceanography on reproductive success on the brown booby (*Sula leucogaster*), a widely distributed species in the Tropics. We monitored 61 nests during the 2019 breeding season at Bona Island, Gulf of Panama, and collected remote sensing information for upwelling, sea-surface temperature, rainfall, chlorophyll-α concentration, wind speed and wind direction. We used egg/chick survival probability to assess reproductive success and a sliding window approach for the statistical analysis. Survival probability increased with maximum chlorophyll-α (CI(β) = 0.19 to 2.54) and decreased with (maximum chlorophyll-α)^2 (CI(β) = -4.19 to -0.31). Based on the sliding window analysis, we identified that maximum chlorophyll-α (linear and quadratic expression) had the strongest influence over survival probability in the 2 to 3 weeks prior to the egg/chick's death. In addition, survival probability decreased with laying date (CI(β) = 0.43 to 1.74), indicating that chicks born earlier in the breeding season had higher chances of survival. Given the high correlation between chlorophyll-α and upwelling, we concluded that upwelling influences the brown booby's reproductive success in the Gulf of Panama, demonstrating that this tropical species follows seasonal pulses similar to those observed in species in polar and temperate regions.

Keywords: brown booby, chlorophyll-α, survival probability, timing of reproduction, seasonal pulses

INTRODUCTION:

The Pacific coast of Central America is a highly dynamic environment (O'Dea et al. 2012), where strong winds from the Caribbean drive seasonal upwelling in certain regions along the Pacific (Xie et al. 2005). In the Gulf of Panama, this oceanographic process causes the usually warm surface waters (SST > 27°C) of the Gulf to cool, promoting nutrient enrichment (NO^{-}_{3}, PO_4^{3-}, $Si(OH)^4$) of the euphotic zone and a peak in surface chlorophyll-α concentration (1.5 mg m^{-3}) (D'Croz and O'Dea 2007). These changes in temperature and nutrient availability drive extensive phytoplankton and zooplankton growth (Forsbergh 1969; D'Croz and O'Dea 2007), which is positively correlated with fish abundance (Forsbergh 1969), and could potentially affect top predators such as seabirds and marine mammals.

Seabirds often live in seasonal environments where timing of breeding (i.e., laying date, chick rearing) is key (Perrins 1969; Verhulst and Nilsson 2008). Many seabirds follow seasonal pulses, matching their breeding events with ocean productivity peaks when food is abundant enough to maintain themselves and their chicks (Perrins 1969). Strong seasonality has been widely documented in seabirds breeding at high latitudes, where laying date, clutch size and fledgling production are often strongly linked to food availability (Shultz et al. 2009; Hatch 2013; Gaston and Elliott 2014). Although tropical seabirds usually have longer breeding seasons, their timing of breeding and reproductive success is also constrained by environmental conditions and food availability. For example, some tropical species adjust their timing of breeding so food availability is higher when they are raising their chicks

(Passuni et al. 2016), while others fail (Champagnon et al. 2018) or skip (Cubaynes et al. 2011) reproduction during unfavorable conditions, like El Niño events.

The brown booby (*Sula leucogaster*) is a long-lived seabird with asynchronous breeding on tropical and subtropical islands. This booby lays clutches of 1-2 eggs and typically produces only one surviving offspring per reproductive attempt (Nelson 1978). Female and male share parental care during 42 ± 3 days of incubation and up to five months of brood care (Nelson 1978). The brown booby is one of the three breeding seabirds at Bona (8° 34’ 25.09’’ N y 79° 35’ 25.99’’ W), a small island of 74.7 ha located at 40 kilometers south of Panama City on the Gulf of Panama (Fig 1.1). This island is considered an Important Bird Area (IBA) and it is protected under the Panamanian law (Comisión de población ambiente y desarrollo 2019). Here, the brown booby breeds almost all year around within a variety of habitats including low-growing shrubs, cacti and rocky cliff faces (Hector Guzmán *personal observation*). The thousands of birds that breed annually in this island are exposed to strong environmental fluctuations due to seasonal upwelling, which generally occurs from January to May, during the dry season (D’Croz and O’Dea 2007). However, little is known about how this oceanographic process affects seabirds reproductive success in the Gulf of Panama.

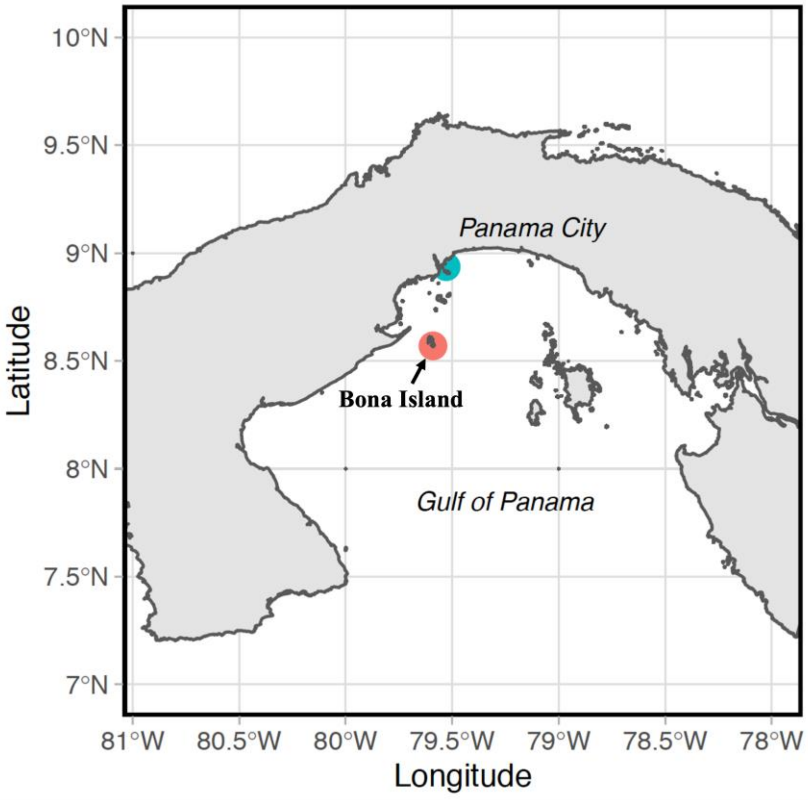
In this study, we look into the potential effects of upwelling on reproductive success of the brown booby, a widely spread tropical seabird. We monitored 61 nests exposed to upwelling and downwelling conditions throughout the 2019 breeding season to test whether the estimated survival probability differ between offspring exposed to upwelling or downwelling conditions at an early life stage (egg/chick). We predicted that survival probability would decrease gradually with time, due to less favorable environmental conditions during downwelling seasons.

METHODS

Field work

We monitored 61 nests (53 unsuccessful and 8 successful nests) at Bona Island (Fig 1.1), between 2 April and 23 August 2019. This period coincided with the reproductive season, during which this colony was exposed to upwelling (January to May) and later downwelling (June to December) conditions (D'Croz and O'Dea 2007). We registered the GPS location of each monitored nest and recorded the number of eggs, chicks and fledglings on a weekly bases or when conditions allowed it. To estimate the age of each fledgling, we used a photographic record of each chick at the nest, as well as the minimum laying date or hatching date (~42 d since egg laying; Nelson 1978). We considered a breeding attempt successful if a fledgling (~90 d old) was recorded in the nest.

Figure 1.1 Location of Bona Island.



Remote sensing

We characterized the oceanographic conditions on each day of our study using remote sensing information (ERDDAP; Simons 2020). Upwelling was estimated using 8-d composites of Ekman's upwelling measures downloaded from the Metop-B ASCAT satellite with a 0.25° resolution. To determine if other climatic variables had an effect on reproductive success, daily measures of rainfall (CHIRPS station, 0.05° resolution) and weekly measures of sea-surface temperature (SST), chlorophyll-α concentration (Aqua MODIS satellite, 0.03° resolution), wind speed and wind direction (Metop-B satellite, 0.25° resolution) were estimated for a 0.5° - 0.5° grid based on the brown booby's maximum foraging distance (50.6 ± 30.5 km; Gilmour et al. 2018).

Statistical analysis

We used a "sliding window" analysis ("climwin" package for R; Van de Pol et al. 2016) to identify the best climatic predictors and determine the periods during which these variables most strongly affected reproductive success. This exploratory approach considered a whole year of environmental data (i.e., the 365 days before the end of the sampling season) to identify the "best" possible window (details in: Van de Pol et al. 2016; MacLeod et al. 2018). First, we used egg/chick survival probability as a proxy of reproductive success and built a Cox Proportional Hazard (PH) model to assess the time-dependent and time-independent factors that influence survival probability. We selected a Cox model with laying date as a baseline model to account for non-climatic effects on survival probability. We then built candidate models for each climatic variable and compared them against the baseline model to find the best descriptive metric (i.e., minimum, maximum, mean) and the form of the relationship (i.e., linear, quadratic). Based on preliminary tests, we considered sliding windows (i.e., time periods relevant for a biological response) up to 12 weeks prior to the event of interest for all the climatic variables. We identified the "best" possible relative climatic window (i.e., one window for every individual) for each climatic variable, and ran randomized models to assess the likelihood that the best window was a result of over-fitting (Van de Pol et al. 2016). We found a relevant climatic window for each of the six climatic variables tested.

To confirm the evidence for multiple climatic signals (i.e., critical climatic periods), the best climatic window identified was extracted for every variable. All variables were centered and a correlation matrix was used to detect collinearity among climatic variables. We then built a baseline model including laying date, and created eleven hypothesis-based climatic models without highly correlated variables in the same model. Models were ranked using the Akaike Information Criterion (AICc), selecting all models within a cumulative

Akaike weight of 0.95 (Burnham and Anderson 2002). All statistical analyses were conducted in R (v.4.0.2; R Development Core Team 2020).

Table 1.1 Models used to explore variation in egg/chick survival probability with oceanographic conditions (n=61). Best-fitting models with a cumulative Akaike weight (*wi*) of ~0.95 are in italics. LD: Laying date; Chl: Chlorophyll-α concentration, SST: Sea-surface temperature; WD: Wind direction; WS: Wind speed; df: degrees of freedom; logLik: log likelihood; AICc: Akaike Information Criterion adjusted from small samples; ΔAICc: differences in AIC_c scores between current model and more parsimonious model.

Model	**Fixed effects**	**df**	**logLik**	**AICc**	**ΔAICc**	**wi**
1	*LD + Chl + Chl²*	*3*	*-148.69*	*303.38*	*0.00*	*0.84*
2	*LD + SST + SST²*	*3*	*-150.69*	*307.39*	*4.01*	*0.11*
3	LD + Rain + Rain²	3	-152.13	310.27	6.88	0.03
4	LD + Upwelling + Chl + Chl² + Rain + Rain² + WD	7	-148.20	310.45	7.070	0.02
5	LD + Upwelling	2	-159.91	323.83	20.45	0.00
6	LD + Upwelling + Chl + Rain + WD	5	-157.91	325.85	22.46	0.00
7	LD + WD	2	-163.22	330.44	27.06	0.00
8	LD + WS	2	-164.21	332.42	29.04	0.00
9	LD + Rain	2	-166.44	336.88	33.49	0.00
10	LD	1	-171.13	344.26	40.87	0.00
11	LD + Chl	2	-171.01	346.03	42.65	0.00
12	LD + SST	2	-171.08	346.17	42.78	0.00

RESULTS

The best supported models included laying date, as well as maximum chlorophyll-α and minimum SST in its linear and quadratic expressions (Table 1.1). However, after model averaging, maximum chlorophyll-α (linear and quadratic) was identified as the only climatic predictor for egg/chick survival probability (Table 1.2). Based on the sliding window analysis, maximum chlorophyll-α (linear and quadratic expression) in the 2 to 3 weeks prior to the egg/chick's death had the strongest influence over survival probability (Fig 1.2). Survival probability increased with maximum chlorophyll-α (CI(β) = 0.19 to 2.54) and decreased with (maximum chlorophyll-α)^2 (CI(β) = -4.19 to -0.31) (Table 1.2). The likelihood of a brown booby chick (or egg) dying increased when chlorophyll-α concentrations were between 0 to 0.42 mg/m^3 and decreased at chlorophyll-α concentrations above 0.58 mg/m^3 (Fig. 1.3). In addition, survival probability decreased with laying date (CI(β) = 0.43 to 1.74), indicating that chicks born earlier in the breeding season had higher chances of survival (Fig. 1.4, Table 1.2). We did not find support for an association between survival probability and upwelling, SST, rain, wind speed or wind direction.

Table 1.2 Summary of the averaged model explaining egg/chick survival probability (n=61).

Predictor	**β**	**SE**	***95%* CI**
Laying date	*0.98*	*0.25*	*0.48 to 1.47*
Maximum chlorophyll 2-3 week (mg/m^3)	*1.37*	*0.60*	*0.19 to 2.54*
Maximum chlorophyll 2-3 week^2 (mg/m^3)	*-2.25*	*0.99*	*-4.19 to -0.31*
Minimum SST 8th week (°C)	-0.36	0.99	-2.30 to 1.58
Minimum SST^2 8th week (°C)	-0.32	0.89	-2.07 to 1.43

Predictors in italics are the only ones with a statistically significant effect on survival probability. SST: Sea-surface temperature

Figure 1.2 The best window (in weeks) for chlorophyll concentration (quadratic expression) opens 3 weeks and closes 2 weeks before the offspring died; the lowest ΔAICc values (red region) indicates the strongest window compared to the null model (no climate effects).

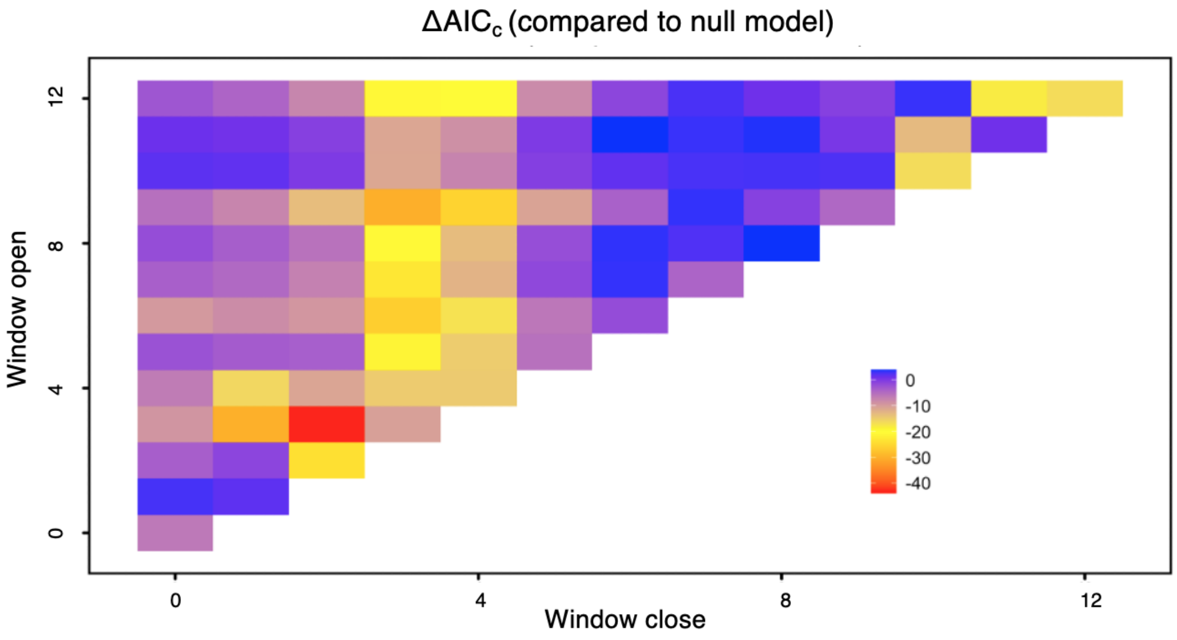


Figure 1.3 Hazard ratio (HR) of an egg or chick dying relative to the maximum chlorophyll-α concentration (linear expression) at sea.

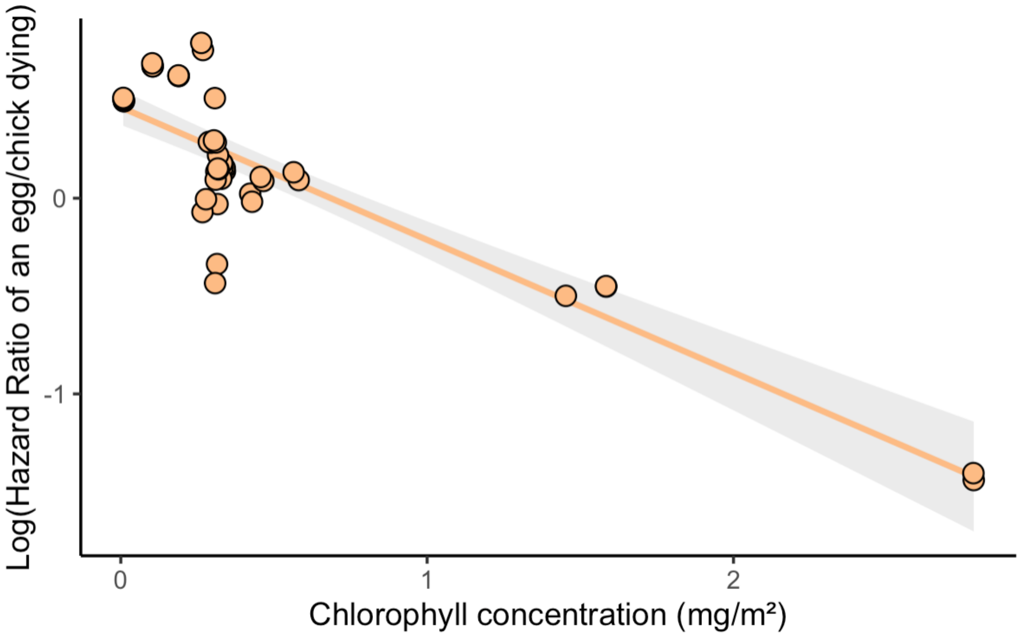
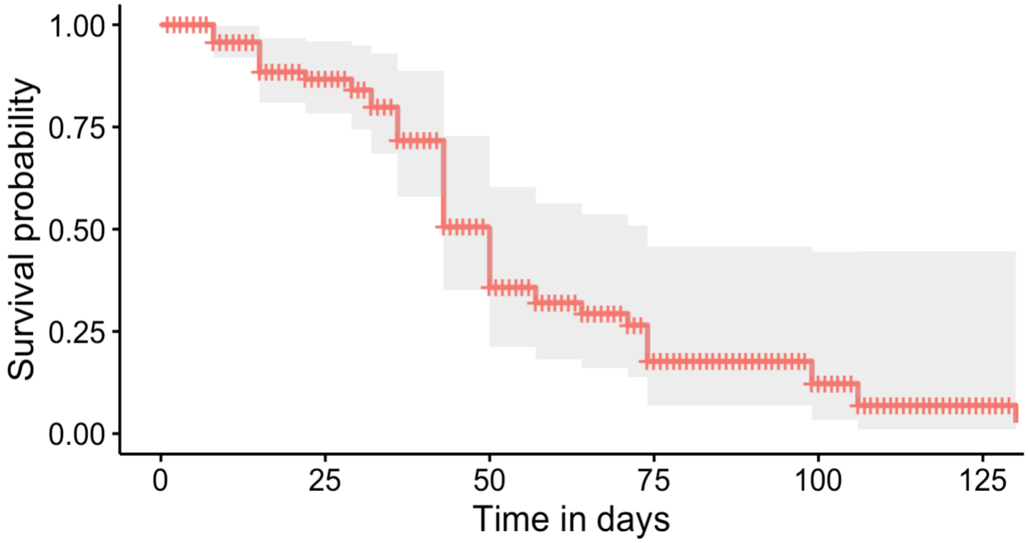
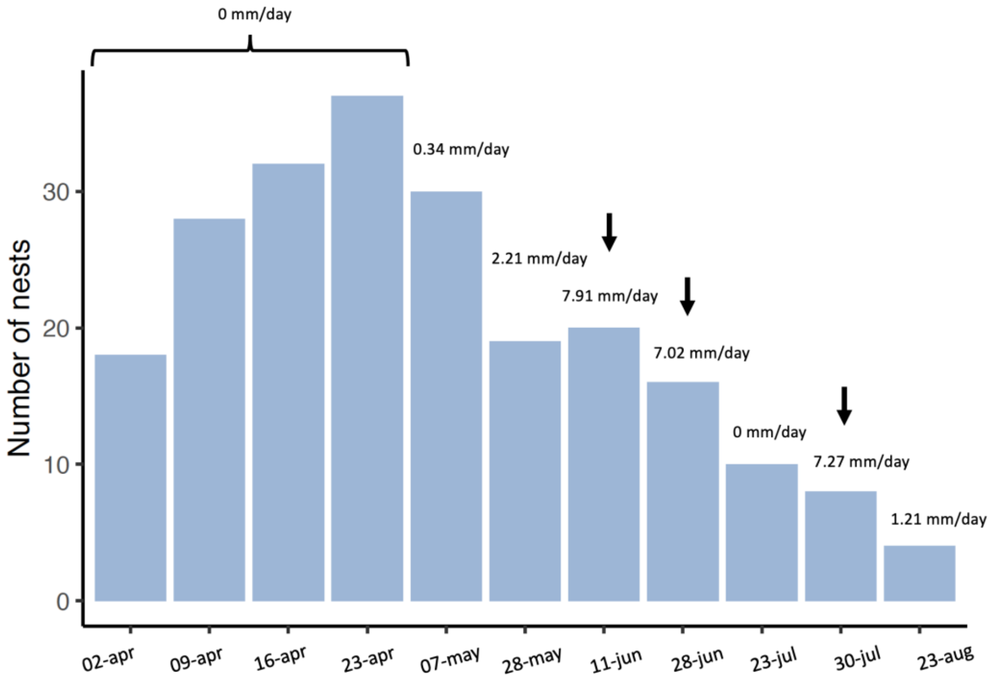


Figure 1.4 Egg/chick survival probability in relation with laying date. The shaded area indicates the 95% confidence interval for the survival curve.



Three big rainfall effects occurred in June 11, June 28 and July 30 that reduced the number of nests at the colony (Fig. 1.5); as ground-nesting birds, many nests were washed out by the heavy rainfall. Although rainfall was not selected in the best fitting models (Table 1.1), steep drops in the number of offspring occurred after each period of heavy rainfall (Hector Guzmán *personal observation;* Fig. 1.5). Nest density was higher at the beginning of the season and gradually decreased as the season progressed, but with steep drops after heavy rainfall late in the season.

Figure 1.5 Number of nests per day. Above each column is the mean average rainfall (mm/day), the arrows indicate each of the three rainfall event.



DISCUSSION

Upwelling conditions throughout the breeding season influenced the reproductive success of brown boobies. This is consistent with the species' strong distributional association with upwelling conditions (Heatwole et al. 1997), as well as links between foraging strategy and prey availability (Castillo-Guerrero et al. 2016). Although brown boobies have the capacity to breed almost all year around, those individuals breeding when chlorophyll-α concentration was higher had offspring with greater chances of survival. Chlorophyll-α concentration is strongly linked to upwelling conditions when SST is cooler and ocean productivity is higher. This would mean that the brown booby is following seasonal pulses, breeding when food availability is greater. Similar results have been found in other tropical seabirds. For example, the Guanay cormorant (*Phalacrocorax bougainvillii*) in the Northern Humboldt Current System, exposed to strong upwelling events, breed when food availability is higher (Passuni et al. 2016). In the same system, the Peruvian booby (*Sula variegata*) and the Peruvian pelican (*Pelecanus thagus*) prefer to adjust their timing of breeding so that chick-rearing coincides with periods of higher resource quality and abundance (Passuni et al. 2016). Moreover, our results are consistent to previously observed patterns of high mortality and low reproductive success on seabirds in the Panama Bright, associated with abnormally warm SST and low primary productivity during strong El Niño events (e.g., El Niño 1982-1983) (Schreiber and Schreiber 1984; Glynn 1988).

Laying date had a negative effect on chick survival. Environmental conditions become less suitable for breeding as the season progresses for most seabirds species (Perrins 1969). At Bona Island, early breeders had greater reproductive success, probably because they breed during the entire upwelling season, when conditions are more favorable and food is abundant. Reproductive success decreased as the season progressed, probably because late breeders experienced downwelling conditions when food was scarce. Our results coincide with a previous study on brown pelicans (*Pelecanus occidentalis*) in the Gulf of Panama (Taboga Island) where early breeders exposed to early upwelling produced more fledglings, and where nest abandonment was correlated to SST (Montgomery and Martínez 1984). Age, breeding experience and body condition are other factors that are known to contribute to the success of early arrivals (De Forest and Gaston 1996; Whelan et al. 2021), and future studies might consider the role of non-climatic variables on seabird reproductive success in tropical environments.

In conclusion, brown booby reproductive success in Panama is highly influenced by upwelling conditions, confirming that some tropical seabirds follow seasonal pulses similar to those registered in species in polar and temperate regions. Future research should explore non-climate effects for seabirds in the region, as well as long term studies to confirm that the pattern reported in this study is consistent over time.

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Connecting paragraph: Chapter 1 examined the effects of upwelling and other oceanographic conditions on brown boobies' reproductive success. This will help understand the effects of natural stressors on tropical seabird fitness. The next chapter, on the other hand, looks at two anthropogenic stressors, climate change and chemical contamination, in the Arctic. More precisely, Chapter 2 looks at the effects of chemical contaminants on the thick-billed murres' endocrine system and foraging plasticity in a climate change context.

Notes on this chapter

This chapter corresponds to the paper titled: “Mercury, legacy and emerging POPs and endocrine-behavioural linkages: implications of Arctic change in a diving seabird” written in collaboration with Kim Fernie, Birgit Braune and Robert Letcher from Environment and Climate Change Canada, Emily S. Choy, Allison Patterson and Kyle H. Elliott from McGill University. This chapter will be submitted to the journal *Environmental Research*.

CHAPTER 2: 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), Hg, hormones and behaviours, in thick-billed murres (*Uria lomvia*) (N = 163) breeding in northern Hudson Bay (2016-18). The blood profile of the murres was dominated by methylmercury (MeHg), followed by much lower levels of sum (∑) 35 polychlorinated biphenyls (PCBs), hexachlorobenzene (HCB) and *p,p'*-

dichlorodiphenyltrichloroethylene (DDE), polybrominated diphenyl ethers (PBDEs) BDE-47, -99 and BDE-100; all other organochlorine pesticides and replacement brominated flame retardants had low concentrations if detected. Inter-annual variations occurred in MeHg, circulating triiodothyronine (T3), thyroxine (T4), corticosterone, 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 behavior, 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 behavior via T3 in relation to variation in sea-ice.

Keywords: mercury, thyroid hormones, foraging behaviour, Arctic, seabirds

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). 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 (*Cepphus grylle mandtii*), a species heavily dependent on sea-ice (pagophilic), have lower chick growth rates during warm years because the preferred prey (Arctic cod, *Boreogadus saida*) occur primarily in waters below 4ºC (Divoky et al., 2015). However, for little auks

(*Alle alle*), decreased sea-ice coverage led to altered diving behaviour, dietary shifts, and increased mercury (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 2.1). Most studies have focused on correlations between contaminant concentrations and behaviours, such as nest attentiveness, lay date and chick feeding rates (Table 2.1). 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., 2015). 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., 2015).

Modification of circulating thyroid and glucocorticoid hormones were reportedly associated with the exposure of Arctic biota to environmental contaminants (Table 2.1) (Dietz et al., 2019). Circulating T3 was negatively associated with polychlorinated biphenyls (PCBs) and polybrominated diphenyl ethers (PBDEs) (Svendsen et al., 2018), and similarly, T3 and metabolic rate were negatively associated with chlordanes but not mercury (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 murres breeding at Coats Island in Hudson Bay. Melting sea-ice has advanced more rapidly than murres 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., 2009, 2005).

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 murres, 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 murres. 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.

Table 2.1 Studies that have investigated the relationship between Hg and POPs, behaviour, reproductive success and the endocrine system in polar bird species. This table is representative rather than exhaustive. Contaminants examined include mercury (Hg), and organohalogens (OHs) such as polybrominated diphenyl ethers (PBDEs), per-and poly-fluoroalkyl substances (PFASs), and legacy persistent organic pollutants (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	OHs	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

MATERIALS AND METHODS

Sea-ice Conditions:

We used a previous methodology (Gaston et al., 2009, 2005) 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 10892, 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 minutes within ~3 hours of collection. The resulting plasma and red blood cells were aliquoted 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 minutes, depth measurements at 1 sec 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 behavior, 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. Methymercury (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 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, oxychlordane, *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 ≤ 0.0037 µg/g ww for PCBs; ≤ 0.012 µg/g ww for OC pesticides; ≤ 0.47 ng/g ww for BFRs excluding PBDEs; ≤ 0.77 ng/g ww for PBDEs. The reporting limits (MRL) were ≤ 0.011 µg/g ww for PCBs; ≤ 0.004 µg/g ww for OC pesticides; ≤ 1.40 ng/g ww for BFRs excluding PBDEs; and ≤ 0.232 ng/g ww for PBDEs. Results are recovery and blank corrected. Concentrations of PCBs and OC pesticides are expressed in µg/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 murres (Table 2.2; Table S2.2), 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.,

2014) 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-transformend for the hormone models, while THg, MeHg and all foraging behaviours were log-transformend 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 Team 2020) (R Core Team, 2020) and significance was considered at $p \leq 0.05$.

RESULTS

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).

Circulating contaminants:

PCBs were detected in 100% of the murres 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 (∑) PCB concentrations. The ∑35PCB concentrations ranged from 0.0006 to 0.02 μg/g ww (Table S2.2). Concentrations of OC pesticides primarily consisted of HCB (100%; 0.004 ± 0.0002 ng/g ww) and *p,p'*-DDE (100%; 0.004 ± 0.0003 ng/g ww), with all of the remaining measured OC pesticides not detected or having low detection rates and concentrations (Table S2.2). In contrast, only 24% of the murres had detectable and very low concentrations of ∑3PBDEs (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 2.2; Table S2.2). 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 2.2).

Table 2.2 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: arithemetic 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	-	-	-	-	-	-	-	-	-	-	-	-
p,p'-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	-	-	-	-	-

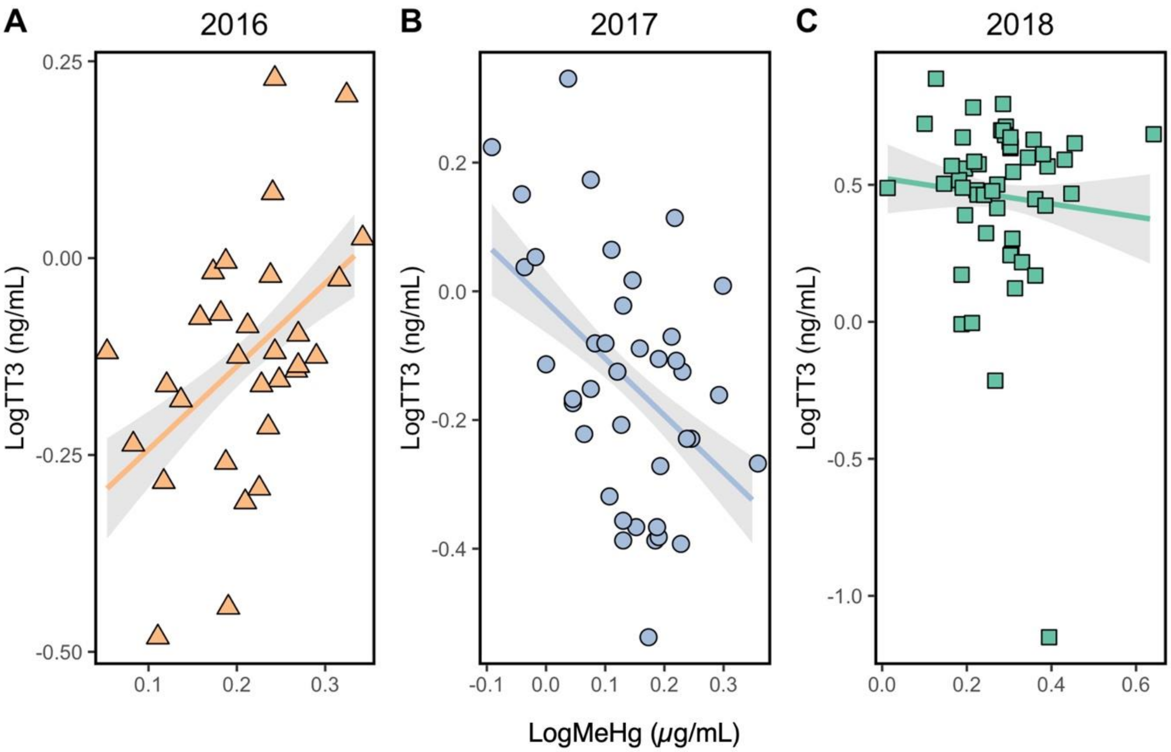
Annual variation in hormones:

Circulating concentrations of THs and CORT measured in the breeding murres are presented in Table 2.2. Circulating TT3 concentrations were similar in 2016 and 2017 (χ^2 = 0.24, p = 0.63) but were higher in 2018 (vs. 2016: χ^2 = 47.85, $p < 0.001$; 2017: χ^2 = 55.94, $p < 0.001$). Circulating FT3 was highest in 2017 (vs. 2016: χ^2 = 6.31, p = 0.01; 2018: χ^2 = 51.30, $p < 0.001$) and lowest in 2018 (vs. 2016: χ^2 = 56.77, $p < 0.001$). Similarly, FT4 levels were higher in 2017 (vs. 2016: χ^2 = 16.01, p = 0.01; 2018: χ^2 = 20.15, $p < 0.001$) but similar between 2016 and 2018 (χ^2 = 1.62, p = 0.20). Circulating TT4 was lower in 2016 than 2017 (χ^2 = 18.85, $p < 0.001$) and 2018 (χ^2 = 24.91, $p < 0.001$), but similar between 2017 and 2018 (χ^2 = 0.004, p = 0.95). CORT was statistically similar in 2016 and 2017 (χ^2 = 0.22, p = 0.64); CORT was not measured in 2018.

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 (ß ± SE=1.05 ± 0.37, p = 0.008) (Fig 2.1A). In contrast, in 2017, TT3 levels decreased with MeHg concentrations (ß ± SE=-0.87 ± 0.29, p = 0.005) (Fig 2.1B), but the relationship was not significant in 2018 (ß ± SE = -0.23 ± 0.45, p = 0.61) (Fig 2.1C). Similarly, FT3 levels were negatively correlated with MeHg in 2017 (ß ± SE = -1.00 ± 0.45, p = 0.03) but not in 2016 (ß ± SE = 0.16 ± 0.38, p = 0.67) or 2018 (ß ± SE= -0.21 ± 0.27, p = 0.44) (Table S2.3).

Fig. 2.1 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.



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 2.3). 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 2.3).

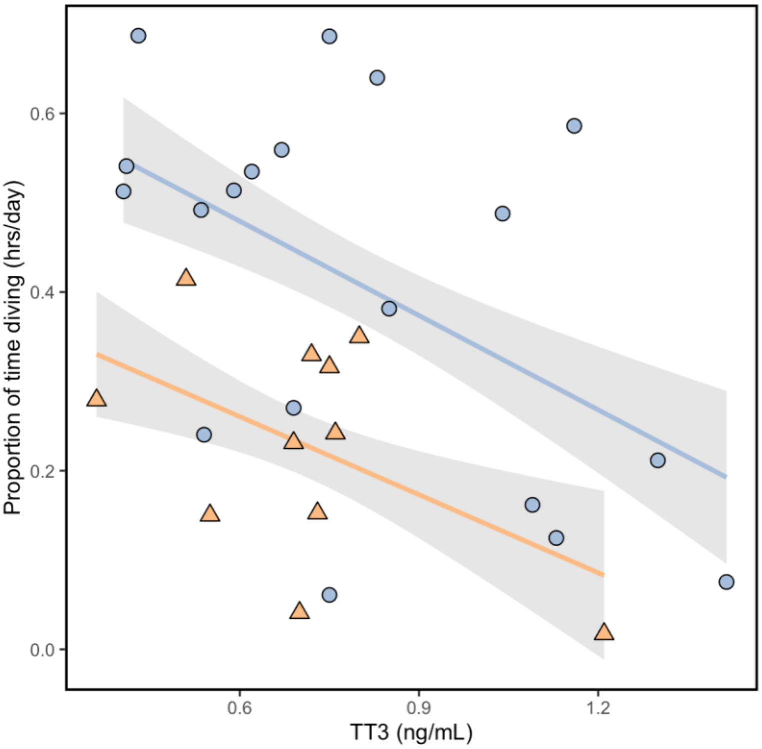
Table 2.3 Summary of the foraging behaviours recorded for the murres from 2016 to 2018. Diving: proportion of time diving (hr/d); Flying: proportion of time flying (hr/d); Swimming: proportion of time swimming (hr/d); Diving depth: average diving depth (m); dives: total number of dives per deployment; n: sample size; Mean: mean; SE: standard error of the mean; Min: minimum; Max: maximum; and p: p value of the Wilcox 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**

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 (ß ± SE = -1.25 ± 0.24, p = 0.0004) and 2017 (ß ± SE = -0.35 ± 0.14, p = 0.024), but not in 2018 (ß ± SE = 0.00005 ± 0.01, p = 0.99) (Fig. 2.2). When two statistical outliers were removed, this relationship was no longer significant in 2016 (ß ± SE = -0.30 ± 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 (ß ± SE = -0.35 ± 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 S2.4).

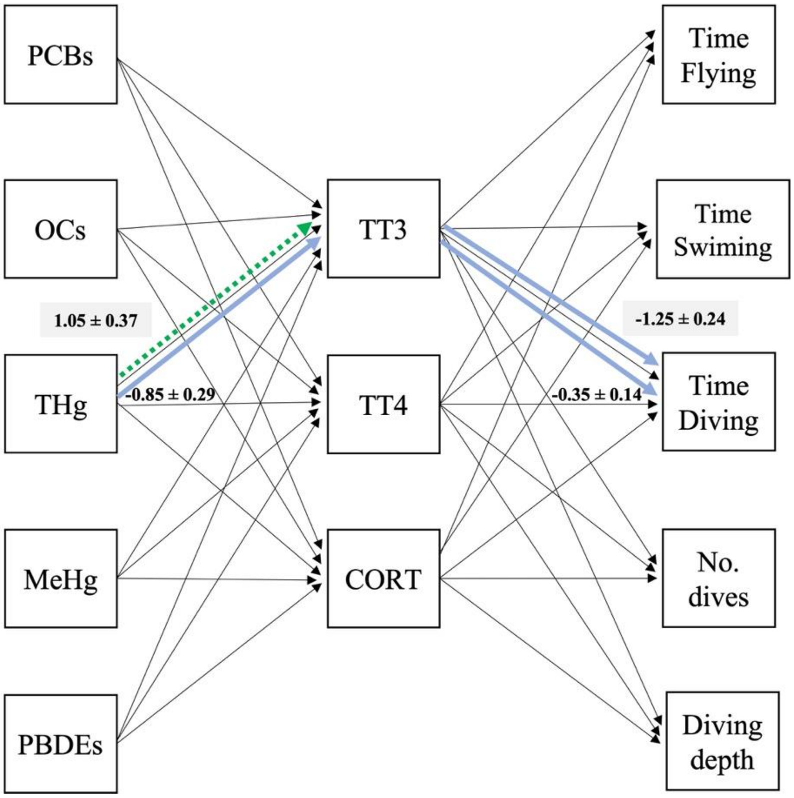
Fig. 2.2 Time spent diving declined with increasing TT3 for thick-billed murres at Coats Island in 2016 (n=12; orange triangles) and in 2017 (n=19; blue circles) but not in 2018 (data not shown). Lines indicate model predictions and the shaded areas represent standard errors.



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. 2.3). 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. 2.3), 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.

Fig. 2.3 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 (ß ± 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).



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 ∑35PCBs, *p,p'*-DDE, HCB, and ∑3PBDEs 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. 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 ∑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; Rigét 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 ± 2 µg/g ww) in the present murres were much higher than previously reported for this species (0.12 ± 0.01 µg/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 µg/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 ± 0.0003 ng/g ww) and HCB (0.004 ± 0.0002 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 eburnean*) (*p,p'*-DDE: 303 ± 38.9 ng/g ww; HCB: 7.94 ± 0.56 ng/g ww) (Lucia et al., 2017) or whole blood of black-legged kittiwakes (*p,p'*-DDE: 3.74 ± 2.27 ng/g ww; HCB: 2.22 ± 0.89 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 (∑3PBDE: 0.11 ± 0.03 ng/g ww) in the present murres, but similar to concentrations in other Arctic seabirds including the northern fulmar (*Fulmarus glacialis*) (0.17 ± 0.22 ng/g ww) and the black-legged kittiwake (0.09 ± 0.04 ng/g ww) (Nøst 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 behavior of the murres.

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. We suspect that the length of time the birds were fitted with the geolocators likely explains the CORT differences between the two studies. That sea-ice breakup (50% of sea-ice coverage) occurred earlier in 2016 and 2017 than the long-term average, may partially explain the similarity in CORT of the murres between these two years; CORT was not measured in 2018 when the breaksup 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; Nøst et al., 2012; Tan et al., 2009). Mean blood MeHg in the present murres in 2016 (0.59 μg/g ww), 2017 (0.46 μg/g ww) and 2018 (0.67 μg/g ww), exceeded the threshold for sub-lethal adverse effects of Hg in birds (e.g., 400 ppb ww or 0.4 μg/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 μg/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 supressed in tree swallows (*Tachycineta bicolor*) having elevated blood Hg concentrations (354 ± 22 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 breaksup 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.

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 behavior 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 (Huserbråten 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 (Amélineau et al., 2019). We hypothesize that with the earlier ice breaksup 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. 2.2). 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., 2015), reflecting the observed association of higher TT3 and reduced dive duration in 2016 and 2017 when sea-ice breaksup 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.

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., 2015). The murres' ability to modify dive duration is a key component of plasticity associated with foraging behavior, and our results may suggest one possible mechanism involved in the adaptability of this pagophilic Arctic seabird to varying climate and sea-ice conditions.

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General Discussion

Extensive research supports the idea that individual stressors can affect different aspects of the life history of wildlife. However, there are still big knowledge gaps regarding multiple stressors, specifically the combined effects of co-occurring stressors. My study contributes to the growing literature on multiple stressors and their combined effects on Tropical and Arctic seabirds reproductive success and performance.

In my first chapter, I assessed the effects of co-occurring natural stressors, upwelling and five oceanographic conditions highly associated with upwelling, in the Gulf of Panama. The analysis of one year of productivity data and remote sensing environmental information allowed me to evaluate the impact of multiple oceanographic conditions on the brown booby's reproductive success. Chlorophyll-α concentration had a strong effect on chick survival probability. Because chlorophyll-α concentration is often considered a good indicator of food availability, high chlorophyll-α concentrations in this time window might indicate greater food availability and, therefore, better breeding conditions for these boobies. Moreover, chick survival probability decreased with laying date, showing that chicks born early in the breeding season had higher chances of surviving than chicks born late in the breeding season. Given that upwelling in the Gulf of Panama occurs early in the breeding season, my results confirm that upwelling has a strong effect over the brown booby's reproductive success. Our findings are consistent to what it has been previously reported for other seabird species in regions highly influenced by upwelling, such as the Gulf of California and the Humboldt Current. Moreover, to our knowledge this is one of the first studies evaluating the effects of upwelling on seabirds in the Gulf of Panama, and sets a precedent for the region.

This study is limited by having only one year of data. Hence, further research should try to confirm the pattern described in this study through a long term study. Having long term information would provide a broader understanding of the natural and anthropogenic threats acting simultaneously in the region and potentially affecting seabirds. Other limitations of this study was the lack of information on the life history of the individuals we monitored. For example, older and more experienced individuals tend to breed earlier and have greater reproductive success. Further studies should take this into account to confirm that the variations in reproductive success over the breeding seasons are truly due to upwelling. Finally, we suggest continue monitoring Bona Island, as well as other seabird colonies in the area, given that long term data would help us understand how changes in seasonal process affect wildlife in the Tropics, information that is especially valuable as seasonal processes like upwelling are expected to intensify and become more frequent with climate change.

In the second chapter, I studied chemical contamination and climate change, two anthropogenic stressor on the rise in the Arctic. Here, I used three years of foraging data, as well as circulating hormones and chemical contaminants concentrations to assess if chemical contamination is affecting the thick-billed murres ability to adapt to climate change, specifically sea-ice loss. PCBs, OC pesticides and PBDEs concentrations were extremely low compared to mercury concentration. Circulating mercury was correlated with total triiodothyronine (T3) levels in the years when sea-ice melted earlier. Because mercury has a high affinity for the endocrine system, high concentrations of mercury could have affected T3 secretion causing endocrine disruption in murres. In addition, time spent diving was negatively correlated with T3 in the same years. This is consistent with our predictions given that T3 is highly associated with basal metabolic rate, therefore high T3 levels potentially increased metabolism and thus shortened dive duration. Our findings indicate that in warm years, high mercury concentration may be disrupting thyroid function, affecting the murres' ability to adjust their time underwater in relation to variation in ice cover.

Having the behavioural plasticity to adapt to the environmental changes currently occurring in the Arctic is key for wildlife in Arctic ecosystem, therefore understanding the impact of endocrine disruptive chemicals (EDCs) like mercury remains a priority. As more studies focus on the combined effects of EDCs and climate change in the Arctic, they may begin to fill the big knowledge gaps regarding the mechanisms behind endocrine disruption and the extent of the effects of these disruptions over wildlife. Future research should try to unravel the mechanism used by mercury to cause apparent thyroid disruption in the murres. Moreover, given that diving is a key behaviour for many seabirds, we recommend that more studies should be done with other diving species to gain knowledge on the effect of EDCs over diving, and the potential indirect effects that endocrine disruption might have on other life history traits.

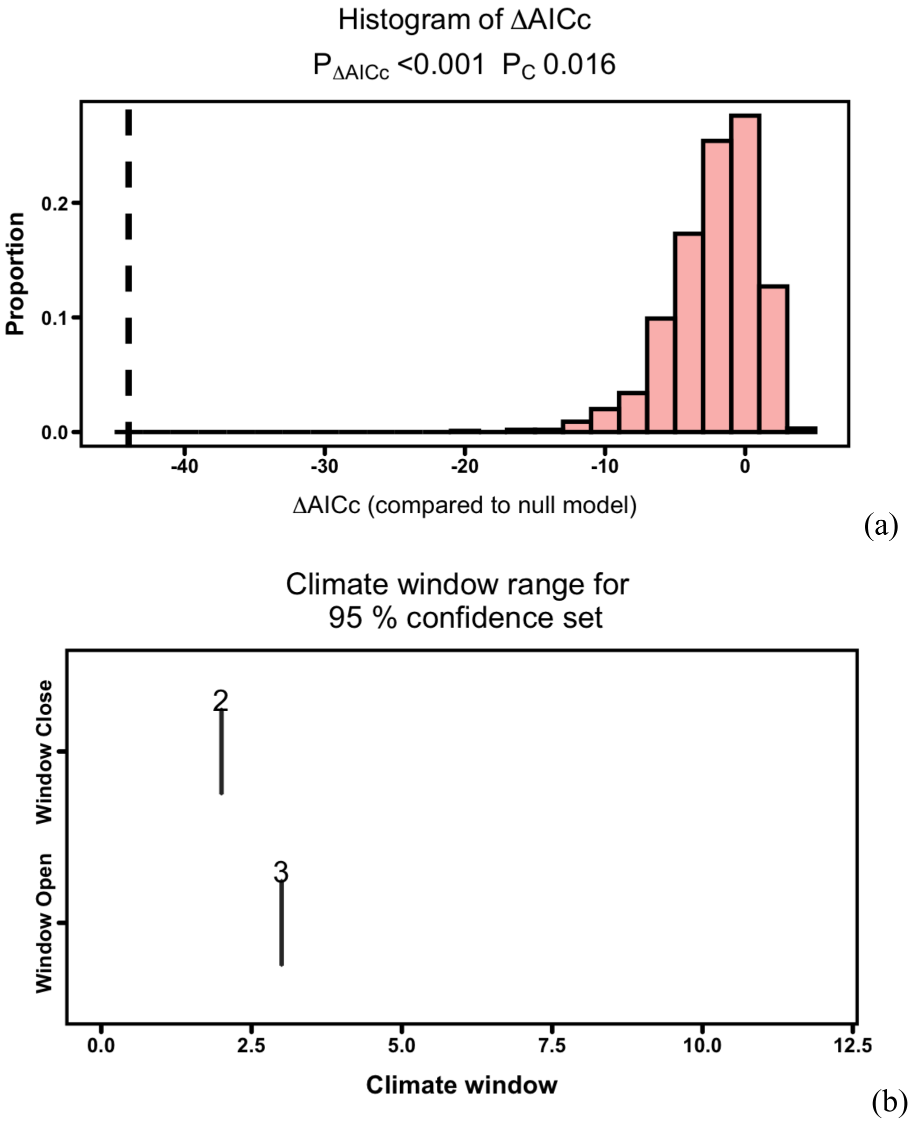
By studying co-occurring stressors using seabirds, it could be possible to assess the impact of interacting multiple natural and anthropogenic stressors in marine environments in both Tropical and Arctic ecosystems. The results could be used to regulate the use of specific contaminants affecting wildlife, as well as assess the impact of current regulations on chemical contaminants like PCBs and OC pesticides.

General Conclusion and Summary

My research aims to address knowledge gaps on multiple natural and anthropogenic stressors affecting seabirds. In the Tropical system (chapter 1), egg/chick survival probability in the brown boobies increased with chlorophyll-α concentration and decreased with laying date. Given that upwelling in the Gulf of Panama occurs early in the breeding season and that chlorophyll concentration is highly correlated with upwelling, we concluded that upwelling has a strong effect over the brown booby's reproductive success. This study sets a precedent on the effects of upwelling on seabirds in the area, and could potentially be used to assess the brown booby's population status and implement management and conservation actions at Bona Island, the most recent protected area in Panama. In the Arctic system (chapter 2), MeHg was associated with total T3 concentrations in the thick-billed murres. This association was positive in 2016 and negative in 2017, but not 2018. Moreover, both in 2016 and 2017, total T3 was negatively associated with the proportion of time the murres spent diving. Through a path analysis we found a causal relationship among MeHg, TT3 and diving behaviour. We concluded that under poor ice conditions (2016 & 2017), MeHg is indirectly affecting the murres diving behaviour potentially by causing a thyroid function disruption. This study, sheds some light on the potential implications of chemical contamination on associated-ice species performance in a climate change context. Potentially, these results could be used to regulate the use of specific contaminants affecting wildlife, and assess the impact of current regulations on chemical contaminants like PCBs and OC pesticides.

SUPPLEMENTARY MATERIALS for Chapter 1

Figure S1.1 Critical climate window analysis for the effects of climate on survival probability. Chlorophyll concentration is the only environmental variable with an effect over offspring survival (see Fig. 1.1 main text). (a) Outcome of the simulations show that the AICc value of the best model (-40, dotted line) does not overlap with the randomized simulated results (histogram) which means that the candidate signal did not occur by chance for chlorophyll. (b) Boxplot shows with a 95% confidence interval that the best climatic window for chlorophyll opens 3 weeks and closes 2 weeks prior to the offspring's dead.



SUPPLEMENTARY MATERIAL Chapter 2

Materials and Methods

Behaviours:

We used a hidden Markov model to classify four behaviours of thick-billed murres (flying, on colony, swimming, and diving) from the accelerometer, GPS, and depth data collected using biologgers. This analysis was adapted from the methods described by Patterson and others (Patterson et al., 2019), and used the *momentuHMM* package (version 1.5.2) in R (McClintock and Michelot, 2018). Wing beat frequency (WBF) was calculated as the mean number of peaks in the Z-axis of the accelerometer data, with an amplitude of at least 0.5 m/s. Pitch is the vertical orientation of the bird's body angle, calculated using the equation in Patterson et al 2019. Pitch values were corrected to be 0 during periods of likely flight (WBF >6), to account for small differences in the orientation of the tag when attached to the bird. Pitch values were smoothed over a 10-second moving window to reduce high frequency noise in the body position signal. Distance from colony was converted to a binomial predictor indicating when birds were far from the colony. Distances <5km were equal to 0 and distances greater than 5 km were equal to 1. Depth data were converted to a binomial predictor for diving, with a value of 1 if depth >1 m and 0 if depth ≤1 m. Because murres must fly to transition from their cliff nests at the colony colony to any other behavioural state, the transition matrix was constrained to prevent transitions between for colony-swimming and colony-diving. Similarly, because murres spend time at the water surface between dives and flights, the transition matrix was constrained to prevent transitions between flying-swimming. Complete starting state distributions are provided in Table S2.1.

Contaminant Analysis:

Prior to analyze the red blood cell samples of individual birds for total mercury (Hg), samples were combusted under a continuous flow of ultra-pure oxygen and the liberated Hg was analyzed by atomic absorption spectrophotometry. Analytical accuracy was determined using a standard reference material (SRM 955c level 4 obtained from the National Institute of Standards and Technology), as well as analyzing two blank samples at the start of each day of analysis. Analytical precision was assessed by analyzing replicate samples. The normal 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. To measure MeHg, we used a Tekran 2700 Automated Methyl Mercury Analysis System according to NWRC Method No. MET-CHEM-HG-01A.

Plasma samples of individual birds were analyzed for polychlorinated biphenyls (PCBs), organochlorine (OC) pesticides, polybrominated diphenyl ethers (PBDEs) and replacement brominated flame retardants (BFRs). Samples were analyzed by gas chromatography with a mass selective detector (Agilent Technologies). Briefly, approximately 1 g wet weight (ww) of aliquots were homogenized with diatomaceous earth and spiked with ^{13}C-labelled PCB/OC/BFR internal standards (PCB: $^{13}C_{12}$-CB28, $^{13}C_{12}$-CB52, $^{13}C_{12}$-CB118, $^{13}C_{12}$-CB153, $^{13}C_{12}$-CB180 and $^{13}C_{12}$-CB194; BFR: BDE-30, BDE-118, BDE-156, $^{13}C_{10}$-*syn*-DCC-CO, $^{13}C_{10}$-*anti*-DCC-CO and $^{13}C_{12}$-BDE-209. Lipids were removed from the tissue with an accelerated solvent extraction (ASE), and all compounds of interest in the extract were separated with 50 % (w/w) sulfuric acid-impregnated silica gel in the form of solid phase extraction. The selected BFRs were analyzed in a first injection, using single quadrupole GC-MS System #6 in the selected ion monitoring mode. The selected PCBs and OCs were analyzed in a second injection using triple quadrupole GC-MS/MS System #5 in the multiple reaction monitoring (MRM). The MS was set in electron capture negative ionization (ECNI) mode for BFR detection/quantification and the MS/MS in electro-impact (EI) mode for PCB/OC detection/quantification.

Table S2.2 Starting values for the state-dependent probability distribution parameters for variables used in the hidden Markov model to classify behavior of thick-billed murres. Starting values for the Gamma distribution are mean (SD, zero-inflation probability), Gaussian distribution are mean (SD), and Bernoulli distribution are probabilities.

Parameter	**Distribution**	**Colony**	**Diving**	**Flying**	**Swimming**
Wing beat frequency (Hz)	Gamma	0.5 (0.5, 0.8)	1 (1,0.05)	7.5 (1, $1*10^{-5}$)	2 (2, 0.25)
Pitch (°)	Gaussian	40 (10)	-5 (30)	0 (5)	-5 (5)
Distance	Bernoulli	$1*10^{-15}$	0.9	0.9	0.9
Diving	Bernoulli	$1*10^{-15}$	$1 – (1*10^{-15})$	$1*10^{-15}$	$1*10^{-15}$

Table S2.2 Frequency of detection rates and quantification limit and range concentrations of the major PCB congeners, OC pesticides and the PBDE congeners (ΣPBDE) measured in the blood of thick-billed murres in 2016. Concentrations are reported in µg/g wet weight (ww) for PCB congeners and OC pesticides, and in ng/g ww for PBDEs.

	Detection rate (%)	Range of Concentrations
PCB congeners		
PCB-28/31	100	0.00002-0.005
PCB-74	53	0.002-0.004
PCB-105	100	0.00002-0.0006
PCB-118	100	0.00004-0.003
PCB-138	100	0.0003-0.001
PCB-153	39	0.0009-0.0015
PCB-187	100	0.0002-0.0007
OC pesticides		
HCB	100	0.003-0.008
p,p'-DDE	100	0.001-0.008
1,2,3,4-tetrachlorobenzene	28	0.001-0.002
Pentachlorobenzene	25	0.0003-0.0004
Dieldrin	3	0.117
1,2,4,5-tetrachlorobenzene	0	-
α-hexachlorocyclohexane	0	-
β-hexachlorocyclohexane	0	-
γ-hexachlorocyclohexane	0	-
Octachlorostyrene	0	-
Heptachlor epoxide	0	-
trans-chlordane	0	-
cis-chlordane	0	-
trans-nonachlor	0	-
cis-nonachlor	0	-
p,p'-DDD	0	-
p,p'-DDT	0	-
Photomirex	0	-
Mirex	0	-
PBDEs		
BDE-47	28	0.08-0.25
BDE-99	18	0.02-0.07

BDE-100	43	0.06-0.13
BDE-153	0	-
BDE-154/BB153	0	-
BDE-138	3	0.68
β-TBECH/BDE-15	0	-
BDE-17	0	-
BDE-28	0	-
BDE-49	0	-
BDE-66	0	-
BDE-85	0	-
BDE-183	0	-
BDE-190	0	-
BDE-209	0	-
BTBPE	0	-
HBB	0	-
syn-DP	0	-
anti-DP	0	-
α-TBECH	0	-
HBCD	0	-
BB-101	0	-

Table S2.3 Summary of statistical models determining possible relationships with methylmercury (MeHg) and circulating hormones, specifically circulating total (T) and free (F) triiodothyronine (T3) and thyroxine (T4) and corticosterone (CORT). The metrics reported are: sample size (n), estimate(β), standard error (SE) and p-value (*p*). Significant relationships are marked with a * ($p \leq 0.05$) and ** ($p \leq 0.01$).

	2016				**2017**				**2018**			
	n	β	SE	*p*	n	β	SE	*p*	n	β	SE	*p*
TT3	30	1.05	0.37	0.008**	39	-0.87	0.29	0.005**	51	-0.23	0.45	0.61
FT3	34	0.16	0.38	0.67	40	-1.00	0.45	0.03*	58	-0.21	0.27	0.44
TT4	36	12.97	17.87	0.47	48	-15.38	15.55	0.33	49	4.81	10.11	0.64
FT4	36	-0.24	0.62	0.70	48	-0.39	0.31	0.21	54	0.05	0.17	0.77
CORT	33	1.63	0.91	0.09	26	1.59	1.47	0.29	0	-	-	-

Table S2.4 Estimates of possible associations of circulating total (T) and free (F) triiodothyronine (T3) and thyroxine (T4) and corticosterone (CORT) in thick-billed murres, with the proportion of time spent diving, flying, swimming, or mean diving depth or the number of dives by the birds. The metrics reported are: sample size (n), estimate(β), standard error (SE) and p-value (*p*). Significant relationships are marked with a * ($p \leq 0.05$), ** ($p \leq 0.01$) and *** ($p \leq 0.001$).

		2016				**2017**				**2018**			
		n	β	SE	*p*	n	β	SE	*p*	n	β	SE	*p*
Diving	TT3	12	-0.29	0.17	0.13	19	-0.35	0.14	0.02*	49	0.00005	0.01	0.99
	FT3	12	-0.005	0.14	0.97	20	-0.10	0.03	0.009**	57	0.046	0.07	0.54
	TT4	14	0.001	0.01	0.87	26	0.003	0.005	0.56	50	0.005	0.003	0.09
	FT4	12	-0.02	0.01	0.13	26	0.01	0.01	0.23	54	-0.0002	0.01	0.98
	CORT	15	0.001	0.001	0.45	19	-0.0004	0.0002	0.15	0	-	-	-
Flying	TT3	12	1.03	0.69	0.21	19	-0.26	0.25	0.32	49	0.01	0.02	0.61
	FT3	12	-0.13	0.16	0.44	20	-0.01	0.05	0.79	57	0.02	0.07	0.82
	TT4	14	0.13	0.02	0.42	26	0.003	0.69	0.82	50	0.01	0.004	0.13
	FT4	12	0.15	0.06	0.06	26	0.03	0.02	0.06	54	0.01	0.01	0.29
	CORT	15	0.001	0.001	0.55	19	-0.0004	0.0004	0.33	0	-	-	-
Swimming	TT3	12	0.04	0.09	0.69	19	0.12	0.12	0.33	49	0.002	0.11	0.82
	FT3	12	-0.17	3.01	0.96	20	0.01	0.02	0.81	57	-0.04	0.04	0.35
	TT4	14	-0.01	0.01	0.14	26	-0.01	0.01	0.32	50	-0.01	0.01	0.20
	FT4	12	-0.01	0.01	0.22	26	-1.06	0.87	0.24	54	-1.44	0.92	0.12
	CORT	15	0.001	0.001	0.41	19	0.0002	0.0001	0.16	0	-	-	-
Mean Diving Depth	TT3	6	2.10	1.22	0.16	19	-0.74	0.40	0.08	49	0.01	0.04	0.69
	FT3	8	-0.02	0.47	0.96	20	-0.05	0.09	0.58	57	0.16	0.15	0.29
	TT4	9	0.05	0.03	0.13	26	-0.005	0.01	0.73	50	0.02	0.01	0.08
	FT4	8	0.14	0.16	0.44	26	0.02	0.03	0.60	54	0.03	0.03	0.24
	CORT	9	0.003	0.003	0.46	19	-0.001	0.001	0.22	0	-	-	-
Number of Dives	TT3	6	2.17	2.19	0.32	17	-2.39	2.23	0.28	49	-2.19	2.19	0.32
	FT3	8	0.67	0.57	0.24	17	-0.66	0.57	0.25	57	-0.99	0.59	0.10
	TT4	9	-0.03	0.05	0.46	23	0.04	0.047	0.43	50	0.02	0.047	0.68
	FT4	8	0.03	0.21	0.89	23	0.01	0.21	0.96	54	-0.08	0.22	0.71
	CORT	9	0.001	0.004	0.71	18	-0.002	0.004	0.60	0	-	-	-

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