

Fredrik Øglænd Hanslin

The Effects of Early-Life Mercury Exposure on Natal Recruitment in Black-Legged Kittiwakes Breeding in Svalbard

Master's thesis in Biology
Supervisor: Børge Moe
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Photo: Fredrik Øglænd Hanslin

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Abstract

The early-life quality of black-legged kittiwakes (*Rissa tridactyla*, Kittiwake) is influenced by numerous ecological and environmental factors which affect the nestlings immediate survival, and can have lasting effects by adjusting the adult phenotype. The kittiwake is a globally vulnerable species, experiencing large population declines caused by a multitude of factors. As kittiwakes occupy some of the uppermost trophic levels in the Arctic marine food webs, they risk high exposure to biomagnifying and persistent pollutants such as mercury (Hg). Hg is an endocrine disruptor that has been shown to negatively affect the reproductive success in adult kittiwakes breeding in the Arctic. In the present study, we investigated the early-life exposure to Hg in kittiwakes breeding in Kongsfjorden on Svalbard, and test whether the accumulated nestling levels of Hg affect the kittiwake's probability of natal recruitment, as well as age of recruitment. Additionally, these individuals were deployed with GLS (Global location sensor) light-loggers, allowing us to track the kittiwakes first years of life and reveal their migratory movements before their return to their natal colony. In following years, the recruited individuals were recaptured to assess their uptake of Hg from the time of fledging to adult life stage. We found low blood concentrations of Hg (0.052 $\mu\text{g/g}$ dry weight) in nestlings, that did not affect the kittiwake's probability, nor age, of natal recruitment. These levels were lower than any observed effect concentration in seabirds ($>0.95 \mu\text{g/g}$ dry weight). The returning kittiwakes had Hg concentrations ~ 45 times higher at recruitment than at fledging (2.35 $\mu\text{g/g}$ dry weight), that decreased throughout the breeding season. The present study shows that Hg concentrations accumulated in the nestling stage are not of concern in this Kongsfjorden kittiwake colony. However, the recruited kittiwakes are exposed to high levels of Hg during their overwintering period in the North-Atlantic Ocean, reaching Hg concentrations above threshold levels for adverse effects on reproductive potential.

Sammendrag

Livskvaliteten tidlig i livet hos krykkje (*Rissa tridactyla*) bestemmes av flere økologiske og miljømessige faktorer som påvirker umiddelbar overlevelse, men som også kan ha langvarige effekter ved å justere den adulte fenotypen. Krykkja er en globalt sårbar art som opplever store populasjonsnedganger forårsaket av mange ulike faktorer. Da krykkjer befinner seg blant de øverste trofiske nivåene i de arktiske marine næringsnettene, risikerer de høy eksponering for biomagnifiserende miljøgifter som kvikksølv (Hg). Hg er en persistent hormonhermer som har blitt vist til å negativt påvirke reproduksjonssuksessen hos voksne krykkjer som hekker i Arktis. I denne studien undersøker vi tidlig-livs eksponeringen for kvikksølv hos krykkjer som hekker i Kongsfjorden på Svalbard, og tester om de akkumulerte nivåene av Hg i reirungene påvirker sannsynligheten for at krykkjene rekrutteres tilbake til kolonien, samt alderen for rekruttering. I tillegg ble disse individene utstyrt med GLS (Global location sensor) lysloggere, som tillot oss å spore krykkjenes første leveår og avdekke migrasjonsmønstrene deres før de vendte tilbake til sin natale koloni. I påfølgende år ble de rekrutterte individene fanget igjen for å måle opptaket deres av Hg fra reirperioden til voksen alder. Vi fant lave blodkonsentrasjoner av Hg ($0.052 \mu\text{g/g dw}$) hos reirungene, som ikke påvirket krykkjas sannsynlighet, eller alder for rekruttering tilbake til fødekolonien. Disse nivåene var lavere enn noen observerte effektkonsentrasjoner hos sjøfugler ($>0.95 \mu\text{g/g dw}$). De rekrutterte krykkjene hadde Hg-konsentrasjoner ~ 45 ganger høyere ved rekruttering enn i reirperioden ($2.35 \mu\text{g/g dw}$), som avtok gjennom hekkesesongen. Denne studien viser at Hg-konsentrasjoner som akkumuleres i reirperioden ikke er bekymringsfulle for krykkjer i denne kolonien. Imidlertid er de rekrutterte krykkjene eksponert for høye nivåer av Hg under overvintringsperioden i Nord-Atlanteren, og oppnår Hg-konsentrasjoner over terskelverdiene for negative effekter på reproduksjonspotensialet.

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Introduction

The early life is an important period for birds, where the offspring's dependency on parental effort for gaining nutrition, and maintaining high body temperature is crucial for the offspring's immediate survival (Coulson & Porter, 1985; Clutton-Brock, 1991; Mock et al., 2009; Ospina et al., 2018). However, early-life conditions also affect the individual on a long term basis by adjusting the adult phenotype (Lindström, 1999; Metcalfe & Monaghan, 2001; West-Eberhard, 2003). Unfavourable conditions during the developmental stages can have several negative long-term effects, including delayed maturation (Alonso-Alvarez et al., 2006), reduced immunocompetence (Birkhead et al., 1999), increased stress and reduced growth rates (Young et al., 2017), all able to affect the lifetime reproductive success of the individual.

The variation in early-life conditions can be affected both by environmental conditions, parental factors, and nest conditions. Environmental conditions include wind speeds (Konarzewski & Taylor, 1989), temperature (Sauve et al., 2022), and food availability (Barrett & Runde, 1980), whereas parental factors include parental age/breeding experience (Coulson & Porter, 1985), parental quality (Groves, 1984), and behaviour such as food provisioning (Bertram et al., 1991) and incubation (Ospina et al., 2018). Randomly determined factors such as hatching order is also shown to have an effect, where the firstborn chick typically outcompetes its sibling for nest resources (Cam et al., 2003; Young et al., 2017). The present study focuses on the importance of early-life quality from an ecotoxicological point of view, investigating the effects of a heavy metal pollutant on post-fledging performance.

Mercury (Hg) is a naturally occurring element in geological sources that commonly is released into the atmosphere during volcanic activity as metallic mercury (Hg^0) (Clarkson, 1997). Hg^0 is a volatile mercury species with a high vapor pressure, and a long atmospheric lifespan (0.8-1.7 years) allowing it to reside in the atmosphere for longer periods of time (Ariya et al., 2015). Eventually, atmospheric Hg^0 is oxidized to inorganic gaseous mercury (Hg^{2+}) by a variety of oxidizing agents, but usually by ozone (O_3) (Iverfeldt & Lindqvist, 1986; Lin & Pehkonen, 1999). Hg^{2+} has the property to partition between gas and solid phases at low temperatures, and is deposited to water and ground surfaces as precipitation (Lin & Pehkonen, 1999). Further, Hg^{2+} is either reduced to Hg^0 , vaporised and recycled back

into the atmosphere (O'Driscoll et al., 2005), or methylated to methylmercury (MeHg) in the presence of methylating bacteria (Kerin et al., 2006).

MeHg is the form of mercury that is of most concern to wildlife and humans due to its bioaccumulating and biomagnifying properties (Morel et al., 1998). MeHg first enters the marine food web by bioconcentrating in phytoplankton through water filtration and diffusion (Lee & Fisher, 2016). It is then bioaccumulated in individual phytoplankton-preying zooplankton over time, and is further biomagnified up the trophic levels of the food web. (Wiener et al., 2002; Baeyens et al., 2003). The high levels achieved due to the correlation between trophic level and Hg caused by biomagnification proves problematic for several top predators (Kidd et al., 1995; Scheuhammer et al., 2007). Seabirds are at the uppermost trophic levels of the arctic marine ecosystems where they typically forage on a range of different fish, crustaceans and zooplankton (Wold et al., 2011). Birds accumulate MeHg through their diet, and are able to excrete MeHg primarily through feathers when moulting, but also through faeces. Females will in addition be able to excrete MeHg through production of eggs (Lewis & Furness, 1991; Ackerman et al., 2019)

Many seabird species are already experiencing population declines due to overfishing, climate change and invasive species (Furness, 2003; Grémillet & Boulinier, 2009; Dias et al., 2019). These factors have caused 30% of the worlds seabird species to be globally threatened following the International Union for Conservation of Nature (IUCN) red list criteria (BirdLife International, 2022). Paleczny et al. (2015) estimates the global population of monitored seabirds to have declined by 70% in the period 1950-2010. Overfishing and climate change can cause shifts in the foraging niche of seabirds, where their preferred food items are either reduced in abundance, or have changed their spatial distribution to match the change in temperature (Perry et al., 2005). These stressors lead to physiological changes that compromise fitness by reducing their aerobic scope (Sokolova, 2013). On top of these stressors, seabirds are faced with an increased release of Hg from industrial activity, where anthropogenic sources are estimated to account for nearly 60% of the world's total emission of Hg (Nriagu, 1989; Pacyna et al., 2006), drastically increasing the circulation of Hg, and hence the bioavailability of MeHg.

MeHg is shown to cause adverse neurological (Wolfe et al., 1998; Seewagen, 2010) and endocrinal (Tan et al., 2009) effects in both humans and wildlife. Negative effects of mercury on the endocrine system have already been observed in the black-legged kittiwake (*Rissa*

tridactyla) in Svalbard (Tartu et al., 2013, 2016). Although there are relatively high Hg levels in adult kittiwakes in Svalbard, mounting evidence show that the Hg exposure is even higher at the non-breeding areas in the North Atlantic (Fort et al., 2014; Albert et al., 2021). Other studies on seabirds indicate that breeding success in adult individuals is negatively affected by increasing Hg levels (Goutte, et al., 2014a, b, 2015; Ackerman et al., 2016). MeHg concentrations are also shown to vary with age (Bighetti et al., 2021). However, few studies have been conducted on seabirds assessing the effects of Hg in the period from early life to adulthood.

The physical properties of Hg make the pollutant capable of long-range atmospheric transport through global distillation, and therefore poses as a threat to the polar regions (AMAP, 2005; O'Driscoll et al., 2005). Global distillation, also called the grasshopper effect, is a process explaining the atmospheric movement of pollutants (typically persistent organic pollutants [POPs]) from low latitudes to higher latitudes (Wania & Mackay, 1996; O'Driscoll et al., 2005). High temperatures at the lower latitudes favour evaporation of Hg, where Hg⁰ is transported with the air currents created by the Coriolis effect before deposition is favoured in colder temperatures at higher latitudes. This process leads to high concentrations of volatile pollutants in the polar regions.

However, the global distillation process of Hg is more complex. The deposition and volatilization of Hg is not solely dependent on the rates of evaporation and condensation, but also the oxidation state of mercury. These redox reactions predominantly determine the rates of volatilization (O'Driscoll et al., 2003). Studies suggest that the rates of these reactions are highly temperature dependant, implying that deposition of Hg²⁺ is favoured at colder temperatures due to the lower reduction rates of Hg²⁺ (Van Loon et al., 2000). There are however uncertainties in these details that require further investigation (Lindberg et al., 2007).

Migration is an energy demanding task that allows animals to benefit from seasonally available resources whilst avoiding unfavourable environmental conditions (Somveille et al., 2015). This is especially evident in polar environments, where the winters are dominated by polar nights and extreme weather conditions. Consequently, most arctic seabird species migrate to lower latitudes during the winter, before returning to their arctic breeding grounds in the spring. The adult black-legged kittiwakes are known to migrate to the Atlantic Ocean, especially concentrated in the north-west, outside Newfoundland and in the Labrador Sea

(Frederiksen et al., 2012). However, little is known about the overwintering grounds and migration routes of the subadult kittiwakes before they return to the breeding colony years after fledging.

Study aims

The present study aims to quantify the levels of Hg accumulated in nestlings of the black-legged kittiwake breeding on Svalbard, and the spatial origin of these contaminants during their first years of life. By using longitudinal data where the nestlings are again sampled at recruitment 2-5 years after fledging, one can test for potential consequences of Hg on individual and population level. The main aim is to i) determine the levels of Hg accumulated in the nestling period, and test whether these levels affect the individual's chance of recruitment or age of recruitment back to the breeding population. I hypothesize that if the measured levels of nestling Hg are above a certain threshold value for adverse effects, then there will be a negative effect of Hg on recruitment, either by compromising survival up until the time of recruitment, or by delaying the age of recruitment, where high concentration individuals will spend more time maturing and catching up before recruiting. I will also ii) reveal where kittiwakes spend their first years of life by using geolocator (GLS) data, and iii) investigate the levels of Hg accumulated in the period from fledging to recruitment back into the colony.

Methods

Study species

The black-legged kittiwake (hereinafter referred to as kittiwake) is a long-lived monogamous seabird that breeds throughout the northern hemisphere. It is one of the most numerous bird species in the world (Callaghan et al., 2021) and is commonly found breeding in bird cliff colonies along the coast with other seabird species such as the Brünnich's guillemot (*Uria lomvia*). During wintering times, adult kittiwakes of Svalbard usually migrate to the North-West Atlantic Ocean which is considered a hotspot for overwintering kittiwakes (Strøm, 2006; Frederiksen et al., 2012)

Globally, the kittiwake is listed as a vulnerable species due to the drastic population decline of >40% over three generations (BirdLife International, 2019). On a global scale, seabird populations declines are caused by a multitude of factors, including climate change, overfishing, bycatch and invasive species (Dias et al., 2019). On the Norwegian Red List, the kittiwake is endangered in mainland Norway due to a severe population decline of 50-80%

over three generations, whereas on Svalbard, it is listed as near threatened due to a population decline of 15-30% (Stokke et al., 2021a, 2021b). The populations trends for kittiwakes in Norway are mainly linked to ecosystem changes resulting in decreased availability of their preferred prey as well as increased predation from avian and mammalian predators (Fauchald et al., 2015a, b).

Kittiwakes are surface feeders, and are only able to capture prey found in the top metre of the ocean surface (Coulson, 2011). Kittiwakes in Kongsfjorden mainly forage on polar cod (*Boreogadus saida*), krill (*Thysanoessa inermis*), and capelin (*Mallotus villosus*), but also forage on other mesopelagic fish, crustaceans, pteropods, and polychaetes (Hop et al., 2002; Wold et al., 2011; Vihtakari et al., 2018). In later years, climate change has caused a change in the species distribution in Kongsfjorden, where there has been observed a shift from Arctic species (e.g. Polar cod and *Themisto libellula*) to more Atlantic species (e.g. capelin and Atlantic herring (*Clupea harengus*)) (Vihtakari et al., 2018). Kittiwakes are central place foragers during the breeding season, and mainly forage within Kongsfjorden during incubation and chick rearing (Chastel, Descamps & Strøm, unpublished data), but may take longer foraging trips outside of Kongsfjorden during the pre-laying period (Goutte et al., 2014c). The adult and nestling diet overlap, indicating that adult kittiwakes feed their offspring the same prey items that they themselves forage on (Thorvaldsen et al., 2015).

Kittiwakes first breed at 3-8 years old, averaging at 4-5 years old (Wooller & Coulson, 1977; Hatch et al., 2020), but are known to return to the colony at least one year prior to recruitment (Porter, 1988). This early return to the colony is linked to acquisition of skills and experience necessary for successful breeding in the colony, and could involve finding a partner, competing for nest sites, and central-place foraging behaviour (Porter, 1988; Cadiou et al., 1994; Collet et al., 2020). Kittiwakes build nests on cliff-ledges providing great protection from ground predators who are usually unable to predate nests on these cliffs. Adult kittiwakes typically lay 1-3 eggs on which they incubate in turns for approximately 30 days before hatching (Hatch et al., 2020). The nestlings heavily depend on parental heat production to maintain high body temperatures, before the parents spend less time in the nest after about 15 days (Coulson, 2011).

Study site and data collection

This study is based on samples collected during the kittiwake breeding season in the colony of Blomstrand in Kongsfjorden, Ny-Ålesund (79°N, 12°E) in the period from 2010-2015

(Fig. 1). The Blomstrand colony along with the neighbouring colony of Krykkjefjellet in Kongsfjorden were actively monitored in the study period when looking for recruited individuals.



Fig. 1: Map of Kongsfjorden showing the study site of Blomstrand, research town Ny-Ålesund, and neighbouring kittiwake colony Krykkjefjellet. Map from TopoSvalbard (Norsk Polarinstitutt).

Kittiwake nestlings ($n = 54$, 24 males, 30 females) were caught in the colony of Blomstrand in early August 2010 at approximately 30 days of age, hence close to fledging. Biometric measurements of body mass (g), tarsus- (mm), skull- (mm), and wing length (mm) were taken upon capture. The clutch size and hatching order were also recorded in each nest. In addition, 2 mL blood samples were taken from the brachial vein using heparinized syringes to avoid coagulation. The chicks were then mounted with light-logging geolocators (Global Location Sensing [GLS]) of the model mk18 before being released. These loggers have a weight of <2.5 g, which allow deployment in large quantities with minimal burden on the individual at the cost of geographical precision. GLS loggers have been shown to not affect behaviour, fitness, nor survival in seabird species (e.g. Kürten et al., 2019; Nicoll et al., 2022).

In the following years (2012-2015), 25 kittiwakes (13 males, 12 females) were observed having returned to the natal colony, and are considered as recruits, and 16 of these were recaptured (10 males, 6 females) and sampled as described above. One of the recaptured GLS

loggers was not functional, and no useable data was retrieved from this logger. Hence, GLS-data was available from 15 chicks recruited to the breeding colony.

Lab analyses

Quantification of THg levels

Total Hg (THg, hereafter Hg [dry weight, dw]) levels were analysed at Littoral Environnement et Sociétés (LIENs, La Rochelle, France) from freeze-dried and powdered red blood cells (RBC), using an advanced Hg analyzer spectrophotometer (Altec AMA 254) as explained in Bustamante et al. (2006). Hg levels for each individual were analysed from two different aliquots to test the repeatability with an average coefficient of variation (CV%) of 2.64% (range: 0.06% - 7.64%) across all individuals. The means for the two samples are used in this study.

Hg concentrations analyzed from red blood cells have been shown to have an half-life of 30-65 days in Great skuas (*Stercorarius skua*) (Bearhop et al., 2000), and 38-65 days in the Cory's shearwaters (*Calonectris diomedea*) (Monteiro & Furness, 2001) depending on the moulting cycle of the animal, and can thus reflect the short-term Hg concentrations of several weeks to months in seabirds.

Molecular sexing

Molecular sexing was conducted at the Norwegian University of Science and Technology (NTNU, Trondheim, Norway). A small drop of blood for sex determination was obtained from each nestling by brachial vein puncture and was immediately stored in 96% ethanol. The DNA-sexing was performed within four months from the blood sampling and followed the procedure of Griffiths et al. (1998). The DNA-sexing procedure is based on the female being the heterogametic (ZW) sex and carrying both the CHD-1-W (chromo-helicase-DNA-binding) gene and the smaller CHD-1-Z gene on the sex chromosome, while the male in contrast is the homogametic (ZZ) sex carrying only the small CHD-1-Z gene (Griffiths et al., 1998).

Stable isotope analyses

Analyses of stable isotopes were conducted at LIENs, La Rochelle, France. Whole blood was freeze-dried and powdered before the relative abundance of $^{15}\text{N}/^{14}\text{N}$ in the tissue was determined using continuous flow mass spectrometer (Thermo Scientific Delta V Plus) coupled to an elemental analyzer (Thermo Scientific Flash 2000). The deviations (δ) of the

relative isotope abundances are calculated by dividing the ratios (R) of $^{15}\text{N}/^{14}\text{N}$ in the sample with the standard ratios for this stable isotope (I).

$$\delta X(\text{‰}) = \left(\frac{R_{\text{Sample}}}{R_{\text{Standard}}} - 1 \right) * 1000 \quad (\text{I})$$

The stable isotope data reflect an organism's diet and foraging environment (Newsome et al., 2007). Stable isotope from red blood cells has a reflective timeframe on dietary information of two months, whereas plasma has a reflective timeframe of one week (Hobson & Clark, 1993). $\delta^{15}\text{N}$ can be used to reflect an organism's trophic level, due to its stepwise increase up the food chain (Minagawa & Wada, 1984; Hobson & Welch, 1992). A higher $\delta^{15}\text{N}$ value represents a higher trophic level. It can also reflect the food quality for an individual, where a higher trophic level diet is linked to higher body mass, but this has not always shown to be the case (Morrison et al., 2014). I therefore assessed the relationship between $\delta^{15}\text{N}$ and body mass for the nestlings in this study, and find a strong positive correlation between the two variables, confirming that $\delta^{15}\text{N}$ is reflective of food quality in these kittiwakes nestlings (Fig. S1).

Spatial analyses of GLS-data

Data on light-levels obtained from the GLS loggers were used to calculate geographical positions using an automated procedure to identify the twilight events (sunrise, sunset) using a threshold method as described in Bråthen et al. (2021). Latitude is determined from the length of the day or night, and longitude is determined from timing of midday or midnight. Hence, positions were estimated twice every day for each logger. Since GLS loggers have low accuracy, they are not recommended for studying movements less than 200 km (Lisovski et al., 2012, 2020), but are good for studying large-scale patterns and movements. The low accuracy is due to factors affecting the light intensity, such as weather, topography, and behaviour, ultimately affecting the latitudinal accuracy (Lisovski et al., 2012). Position estimation is also prevented during the polar summer, when the birds are exposed to constant sunlight. At this time, there are no twilight events to be identified, and therefore no positions to be estimated. Furthermore, daylength is equal at all latitudes at spring and autumn equinox, which makes estimates of latitude unreliable. Positions are, therefore, removed for three weeks at each side of apparent equinox (8 September – 20 October and 20 February – 3 April, Bråthen et al., 2021). The chosen light-threshold for sunset and sunrise corresponds to

the sun being approximately -3 degrees below the horizon, and at this sun elevation angle the apparent equinox is closer to December than the standard equinox.

Statistics

Analyses of the data are performed in R (version 4.0.2) with a significance level of $\alpha = 0.05$. Dispersion parameters are given as standard deviations unless stated otherwise. To test the effects of Hg, sex, trophic level ($\delta^{15}\text{N}$), and sibling status (singleton, sibling α and sibling β) on the probability of recruitment, a logistic regression was fit with a generalized linear mixed-effect model (GLMM) from the 'lme4' package using a binomial distribution and logit-link, with the nest as a random variable (Bates et al., 2014). Recruitment is represented by resight data as a binary variable, i.e., observed (1) or not observed (0) in the colony 2-5 years after fledging. Introducing nest as a random variable improves the estimates of the predictors by accounting for variation produced between nests that is not covered by the predictors (e.g. parental fitness and breeding experience). The alternative when accounting for the effects of nest is to include nest as a fixed variable in the model. However, I am not interested in estimating the effects of nest, just account for it. Adding predictor variable as a fixed effect also increases the degrees of freedom, reducing the power of the model. The same predictor variables were modelled against the year of recruitment using a linear mixed-effect model (LMM), with nest as a random variable as explained above.

Chick age (days), trophic level ($\delta^{15}\text{N}$), sibling status (singleton, sibling α , and sibling β), and Sex were modelled against the nestling levels of Hg in a GLMM with nest as random effect, to explore how these variables contributed to the early-life accumulation of Hg .

To test the difference in Hg levels in the individuals between nestling and adult stages, a linear model (LM) was used to model the age as a categorical predictor variable (Nestling, Adult) against the levels of Hg. Hg levels were log-transformed to fulfil the assumption of homoscedasticity, as nestlings show much lower values and therefore smaller variation in Hg than adults. The effects of sex, year of sample and sampling day within each year after June 15th (squared) on the accumulation of Hg from fledging to recruitment were also modelled in a LM.

Diagnostic plots for all models were examined using the 'DHARMA' package (Hartig, 2022), and multicollinearity between predictor variables was assessed by determining the variance inflation factor (VIF) from the 'car' package (Fox & Weisberg, 2018), to investigate whether the estimates for predictor variables are reliably computed.

Results

Nestling Hg levels

A total of 54 chicks were sampled during the nestling stage just prior to fledging in 2010. Nestling levels of Hg measured on average $0.052 \pm 0.02 \mu\text{g/g dw}$, which is lower than concentrations associated with adverse effects in seabird (Ackerman et al., 2016, Fig. 2A). Hg concentrations in the nestling stage were positively correlated with the age, and the trophic level of the individual (Table 1, Fig. 2B, Fig. 3C). There were no differences between sex or between individuals with different sibling status.

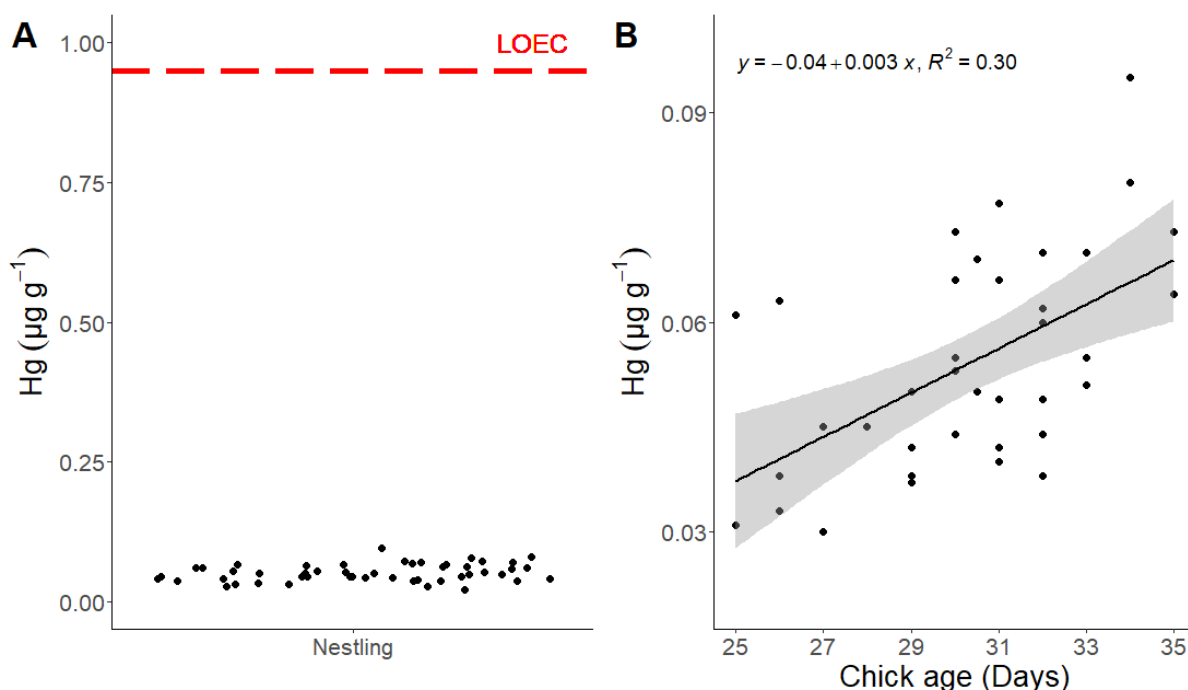


Fig. 2: (A) Nestling levels of Hg ($\mu\text{g/g}$) accumulated in the nest. LOEC (Lowest observed effect concentration) refers to the lowest concentration of Hg ($0.2 \mu\text{g/g ww}$ in blood, transformed to $0.95 \mu\text{g/g dw}$ in blood assuming a water content of 79%) shown to have any adverse effect in seabird following Ackerman et al., (2016). All nestlings are plotted with jitter on the x-axis to provide spread and visualize all individual values. (B) Linear regression between Chick age (Days) and nestling Hg ($\mu\text{g/g dw}$) with the regression formula and coefficient of determination (R^2). Grey area represent the 95% confidence interval.

Probability of recruitment

In total, 25 of the initial 54 nestlings were resighted in the colony after 2-5 years, and are considered to have recruited into the colony.

A logistic regression between nestling Hg levels and recruitment yielded a significant positive relationship between Hg concentrations and the probability of recruitment ($p = 0.030$, Fig. 3A, Table S1). However, the probability of recruitment also related statistically significantly to nestling trophic level ($p = 0.002$, Fig. 3B, Table S2) and nestling trophic level correlated positively with nestling Hg level ($p = 0.001$, Fig. 3C). This relationship was disentangled in a GLMM including both nestling Hg and trophic level along with, sibling status and sex modelled against recruitment with nest as a random variable. From this analysis there is no effect of Hg ($p = 0.181$, Table 2) on the probability of recruitment. The variables best explaining the probability of recruitment was trophic level where high trophic level individuals had higher chances of recruiting back to the colony, however not entirely reaching statistical significance ($p = 0.061$). There was no significant effect of sibling status ($p > 0.104$), or of sex ($p = 0.355$) on the probability of recruitment.

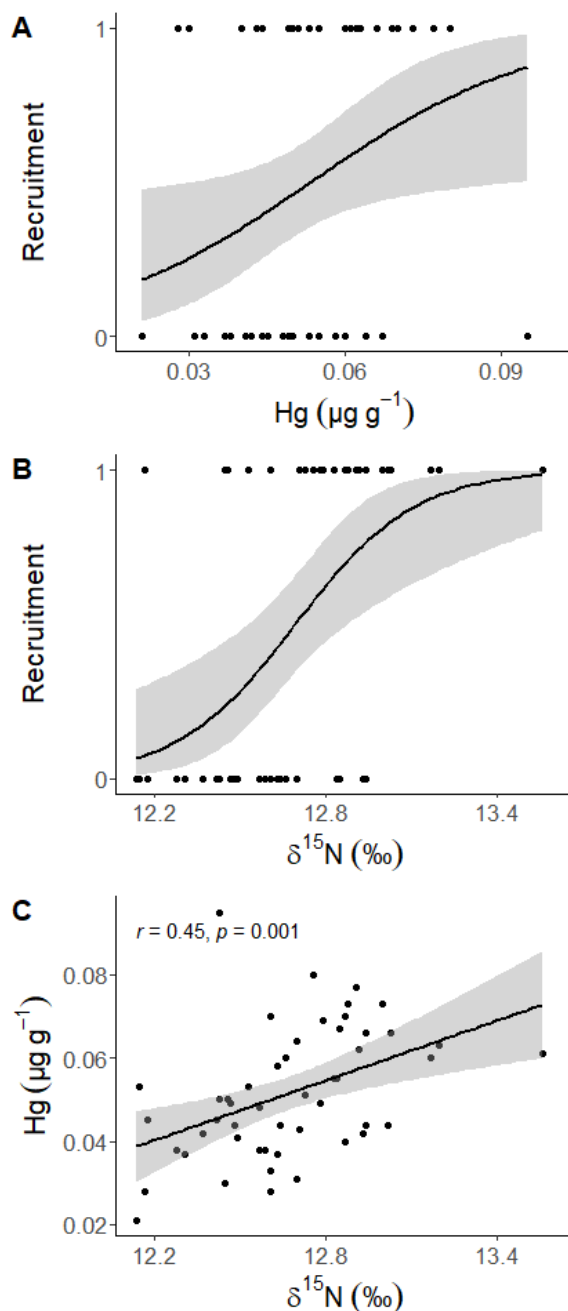


Fig. 3: Logistic regressions of the effect of (A) Hg ($\mu\text{g g}^{-1}$), and (B) $\delta^{15}\text{N}$ (‰) on the probability of recruitment. (C) shows the significant correlation between Hg and $\delta^{15}\text{N}$ causing the positive effect of Hg on the probability of recruitment with p-value (p) and Pearson's coefficient of correlation (r). Grey areas represent the 95% confidence intervals.

Table 1: Effect of Age (days), $\delta^{15}\text{N}$, Sibling status (singleton, sibling α , sibling β) and Sex on the Hg levels accumulated in the nestling period. Coefficients for each predictor variable (*Estimate*), 95% confidence intervals (*95% CI*), p-values (*p*), sample size (Observations), the variance produced by the random effect (Nest variance), sample size for random variable (N_{Nest}), residual variance, marginal R^2 and conditional R^2 .

<i>Fixed coefficients</i>	<i>Estimate</i>	Hg	
		<i>95% CI</i>	<i>p</i>
(Intercept)	-0.304	-0.545 – -0.064	0.015
Age (days)	0.003	0.001 – 0.005	0.001
$\delta^{15}\text{N}$	0.021	0.003 – 0.039	0.027
Sibling α -chick	-0.001	-0.013 – 0.011	0.845
Sibling β -chick	0.002	-0.010 – 0.014	0.783
Sex [M]	0.000	-0.009 – 0.010	0.936
<i>Random effects</i>			
Nest variance	0.00009		
N_{Nest}	30		
Residual variance	0.00007		
Observations	38		
Marginal R^2 / Conditional R^2	0.371 / 0.727		

Age of recruitment

The recruiting birds recruited at an average age of 3.0 ± 0.8 years old. The age of recruitment was not affected by nestling concentrations of Hg ($p = 0.718$), nor truly explained by any of the measured variables (Table 2). Most of the variation is explained between nests as observed by the relatively high conditional R^2 compared to the marginal R^2 . There is however a tendency of males recruiting at earlier ages (2.7 ± 0.6 years) than females (3.4 ± 0.8 years), with all but one recruited male having returned to the colony by 2013 (Fig. 4).

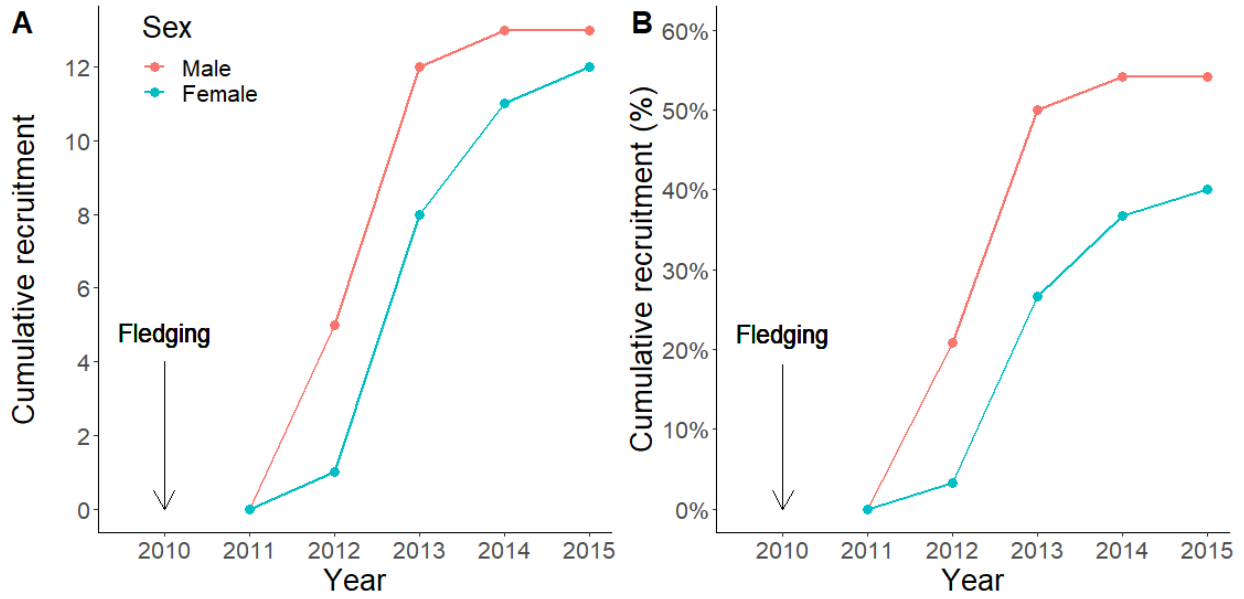


Fig. 4: Lineplot for (A) the cumulative number, and (B) the cumulative percentage of natal recruits from the initial 54 individuals for both sexes based on their year of recruitment since fledging in 2010.

Table 2: Results from the generalized linear mixed-effects model analysing the probability and age of natal recruitment in relation to nestling Hg, $\delta^{15}N$, Sibling status (singleton, sibling α , sibling β). Coefficients for each predictor variable in Log-odds (*Estimate*), 95% confidence intervals (*95% CI*), p-values (*p*), sample size (Observations), the variance produced by the random effect (Nest variance), sample size for random variable (N_{Nest}), residual variance, marginal R^2 and conditional R^2 are shown.

<i>Fixed coefficients</i>	Probability of Recruitment			Age of Recruitment		
	<i>Estimate</i>	<i>95% CI</i>	<i>p</i>	<i>Estimate</i>	<i>95% CI</i>	<i>p</i>
(Intercept)	-112.8	-230.1 – 4.4	0.059	16.7	-3.0 – 36.3	0.090
Nestling Hg	60.6	-28.2 – 149.5	0.181	-5.0	-33.8 – 23.9	0.718
$\delta^{15}N$	8.5	-0.4 – 17.4	0.061	-1.0	-2.6 – 0.6	0.194
Sibling α -chick	2.0	-1.1 – 5.1	0.214	-0.2	-1.2 – 0.9	0.753
Sibling β -chick	3.8	-0.8 – 8.4	0.104	-0.1	-1.1 – 0.9	0.841
Sex [M]	1.2	-1.3 – 3.6	0.355	-0.5	-1.2 – 0.3	0.209
Random effects						
Nest variance		0.77			0.59	
N_{Nest}		34			18	
Residual variance		3.29			0.10	
Observations		44			22	
Marginal R^2 / Conditional R^2		0.652 / 0.718			0.164 / 0.881	

Early-life migration

Tracking data from the 15 recaptured and functioning loggers show that the subadult kittiwakes occupy large areas in the North Atlantic Ocean during the overwintering period from the coast of Newfoundland, Canada to the coast of Portugal and Spain (Fig. 5). At the time of spring migration, the kittiwakes migrate up northwards, either along the west coast of Greenland, or in the Northern Barents Sea. During the breeding season, the subadult kittiwakes are typically found at areas around Svalbard, but not necessarily at the natal colony in Kongsfjorden. No individuals were resighted in the natal colony in 2011 (Fig. 4), i.e., the first summer after fledging. The tracking data shows that 8 kittiwakes were at the west coast of Greenland, while 7 kittiwakes were at the east coast of Greenland and the northern Barents Sea in July - October 2011 (Fig. 5).

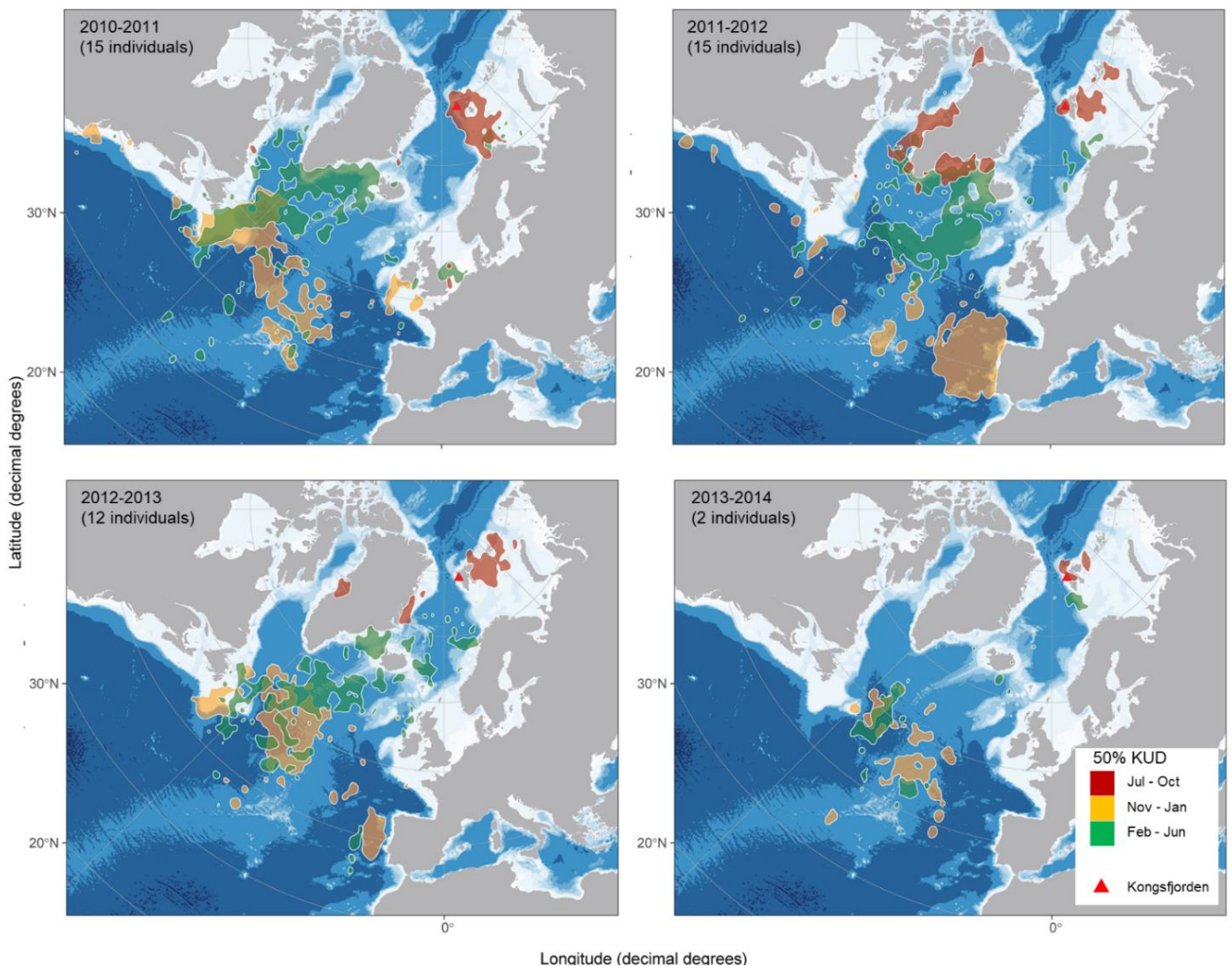


Fig. 5: Map showing the tracking data from GLS-loggers for each of four years tracked from July to June with sample size shown for each year (2010-2011, 2011-2012, 2012-2013, 2013-2014). The maps show 50% kernel utilization distribution which represent the core areas used by the kittiwakes. Red = late summer-autumn distribution from July to October, yellow = Late autumn-winter distribution from November to January, and green = Late winter-summer distribution from February to June.

Records of constant daylight clearly indicate that birds were at high latitudes, and there are only few positions in July and August (and June, as well). In their first summer after fledging, 8 of the kittiwakes spent the summer in West Greenland before eventually recruiting back to Svalbard 1-3 years later.

Accumulation of Hg from fledging to recruitment

From the recruited individuals, 16 were recaptured and sampled to assess the Hg accumulation from fledging to recruitment. After recruiting back into the colony, the kittiwakes had accumulated significantly higher levels of Hg as returning adults ($1.963 \pm 0.8 \mu\text{g/g dw}$) than as nestlings ($0.052 \pm 0.02 \mu\text{g/g dw}$) ($p < 0.001$) (Fig. 6, Table S3).

When investigating the accumulated Hg levels by sex, year, and sampling day within each year, there is a strong effect

of sampling day within each year, where the Hg levels measured decrease throughout the breeding season ($p = 0.008$, Fig. 7A, Table 3). When correcting for the effect of sampling day, the returning kittiwakes averaged a Hg concentration of $2.35 \pm 0.5 \mu\text{g/g dw}$ on June 15.

There is no effect of year of recruitment on Hg concentrations (ANOVA, $p = 0.401$). However, the entangled structure of year sampled, and day sampled within year makes it difficult to accurately estimate the effects of year (Fig. 7A, Fig. 8). Males accumulate significantly higher levels of Hg than females from fledging to recruitment ($p = 0.041$, Fig. 7B, Table 3).

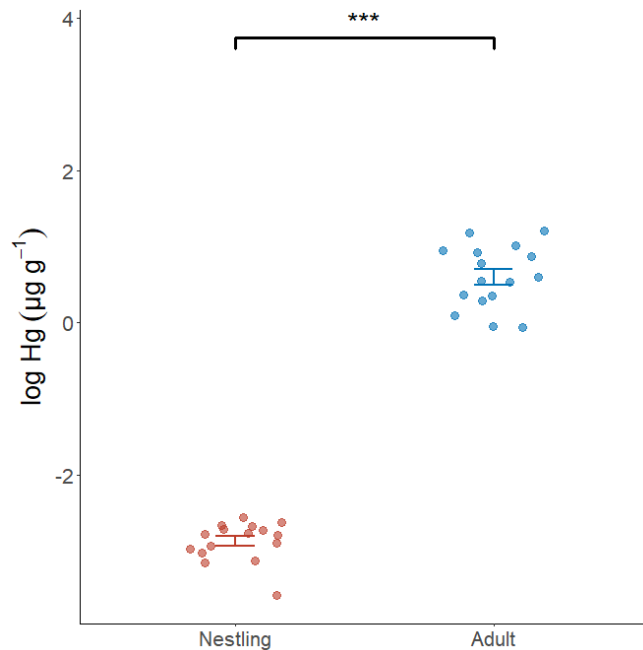


Fig. 6: The log Hg concentrations ($\mu\text{g/g}$) in the nestling period and when they return to the colony to as adults. Whiskers show the standard error of the mean. Significance code: *** = $p < 0.001$.

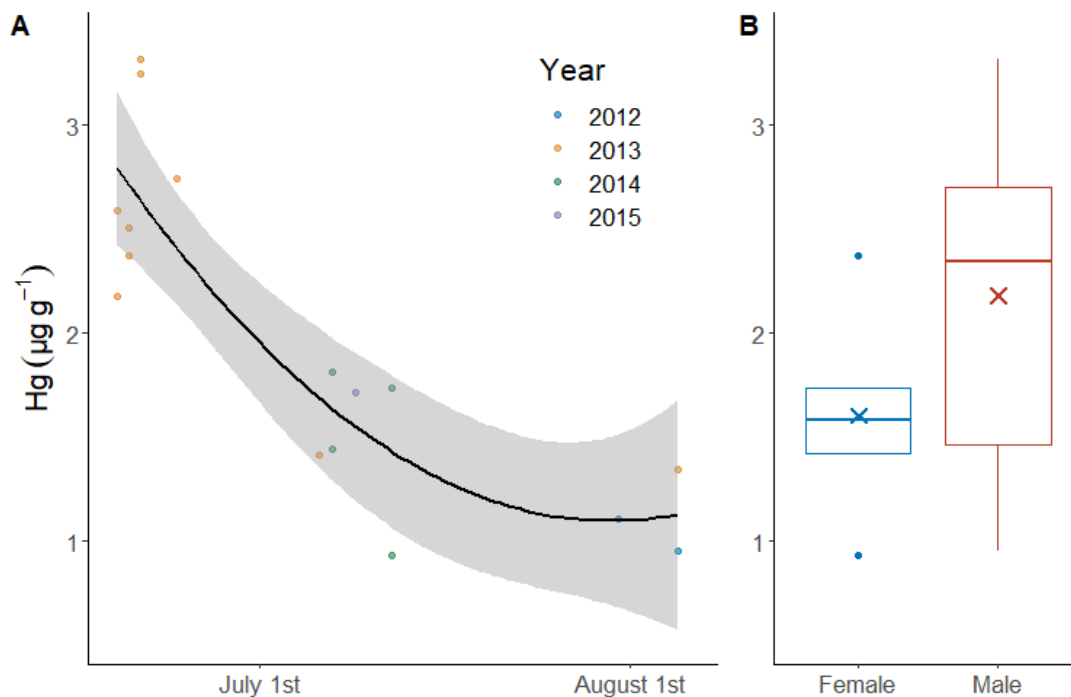


Fig. 7: (A) The seasonal decrease of Hg ($\mu\text{g/g}$) throughout the breeding season for the different years of recruitment (Year), and (B) the sex differences in accumulated Hg levels from nestling to adult. Boxes refer to the 25th and 75th percentile which is the interquartile range (IQR). The whiskers cover data points within 1.5x IQR outside the IQR. Data points outside 1.5x IQR are regarded as outliers and shown as dots. Line = median, cross (\times) = mean.

Table 3: Results from the linear model analysing accumulated levels of Hg as returning adults in relation to day sampled within year (Day^2), year sampled (Year), and Sex. Day of sample was entered as a second degree term to account for a curved relationship to the dependant variable. Coefficients for each predictor variable (*Estimate*), 95% confidence intervals (95% *CI*), p-values (*p*), sample size (Observations), R^2 and R^2 -adjusted are shown. The intercept represents the estimate for Females on June 15 in 2012. Day of sample refers to days after June 15 within each year.

<i>Predictors</i>	Accumulated Hg		
	<i>Estimate</i>	<i>95% CI</i>	<i>p</i>
(Intercept)	1.66	0.44 – 2.89	0.013
Day^2	-0.0006	-0.0009 – -0.0002	0.008
Year [2013]	0.41	-0.62 – 1.44	0.401
Year [2014]	-0.07	-1.17 – 1.04	0.897
Year [2015]	0.30	-1.11 – 1.71	0.645
Sex [M]	0.63	0.03 – 1.23	0.041
Observations	16		
R^2 / R^2 adjusted	0.813 / 0.720		

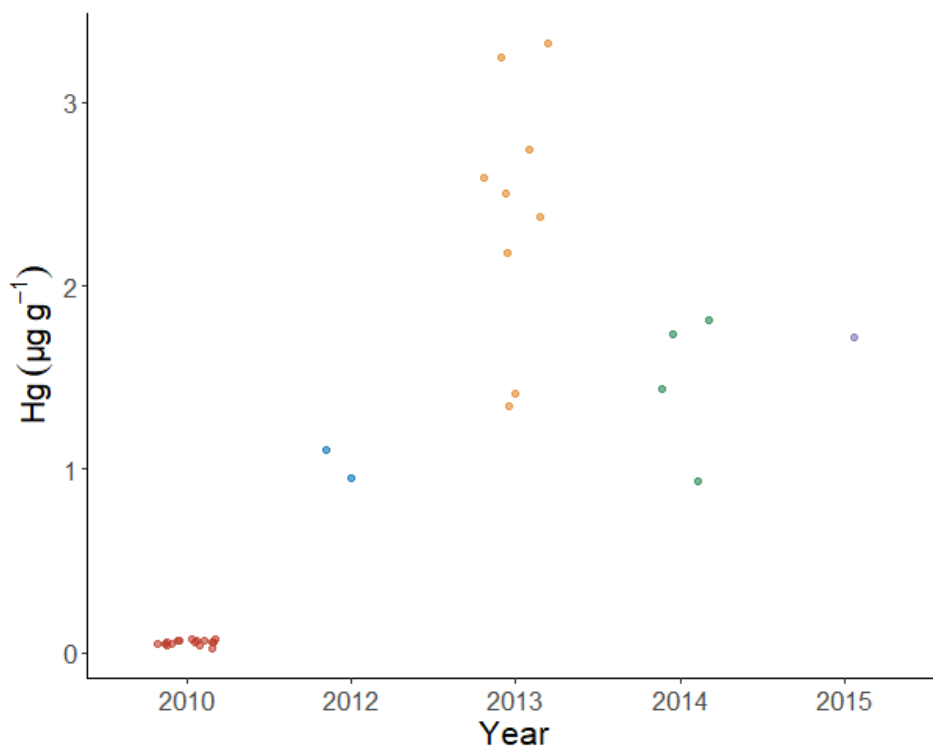


Fig. 8: Hg concentrations ($\mu\text{g/g}$) by year from their nestling stage in 2010, and their returning years in 2012, 2013, 2014 and 2015.

Discussion

Recruitment and nestling Hg levels

The hypothesis that higher Hg levels are related to lower probabilities of recruitment is not supported by the present study (Table 2). Nestlings had an average blood Hg concentration of only $0.052 \mu\text{g/g dw}$, a concentration which is far below the lowest observed effect concentration reported by Ackerman et al. (2016) (Fig. 2A). Hence, the Hg levels accumulated by the kittiwake nestlings before fledging are too low to have an adverse effect on the individual and do not influence the probability of recruitment. However, it is important to note that the threshold values for adverse effects of Hg during the developmental stages are not known, and that they may possibly be lower than the threshold values seen in adults due to complications during development having large physiological impact (e.g. Birkhead et al., 1999; Alonso-Alvarez et al., 2006; Young et al., 2017).

The low Hg concentrations in the fledglings could be caused by three factors: the Hg-levels in their prey, the age of the individual, and the maternal Hg-levels. On a large scale, the Hg exposure observed in seabirds during the breeding season in Kongsfjorden and other eastern Arctic colonies are shown to be relatively low compared to that found in western Arctic colonies (Albert et al., 2021). Accumulation of Hg is also time-dependent, with more Hg

accumulated due to a higher total amount of feeding events (Bearhop et al. 2000). This is clearly demonstrated also in the present study as the Hg-level increase with age of the chicks (Fig. 2B). Lastly, the maternal Hg-levels influences the nestling concentrations of Hg, as the adult female is able to deposit 13-24% of its own burden of Hg into the entire clutch (Ackerman et al., 2019). In further studies it would therefore be interesting to investigate the relationship between maternal and offspring levels of Hg in the Svalbard kittiwakes to obtain a perspective of how much of the accumulated nestling levels of Hg are caused by food, and how much is caused by the maternal transfer of Hg derived from outside of Svalbard.

Nestling Hg concentration were statistically positively associated to the probability of recruitment (Fig. 3A). However, this apparent positive effect is most likely due to the underlying correlation between Hg levels and trophic level (Fig. 3B), where higher trophic level prey contains higher levels of Hg. Trophic level of the individual is also reflective of the food quality, and is positively correlated with nestling body mass (Fig. S1). Trophic level may also be reflective of parental quality, where high quality parents could be able to gather high quality food for their offspring. The observed positive effect of trophic level is therefore expected, as nutrition in the developmental stages is one of the most important indicators for performance during the first independent stages (Metcalf & Monaghan, 2001), allowing the individual to survive up until the time of recruitment.

No effect of sibling status on the recruitment probability was observed, but both α - and β -chicks tended to have higher chances of recruitment compared to singletons. This might seem unintuitive as a larger clutch size implies that the individuals compete for nest resources to a larger extent than a singleton chick (Brockelman, 1975). However, clutch size could also be reflective of parental quality, where parents who are able to raise two chicks, also are able to provide sufficient food for two offspring, thus increasing their chances of recruitment (Coulson & Porter, 1985).

Hg was also hypothesized to delay the kittiwakes age of recruitment, as high Hg individuals might spend more time maturing and catching up before recruiting. In the present study, there is no clear effect on the age of recruitment of the nestling Hg levels, nor any of the other predictor variables. The variation in the age of recruitment was however partly explained by nest as a random factor (Table 2). This may again point to a potential role of parental quality. There is observed a trend between sexes, with males recruiting earlier than the females (Fig. 4). Previous studies conducted on sex differences in natal recruitment in kittiwakes

showed that 80-82% of the natal recruits in a low philopatry population were males (Wooller & Coulson, 1977; Coulson & Coulson, 2008). The explanation for this is linked to reduced chances of inbreeding with close relatives, and the male's role to obtain a nest site, which could be more difficult to obtain in a foreign colony as a dispersing individual. Males also tend to recruit earlier to the colony, and reproduce at a younger age than females (Wooller & Coulson, 1977). This is supported by the findings in the present study. However, fieldwork in the Blomstrand colony was not continued after 2015. Individuals could therefore have been recruited into the colony in a later year, although most individuals are expected to return within 5 years after fledging (Wooller & Coulson, 1977). The sample sizes for each sex and year of return are also fairly low, and the results regarding the sex-related difference in recruitment should therefore be interpreted with caution.

Early-life migration and dispersion

Tracking data from the GLS-loggers reveal that the subadult kittiwakes explore large areas across the North-Atlantic Ocean during the winter, similar to that previously shown for adult kittiwakes (Frederiksen et al., 2012). A total of 8 returning kittiwakes spent their first summer in close proximity to breeding kittiwake populations in Greenland, before eventually returning to Kongsfjorden (Fig. 5). It is important to note that these data only show the birds that returned to the Svalbard colony and were recaptured. Despite being considered a highly philopatric species, there are still possibilities of dispersion and establishment in other colonies that is not covered in the present study.

With several individuals having spent their summer in West Greenland, the possibility of kittiwakes having dispersed and established in other populations is not unlikely. The philopatry rate in kittiwake populations have been shown to vary a lot, ranging from populations containing 33% to 91% philopatric individuals (Coulson, 2016). There has not been conducted any similar studies on the philopatry of kittiwakes in the Kongsfjorden population or nearby Svalbard populations, so it is difficult to estimate the proportion of philopatric individuals for these populations. Little is also known about the post-fledging survival rates of kittiwakes, although Coulson (2011) estimates an average survival of 36% from fledging to breeding based on adult survival rates in a stable British population. In the present study, I observed that 48% of the nestlings both survived and were recruited back into the colony. Accounting for possible dispersers to other colonies or late recruiters might yield a slightly higher percentage of surviving fledglings. If the estimate of 36% post-fledging survival up until breeding is representative for kittiwakes, then it seems likely that this

Svalbard population is highly philopatric. In a high philopatry population, natal recruitment is strongly related to early-life survival. This allows for further interpretation of the effect of early-life Hg levels on survival, where the measured nestling Hg levels do not affect the survival in the time from fledging to recruitment.

Even though Svalbard kittiwakes seem to be highly philopatric, dispersion is a necessity to maintain gene flow, allowing for a larger genetic variance suitable for adaptation. Currently, there are no optimal solutions of dealing with non-returning birds and disentangling mortality from dispersal. Observations of alive individuals is the only certainty one has that confirms survival, whereas unobserved individuals can either be dead or alive. From the closely monitored populations in Kongsfjorden, one of the returning kittiwakes was recaptured in Krykkjefjellet, a neighbouring colony located about 10 km southeast of Blomstrand (Fig. 1). However, with the large distribution of the kittiwake, one cannot rely on observing individuals in other colonies even though fieldwork is carried out in several widespread kittiwake colonies. Therefore, one would also need to track dispersing individuals to fully understand the migratory movements of the kittiwake.

Accumulation of Hg from fledging to recruitment

Kittiwakes had substantially higher levels of Hg as returning adults than as nestlings (Fig. 6, Table S3). This is in line with previous findings in seabirds (e.g. Thompson et al., 1991; Stewart et al., 1997; Tavares et al., 2013), and is mainly related to the exposure time to Hg since last moulting. The returning adults have been exposed to Hg for a longer period of time, than the nestlings at ~30 days old.

No differences in Hg accumulation between the years of return were observed (ANOVA, $p = 0.401$). This result suggests that returning adults have reached a stable state of uptake and excretion of Hg, where Hg levels do not continue to increase with age after reaching the adult stage. The same stability of Hg in adults have previously been shown (Furness & Hutton, 1979; Hutton, 1981; Furness et al., 1990a; Tavares et al., 2013).

There is a strong effect of day sampled within year, where the blood levels of Hg are decreasing throughout the breeding season (Fig. 7A). This trend is observed due to the use of blood samples, where Hg stays in RBCs for several weeks or months (Bearhop et al., 2000; Monteiro & Furness, 2001). This implies that our samples reflect the Hg at the time of sampling and back in time, to late stages of migration. Studies have shown that the global distribution of Hg is not homogenous, and that seabirds are exposed to higher Hg levels in the

North-Atlantic Ocean (Fort et al., 2014; Albert et al., 2021). The sampled levels of accumulated Hg at recruitment are therefore influenced by the time since foraging in the North-Atlantic Ocean. Lower rates of accumulation in Kongsfjorden compared to the North-Atlantic creates the declining trend of blood Hg over time. The time of sampling is therefore important for blood concentrations of Hg, assuming that the time of sampling is not related to their time of return to the colony.

When correcting for the temporal decrease throughout the breeding season, the kittiwakes average a Hg concentration of 2.35 $\mu\text{g/g dw}$ on June 15, in the pre-laying period. This concentration is above the threshold level for shown adverse effects on reproduction in kittiwakes (Tartu et al., 2013, 2016). Even though the recruited kittiwakes in the present study are yet to breed, it can still be observed that they already at recruitment have accumulated high Hg concentrations able to negatively affect reproductive potential.

A difference in Hg accumulation is observed between the sexes, in which males have higher levels of Hg at recruitment compared to females (Fig. 7B). Different explanations have been suggested as to why differences between sex are found in accumulation of Hg. Typically, the differences are hypothesised to be caused by females having an extra route of excretion through eggs, or by sexual dimorphism, where the larger sex can forage at higher trophic levels, yielding higher concentrations of Hg (Bighetti et al., 2021). In the present study, however, the recruited females are yet to reproduce and produce eggs, and have consequently not excreted Hg through egg formation. The $\delta^{15}\text{N}$ levels of the individuals were not significantly different among the sexes (Fig. S2), despite the male kittiwake on average are 11.1% larger than the female (Table S4). However, similar $\delta^{15}\text{N}$ levels at the time of sampling does not rule out the explanation of trophic level on sex differences due to different reflective timeframes of Hg and $\delta^{15}\text{N}$ from RBCs. It is possible that males had foraged at higher trophic levels in the timeframe reflected by the Hg data, while not being reflected in the larger timeframe of $\delta^{15}\text{N}$. Mismatching timeframes are also shown in the relationship between returning adult Hg and $\delta^{15}\text{N}$ levels, which do not positively correlate (Fig. S3). It is also worth to note that the sample sizes for these data are low ($n = 6$ females, $n = 10$ males), which allows for more stochasticity in these data and the results should therefore be interpreted with caution.

Concluding remarks

The subadult migrating kittiwakes are observed occupying large areas in the North-Atlantic Ocean during their overwintering period similar to the adult kittiwakes. The high Hg levels accumulated at recruitment are suggested to derive from these overwintering grounds, where seabirds are exposed to higher concentrations of Hg. From the present study, it is clear that nestling Hg levels do not negatively affect the kittiwake's probability of recruitment. This is suggestively explained by the low levels of Hg accumulated in the nestling period, that is below a threshold level for adverse outcomes. Although natal recruitment in this kittiwake population is not adversely affected by the measured Hg levels, one cannot exclude the possibility that natal recruitment and early-life survival in populations facing higher levels of Hg are negatively affected. Therefore, studying the effects of nestling Hg-levels on recruitment in populations with higher local concentrations of Hg could prove important to expand the knowledge on the threshold value for adverse effects, and aid in the conservation of the red-listed kittiwake.

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Supplementary information

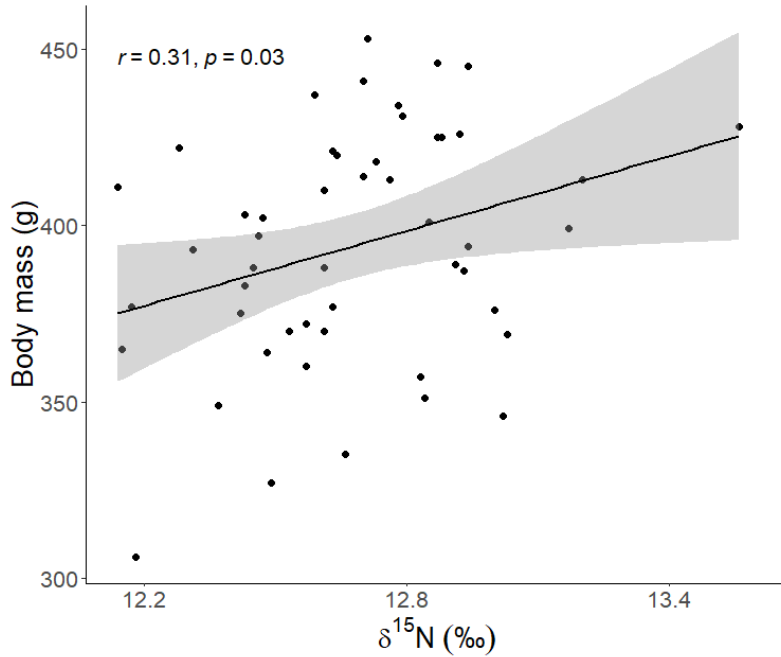


Fig. S1: Correlation plot between nestling body mass (g) and trophic level ($\delta^{15}\text{N}$), with Pearson's coefficient of correlation (r) and the p-value (p). Grey areas represent the 95% confidence intervals.

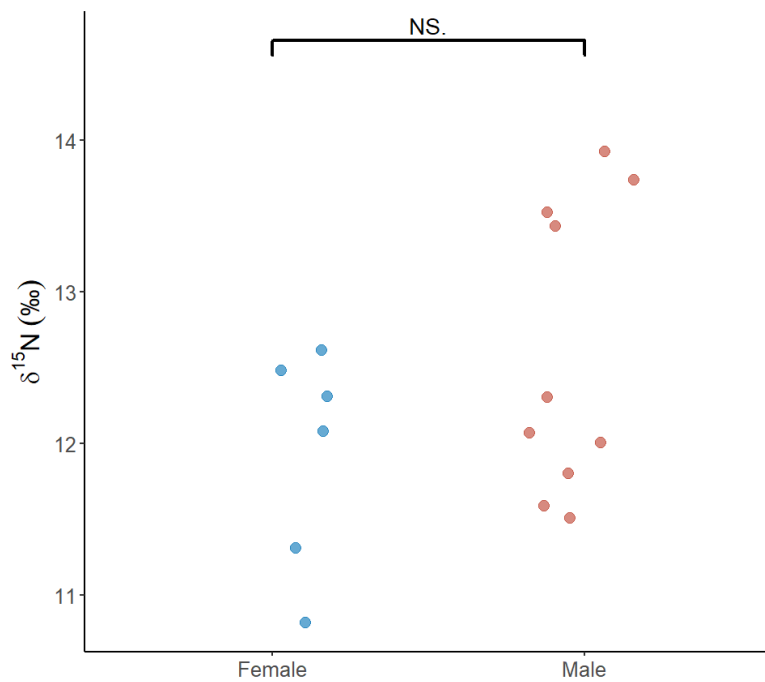


Fig. S2: The trophic level ($\delta^{15}\text{N}$) for the difference sexes in the recruited kittiwakes, showing a non-significant difference (NS.).

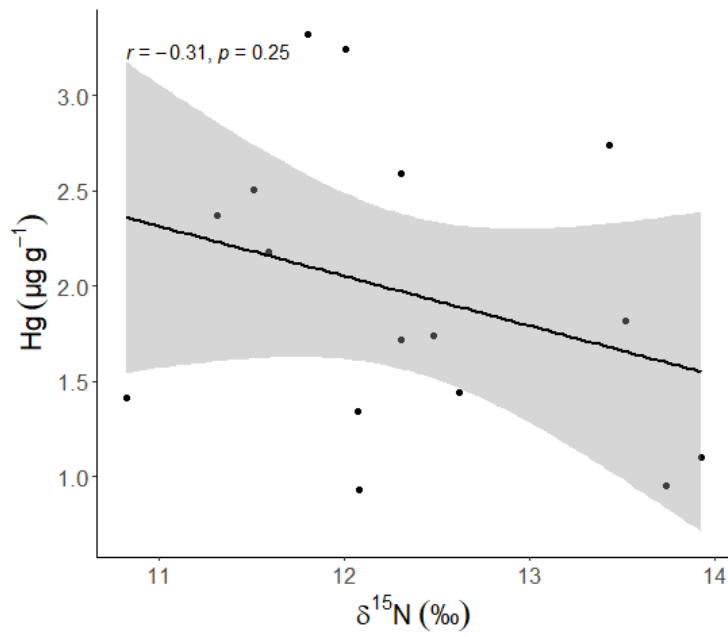


Fig. S3: Correlations between trophic level ($\delta^{15}\text{N}$) and Hg ($\mu\text{g/g dw}$) levels in the recruited adults, not showing the positive relationship as seen in nestlings. Pearson's coefficient of correlation (r) and the p-value (p) are shown. Grey areas represent the 95% confidence intervals.

Table S1: The effect of Hg as the only predictor variable on the probability of recruitment. Coefficient for the predictor variable in Log-odds (*Estimate*), 95% confidence interval (*95% CI*), p-value (*p*), sample size (Observations) and R^2 Tjur are shown.

Probability of Recruitment			
<i>Predictors</i>	<i>Estimate</i>	<i>95% CI</i>	<i>p</i>
(Intercept)	-2.47	-4.89 – -0.36	0.030
Hg	46.33	6.93 – 92.00	0.030
Observations	50		
R^2 Tjur	0.111		

Table S2: The effect of trophic level ($\delta^{15}\text{N}$) as the only predictor variable on the probability of recruitment. Coefficient for the predictor variable in Log-odds (*Estimate*), 95% confidence interval (*95% CI*), p-value (*p*), sample size (Observations) and R^2 Tjur are shown.

Recruitment			
<i>Predictors</i>	<i>Estimate</i>	<i>95% CI</i>	<i>p</i>
(Intercept)	-60.97	-104.75 – -26.70	0.002
$\delta^{15}\text{N}$	4.80	2.10 – 8.25	0.002
Observations	50		
R^2 Tjur	0.264		

Table S3: The effect of life stage on the natural logarithmic blood levels of Hg. Coefficients for each predictor variable (*Estimate*), 95% confidence intervals (*95% CI*), p-values (*p*), sample size (Observations), R^2 and R^2 -adjusted are shown. Intercept refers to Hg levels for returning adults.

Log Hg			
<i>Predictors</i>	<i>Estimate</i>	<i>95% CI</i>	<i>p</i>
(Intercept)	0.60	0.42 – 0.77	<0.001
Nestling	-3.47	-3.72 – -3.22	<0.001
Observations	32		
R^2 / R^2 adjusted	0.965 / 0.964		

Table S4: Average body mass with standard deviations for both sexes of returning adult kittiwakes.

Body mass (Mean \pm SD)	
Male	406.6 \pm 19
Female	365.8 \pm 20



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