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Master's thesis in MSc Biology
Supervisor: Børge Moe
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May 2022

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Kunnskap for en bedre verden

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ABSTRACT

Feeding ecology plays a crucial factor for the performance of seabirds, and even set limits for where and how they can breed successfully. Among the several methods that exist to study seabird diet, examination of stable isotope levels has been used extensively. The ratios of stable isotopes in nitrogen (δ^{15}N) and carbon (δ^{13}C) pass from prey to predator through ingestion. δ^{15}N is used to measure the trophic level of the organism, as the ratio of the heavier isotope to the lighter isotope increases in a predictable manner up through the trophic levels. δ^{13}C is used to find the habitat and food type of the species. Only short-term (up to a month) diet can be deduced from the stable isotopes in the blood, as blood has a high turnover rate. Blood was sampled from Long-tailed skuas breeding in Svalbard and in Sweden, and from Arctic terns breeding in Svalbard. The first goal of the study was to investigate the feeding ecology of the Long-tailed skuas breeding in Svalbard, at the edge of the species' breeding distribution, by comparing the stable isotopes with the Arctic terns breeding in Svalbard and with the Long-tailed skuas breeding in Sweden, a core breeding area. The Long-tailed skuas in Sweden consume rodents such as lemmings during breeding, but there are no native rodents in Svalbard. It is important to find out what prey this population can sustain themselves on during breeding in Svalbard. Specifically, we ask whether these birds maintain their marine lifestyle, from the non-breeding season, instead of switching to terrestrial prey during breeding. We expect this, because Long-tailed skuas have been observed to kleptoparasite Arctic terns and regurgitations from Long-tailed skuas have contained fish. As expected, they were in the highest trophic level of our study populations and had δ^{15}N-values significantly more similar to the Arctic terns breeding in Svalbard than to the Long-tailed skuas breeding in Sweden. In addition, they had significantly higher δ^{13}C-values compared to the Swedish population. Showing that the Long-tailed skuas breeding in Svalbard have a pelagic marine feeding ecology towards the top of the food web, during the breeding season. The second goal was to assess the consequences of diet on contaminant levels. Specifically, we compared the Hg (mercury) levels of the different populations of Long-tailed skuas and the Arctic terns. Assuming a terrestrial diet for the Swedish birds and a marine diet for the Svalbard birds we predicted lower overall Hg levels in the Swedish birds compared to the Svalbard birds. This was not the case. The results showed significantly lower Hg levels in the Arctic terns, and both populations of Long-tailed skuas had statistically the same results, with the Svalbard population having a higher variance. This study highlights the importance of the difference in integration periods of stable isotopes and Hg in blood, as well as the flexibility in diet for Long-tailed skuas.

SAMMENDRAG

Næringsøkologi er en viktig faktor for sjøfuglers liv, og setter grensene for hvor og hvordan de kan lykkes med å hekke. En av flere velbrukte metoder for å studere kosthold til sjøfugl er å studere deres stabile isotopnivåer. Forholdet mellom stabile isotoper i nitrogen ($\delta^{15}N$) og karbon ($\delta^{13}C$) går fra byttedyr til rovdyr gjennom fordøyelsen. $\delta^{15}N$ brukes til å måle organismens trofiske nivå fordi forholdet mellom den tyngre og den lettere isotopen øker forutsigbart opp gjennom de trofiske nivåene. $\delta^{13}C$ brukes til å finne artens habitat- og mattype. Kun korttidskosthold (opptil en måned) kan bli målt fra stabile isotoper i blod, fordi blod har en så høy omløpshastighet. Blod ble tatt fra fjelljo som hekket på Svalbard og i Sverige, og fra rødnebbterner som hekket på Svalbard. Studiens første mål var å undersøke næringsøkologien til fjelljo som hekket på Svalbard, som er i utkanten av artens hekkeutbredelse, ved å sammenligne deres stabile isotopverdier med de fra rødnebbternene som hekker på Svalbard og med fjelljoen i Sverige, i artens kjerneområde for hekking. Fjelljoen som hekker i Sverige spiser smågnagere, blant annet lemmen, under hekketiden, men det er ingen naturlige smågnagerbestander på Svalbard. Det er viktig å finne ut av hvilke byttedyr fjelljoene som hekker på Svalbard spiser. Vi undersøkte spesifikt om disse fuglene beholder sin marine livsstil fra utenom hekketiden, isteden for å bytte til terrestriske byttedyr under hekkingen. Vi antar dette fordi fjelljoen har blitt observert å kleptoparasittere rødnebbternen, og oppgulp fra fjelljoer har inneholdt fisk. Som forventet fant vi at de var på det høyeste trofiske nivået sammenlignet med de andre populasjonene i studien, og hadde $\delta^{15}N$-verdier som var signifikant mer lik rødnebbternene som hekket på Svalbard enn fjelljoene som hekket i Sverige. I tillegg hadde de signifikant høyere $\delta^{13}C$-verdier enn den svenske populasjonen, som viser at fjelljoene som hekker på Svalbard har en pelagisk marin næringsøkologi mot toppen av det trofiske nettet i hekketiden. Det andre målet med studien var å vurdere konsekvensene kostholdet hadde på forurensingsnivåene i blodet. Spesifikt så sammenlignet vi Hg-nivåer (kvikksølv) i de forskjellige populasjonene av fjelljo og rødnebbterner. Vi antok at de svenske fuglene hadde et terrestrisk kosthold og at Svalbardfuglene hadde et marint kosthold, og forventet lavere Hg-nivåer i de svenske fuglene sammenlignet med Svalbardfuglene. Det var ikke riktig. Resultatene viste signifikant lavere Hg-verdier i rødnebbternene og begge fjelljopopulasjonene hadde statistisk sett de samme resultatene, men Svalbardpopulasjonen hadde en høyere varians. Denne studien framhever hvor viktig forskjellen i integrasjonsperiodene er for stabile isotoper og Hg i blod, i tillegg til fleksibiliteten i fjelljoens kosthold.

PREFACE

This Master's thesis was written at the Department of Biology, Norwegian University of Science and Technology (NTNU), Trondheim, in collaboration with the Norwegian Institute of Nature Research (NINA). I have been supervised by Børge Moe, Institute of Biology and NINA, and by Sveinn Are Hanssen (NINA). I participated in the field season of 2021 (June-July) in Kongsfjorden, Svalbard. Permissions to conduct the field work and sampling were granted by the Governor of Svalbard (Sysselmannen) and the Norwegian Food Safety Authority (Mattilsynet).

Trondheim, May 2022

Solveig Aanensen

CONTENTS

INTRODUCTION

Animals require food for energy to survive and reproduce. The food availability affects where animals can live, and when they can use specific habitats. Seabirds are a group of animals that use central place foraging during the breeding period (Elliott et al., 2009). They commute between their nests and the feeding grounds, and are dependent on sufficient availability of prey within a limited distance from the nest to be able to both feed themselves and incubate their eggs, or help their partner and provide frequent meals for the offspring. After the breeding season, they are no longer tied to the nest and breeding site and they can migrate long distances to find areas with better seasonal food conditions in offshore or inshore waters. Since food and prey play such a crucial factor for the performance of seabirds, and even set limits for where and how they can breed successfully, it is crucial to study their diet. Among the several methods that exist to study seabird diet (Barrett et al., 2007), examination of stable isotope levels has been used extensively. Measuring of blood levels of stable isotopes are widely used in ecophysiological studies. Blood sampling is non-invasive and can be easily performed on many individuals, as well as repeatedly within the same individuals at different times.

Stable isotopes

The ratios of stable isotopes in nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) pass from prey to predator through ingestion (Bearhop et al., 2004). The ratio of the heavier isotope to the lighter isotope increases in a predictable manner up through the trophic levels. For nitrogen, the rate is 3-5‰ per trophic level in marine systems (Hobson & Welch, 1992; Renaud et al., 2011), and for carbon it is 1‰ (Bearhop et al., 2004), though the stable isotope value of carbon is most often used to find the carbon source, such as the habitat and food type of the species (Ceia et al., 2014). Specific items in the diet cannot be determined through the use of stable isotopes alone, but carbon can give an idea of the oceanographic region the bird feeds on (Barrett et al., 2007). In nearshore waters, the food for seabirds have a higher ratio of 13C in relation to 12C, compared to offshore waters. And the 13C-isotope is more prevalent in high latitudes than close to the equator, making it possible to track wide-ranging movements and winter habitats in tissues with slow turnover rates. $\delta^{13}C$ also differ strongly between terrestrial and freshwater food webs, and marine food webs.

Analyses on stable isotopes are conducted on proteins in animal tissues (Dalerum & Angerbjörn, 2005). Different tissues have different metabolic rates, or turnover rates, making

the time the isotopes reflect the isotopic values of the diet differ throughout the animal's body (Barrett, 2007, Bearhop et al., 2004). Blood has a high turnover rate, the plasma of the blood completely replenishing within 24 hours in some species, and up to a few days in others, while red blood cells (RBC) take 3-4 weeks to replenish (Ceia et al., 2014). This means that only the short-term diet can be deduced from the stable isotopes in the blood. And since plasma, in some species, only has a turnover rate of one day, the stable isotope ratios only are only reflective of the last (few) meal(s), and as such may vary considerably between days. Therefore, these values may vary wildly between individuals as well as between days and should thus be used with caution if the sample size is small (Dalerum & Angerbjörn, 2005). Other tissues, such as bone or scales have a much slower turnover rate and can thus give information on the diet for several seasons or even years (Bearhop et al., 2004). Some tissues are even metabolically inert after formation, saving the elements in a time capsule, reflecting the diet of the animal during the time the tissue was formed. This is the case e.g. in hair, feathers, baleen or claws.

The isotope ratios are also affected by the physiological state of the animals (Dalerum & Angerbjörn, 2005). Water-stressed or starving animals have been shown to have higher 15N-isotope rates than non-stressed animals, mainly due to the recycling of nitrogen in the tissues; animals nursing offspring or hibernating also increases 15N-isotope rates. It has been suggested that age also influences isotope ratios, possibly linked to a specific metabolism during growth, but the mechanisms for this are, ultimately, still unknown.

Comparisons between different tissues within a species, may reveal temporal variations in the diet, because the tissues have different turnover rates giving information on different time scales (Albert et al., 2020; Dalerum & Angerbjörn, 2005). Assuming a species has two distinct seasonal diets (e.g. because of migration), tissues with fast turnover rates would reflect the current diet, while a tissue with a sufficiently slow turnover rate would reflect the average diet over several seasons.

Mercury (Hg)

The diet of seabirds is also the source for pollutants to enter the body. Pollutants, such as mercury (Hg), accumulate in the diet through the trophic web. Hg poses major risks for wildlife and human health, and has been found to be one of the most toxic elements for seabirds (Renedo et al., 2020; Savinov et al., 2003). Hg biomagnifies through the food web, particularly in its

methylated form (methylmercury, MeHg) which is its most potent neurotoxic form (Campbell et al., 2005; Renedo et al., 2020). MeHg production in the ocean mainly occurs through biotic methylation of inorganic Hg (Renedo et al., 2020). In the Arctic marine biota, there are high concentrations of Hg, despite its limited direct anthropogenic input (Renedo et al., 2020). This is because the Arctic ocean is a sink for contaminants, with sea-ice melting, direct atmospheric deposition and continental inputs from soil erosion and riverine circulation, all transporting contaminants, such as Hg, up from lower latitudes (Albert et al., 2020; Ariya et al., 2005; Renedo et al., 2020). Savinov et al. (2003) found that the seabirds breeding in Kongsfjorden, Svalbard had the highest Hg concentrations compared to Greenland, Canada and northeast Siberia.

Seabirds' exposure to distinct environmental MeHg sources in marine environments and their place in the food webs have made them a favorite to study and use as bioindicators for Hg exposure in marine food webs, including in the Arctic (Evers et al., 2005; Renedo et al., 2020). They obtain Hg via ingestion of contaminated prey and store it in a body reservoir until it can be eliminated.

Once ingested, Hg stays in the blood for a few weeks up to a few months, before moving on to the liver, where some of the more toxic MeHg is likely converted to inorganic Hg (Albert et al., 2019; Bond, 2010). Hg in blood thus informs about more recent intakes than e.g. feathers and liver, and is traditionally thought to reflect intake at the sample site (Evers et al., 2005), but newer studies lengthen this time-frame by several months (e.g. Lavoie et al., 2014). Albert et al. (2019) concluded that blood sampled during the breeding period might reflect the diet from the winter sites or late migration to chick-rearing. Once Hg is assimilated, it is transported and distributed to the different organs, where it can be demethylated as a protective mechanism against Hg toxicity, and/or stored. Hg in internal organs such as liver, brain, kidney and muscle thus inform about longer term Hg contamination compared to blood. In birds, the largest Hg reservoir is the liver, while the kidney stores less and muscle stores the least (Jæger et al., 2009; Kim et al., 1996), where Hg will be stored until excretion through guano, eggs and feathers (Albert et al., 2020; Bond, 2010). Eggs are only produced at the breeding sites and is only an available excretion pathway for females. Molting of feathers is the primary route for Hg excretion in birds, having the capacity to hold up to 70-80% of body burdens (Lavoie et al. 2014).

Changes in feeding behavior will affect Hg ingestion, particularly if there are dietary shifts between fish (which are generally higher in Hg) and invertebrates (especially copepods and amphipods, which are generally lower in Hg) (AMAP, 2005). Higher Hg concentrations can be found in seabirds measured at the wintering sites caused by seasonal dietary shifts towards higher fish consumption (Albert et al., 2020).

Study species

The migratory seabird Long-tailed skua (*Stercorarius longicaudus*) has a circumpolar distribution. This species normally undergoes a transition from a marine diet in the non-breeding season (Aug/Sept-May) to a terrestrial diet in the breeding season (May/Jun-Aug) (Andersson, 1981; Wiley & Lee, 1998). It spends its wintering months on the western and southern coast of Africa, feeding pelagically on mainly fish and kleptoparasiting other seabirds (Gilg et al., 2013; van Bemmelen et al., 2017), and the summer months breeding in the Arctic tundra, feeding mainly on rodents (Andersson, 1981). The reproductive success is highly dependent on the abundance of lemmings, they do not breed in years with low densities of lemmings, and lay 1-2 eggs in high density years (de Korte, 1977, 1984). Lemmings are common in the alpine and Arctic tundra areas such as Greenland, Northern Scandinavia, Siberia, Alaska and Canada, but there are no lemmings in Svalbard. The Long-tailed skua also supplements their diet with some arthropods and the previous year's berries throughout the breeding season, and new berries when they start ripening (de Korte & Wattel, 1988).

In Disko Bay, west Greenland, there are no lemmings, so the Long-tailed skuas breeding there use kleptoparasitism as their main food source (Kampp, 1982). Breeding birds pursue Arctic terns (*Sterna paradisaea*) at sea, while nonbreeding birds pursue the Arctic terns overland near their colonies. In the north of Russia Long-tailed skuas mostly target Black-legged Kittiwakes (*Rissa tridactyla*), Sabine's Gulls (*Xema sabini*) and Arctic terns but can also chase other birds, mainly chicks and juveniles (Wiley & Lee, 1998). Long-tailed skuas breeding near coast also consume fish and zooplankton.

First age at breeding is between 3-5 years old (de Korte, 1985; Andersson 1976), depending on the lemming density that year (Julien et al., 2013). Most studies report a longevity of 8-9 years, (van Bemmelen, 2010; Clapp et al., 1982) but note that it is likely higher, with a yearly survival rate of 0.91 and with the oldest recorded bird being 22 years old (Julien et al., 2013). In the

years before first breeding, Long-tailed skuas may still come back up north from their wintering sites, to learn the lay of the land and look for a territory for themselves (van Bemmelen, 2010). The Long-tailed skua is monogamous, couples keep together during the entire breeding period, they alternate brooding/incubation, defending the territory and hunting during this time (de Korte, 1977, 1984). They also breed with the same partner for many years. They defend territories that they come back to every year, even in the years when they don't lay eggs. They come to their territories between the last week of May and the first week of June, and if they lay eggs that year they will have done so by the end of June (Gilg et al., 2013).

Objectives

The first objective of the present study is to investigate the feeding ecology of the Long-tailed skua breeding in Svalbard. There are no lemmings or rodents available in Svalbard, and this population is at the edge of the breeding distribution of this species. It is important to find out what prey this population can sustain on during breeding in Svalbard. Specifically, we ask whether these birds maintain their marine lifestyle, from the non-breeding season, instead of switching to terrestrial prey during breeding. Based on previous observations, we expect this, because Long-tailed skuas have been observed to kleptoparasite Arctic terns and regurgitations of Long-tailed skuas have contained fish. We therefore compare stable isotopes (δ^{15}N, δ^{13}C) and trophic niche of Long-tailed skuas in Svalbard with Arctic terns in Svalbard and Long-tailed skuas in Sweden.

The second objective is to assess the consequences of diet on contaminant levels. Specifically, we compare the Hg levels of the different populations of Long-tailed skuas and the Arctic terns. Assuming terrestrial diet (lemmings) and marine diet (mainly fish) of birds in Sweden (Long-tailed skuas) and in Svalbard (Long-tailed skuas and Arctic terns), respectively, we predict lower overall Hg levels in the Swedish birds compared to the Svalbard birds.

The Long-tailed skuas from both Sweden and Svalbard have similar migration and distribution during the 9-month non-breeding season (van Bemmelen et al., 2017, Gilg et al., 2013). Assuming similar marine lifestyle and diet for both populations during the non-breeding season, the difference between the two populations in stable isotopes or Hg will be caused by the difference in their summer diets.

METHODS

Capture and sampling

Observations and sampling have been done over the last 10 years. The dataset in this study was sampled in the breeding period (June-July) between 2011 and 2015 (**table 1**). In Ammarnäs, Sweden, a population of Long-tailed skuas were sampled in 2014 (n=9). In Kongsfjorden, Svalbard, a population of Long-tailed skuas (n=12) were sampled in 2011, 2012 and 2014, and Arctic terns (n=4) were sampled in 2012.

Table 1: *Sample location, sample date and types of analyses taken for the different populations. Analyses included whole blood (WB), red blood cells (RBC), plasma, and mercury (Hg).*

Species	Location	Sample date	Analyses
Long-tailed skua	Svalbard	02.07.2011	WB, RBC, Plasma, Hg
Long-tailed skua	Svalbard	02.07.2011	WB, RBC, Plasma, Hg
Long-tailed skua	Svalbard	06.07.2011	WB, RBC, Plasma, Hg
Long-tailed skua	Svalbard	06.07.2011	WB, RBC, Plasma, Hg
Long-tailed skua	Svalbard	29.06.2012	WB, RBC, Plasma, Hg
Long-tailed skua	Svalbard	29.06.2012	WB, RBC, Plasma, Hg
Long-tailed skua	Svalbard	08.07.2012	WB, RBC, Plasma, Hg
Long-tailed skua	Svalbard	08.07.2012	WB, RBC, Plasma, Hg
Long-tailed skua	Svalbard	22.06.2012	WB, RBC, Plasma, Hg
Long-tailed skua	Svalbard	22.06.2012	WB, RBC, Plasma, Hg
Long-tailed skua	Svalbard	22.06.2012	WB, RBC, Plasma, Hg
Long-tailed skua	Sweden	Mid-June 2014	WB, Hg
Long-tailed skua	Sweden	Mid-June 2014	WB, Hg
Long-tailed skua	Sweden	Mid-June 2014	WB, Hg
Long-tailed skua	Sweden	Mid-June 2014	WB, Hg
Long-tailed skua	Sweden	Mid-June 2014	WB, Hg
Long-tailed skua	Sweden	Mid-June 2014	WB, Hg
Long-tailed skua	Sweden	Mid-June 2014	WB, Hg
Long-tailed skua	Sweden	Mid-June 2014	WB, Hg
Long-tailed skua	Sweden	Mid-June 2014	WB, Hg
Arctic tern	Svalbard	04.07.2012	WB, Hg
Arctic tern	Svalbard	04.07.2012	WB, Hg
Arctic tern	Svalbard	04.07.2012	WB, Hg
Arctic tern	Svalbard	04.07.2012	WB, Hg

Long-tailed skuas were captured while incubating by the use of a remote-controlled snare trap or a hand-held netgun. The four Arctic terns were captured using a hand-held netgun or a mist-net at late incubation/early chick-rearing. All birds were banded with a metal or plastic ring engraved with a unique code, if caught for the first time, otherwise the existing code was recorded. The birds were weighed to the nearest 1g using a Pesola spring balance. Tarsus and head-bill length was measured with a caliper to the nearest 0.1 mm, and wing length and outer central tail feathers were measured with a metal ruler to the nearest 1mm. Then, 1-2mL of blood was sampled (< 1ml for the terns) using a heparinized syringe from the brachial vein to measure stable isotopes (δ^{15}N and δ^{13}C) and Hg concentrations.

Previous observations

Over the period 2010-2021, our field team has anecdotally observed foraging behavior of Long-tailed skuas in Svalbard. On several occasions the Long-tailed skuas have been observed to kleptoparasite Arctic terns. In addition, they have often been observed to sit on cliffs and on the tops of icebergs scouting across the fjord, looking for fish in the water or Arctic terns coming back with food. They have also been observed walking along the shoreline plucking small items, most probably crustaceans. Sometimes they have also been observed plucking small items on the ground in the breeding territory, most probably insects.

During capture and handling, sometimes, though rarely, the birds vomit food. All the samples have been of fish, probably Polar cod (*Boreogadus saida*), Capelin (*Mallotus villosus*), Atlantic cod (*Gadus morhua*) or Atlantic herring (*Clupea harengus*), which are the most likely fish species available for seabirds in Kongsfjorden (Vihtakari et al., 2018). The samples were partly digested, and proper species identification were difficult by visual inspection. We chose, however, not to subject the samples to otolith analysis, since correct species identification of these relatively few fish samples would not alter the conclusions in this study.

Lab analyses

Laboratory analyses of blood on Hg concentration and stable isotopes were performed at the Littoral Environment et Sociétés laboratory (LIENSs, La Rochelle, France). For the analyses on the stable isotopes, the isotopic niche of δ^{15}N is being used as a proxy to trophic status and diet (Bearhop et al., 2002; Hobson & Clark, 1992; Cherel et al., 2010), and δ^{13}C as an indicator of foraging habitat (Hobson & Clark, 1992; Hoffman & Rasmussen, 2022; Cherel & Hobson,

2007). The stable isotope analyses were performed on the whole blood samples from Long-tailed skuas in Svalbard, as well as on plasma and red blood cells (RBC), separately. While the blood samples from the Long-tailed skuas in Sweden and Arctic terns were only analyzed as whole blood. Blood plasma regenerates after a few days and so gives a picture of the trophic ecology of the last few meals, while the dietary time frame offered for RBC is 3-4 weeks as that is their regeneration time (Ceia et al 2014). When comparing the different species and the different populations, whole blood was used. The whole blood of the Long-tailed skuas in Sweden may include the diet of the last leg of the migration route to the breeding sites, so in total there might be a slight mix of terrestrial and marine foods in those samples.

Prior to analysis the samples were freeze-dried and powdered. Lipids were extracted from dried plasma samples prior to stable isotope analysis using a 2:1 chloroform:methanol solution. Subsamples of homogenized blood, (RBC, whole blood, or lipid-extracted plasma) powder were then weighed to ~0.3 mg with a microbalance and packed in tin containers. The relative abundances of C and N isotopes were determined using a continuous flow mass spectrometer (Thermo Scientific Delta V Plus) coupled to an elemental analyzer (Thermo Scientific Flash 2000). Results are expressed in the δ unit notation as deviations from standards (Vienna Pee Dee Belemnite for δ^{13}C and N_2 in air for δ^{15}N) following the formula:

$$\delta^{13}\text{C or } \delta^{15}\text{N} = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \times 1000, \text{ where R is } {}^{13}\text{C}/{}^{12}\text{C or } {}^{15}\text{N}/{}^{14}\text{N, respectively.}$$

Replicate measurements of internal laboratory standards (acetanilide, every 20 samples) indicate measurement errors <0.10‰ for δ^{13}C and <0.15‰ for δ^{15}N values. The C:N mass ratios of the samples were calculated as the ratio between the mass percentages in carbon and nitrogen.

Hg reflects the trophic ecology of the last weeks to several months (Albert et al., 2019; Lavoie et al., 2014; Monteiro & Furness, 2001). Analyses on Hg were performed on a subsample of ~0.2 mg of homogenized whole blood, for all study populations, using an Advanced Mercury Analyser spectrophotometer (Altec AMA 254 – detection limit of 0.05 ng of dry weight (dw)). For each sample, analyses were repeated two times to ensure the relative standard deviation for the aliquots was <10%. Subsequently, the mean of the repeated Hg measurements was used for statistical analysis. To ensure the accuracy of measurements, certified reference materials

(CRM: lobster hepatopancreas TORT-2) were analyzed every 10 samples. In addition, blanks were run prior to the analyses.

Statistical analyses

All statistical analyses were performed using R v.4.1.1 (R Development Core Team, 2021). A significance level of $p < 0.05$ was used for all tests. The means and standard deviations were found for each group of samples: for both of the isotopic niches for the whole blood of the different bird populations, for the different blood components of the Long-tailed skuas breeding in Svalbard, and for the Hg concentrations for the different bird populations. Then, linear models (lm) were fitted and the summary function (t-statistics) was used to determine whether the difference in the mean was significantly different between the different groups in all those categories.

The R package "Stable Isotope Bayesian Ellipses" (SIBER v.2.1.6, Jackson et al., 2011) was used to determine the isotopic niche in the birds and to display it on an isotopic biplot (**figure 1**, **figure 2**). The standard ellipses contained ~95% of the data after correcting for small sample size (SEAc).

The Hg concentrations for the different bird populations were displayed using a box plot (**figure 3**) showing the 25-75% quartile range, and the median bar (thick, black line). The whiskers extend from the boundaries of the box to the 1.5x interquartile range (IQR) of the boundaries. Data beyond the whiskers are plotted as points (outliers).

RESULTS

Stable isotopes

Stable isotope analyses in whole blood showed that Long-tailed skuas breeding in Sweden had the lowest values for both $\delta^{15}N$ and $\delta^{13}C$ (**figure 1, table 2**), whereas Long-tailed skuas breeding in Svalbard had the highest stable isotope values. Arctic terns had intermediate values for both $\delta^{15}N$-values and $\delta^{13}C$-values. The difference between Long-tailed skuas breeding in Svalbard and in Sweden was significant ($p<0.01$) for both nitrogen and carbon, but the difference between Arctic terns and Long-tailed skuas breeding in Svalbard was only significant for nitrogen ($p<0.01$) and not for carbon ($p=0.77$).
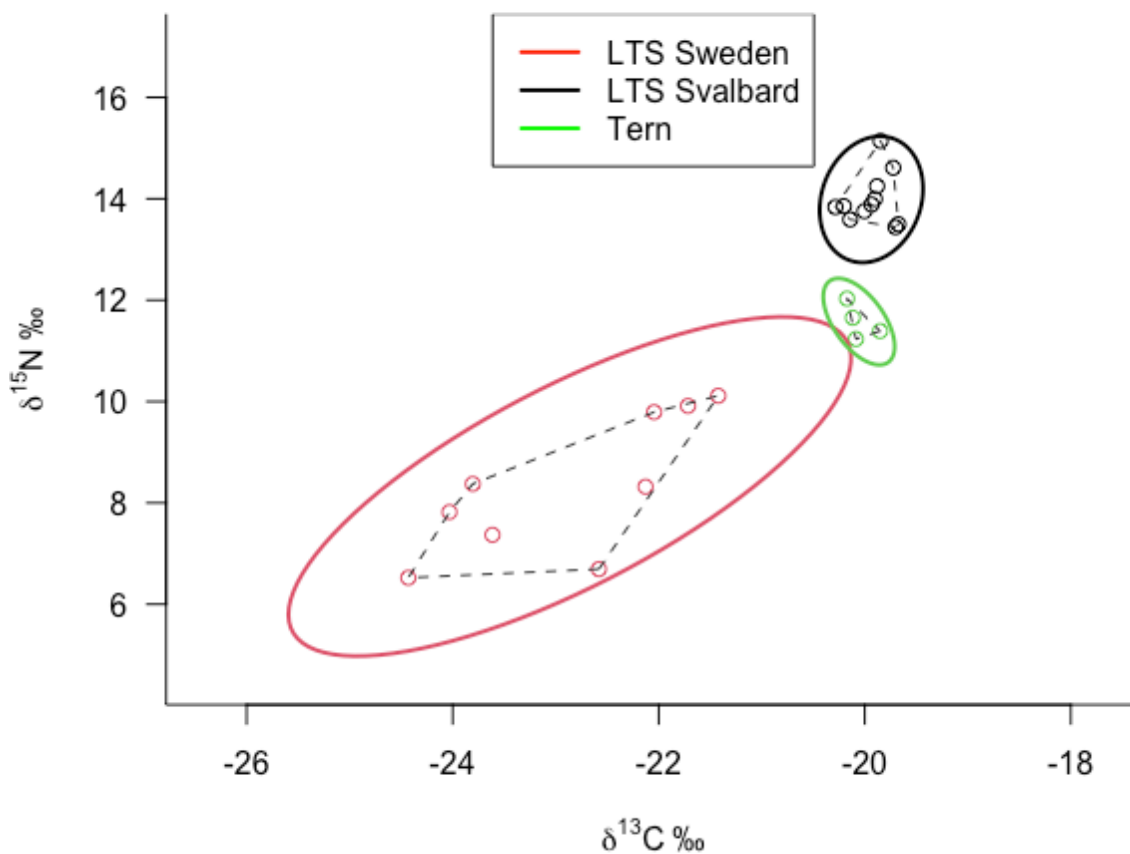

Figure 1: *Isotopic niche space estimated through blood of Long-tailed skuas both in Svalbard (LTS Svalbard) and in Sweden (LTS Sweden), and in Arctic terns (Tern). $\delta^{15}N$ and $\delta^{13}C$ values and standard ellipse areas corrected for small sample sizes (SEAc) using stable isotope Bayesian ellipses in R (SIBER). Ellipses are covering 95% of the stable isotope data. Stippled lines mark the borders of values measured for each population.*

Table 2: *Mean and ±SD of isotopic values for Long-tailed skuas (LTS) breeding in Sweden and Svalbard, and Arctic terns (AT) breeding in Svalbard measured in whole blood (WB). As well as in plasma and red blood cells (RBC) in Long-tailed skuas breeding in Svalbard.*

Population	Blood part	δ^{15}N (‰)	δ^{13}C (‰)	n
LTS Sweden	WB	8.32 ±1.37	-22.86 ±1.12	9
AT Svalbard	WB	11.58 ±0.35	-20.06 ±0.14	4
LTS Svalbard	WB	13.98 ±0.49	-19.92 ±0.20	11
LTS Svalbard	Plasma	14.82 ±0.36	-20.04 ±0.43	11
LTS Svalbard	RBC	13.67 ±0.39	-19.77 ±0.20	11

Stable isotope analyses where also conducted on blood components for the Long-tailed skuas breeding in Svalbard to discern the difference between the diet during migration and during breeding. Plasma had the highest δ^{15}N-values but the lowest δ^{13}C-values (**table 2, figure 2**). RBC had the lowest δ^{15}N-values but had intermediate δ^{13}C-values. The difference between whole blood and plasma was significant for nitrogen ($p < 0.01$) but not for carbon ($p = 0.68$), and the difference between whole blood and RBC was not significant for either nitrogen ($p = 0.31$) or carbon ($p = 0.49$).
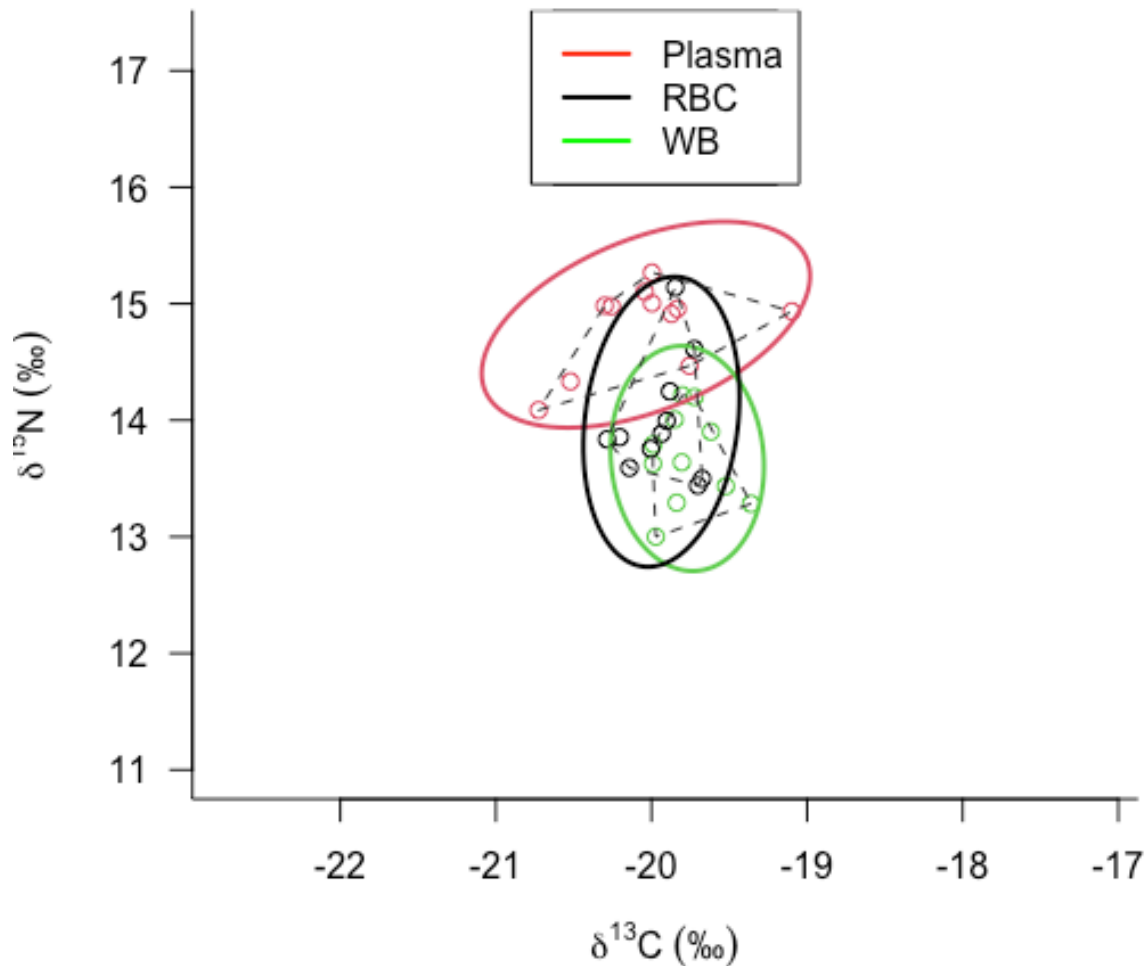
Figure 2: *Isotopic niche space estimated through plasma, red blood cells (RBC) and whole blood (WB) for Long-tailed skuas breeding in Svalbard. $\delta^{15}N$ and $\delta^{13}C$ values and standard ellipse areas corrected for small sample sizes (SEAc) using stable isotope Bayesian ellipses in R (SIBER). Ellipses are covering 95% of the stable isotope data. Stippled lines mark the borders of values measured for each population.*

Mercury (Hg)

Hg analyses in whole blood showed that Long-tailed skuas breeding in Svalbard had the highest Hg concentrations (**table 3, figure 3**), Arctic terns had the lowest concentrations, and Long-tailed skuas breeding in Sweden had intermediate concentrations. The difference between Long-tailed skuas breeding in Svalbard and in Sweden was not significant (p=0.60), but the difference between Arctic terns and Long-tailed skuas breeding in Svalbard was significant (p<0.01).
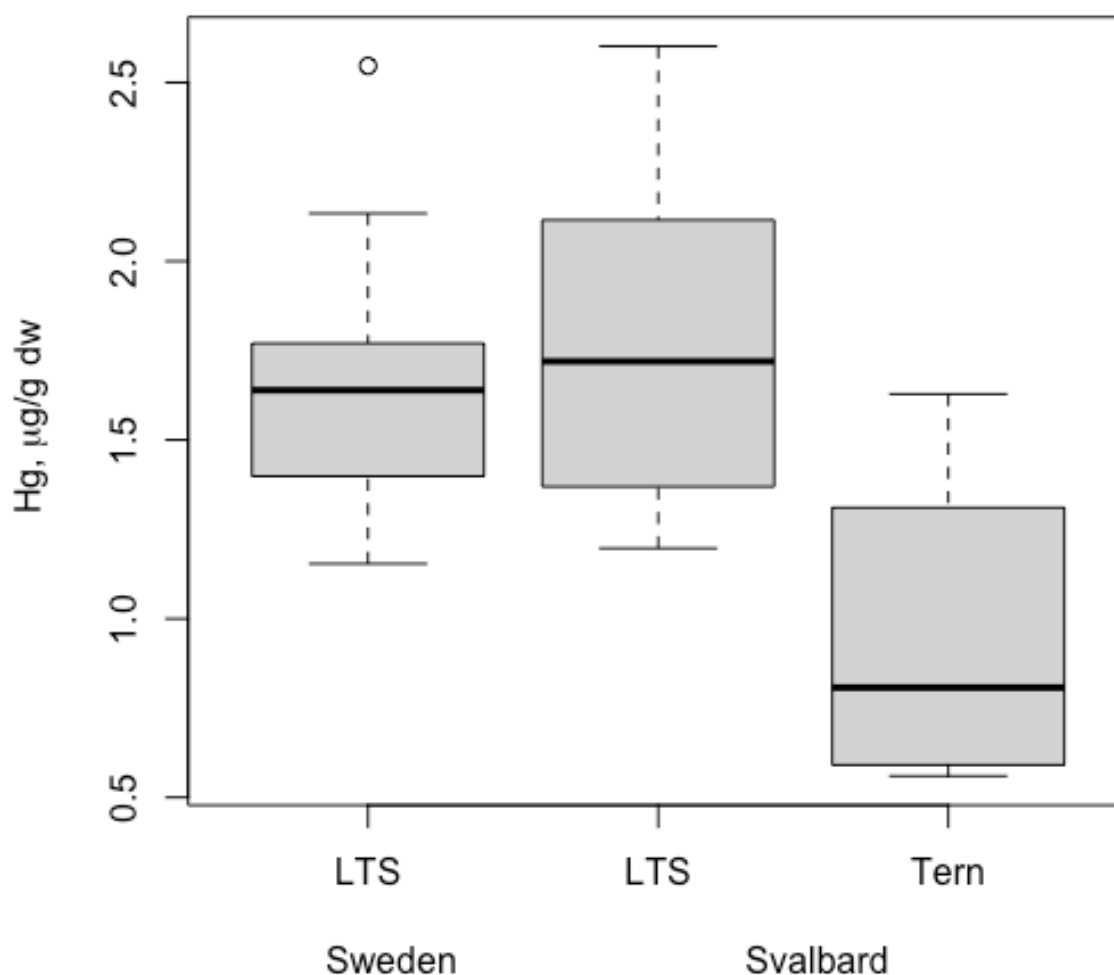
Figure 3: *Mercury (Hg) concentrations measured in blood (µg/g dw) for Long-tailed skuas (LTS) both in Svalbard and in Sweden, and Arctic terns (Tern) in Svalbard. The boxplot represents the 25-75% quartile range, and the median bar. The whiskers extend from the boundaries of the box to the 1.5x interquartile range (IQR) of the boundaries. Data beyond the whiskers are plotted as points (outliers).*

Table 3: *Mean and ±SD of mercury (Hg) concentration values for Long-tailed skuas (LTS) breeding in Sweden and Svalbard, and Arctic terns (AT) breeding in Svalbard measured in blood.*

Population	Hg (µg/g dw)	n
LTS Sweden	1.69 ±0.43	9
LTS Svalbard	1.79 ±0.47	11
AT Svalbard	0.95 ±0.49	4

DISCUSSION

The aim of the present study was to investigate the feeding ecology of the Long-tailed skuas breeding in Svalbard and assess the consequences of diet on Hg contaminant levels. As expected, they were in the highest trophic niche of our study populations and had δ^{15}N-values significantly more similar to the Arctic terns breeding in Svalbard than to the Long-tailed skuas breeding in Sweden. In addition, they had a significantly higher δ^{13}C-value compared to the Swedish population. This shows that the Long-tailed skuas breeding in Svalbard have a pelagic marine feeding ecology towards the top of the food web, during the breeding season. The Hg levels were predicted to be significantly lower in the Swedish birds compared to the Svalbard birds, as a result of their having a terrestrial diet compared to the marine diet of the Svalbard birds. This was not the case. The results show significantly lower Hg levels in the Arctic terns, and both populations of Long-tailed skuas had statistically the same results, with the Svalbard population having a higher variance.

Stable isotopes

To measure the trophic levels present in a food web, one first measures the δ^{15}N-values of the lowest producer in the food web, and then the δ^{15}N-values of its predator, then the δ^{15}N-values of that one's predator, etc., all the way up to the top predator (Hobson et al., 2002). It is then possible to record the incremental increase between the levels. Any individual that has values measured somewhere between those levels will necessarily consume prey on multiple trophic levels, decreasing their values from fitting completely into the trophic level of the predator consuming only the prey on the highest trophic level. However, most studies studying the trophic levels of one or multiple species don't have the possibility to measure the δ^{15}N-values of each organism in the food chain of their study species. This means that they have to calculate the trophic levels of their species based on the δ^{15}N-values they have, and compare it to previous studies of similar food webs. There are several different values used in the calculations for food chains with seabirds as top predators. The ranges used are either 3-5‰ per trophic level (Renaud et al., 2011; Hobson & Welch, 1992), or 2-4‰ (Hobson & Clark, 1992; Hobson et al., 1995). Although Hobson et al. (2002) did measure each trophic level up to top avian and mammalian predators in their study and found that the trophic enrichment factor between the avian predators and their prey (2.4‰) was different from all other predators and their prey (3.8‰), in the food web of the North Water Polynaya area. A study on a Kongsfjorden food web used 3.8‰ as the trophic enrichment factor for all organisms expect the piscivorous birds, where they used 2.4‰,

based off of a study on fish-fed cormorants conducted in 1991 (Ruus et al., 2015). They did not calculate the enrichment factor between the trophic levels themselves.

Long-tailed skuas in Svalbard vs Sweden

The Long-tailed skuas breeding in Svalbard had the highest trophic level of the three populations sampled in this study (**figure 1, table 2**). With an average δ^{15}N-value of 13.98‰ (±1.15‰), that is 5.66‰ higher than the Swedish population (8.32‰, ±1.8‰), which is at least one whole trophic level above the Swedish population, even when using the highest range of 3-5‰ per trophic level, and 2.4 trophic levels higher using 2.4‰ as the trophic enrichment factor. Which means that they would have to have different diets on the breeding grounds. This conclusion is further strengthened by the difference in the δ^{13}C-values.

The carbon source is mainly used to distinguish between different habitats (Hobson & Clark, 1992, Barret et al., 2007). The δ^{13}C-values measured in the Long-tailed skuas breeding in Sweden has an average of -22.86‰, with a large variation (±3.01‰), while the Long-tailed skuas breeding in Svalbard has an average of -19.94‰, and very little variation (±0.62). The great variance in the data for the Swedish population could be caused by the blood samples having some of the marine migration diet still present, skewing the data to a higher trophic level and higher δ^{13}C-values. This is highly likely as they reach Ammarnäs by late May/early June and where sampled in mid-June, and RBC have a turnover rate of 3-4 weeks (Ceia et al., 2014). Another component is that they are known to have quite a broad diet in their breeding years (which 2014, the sampling year, was), ranging from last year's berries, to a lot of insects and spiders, to rodents such as lemmings (de Korte & Wattel, 1988). Lemmings have low δ^{15}N-values, (mean= 2.27‰, for Norway lemmings (*Lemmus lemmus*), mean=0.08‰, for Wood lemmings (*Myopus schisticolor*) (Calandra et al., 2015)), and berries and arthropods, being at even lower trophic levels, will skew the data lower for the nitrogen source. The carbon source was also more marine than was measured in the lemmings (mean=-24.52‰, for Norway lemmings, mean=-28.69‰ for Wood lemmings (Calandra et al., 2015)). The trophic ecology measured in the blood will then be very varied, as was the case here.

There is no overlap between the δ^{15}N or the δ^{13}C-values in the two Long-tailed skua populations, meaning that their feeding ecology at the breeding sites are completely different. The higher δ^{15}N-values of the Svalbard population shows that they should feed on a higher trophic level than lemmings are at. Comparing the δ^{13}C-values with the Arctic terns, however,

shows that they have the same carbon source as the Svalbard population of Long-tailed skuas, so they should have a pelagic marine diet. The range of δ^{13}C-values measured in the Swedish population, and how close the extreme values comes to the values for the marine-feeding birds, further shows that they still have some of the marine migration diet in their blood.

Arctic terns vs Long-tailed skuas in Svalbard

The trophic levels of the Arctic terns are lower than the Long-tailed skuas breeding in Svalbard (**figure 1, table 2**), at 11.58‰ (±0.45), a 2.4‰ decrease. Using the highest range (3-5‰), this is not a full trophic level difference. However, using the value Hobson and Clark (1992) found in their study on captive-reared birds (2.4‰), this is precisely one trophic level difference (see also Hobson et al., 2002). No matter which value is the most correct to use here, the Arctic terns and the Long-tailed skuas breeding in Svalbard does not have identical nitrogen levels, and so they do not have an identical diet. This conclusion is strengthened when looking at the plasma values measured in the Long-tailed skuas, they are even higher than the whole blood values, with a mean of 14.82‰ compared to 13.98‰. This is not a whole trophic level difference (0.84‰), but by comparing the plasma values of the Long-tailed skuas and the whole blood values of the Arctic terns, the Long-tailed skuas are 3.24‰ higher. Even comparing the whole blood of Arctic terns to the RBC of Long-tailed skuas, the skuas are 2.09‰ higher, which would be on different sides of the spectrum of the same trophic level. So, it seems that the diets the two species have when breeding in Svalbard are not entirely identical.

The Arctic terns exhibit considerable plasticity in their diet, feeding on terrestrial insects, zooplankton, crustaceans and fish (predominantly polar cod) (Savinov et al., 2000; Fauchald et al., 2015). If the Long-tailed skuas kleptoparasite the Arctic terns, as they are hypothesized and observed to do, perhaps only the fish are big enough for the Long-tailed skuas to see in their beaks, and thus when the terns catch fish this is when the skuas kleptoparasite them. This results in the Long-tailed skuas having a higher ratio of fish and the Arctic terns having a higher ratio of zooplankton and crustaceans in their diets. This would explain why the δ^{15}N-values are lower in the Arctic terns, as the zooplankton and crustaceans are on lower trophic levels than fishes are. Also, the δ^{13}C-values are not significantly different (p=0.71), the Long-tailed skuas having an average of -19.94‰ and the Arctic terns having an average of -20.06‰, and both have very little variation (±0.62 and ±0.32, respectively). Renaud et al. (2011) measured mean δ^{13}C-values between -22.3‰ and -17.4‰ for fishes and seabirds in Kongsfjorden, so both the skuas and the terns have values corresponding to a marine diet.

The Long-tailed skuas seem to have a dietary shift during breeding. The high turnover rate of the plasma shows the diet of the last few days (Ceia et al., 2014). The δ^{15}N-values measured in the plasma (mean=14.82‰) and the RBC (mean=13.67‰) were significantly different (p<0.01) (**figure 2, table 2**). The birds were sampled at the very end of June or beginning of July (see **table 1**) and so the samples don't have any, or have barely any, of the migration diet still in the blood. So, the difference in the plasma and RBC values represents a change in the diet over time in the breeding area. The Long-tailed skuas then possibly feed on a higher ratio of crustaceans and copepods when first arriving at the breeding site and incorporating a higher ratio of fish later. Probably because the Arctic terns arrive at the breeding sites around the same time as the skuas (Egevang et al., 2010; Gilg et al., 2013), and so at the beginning there are very few terns to kleptoparasite, so they need a different food source. This food being crustaceans and zooplankton is also probable because while the carbon source is the same for both plasma and RBC (the difference is nonsignificant: p=0.079), there seems to be some difference there, which would be explained by the incorporation of some coastal food (crustaceans and zooplankton plucked from the shoreline) during breeding and not just pelagic food (kleptoparasite terns who have fished in the fjord).

Considering the sample size for Arctic terns was only 4, it is possible that this gives a bias in the results. The Arctic terns have a good deal of plasticity in their diet, so the 4 individuals we sampled could have very similar diets, underrepresenting the diversity and skewing the data in one direction. It is possible that a larger sample size would have given a higher mean δ^{15}N-value, showing that kleptoparasitism affects the diet less in the population as a whole, than it did these 4 individuals. In addition, they were sampled during late incubation/early chick-rearing and thus might preferentially feed their chicks fish while consuming lower trophic level prey themselves, as was recorded by Fauchald et al. (2015). It is not likely that the δ^{15}N-values would have been much lower in a larger sample size, as they were very similar to those in a zooplankton-feeding bird, little auk (*Alle alle*), measured by Jæger et al. (2009).

Mercury (Hg)

Marine-feeding organisms typically exhibit higher Hg concentrations than terrestrial-feeding organisms (Clatterbuck et al., 2021). Thus, the terrestrial feeding ecology of the Long-tailed skuas breeding in Sweden were predicted to cause this population to have lower Hg levels than

the birds breeding in Svalbard and having a marine feeding ecology. However, these were not the results found in this study. The Arctic terns had the lowest Hg levels (**figure 3, table 3**). The populations of Long-tailed skuas had similar Hg levels, they had similar lower values, but the Svalbard population had a greater variation. Why the populations of Long-tailed skuas had such similar Hg concentrations cannot be explained by the diet at the breeding grounds.

The turnover rate of the stable isotopes measured ($\delta^{15}N$, $\delta^{13}C$) is not the same as the turnover rate of Hg, therefore they reflect the diet at different time spans. The turnover rate of stable isotopes in the blood is a few weeks (Ceia et al., 2014), but the turnover rate of Hg in the blood is longer. The literature on blood Hg retention in seabirds give different rates. Albert et al. (2019) concluded that Hg concentrations measured during chick-rearing could inform of the uptake from late migration and up to the sample date, using two studies: Hg half-life measured in Great skua (*Stercorarius skua*) were 30 days (Bearhop et al. 2000), and Hg half-life measured in Cory's shearwaters (*Calonectric borealis*) were 45-60 days (Monteiro & Furness, 2001). Monteiro and Furness (2001) dosed their birds with Hg and measured them periodically for up to 140 days, and up to the end they still measured a declining Hg concentration. The half-life measure is not a measure of when Hg is depleted in the blood stream, and so can inform on trends on a temporal (and spatial, in migrating species) scale, rather than accurate concentrations, of Hg, especially as time between intake and sampling increases.

Hg excretion pathways also confounds the accuracy over longer time spans. Molting of feathers is the primary route for Hg excretion in birds, having the capacity to hold up to 70-80% of body burdens (Lavoie et al. 2014). Arctic terns have a full-body and wing feather molt that starts and finishes shortly before leaving the wintering sites (Voelker, 1997; Egevang et al., 2010), and Long-tailed skuas molts two times a year (continuously at the wintering site, first body plumage, then wing- and tail feathers, then body plumage again) before leaving the wintering sites (van Bemmelen, 2019; Wiley & Lee, 2020). In females, egg-laying is a great source of Hg unloading (Albert et al., 2019, 2020; Monteiro & Furness, 2001), and the samples in this study was taken after egg-laying, reducing the overall Hg levels compared to first arrival at the breeding sites, but the birds in this study was not sexed, so this was neither measured nor accounted for in the results. The timing-specific excretion pathways make these results not a true representation of the Hg concentrations found in these birds at the wintering sites, but the higher the Hg concentrations at the wintering and stopover sites are, the more it will be present in and affect the birds also at the breeding sites.

All three populations studied have the same stopover sites, arriving in late May in the North Atlantic Drift Province, where they have a marine pelagic feeding ecology (Egevang et al., 2010; van Bemmelen, 2019). Considering the similar arrival times, it is possible that the Long-tailed skuas also kleptoparasites the Arctic terns even there. Long-tailed skuas are known to kleptoparasite seabirds at their wintering sites on the south and southwest coast of Africa (Gilg et al., 2013). The Arctic terns overwinter on the pack ice of the Southern Ocean, where a key prey species for many seabirds, and is theorizes to also be ingested by Arctic terns, lives: the Antarctic krill (*Euphausia superba*) (Egevang et al., 2010). A study on food webs in the Southern Ocean found that mean Hg concentrations in Antarctic krill measured in two years were between 0.01-0.04 (μg/g) and the seabirds measured had concentrations between 0.22-3.88 (μg/g), with the seabirds with higher relative consumption of Antarctic krill and other zooplankton having the lowest Hg concentrations (Seco et al., 2021). However, it should be noted that Arctic terns did not feature in this study and knowledge of the diet at the wintering sites is difficult to obtain, there are few studies on this in general for seabirds, so there are possibly other unknown prey items in both Arctic terns' and Long-tailed skuas' diets. Different areas of the world and different habitats have different Hg concentrations (Albert et al., 2019, 2020; Evers et al., 2005; Renedo et al., 2020) and Hg concentrations and trophic level have been linked in several studies (Atwell et al., 1998; Evers et al., 2005; Lavoie et al., 2014; Seco et al., 2021) so the lower Hg concentrations in Arctic terns probably signify that they generally feed on lower trophic levels than the Long-tailed skuas in their wintering sites, or at the very least that they have different prey items at this time.

The lower Hg levels in Arctic terns could also be caused by kleptoparasitism. It creates an involuntary shift in the Arctic terns towards a higher concentration of crustaceans and zooplankton and a lower concentration of fish, while simultaneously causing a voluntary shift in the Long-tailed skuas towards a higher concentration of fish, and lower concentrations of lower trophic level prey. Changes in feeding behavior will affect Hg ingestion, particularly if there are dietary shifts between fish (which are generally higher in Hg) and crustaceans (which are generally lower in Hg) (AMAP, 2005). Kleptoparasitism does not cause the terns to completely lack Hg concentrations caused by ingestion of fish, though, as the skuas does not steal all of their food (Fauchald, et al., 2015). So, while this might be a contributing cause, the possible different trophic levels of their diets and the regional differences at the wintering sites is more likely the main cause for the great variation in Hg concentrations. If this is the case, it

shows that there is not a complete unloading of the Hg between the departure of the wintering sites and the sample dates – a span of at least 5 months, an unloading time hinted at in some studies (Bearhop et al. 2000; Monteiro & Furness, 2001; Lavoie et al., 2014).

The slightly higher maximum values measured in the Long-tailed skuas breeding in Svalbard might be because they keep the marine diet year-round, while the Swedish population has a terrestrial diet for 3 months. Because organisms with a marine feeding ecology typically exhibit higher Hg concentrations than those with a terrestrial feeding ecology (Clatterbuck et al., 2021), the Swedish population would accumulate less Hg for 3 months of the year than the Svalbard population would in that time. Although, in this study the difference in their blood Hg concentrations was non-significant (p=0.61), the Swedish population still had traces of the marine migration food during sampling. If they had been sampled later in the breeding season, the difference between them and the Svalbard birds would probably have been larger, and possibly even significant. Even then, it seems that having the same feeding ecology for 9 months of the year is a contributing cause to why the different breeding populations have such similar Hg levels, especially because the Hg concentrations measured have the same lower values. If the Hg accumulated during the wintering sites were to completely disappear from the blood, then we should see that the lowest Hg values measured in the Swedish birds is lower than the Svalbard birds. Perhaps this happens later in the breeding season than was measured in this study.

CONCLUSIONS AND FUTURE WORK

The feeding ecology of the Long-tailed skuas at the edge of their breeding distribution was investigated and compared with local Arctic terns and with Long-tailed skuas in the core breeding areas. We found that the Arctic population kept a pelagic marine diet even in the breeding season, most likely by kleptoparasiting Arctic terns. This was showed through δ^{15}N-values being significantly more similar to the Arctic terns breeding in Svalbard than to the Long-tailed skuas breeding in Sweden. In addition, they had a significantly higher δ^{13}C-values compared to the Swedish population, indicating a more marine diet. Further, we investigated the effect this dietary difference had on the Hg concentrations found in the blood during breeding. Lower Hg concentrations in Arctic terns, and similar Hg concentrations in the two populations of Long-tailed skuas indicated that the Hg absorbed through the diet earlier in the year, in the non-breeding period, were still present to some degree in the breeding period. Exactly how long Hg stays in the blood, and how representative these recordings are of the concentrations at the wintering areas or the stopover areas, is unknown, as the current literature gives different and imprecise time frames. More studies need to be conducted on how the Hg moves throughout the body of seabirds, and how the concentrations in different tissues change year-round.

The use of stable isotope analyses to study diet is becoming more and more common. However, most studies investigating the trophic levels of one or multiple species does not have the possibility to measure the δ^{15}N-values of each organism in the food chain of their study species. This means that they have to calculate the trophic levels of their species based on the δ^{15}N-values they have and compare it to previous studies of similar food webs. This gives an average of what the diet consists of, but not how much of each prey item is in the diet. This may conceal the prey items on the extreme ends of the range of the trophic levels the organism feeds on, as well as the diversity of prey items with similar δ^{15}N-values. Studies on feeding ecology and diet therefore cannot only rely on stable isotope analyses but needs an observational aspect as well.

The current literature on the ranges included per trophic level for birds seem to site primarily one study on captive reared quail and crows (Hobson & Clark, 1992). Subsequent studies including seabirds either use this value, or values found in different parts of the studied food

webs. More studies on the enrichment of nitrogen through the trophic levels are needed for different types of foodwebs.

Future studies should also measure stable isotopes in chicks. In this study only adults were measured, because the fieldwork period coincided with brooding and not hatching, but data on chicks, both through blood/down samples as well as having cameras on the nests, would give an even clearer idea of the breeding diet, as well as possible differences between what the adults eat and what they feed their chicks. It is possible that they feed newly hatched chicks more insects, as that can be found within their territories. This would enable them to keep a lookout for predators as well. The Arctic fox (*Vulpes lagopus*) is the main predator for the chicks, and very few hatched chicks survive the first year. There is also a possibility that the Long-tailed skuas have a difficult time utilizing the marine food for breeding, as the adult survival is high, but there are only about 10 territorial couples in Kongsfjorden every year. While there are large populations of Black-legged kittiwakes (*Rissa tridactyla*) and Arctic terns breeding, having a marine diet. The marine diet seems good for survival 9 months of the year for the Long-tailed skuas, but seems suboptimal for breeding, at least compared to lemmings in high density-lemming years. The limiting factors for the low population and low breeding success should be investigated in future studies.

Most Long-tailed skuas breed in areas with large rodent populations, breeding in high density-lemming years. The population in Kongsfjorden, Svalbard is at the edge of this breeding distribution, with a marine diet, showing the flexibility of seabirds in general, and Long-tailed skuas in particular, in their feeding ecology. Prompting the question of the possibility of other species also being able to breed in areas without access to their main prey item. In a drastically changing world, studying seabirds' diets and their flexibility is vital to understand the enduring viability of their populations.

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