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Diet variability in black-legged kittiwakes (*Rissa tridactyla*) in Kongsfjorden in relation to ongoing environmental changes

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Abstract

The Atlantification of the European Arctic is defined as Atlantic water masses increasing their influence further North. This process, which is induced by climate warming, leads to changes in the physical and biological environment of the marine ecosystems. Decreased sea ice cover, increased sea surface temperature and increased salinity, as well as incoming boreal species, introduce potential threats to the local organisms. Colony breeding seabirds, such as black-legged kittiwakes (*Rissa tridactyla*), can be used for biomonitoring of the occurring changes in marine ecosystems. Diet samples can indicate how the communities of prey species are changing and how these variations affect the energy budget of the birds. Calorimetry analyses revealed that the energy content in the diet samples of kittiwakes in Kongsfjorden declined from 2012 to 2020, but only a small proportion of the variability can be explained by time. While Atlantic-type conditions in summer, measured in salinity, increase in frequency, Arctic prey species decrease in frequency of occurrence in the diet samples of the birds. In Atlantic-type summers, the energy content in the diet samples was mostly lower. The median clutch size decreased over time, while in general there were larger clutches in years with Arctic-type conditions. However, not all Atlantic-type summers resulted in low energy content in the diet samples and low clutch sizes. Some Atlantic prey species could be a qualitatively high substitute for Arctic prey species. Especially the Atlantic *Mallotus villosus* could be a good replacement for the Arctic *Boreogadus saida*, as energy densities of both species were very similar. The effect of the Atlantification on the kittiwakes appears to be moderate for the given study period. My results indicate that black-legged kittiwakes are suitable biomonitors for the conditions in Kongsfjorden and suggest, that the Atlantification leads to decreased energy availability during breeding season and therefore reduced reproductive success. To be able to learn more about the influence of the Atlantification of the European Arctic, future studies should consider including diet samples from areas, where the population decline has been stronger than in Svalbard, such as mainland Norway.

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1. Introduction

1.1 The Arctic environment

Polar environments are characterized by intense seasonality. Light, temperature and nutrient availability are highly unevenly distributed throughout the year and follow predictable cycles (Svendsen et al., 2002). The seasonal environment leads to narrow, neatly timed windows of favorable conditions for local organisms, which in turn have evolved a range of adaptations (Alerstam et al., 2003; Liess et al., 2015; Varpe, 2017). Short but intense vegetation and growth phases for organisms at low trophic levels, such as phytoplankton, determine the energy transfer through the food chain (Varpe & Fiksen, 2010; Winder & Cloern, 2010). For seabirds, such as black-legged kittiwakes, hereafter called kittiwakes (*Rissa tridactyla*), the Arctic provides opportunities, such as high food availability in summer, reduced parasite load and decreased predation, which makes the area a suitable breeding habitat (McKinnon et al., 2010; Piersma, 1997; Schekkerman et al., 2003).

Due to climate warming, the Arctic and its inhabitants are experiencing great changes (e.g.: Carmack et al., 2015; IPCC, 2022; Lind et al., 2018). Alterations of the physical conditions can lead to asynchrony of the delicate timing which can have large effects on trophic interaction (Ji et al., 2013; Søreide et al., 2010). With the abiotic and biotic factors altering, also the feeding environment and therefore breeding conditions for the kittiwakes change (Barrett, 2007).

1.2 Atlantification

Over the recent decades, the impact of waters from lower latitudes has been increasing and the Arctic Ocean has warmed significantly (Asbjørnsen et al., 2020). This “borealization” has been occurring in different areas that support southern water masses accessing Arctic seas. In the European Arctic, where this process has been observed to be especially severe, it was called “Atlantification” (Årthun et al., 2012). The Atlantification is characterized Atlantic waters, that have become warmer and saltier, reaching North and is estimated by different physical proxies such as water temperature, salinity and extent of sea ice cover as well as biological proxies consisting of distinct species appearances (Asbjørnsen et al., 2020; Barton et al., 2018; Descamps et al., 2019). The Atlantification has been increasing with developing global warming which was measured through the proportion of Atlantic waters in the whole water body of different Arctic fjords of Westerns Spitsbergen. In peak years, Atlantic waters

increased to up to 30% of the water body (Bloszkina et al., 2021). Due to arising higher temperatures and increased salinity, many fjords of Spitsbergen have been free of ice cover the past decades (Lind et al., 2018). Polar cod (*Boreogadus saida*), that different organisms at higher tropic levels, such as kittiwakes, prey on, has a life history adapted to sea ice, and therefore faces hardship coming the new conditions (Eriksen et al., 2020). Furthermore, incoming boreal waters transport boreal organisms with them, which can survive and reproduce in the warming environment. Changing conditions in favor of the less strongly adapted boreal species, alter different points in the food web and the trophic cascade that follows (Barton et al., 2018).

Different studies found evidence for boreal species in former Arctic ecosystems which have entered higher latitudes only recently and expanded their ranges North. In 2013 for example, the Atlantic mackerel (*Scomber scombrus*) was recorded in Isfjorden, Svalbard, for the first time (Berge et al., 2015). Kujawa et al. (2021) found Atlantic species such as *Melonis affinis* in the benthic foraminifera fauna in Rijpfjorden in Northern Svalbard. A study about the distribution of gelatinous plankton species in the Fram strait revealed a general extension of the distribution northwards. Taxa, that are associated with warmer water temperatures, were found further North (Mańko et al., 2020). These shifts in species distributions indicate the ongoing changes in relation to the Atlantification. Species from different regimes, that previously would not have been able to sustain themselves as far North, exploit new niches in the established Arctic food webs. The Atlantification can thus be seen as a threat to the Arctic species which are outcompeted as conditions change in favor of less specialized boreal species (Csapó et al., 2021; Søreide et al., 2010).

Gaston and Elliott (2014) studied seabirds (*Uria lomvia*) around the Hudson Bay in North-East Canada from 1981-2013 and found that the diet composition was strongly affected by the sea ice conditions. They found a steady increase of capelin (*Mallotus villosus*) at the expense of a decrease in polar cod over the study period, which suggests that the borealization is also happening in the Canadian Arctic (Gaston & Elliott, 2014). Because of the feeding ecology of marine food webs, organisms that are situated at a high trophic level, such as seabirds, can report on species compositions and changes in the lower trophic domain. The changes in the basal steps become visible through the effects they have on higher trophic levels.

1.3 Seabirds as biomonitors

Biomonitoring are “organisms that contain information on the quantitative aspects of the quality of the environment” (Markert et al., 2003). In other words: Biomonitoring can be used, to learn about conditions in ecosystems.

Colonially breeding seabirds, as predators and central place foragers, can deliver information on the status of marine ecosystems. They can cover large areas for their foraging and frequently return to their colonies (Elliott et al., 2009; Gaston & Elliott, 2014). Diet samples can be used for biomonitoring, as the diet of seabirds reflects the underwater environment they forage in, and therefore also ongoing changes (Vihtakari et al., 2018). Kittiwakes are suitable biomonitors of the conditions in the marine ecosystems, as they are well studied and very abundant (CAFF, 2020). The birds breed in colonies on cliffs and can be caught during the breeding period because they display protective behavior towards their nesting sites and eggs/chicks. Kittiwakes remain on their nests for quite long in possibly dangerous situations before leaving for the sake of their own lives and can therefore be caught easily. Because of their behavior of regurgitating their stomach content, which is a response to stress or a tactic for predator distraction, diet samples can be obtained in a non-invasive way (Acampora et al., 2017; Barrett, 2007). In Kongsfjorden, kittiwakes mainly forage in the fjord close to their colony during breeding season, as expected by the optimal foraging theory (Thaxter et al., 2009). Therefore, the birds indicate the variability in the fjord's ecosystem.

The composition of the diet of kittiwakes in Kongsfjorden has been monitored over many decades. In the 1980s and 90s, fish used to dominate the diet samples of the kittiwakes during the breeding seasons (Mehlum & Gabrielsen, 1993). In 1992, Gabrielsen et al. found only polar cod (*Boreogadus saida*), *Thysanoessa inermis* and *Themisto libellula* in the diet samples (Lønne & Gabrielsen, 1992). Atlantic fish species appeared for the first time in regurgitation samples from Kongsfjorden in 2005, while the intermediate *Thysanoessa inermis* had already been found since the first recorded sampling in 1982 (Vihtakari et al., 2018). Over the period of the mid-80s to 2018, polar cod was the most important prey species for kittiwakes in the fjord and most frequently found. Still, this Arctic species has been declining in frequency of occurrence in diet samples. On the other hand, Atlantic species such as capelin (*Mallotus villosus*) and herring (*Clupea harengus*) and intermediate species such as *Thysanoessa inermis* have been increasing (Vihtakari et al., 2018). Atlantic fishes, that are generally larger in body size, have a faster growth rate and a more generalist feeding pattern, can outcompete Arctic fish species such as the polar cod (Csapó et al., 2021). A positive correlation was found between high sea ice extends and frequency of occurrence of Arctic species and vice versa, low sea ice extends and frequency of occurrence Atlantic species Vihtakari et al., (2018). Further, a more diverse diet and a higher share of Atlantic species such as capelin (*Mallotus villosus*) or Atlantic herring (*Clupea harengus*) was found after 2004 (Lønne & Gabrielsen, 1992, Vihtakari et al., 2018).

1.4 Possible shifts in the energetics of the food web

Since boreal and polar species derive from regions with different ecological requirements, the energetics of the species could be different. Prey species that contribute an important share of the diet of kittiwakes, such as the Arctic species polar cod (*Boreogadus saida*) and the Intermediate *Thysanoessa inermis*, were found to have around 21 to 22 KJ/g in dry weight (DW) and 27 KJ/g DW respectively (Harter et al. 2013; Nowicki, publishing in progress). The Atlantic herring (*Clupea harengus*) on the other hand, was found to only contain around 17 to 19 KJ/g DW of dry weight (Bernreuther et al., 2013). Atlantic species exploiting Arctic ecosystems could therefore change the energetics of the food webs. The energy expenditure is expected to be especially high in polar seabirds because of high activity rates and low temperatures (Gabrielsen et al., 1988). Kittiwakes are known to have the highest daily energy expenditure during the period of chick rearing (Fyhn et al., 2001). The birds are therefore sensitive to changes in the energy budget, especially during summer.

Reiertsen et al. (2014) have investigated the effect of prey density on adult survival and found that kittiwakes in the Southeast Barents Sea are especially reliant on the local capelin populations. In the British North Sea, the breeding success used to be correlated to lesser sandeel (*Ammodytes marinus*) populations (Frederiksen et al., 2004). After a strong decline in the stocks due to fisheries in the mid-90s, the kittiwake population also declined drastically. A ban of sandeel fisheries in the area led to population recovering until 2002. Afterwards, the numbers dropped again due to rising water temperatures (Frederiksen et al., 2004). The increase in temperature seemed to compromise the recruitment of the main prey. Also, in the southern Barents Sea the local sandeel population seems to be crucial for the kittiwakes. Higher sandeel larval biomass leads to a higher breeding success in the following year (Frederiksen et al., 2006). Through this bottom-up control of the food web, an increase in sea surface temperature is therefore likely to negatively affect the population health of kittiwakes (Frederiksen et al., 2004, Frederiksen, 2010).

When the chicks of black-legged kittiwakes hatch, they cannot regulate their body temperature and rely on their parents brooding (Coulson, 2011). Increasing their weight and body fat amount is therefore crucial for their survival. Because the energy is transferred from the adults to the chicks through regurgitation, chicks rely heavily on the quality of the food the parents provide which is hence crucial for the population health (Jodice et al., 2006; Moe et al., 2009). Previous studies have shown that Atlantic species increase in abundance in diet samples in Svalbard. Still, the decline in numbers in Kittiwakes in Svalbard is nowhere near

the decline in mainland Norway. While in 2005 there were still about 336.000 breeding pairs in Mainland Norway and 270.000 in Svalbard, in 2013 there were only 87.000 pairs left and 245.000 pairs respectively. This means a decline of around 70% in mainland Norway, but only 10% in Svalbard (CAFF 2020; Fauchald et al. 2015). One possible explanation could be that kittiwakes in Svalbard are able to exchange energy-rich Arctic food with energy-rich Atlantic food. Descamps et al. (2019) found that the sea ice extend is positively correlated with the proportion of Arctic prey species in the diet samples. But they could not find a relationship between breeding success and average diet composition of the parent birds (Descamps et al., 2019). So maybe the Atlantification of the food web is not leading to less favorable conditions for black-legged kittiwakes in the short run? Renaud et al. (2018), investigated how the shift from the Arctic species *Calanus glacialis* and *Calanus hyperboreus* to the boreal species *Calanus finmarchicus* influenced the total lipid content in the food web. They found that, even though *Calanus finmarchicus* is smaller and has less energy per individual, their shorter generation lengths and higher turnover rate still lead to a net increase of lipids in the ecosystem. Perhaps, this could also account for other steps in the food web, where boreal species replace Arctic species. As Descamps suggests, research on whether Atlantic prey is energetically suboptimal is needed (Descamps & Ramírez, 2021).

1.5 Study aims

With this project, by using calorimetry on the diet samples of kittiwakes, I will estimate the energy budget for kittiwakes in Kongsfjorden during breeding season and describe the diet composition and energy content of selected prey items.

First, I will ask if the energy content in the diet gradually declines over time as a consequence of the ongoing Atlantification and the related diet variability.

Further, I will test if years with more Arctic waters, as determined by physical proxies, are associated with diets of higher energy content.

Lastly, I will investigate if there is a positive relationship between the energy content of the diet and the breeding success of kittiwakes.

2. Material and Methods

The project was registered in “Research in Svalbard” under the RIS ID 11844. The permission to catch a limited number of kittiwakes for sampling and ringing during the field work period was granted by the Governor of Svalbard.

2.1 Study site and time

Diet samples of black-legged kittiwakes were collected in Kongsfjorden, a fjord on the west coast of Spitsbergen, the biggest island of the Svalbard archipelago. Over a period of 2012 - 2020 a total number of 343 collected diet samples were available in four different colonies along the fjord (see figure 1). 149 of these samples were collected in Krykkjefjellet ($78^{\circ}53'46''\text{N}$, $12^{\circ}11'43''\text{E}$), 77 in Blomstrandhalvøya ($78^{\circ}59'37''\text{N}$, $12^{\circ}7'46''\text{E}$), 12 in Observasjonsholmen ($78^{\circ}56'20''\text{N}$, $12^{\circ}17'5''\text{E}$), 6 in Ossian Sarsfjellet ($78^{\circ}56'17''\text{N}$, $12^{\circ}26'21''\text{E}$) and for 99 the colony was unknown (see table 1). All samples were conducted between late May and August during the breeding season of the kittiwakes. The breeding stages in which the samples were collected ranged from pre-laying, incubating and chick rearing periods and both sexes were sampled.



Figure 1: Inlay map: Overview of Svalbard with the location of the study site Kongsfjorden (red rectangle), made with the ggOceanmaps package in R. Main map: Detailed map of Kongsfjorden with exact locations of the sampled colonies of black-legged kittiwakes and the Mooring Dirigible Italia, made with TopoSvalbard, NPI.

2.2 Study species

Black legged kittiwakes are long-lived, medium sized seabirds and the most numerous gull species in the world (CAFF, 2020). In 1991, the world's population of breeding kittiwakes was estimated to 6-8 million pairs (Anker-Nilssen et al. 2000). According to the IUCN Red List of Threatened Species, black-legged kittiwakes are now considered vulnerable on a global and European scale due to decreasing population trends (The IUCN Red List of Threatened Species, 2019). In 2020 the estimated number of pairs was only 4 million which means a decrease of the global population of up to 50% in three decades (CAFF, 2020). Around half of the worldwide population is being supported in Europe (CAFF, 2020). All over mainland Norway, kittiwake colonies have been declining drastically over the past 2-3 decades which seems to be a direct consequence of warming sea surface temperatures. Some colonies have already disappeared, others are predicted to go extinct within the coming five to nine decades (Barrett 2007; Sandvik et al. 2014).

In Svalbard the subspecies *Rissa tridactyla tridactyla* is one of the most abundant seabirds and the most numerous gull species (Anker-Nilssen et al. 2000). There are about 215 colonies known in the archipelago, with an estimated breeding population of 245.000 pairs in 2013. Since 1995, a decline in numbers has been observed. Normally, the birds start egg-laying in Svalbard in June. Typically, the clutch will consist of two eggs but depending on the environmental conditions, the birds can also lay one or three eggs, which are incubated for about 27 days (Coulson, 2011). The chicks are fed by both parents after they fledge at an age of five to six weeks (Anker-Nilssen et al. 2000).

As generalist surface feeders, kittiwakes often feed in flocks indiscriminately on various prey items within their reach. These include fishes of a size from up to 20 cm as well as different invertebrates (Anker-Nilssen et al. 2000). Kittiwakes from colonies within Kongsfjorden mostly forage in the inner fjord and near the tidewater glacier fronts (Bertrand et al., 2021; Varpe & Gabrielsen, 2022).

2.3 Sample collection

The project is part of a long-term monitoring project of different seabird colonies in Svalbard. Every summer, the population health of the colonies was monitored and different measurements on breeding birds and chicks were taken. Adult birds were caught using a telescope noose pole. While one participant caught the bird from the nest, the other collected it from the noose as quickly as possible in order to minimize the handling time and stress for the birds (see figure 2). Depending on the location of the ledges, the kittiwakes can either be

caught from below or above the bird cliff. The birds were colored with permanent markers to prevent too early recapture.



Figure 2: William Jouanneau and Manrico Sebastiano catching a black-legged kittiwake from its nest for sampling and measuring in the colony Krykkjefjellet.

Collected data include the timing of the different phases of breeding periods; closer: pre-breeding, breeding, and chick rearing as well as the hatch date and the number of eggs and chicks. Standard biometric measurements were taken for all caught individuals. These include body mass (measured to the nearest 2g, using a Pesola spring balance), wing length (using a wing ruler), skull size and tarsus size (using a caliper; see figure 3). The sex was determined in the field by skull size and verified with previously collected DNA sexing data. Breast feather samples were taken for later molecular sexing. Lastly, 2.5 ml of whole blood were sampled from the alar vein, with a heparinized 5 ml syringe and a 25-gauge needle.



Figure 3: Nora Stampe (right) measuring the skull size of a black-legged kittiwake in the colony Krykkjefjellet.

The samples used in this project were spontaneously regurgitated diet samples that some birds provided after being caught. The samples were either caught directly or picked up and placed in zip lock bags, which resulted in different amounts of corresponding material such as sand or moss. Naturally, the samples differ in weight, size, and content. All samples were kept cold during the working day and stored at -18°C upon arrival in the lab for further analysis.

2.4 Regurgitate analysis

The content of the diet samples was analyzed in the laboratory facilities of the Norwegian Polar Institute in Tromsø. Since the beginning of the project, different participants were involved in assessing the samples. Therefore, a template was used to maintain consistency over the time. The different prey items were identified to the lowest possible taxon, using a stereomicroscope and identification literature (Campana 2004; Härkönen 1986). Fish species were identified by body morphology or otolith morphology. The frequency of occurrence of the different prey species was determined by presence or absence. If possible, the individuals of the prey species in the samples were counted.

2.5 Sample procession

The diet samples obtained over the years were stored in the freezer facilities of the FRAM center in Tromsø. Due to the random nature of the sample availability, different numbers of diet samples were available for further analysis from each year (see table 1). Between 10 and 15 diet samples of adult kittiwakes were randomly chosen from each year for analysis, which were conducted in the laboratory facilities of The University Center in Svalbard (UNIS), Longyearbyen.

Table 1: Number of diet samples available for analysis and number of samples used for semimicro calorimetry.

	2012	2013	2014	2015	2016	2017	2018	2019	2020	Total
Number of available diet samples	69	58	26	43	53	35	20	16	23	343
Number of used samples	15	14	10	12	10	10	11	10	10	112

2.6 Semimicro bomb calorimetry

The samples were dried for 18 – 24 hours in a freeze drier and the dry weight was measured, using an analytical balance. The dry samples were homogenized, after large pieces of contamination, such as moss, were removed, using a pestle and mortar. Some samples, mainly those containing larger pieces of fish, were additionally grinded to receive higher homogeneity. The material was then pressed into pellets of 0.15-0.35 g, depending on the density of the samples, with the Parr ® 2812 Pellet Press. The pellets were placed in the bomb of the calorimeter and attached to 10 cm of combustible fuse wire. The bomb was filled with oxygen and placed in a container with 400 g of water. After the apparatus was started, the sample, attached to the fuse wire, was ignited and all combustible parts were burned. The released thermal energy heated the water surrounding the bomb and the caloric content was determined through the amount of warming. The used calorimeter was the Parr ® 6725 Semimicro Oxygen Bomb Calorimeter (see figure 4) and provided values for the energy content in the samples in calories per gram of dry weight (cal/g DW), which were then converted into Kilojoule per gram of dry weight (KJ/g DW), by dividing the value by 239,006 (Woan, 2000).

The calculation for the heat of combustion is as follows:

$$H_c = \frac{WT - e_1 - e_2 - e_3}{m}$$

With:

H_c = Gross heat of combustion.

W = Energy equivalent of the calorimeter being used.

T = Observed corrected temperature rise.

e_1 = Heat produced by burning the nitrogen portion of the air trapped in the vessel to form nitric acid.

e_2 = The heat produced by the formation of sulfuric acid from the reaction of sulfur dioxide, water, and oxygen.

e_3 = Heat produced by the heating wire and cotton thread.

m = Mass of the sample.

(Parr Instrument Company, 2022)

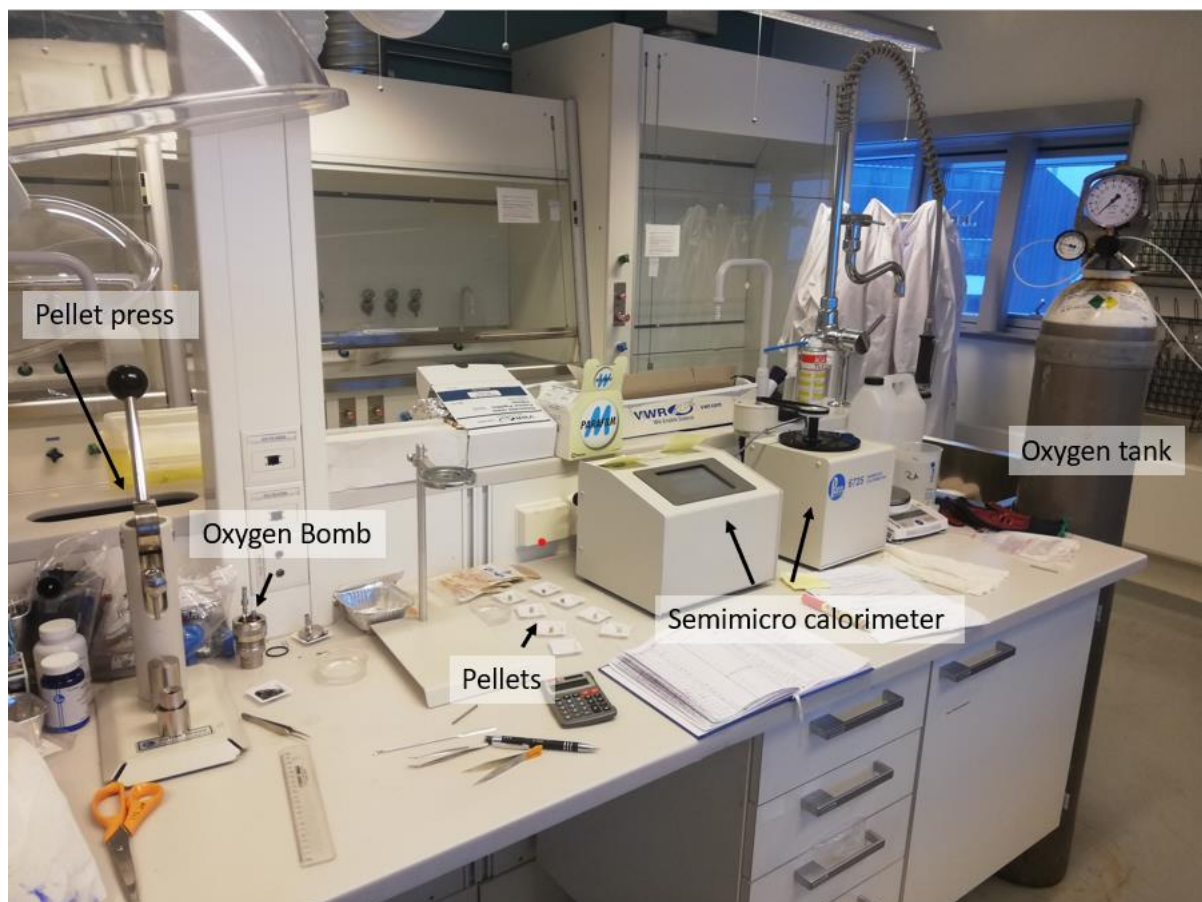


Figure 4: Set up of semimicro bomb calorimeter in the laboratory facilities of UNIS in Longyearbyen.

2.7 Quality insurance

Due to high levels of salt in the samples, there was corrosion of the internal parts of the bomb, with parts having to be replaced frequently. To secure the quality and credibility of the calorimeter output, standardized benzoic acid tablets (0.2 g) were regularly used for calibration after parts were exchanged. The benzoic acid tablets have an error margin of $\pm 0.9\%$, while the error margin of the samples can be different, depending on the degree of homogeneity. Further, samples with too little volume had to be spiked up with benzoic acid in order to meet the minimum energy density required by the calorimeter to guarantee trustable output. At least two pellets were measured from each sample. If the difference in the caloric output was higher than 5%, a third pellet was examined.

2.8 Mooring

The data on the physical parameters in the fjord was provided by the Italian Arctic Data Center (IAD). It was collected by the permanently installed instrument “Mooring Dirigible Italia”, belonging to the Italian Polar Research center ISP (Istituto di Scienze Polari). The Mooring Dirigible is situated in the inner part of Kongsfjorden, close to where the sampled colonies are found (See Figure 1) and its exact location is $78^{\circ}54'863''\text{N}$, $12^{\circ}15'530''\text{E}$, where the fjord has a depth of around 100 m. The instrument collects hourly information on water temperatures, current speed, conductivity, particle flux, turbidity, oxygen saturation and acoustic release (IAD, 2022; Li et al., 2022). Data used in the project include water temperature at 35 m and 85 m water depth, as well as conductivity, converted into salinity in 85 m.

In contrast to water temperature, salinity reacts less sensitive to short term changes and random influences (Li et al., 2022). Further, based on salinity, the water body is easily categorizable as Atlantic or Arctic after the classification of Svendsen et al., 2002 (see table 3). The salinity is less dependent on the depth and hence can easier be adapted for analysis. It has therefore been decided to use salinity as the physical proxy for Atlantification for this project.

2.9 Data analysis

To enable good comparison and because it is common practice in literature, calorimetry data was converted to KJ/g DW (e.g.: Brekke and Gabrielsen 1994; van Pelt et al. 1997). If a third pellet had to be measured to ensure quality, the value most divergent from the others was removed. If samples had to be spiked up with benzoic acid, the first attempts delivering too

low heat release were also removed. The prey items in the samples were classified as Arctic, Intermediate or Atlantic according to Vihtakari et al., (2018) which was added to the dataset. The data on the physical conditions was downloaded from the Italian Arctic Data Center (IAD, 2022) and converted into comma-separated values files. To compensate for extreme values deriving from disturbance, for instance when changing batteries, the salinity data was comprised into one median value per day, as per (Li et al., 2022). In order to find out the effect during the time most crucial for the kittiwakes, it was decided to use only data from June and July for statistical analysis with the caloric data. The values were classified as Arctic- or Atlantic-type, which was adapted from Svendsen et al. (2002).

The data for the breeding success of the birds was calculated as > 12 days old chicks per active nests, after Moe et al., (2009). For the clutch size, data on the maximum clutch size per active nest was used. Data on the reproductivity was adapted from Moe et al. (2009) and for the clutch size given as average. For the years from 2012 – 2020 The French Polar Institute (IPEV) provided the data on the reproductivity. It was one data set for each year and had to be combined into one file. The same was accounting for the data of the diet samples and the content, which were provided by Geir Wing Gabrielsen from NPI.

To be able to combine the data sets, and to provide stability against outliers, one yearly median of caloric content, salinity, and clutch size from 2012 - 2020 were calculated. Further, merging different datasets also required homogeneous data of time, which was converted into annual values.

Table 2: Classifications of water masses in Kongsfjorden.

Water mass	Temperature in °C	Salinity in psu
Atlantic water	3.0-7.0	34.9-35.2
Transformed Atlantic water	1.0-7.0	34.7-34.9
Surface water	1.0-7.0	30.0-34.0
Intermediate water	1.0-7.0	34.0-34.7
Local (Arctic) water	-0.5-1.0	
Winter-cooled water	-1.9- -0.5	34.4-35.0

Adapted from: Svendsen et al., 2002.

Table 3: Breeding success and clutch size (mean until 2008, median from 2012) of black legged kittiwakes in Kongsfjorden.

Year	Clutch size	Breeding success	Year	Clutch size	Breeding success
1997	1.81	1.1	2009		
1998	1.77	0.94	2010		
1999	1.64	0.74	2011		
2000	1.73	1.02	2012	1.99	0.92
2001			2013	1.91	0.65
2002	1.3	0	2014		
2003	1.53	0.25	2015		
2004	1.5	0.58	2016	1.93	
2005	1.96	1.31	2017	1.82	
2006	1.74	0.55	2018	1.89	
2007	1.9	1.27	2019	1.27	
2008	1.86	0.98	2020	1.79	1.24

Combination of data from Moe et al., 2009 (1997 - 2008) and data provided by Olivier Chastel from CNRS (2012 - 2020).

All statistical analyses were performed using R 4.1.3 (R Core Team 2022). Correlations of normally distributed data were tested using linear regressions with single and combined data sets. In case of the trend of energy content in the diet samples, a linear mixed effect model was additionally used to examine clustering of the data. The statistical significance level was set to $p \leq 0.05$ for all tests. Figures were created using the package ggplot2 (Wickham, 2011).

3. Results

3.1 Research question one – Energetic content in diet samples

In most years from 2012 to 2020, prey items of the classifications Arctic, Atlantic and Intermediate appeared intermixed in the diet samples of the black-legged kittiwakes from Kongsfjorden (see figure 5.a). Arctic species were found every year until 2015, which otherwise contained almost only intermediate prey items, and then again in 2016 and 2020. The years between were characterized to similar parts by Atlantic, Intermediate, and not determined prey items. The size of the bars in figure 5.a does not show the size or weight of items found, but only the frequency of occurrence, hence the absence or presence, counted.

The classifications used in figures 5.a mirror diet samples containing the following prey items:

Arctic: *Boreogadus saida*, *Themisto libellula*, *Limacina*

Atlantic: *Mallotus villosus*, *Clupea harengus*, *Meganyctiphanes norvegica*, *Gadus morhua*, *Themisto abyssorum*

Intermediate: *Nereis*, *Thysanoessa inermis*, *Chaetognatha*, *Latirus maculatus*, *Lumpenus lamprætaeformis*, *Pandalus borealis*

Mesopelagic: *Pasiphaea tarda*, *Arctozenus risso*.

Overall, the samples consisting only of the Arctic species polar cod (*Boreogadus saida*) had 22.4 KJ/g DW, a relatively high average energy content, but the Atlantic species capelin (*Mallotus villosus*) had a similar mean value of 22.43 KJ/g DW (see figure 5.b). The mesopelagic spotted barracudina (*Arctozenus risso*) had even a much higher energy content, with on average 25.471 KJ/g DW weight, while the samples containing the species Atlantic cod (*Gadus morhua*) were lowest in energy density, with 17.21 KJ/g DW. *Pandalus borealis* is considered Intermediate, and the energetic values were very similar between the pellets. Figure 5.b has only taken samples into account, which contained one prey species only, since in mixed samples it was not comprehensible which item accounted for what amount of the total energy.

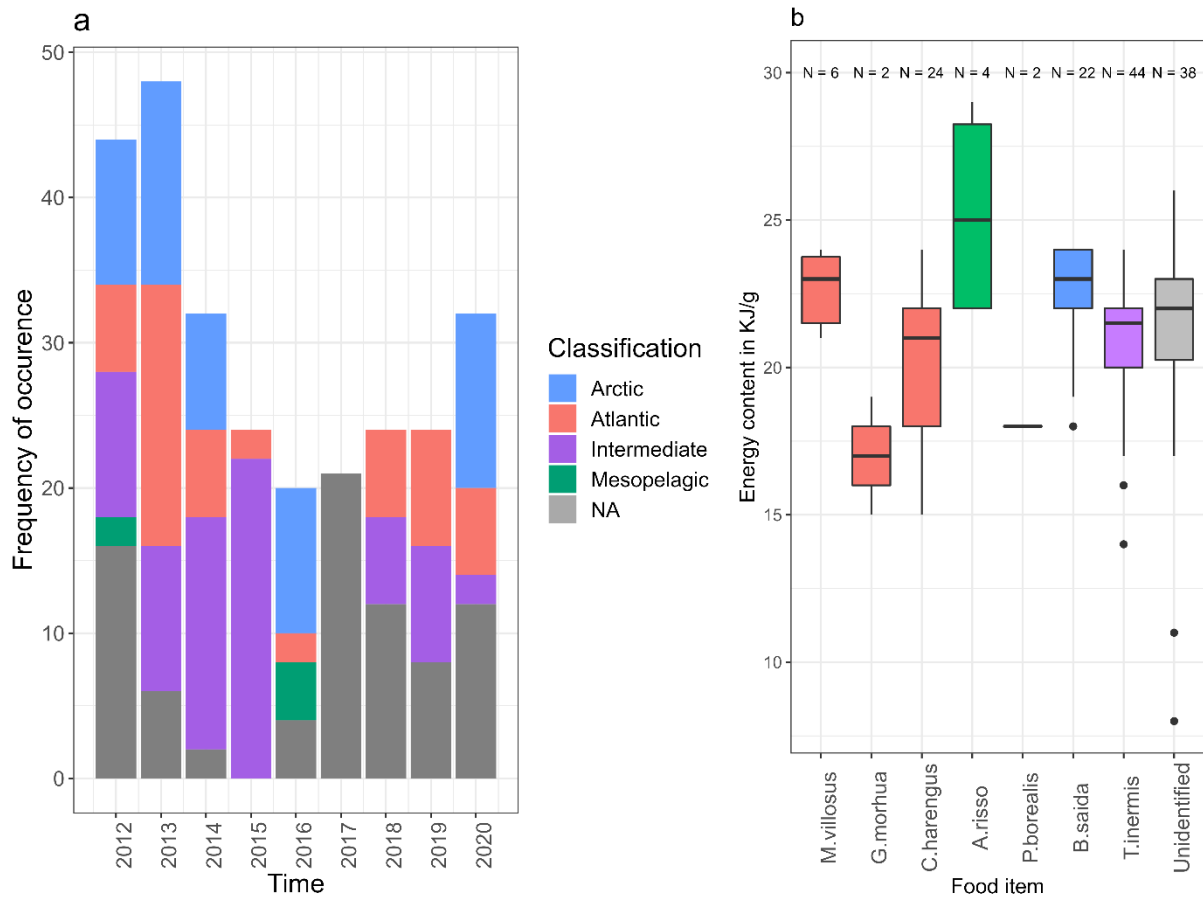


Figure 5: Panel a: Frequency of occurrence of classified prey in diet samples of kittiwakes per year. Panel b: Energy content of classified prey items in KJ/g DW, pooled across years, with N = number of pellets tested per item, only samples containing one single prey item were considered. *P. borealis* is an Intermediate species. Classification after Vihtakari et al. (2018).

In the analyzed diet samples from 2012 to 2020, the median energy content per year was between 19,5 KJ/g DW, in 2019 and 22,5 KJ/g DW, in 2012 (see figure 6). The sample with the highest energy content (28,7 KJ/g DW) was found in 2016, collected in mid-July from the Krykkjefjellet colony and contained spotted barracudina (*Arctozenus risso*). The sample with the lowest energy content was found in 2019 with 8,5 KJ/g DW, containing unidentified fish and was collected from an unspecified colony in Kongsfjorden in late June. Of all years, 50% of the data, hence the second and third quartile, lay between 17,6 KJ/g DW and 23,7 KJ/g DW. The years with relatively low energy content were 2015, 2017, 2019 and 2020. Higher energy content was found in the diet samples from 2012, 2013, 2014 and 2016. The highest variance within the years was found in 2016, 2019 and 2020. The energy content of the kittiwake diet in Kongsfjorden declines significantly over time (see Figure 6, linear regression with all data points, Adjusted $R^2 = 0.086$, $p < 0.0001$).

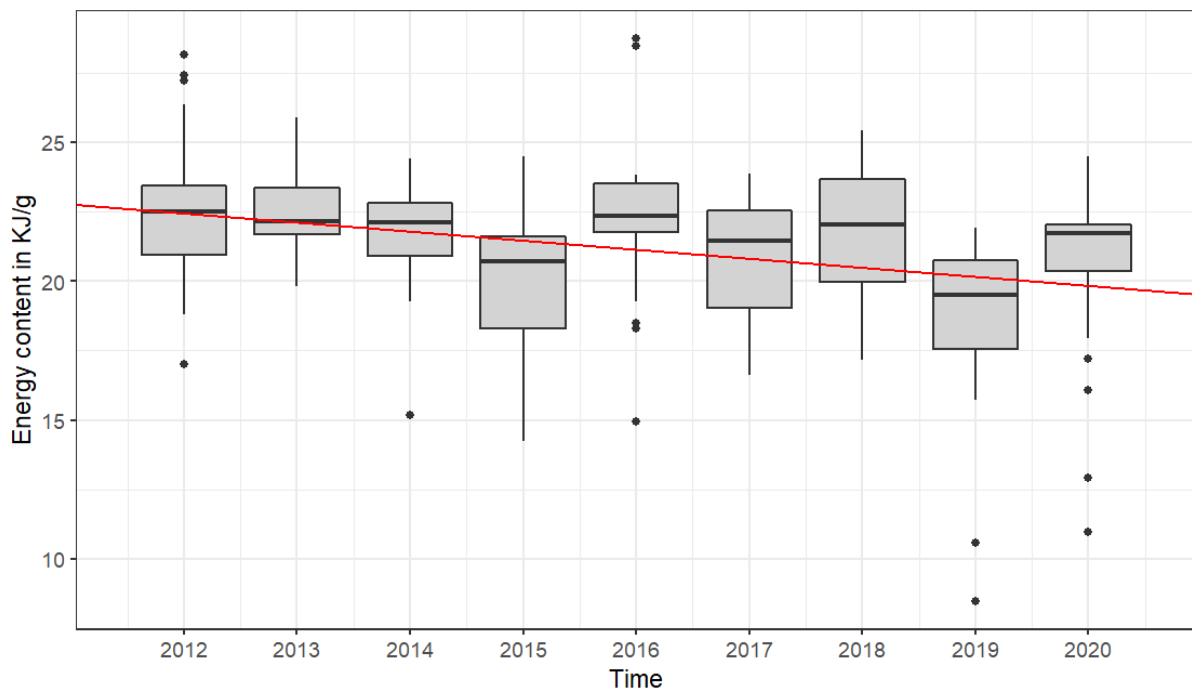


Figure 6: The distribution of energy content in diet samples measured in KJ/g DW from kittiwakes per year, determined with a semimicro calorimeter, with linear regression line (red line).

3.2 Research question two - Physical proxies determining Atlantification

The salinity in 85 m in Kongsfjorden develops with recognizable, but not very pronounced seasonal trends (see figure 7.a, as compared to temperature in figure Appendix 1). The periods with the lowest daily median salinity were the late winter, late summer, and autumn months of 2012, the first half of 2015, early months of 2018 and the winter months of 2019/2020 and exhibited salinities of 34.2 – 34.5 practical salinity unit (psu). The outstanding values in 2012, 2016 and 2017 probably derive from technical work on the sensors and will not be included in this analysis. The periods with the highest salinity were in autumn of 2014, late months of 2016, and most of mid-2016 until late 2018, as well as mid-2019, with around 35.0 – 35.1 psu. The blue line indicates the threshold, until which salinity the water mass can be classified as Arctic and the red line marks the threshold from which water masses can be classified as Atlantic. While considerable parts of 2012 and 2013 were still within the Arctic regime, the water masses changed to mostly intermediate in 2014, where also Atlantic classification was reached for the first time over the period. In 2015, the salinity decreased again, reaching far in the Arctic regime, to then fulfill a steep increase into the Atlantic classification. The water

masses stayed mostly Atlantic in 2016 and 2017 and decreased to largely intermediate again in 2018 and 2019. 2020 was a mostly Arctic year again.

For better reliability, daily median salinity values were condensed to one single value per year (see figure 7.b). For each data point, only the months June and July were considered in order to better reflect the physical conditions in the water column during the breeding period of the kittiwakes. Each point therefore reflects the median salinity of June and July of each year. The blue line indicates again the threshold until where the water is classified as Arctic (see explanation above) and the red line indicates from which salinity the water column turns to being classified as Atlantic. The summers of the years 2012, 2013 and 2018 can therefore be classified as Arctic-type summers, and the summers of the years 2016, 2017 and 2019 as Atlantic-type. The remaining years lay in between in intermediate salinity in June and July.



Figure 7: Panel a: Daily median salinity in Kongsfjorden at 85 m depth in psu (practical salinity unit) over time. Straight blue line, 34.7 psu: upper limit for Arctic waters, red line, 34.9 psu: lower limit for Atlantic waters. Panel b: Median values of salinity of June and July in each year. Red area: Atlantic water regime, blue area: Arctic water regime, white area: Intermediate water regime.

For better comparison, the energy data of the kittiwake diet samples was comprised into one median value per year (see figure 8.a). The blue bars indicate which summers were previously classified as Arctic and the red bars the Atlantic summers, respectively. The years with the highest median caloric content were 2012 and 2013 (both Arctic), 2014 (Intermediate), further 2016 (Atlantic) and 2018 (Arctic). The lowest median energy content was found in 2015 (Intermediate) and 2017 and 2019 (both Atlantic). Years with Atlantic summers have delivered diet samples with lower caloric content than years with Arctic summers (exception: 2016). Nevertheless, years with intermediate summers do not necessarily show intermediate energy content. In general, the median energy content in the diet samples of the kittiwakes decreased over time.

The median energy content of the diet samples of the kittiwakes declines with increasing median salinity in June and July (see figure 8.b). Nevertheless, the trend is not statistically significant (linear model, adjusted $R^2 = -0.012$, $p = 0.373$). When testing with categorical values, the energy content in the diet samples is higher in Arctic years than in Atlantic years (see figure 8.c). The intermediate years lay between the other two categories. This trend is however not statistically significant (linear regression, intercept (Arctic) = 22.2384, estimate Intermediate = -0.7096, $p = 0.394$, estimate Atlantic = -1.1376, $p = 0.192$).

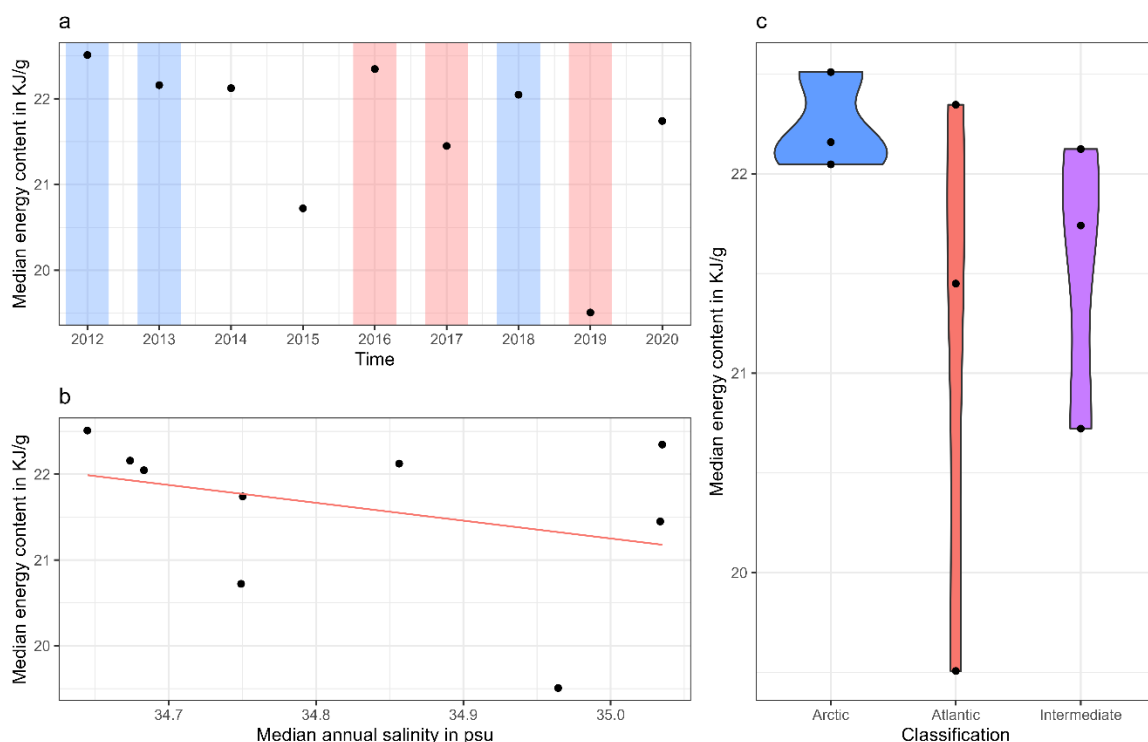


Figure 8: Y-axis in all panels: median energy content in diet samples in KJ/g DW. Panel a: Medians of energy content in KJ/g DW for each year. Blue bars: years classified as Arctic, red bars: years classified as Atlantic. Panel b: Median energy content of kittiwake diet samples in KJ/g DW per year over median salinity of June and July in psu per year. Red line: linear regression. Panel c: Violin plot of medians of energy content in KJ/g DW after Classification of the water column.

3.3 Research question three – Reproductive success

The breeding success of kittiwakes in the Krykkjefjellet colony shows strong interannual variation (see figure 9.a). The years with the highest breeding success were 1997, 2005, 2007 and 2020. The period with the lowest breeding success was 2002 to 2004 while the absolute lowest breeding success was found in 2002 with a value of 0. In 2005, the highest breeding success was documented with 1.31 chicks, older than 12 days, per active nest. Especially between 2013 and 2020 many data are missing (see table 1), which results in a large error margin bar in this period. In the years critical for this project, where a classification of the situation in the fjord was possible, only 2012, 2013 and 2020 had data for breeding success available. When testing for the relationship between breeding success and clutch size, to be able to validate the proxy, high correlation indicates that clutch size could be a suitable alternative for breeding success (linear model, adjusted $R^2 = 0.607$, p -value < 0.001). It has therefore been decided to use the clutch size rather than the breeding success as a proxy for the reproductive success of the birds.

Also for the clutch size, data is incomplete for the period of 1997 to 2020. The years of 2009 to 2011 and 2014 and 2015 are lacking (see table 3). The clutch size of the kittiwakes in Krykkjefjellet displays a similar trend to the breeding success until the year 2008 (see figure 9.b). From 1997 the clutch size decreases steadily until 2002, with 1.51 eggs on average. Afterwards, there is a change in trends and the clutches increase again until 2012. After 2012, hence in the period most important for this project, the clutch size decreases steadily until 2020. In 2019 the median clutch size reaches a so far matchless low of 1.27. The maximum median clutch was found in 2012 with 1.99. The blue and red bars indicate the years with summers classified as Arctic and Atlantic respectively. For most years, the clutch size in Arctic-type summers lies above the clutches in the Atlantic-type summers. An exception is the summer of 2016, which was classified as Atlantic but had, with a value of 1.93, a higher clutch size than the Arctic summers of 2013 and 2018 with clutch sizes of 1.91 and 1.89 respectively. During the period most important for this project (2012 to 2020), from when diet samples of the birds were available, the clutch size displays a steady decreasing trend. This decrease is not statistically significant (linear model, adjusted $R^2 = 0.2$, $p = 0.175$).

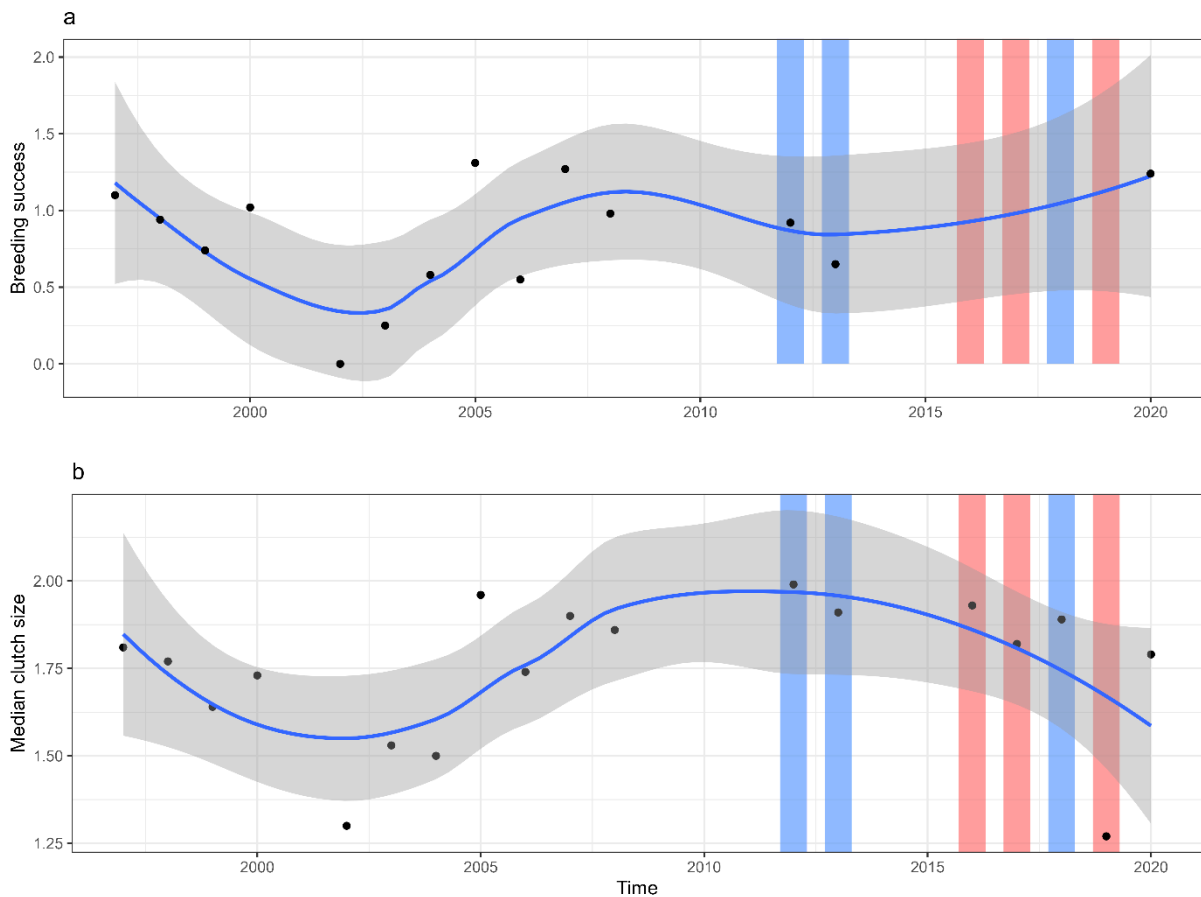


Figure 9: Panel a: Breeding success, measured in chicks older than 12 days per active nest over time in Krykkjefjellet. Blue line: fitted averages with standard error margin. Blue bars: years with summers classified as Arctic, red bars: years with summers classified as Atlantic. Panel b: Median clutch size of kittiwake nests in Krykkjefjellet over time. Blue line: fitted averages with standard error margin. Blue bars: years with summers classified as Arctic, red bars: years with summers classified as Atlantic.

The clutch size of the kittiwakes in the colony Krykkjefjellet increases with increasing energy content in the diet samples (see figure 10.a). A linear regression reveals that this trend is highly statistically significant (linear model, adjusted $R^2 = 0.976$, $p < 0.0001$). The outstanding value in the median energy content of the diet samples of 2019 might have had a positive effect on the trend. When excluding this value from the analysis, the trend remains significant (see figure 10.b; linear model, adjusted $R^2 = 0.821$, $p = 0.008$). There is a strong positive correlation between the clutch size and the available energy for breeding in black-legged kittiwakes in the colony Krykkjefjellet in Kongsfjorden.

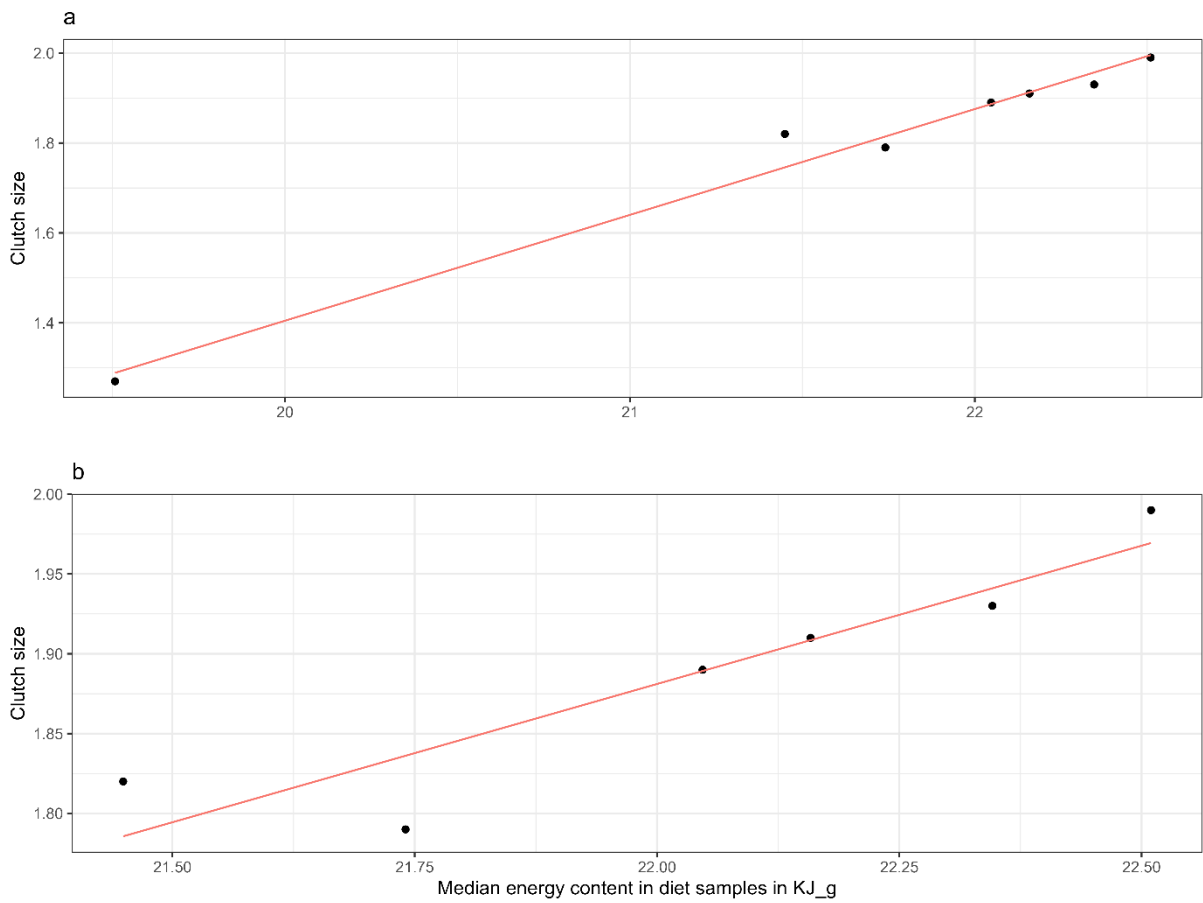


Figure 10: Panel a: Clutch size of kittiwakes from 2012 to 2020 in Krykkjefjellet over the annual median energy content in KJ/g DW in diet samples. Red line: linear regression. Panel b: Clutch size of kittiwakes from 2012 - 2020 in Krykkjefjellet over annual median energy content in KJ/g DW in diet samples. Without extremely low KJ/g DW value in 2019. Red line: linear regression.

4. Discussion

Black-legged kittiwakes are predators in Arctic ecosystems and as such commonly used as bioindicators for the conditions in the marine environment they forage in (Barrett 2007; Frederiksen et al. 2004; Vihtakari et al. 2018). My study indicates that kittiwakes in Kongsfjorden can be used to monitor the variability in the food web. Their reproductive success is strongly connected with their energy budget during breeding season, which furthermore was negatively correlated with ongoing Atlantification. The aim of this study was to provide new knowledge on how climate change affects the black-legged kittiwake nesting in Svalbard and their forage environment.

4.1 Main findings

While all tested years (2012-2020) had Intermediate and Atlantic prey in the samples, Arctic species were lacking in 2015 and 2018-2019. Mesopelagic species, which had the highest energy content, were found only in 2012 and 2016. While the Arctic species *Boreogadus saida* had a higher energy density than the Atlantic species *Gadus morhua* and *Clupea harengus*, the also Atlantic *Mallotus villosus* delivered similar values to polar cod. Answering the first research question, the energy content in the diet samples declined significantly over the project period of 2012 – 2020, though not gradually but rather situational. This trend was of moderate magnitude and only a small proportion of the variability can be explained by time.

With the classification of the water masses in Kongsfjorden, implemented by (Sundfjord et al., 2017), I categorized the summers of my project period as Arctic-, Atlantic- or Intermediate-type. Assuming the conditions in the water body have the highest influence on kittiwakes while breeding, we decided to use the data of June and July only. Using the salinity of June and July as a proxy for the Atlantification during the breeding period, I categorized 2012, 2013 and 2018 as Arctic-type summers. 2016, 2017 and 2019 were years with Atlantic-type summers and in 2014, 2015 and 2020 the conditions were Intermediate. Arctic-type summers produced in general diet samples with higher, less variable energy density than Atlantic-type summers, except for the Atlantic summer of 2016. The second research question, if years with more Arctic water are associated with diets of higher energy content can be answered in the affirmative. With increasing salinity, hence increasing Atlantification, the energy content in the diet samples decreased, though not significantly. Since data on the breeding success of kittiwakes in Kongsfjorden was lacking for most years,

I decided to focus on the clutch size as the next best proxy for reproductive success. Arctic-type summer had in general bigger clutches than years with Atlantic-type summers. Also here, the Atlantic summer of 2016 was an exception with a high median clutch size. From 2012 to 2020, the median clutch size in the colony Krykkjefjellet declined, but not significantly. Further, with increasing median energy in the diet samples, the clutch size increased significantly. Using the best available proxy for the reproductivity, the question on whether energy content in the diet samples was positively correlated with the clutch size of the kittiwakes could be answered affirmatory.

The years where Arctic prey was found coincide mostly with years with high energy ratios, especially in 2012, 2013 and 2016. I found low energy content in the diet mostly when no Arctic prey was found in the samples such as 2015 and 2019. Looking into the energy content of the food items, I found that the Arctic species *Boreogadus saida* had higher energy content than the Atlantic species *Clupea harengus* and *Gadus morhua*. Arctic summers, with low salinity, had high energy values in the diet samples and almost all had a high share of Arctic items in the diet. Also, the median clutch size in Arctic summers was generally high. Furthermore, years with Atlantic summers had mostly lower energy in the diet samples and lower clutch sizes. Additionally, Atlantic prey was found to be usually less energy dense, and the energy content was more variable.

4.2 Interpretation of the results

These findings support the hypothesis, that Arctic prey is the qualitatively better food source over Atlantic prey (e.g.: Descamps and Ramírez 2021; Piatt et al. 2020). It leads to the conclusion, that kittiwake populations decrease as a response to more Atlantic water and therefore more Atlantic prey, that is less energy dense, hence less beneficial food sources. This idea is supported by Piatt et al. (2020) who found that seabirds in the North Pacific declined as a response to higher water temperatures which had led to decreasing quantity and quality of the main prey fishes. Descamps and Ramírez (2021) found that low sea ice extent in the Arctic led to low recruitment of polar cod which was correlated with declining sea bird colonies. However, they found a response only with a two-year lag, which could indicate that sea ice extend might not be the main driver. Frederiksen (2010) stated that decreasing food quality, especially during breeding season, is a large threat for seabirds. Their feeding ecology during breeding does not allow the birds to follow their prey species, but they are dependent on local food sources (Frederiksen, 2010). Assuming the Atlantification has a negative

influence on the energy budget of kittiwakes in Kongsfjorden, this would follow the prediction of the junk-food-hypothesis which expects that the productivity of seabirds declines as a response to decreasing food quality (Jodice et al. 2006; Romano et al., 2006). These studies, as well as my own findings, support the idea that Arctic seabirds suffer from the Atlantification, and that population decrease can, to some extent, be explained by resulting diet variability. Parent birds are not able to deliver sufficient energy to their chicks, which leads to low reproductivity in Atlantic years, that will likely increase in frequency as climate change advances (Carmack et al., 2015; Lind et al., 2018).

On the other hand, the diet samples from the years 2016 and 2018 were strikingly different and do not fit the previous ideas. 2018 was a year with an Arctic summer, that had high energy in the diet samples. However, identified prey items in the samples did not contain Arctic species. Because of higher stability against seasonal changes and easy classification as Arctic or Atlantic, we decided to use salinity as a proxy for the Atlantification only. Nevertheless, temperature data from 35 m and 85 m depth in Kongsfjorden, were included in the appendix (see Figure Appendix 1). Due of high salinity values, I classified the summer of 2016 as Atlantic type. Yet, 2016 had second highest median energy content in the samples and the second highest median clutch size, after the Arctic summer of 2012. It could be argued that the regime shift had only just happened, maybe not completely been proceeded in the summer of 2016. This can however not be the case, as the year before had already had Atlantic conditions. Also, in 2015, median energy content and median clutch size were much lower than in 2016. My results show that Arctic species are mostly more energy dense than Atlantic species, but not exclusively. In fact, the samples of the Atlantic capelin were very similar in energy content to the Arctic species polar cod. Previous studies on the energy budget of these two species found very similar results: while in my study, polar cod had a mean energy content of, 22.4 KJ/g DW, and capelin 22.43 KJ/g DW, Harter et al. (2013) measured between 21.6 and 22.2 KJ/g DW in polar cod and Hedeholm et al., (2011) found 20.86 KJ/g DW in capelin (see table Appendix 2).

These results enhance the idea that Arctic prey is not per se higher quality food for kittiwakes. It seems likely that the amount of energy a birds gets from its prey depends on which species it forages. Already in 1996, Barrett & Krasnov Barrett (1996) connected decreased population health in seabirds in the Barents Sea with collapsing capelin populations in that period. They found that shifts in the species composition toward less energy dense fishes such as *Clupea harengus*, which in my study had a mean energy content of 20.39 KJ/g DW, while Bernreuther et al. (2013) measured between 17.23 and 19.05 KJ/g DW, kittiwakes suffered

from reduced breeding success and were struggling to maintain a positive population trend. Gaston and Elliott, (2014) conducted a study on diet change in Brünnich's guillemot (*Uria lomvia*) in Canada. They found that in the mid-1990s there was a shift from the former main prey species polar cod, to the then dominating capelin, which did not lead to a decrease of the breeding success of the birds. These findings suggest that there is a similar shift in the food web happening in the Canadian Arctic and that capelin could be good substitute for polar cod. Brekke and Gabrielsen, (1994) studied the assimilation efficiency of different seabirds feeding on *Boreogadus saida* versus *Mallotus villosus* and found a slightly higher efficiency for kittiwakes feeding on polar cod than on capelin. On the other hand, they stated that capelin had a higher fat content and calculated that Kittiwakes needed 215 g of polar cod per day, while they only needed 130 g of capelin to meet their minimum energy requirements. These findings suggest that capelin is not only a crucial part of the marine ecosystem of the Arctic. It also seems to be a suitable replacement for polar cod for the kittiwakes in terms of energy availability.

Nonetheless, the unexpectedly high values of energy content in the diet and clutch size in 2016 cannot be explained by the high share of capelin. In fact, there was no capelin identified in those samples, but rather a large share of polar cod despite the Atlantic conditions. As seen in figure Appendix 3 however, capelin decreases in frequency of occurrence in the diet samples over time and were only found in 2012 and 2013. Nevertheless, data from Vihtakari et al. (2018) suggest, that capelin was also found in 2016 and 2018 in diet samples from Kongsfjorden, which might have been overlooked by my analysis due to random selection of the samples. Instead, I found a high amount of polar cod in the samples of the Atlantic summer of 2016. Further, the unmatched high values from 2016, deriving from *Arctozenus risso* could be an indicator, that mesopelagic species could be a valuable food source for kittiwakes in Kongsfjorden. This cannot be concluded from this study, as these were the only samples where the species was found. On the other hand, 2016 and 2018 had a lot of unidentified fish, which could have been both, polar cod, and capelin. Also, the high energy content in 2016 could derive from *Thysanoessa inermis* which is also very high in energy, as measured by Nowicki et al. 2022, with up to 27.06 KJ/g DW (publication in progress).

Overall, the Atlantification has a negative impact on the population health of black-legged kittiwakes breeding in Kongsfjorden. Nonetheless, the decline in populations on Svalbard is nowhere near the devastating situation on the mainland. It seems that Arctic prey species are in general higher in quality than Atlantic prey. It needs to be taken into account which Atlantic species the birds prey on, as there are high interspecific variations in energy density.

Especially capelin could be a suitable exchange for polar cod in terms of energy availability and might, if it keeps established further North, be a possibility for breeding seabirds to meet their energy requirements despite the ongoing Atlantification.

4.3 Assessment of reproduction

The clutch size was the next best proxy for reproductive success, as the breeding success was not available. This was revealed by a linear regression with highly significant correlation between the two proxies. Nevertheless, the clutch size could be biased by the breeding strategy of the birds. Black-legged kittiwakes mostly lay two eggs, unless conditions differ a lot from the mean (Coulson, 2011). In 2012, 2016, 2018, three egg clutches occurred when the general clutch size was high in Arctic summers (see table Appendix 1) and in 2012, the relative number of three-egg clutches was at almost 10%, which was also the year with the highest median energy in the diet samples. Still, in 2019, when the median clutch size was detrimental, there was still one nest with three eggs. On the other hand, in 2017, when the clutch size was relatively high, there were no three-egg clutches at all. This enhances the theory, that kittiwakes could lay three egg clutches mostly in favorable years. Using the clutch size as a parameter for population reproductivity does not consider for instance storms during which the clutch can be lost or the predation pressure on the nests. Further, it could be interesting to investigate, if the bird ID adds a random effect to the clutch size. Perhaps, some birds could be more prone to laying three eggs than others.

4.4 Strengths and weaknesses

The kittiwake colony Krykkjefjellet in Kongsfjorden has been followed for more than 40 years. A long-term study such as this one produces a unique and valuable dataset. Nevertheless, diet samples as well as data about population health were collected by different people, in different colonies and not every year at the same time. Especially the data about the breeding success was collected very inconsistently and only a very limited amount of data exists. Further, the process of collecting data on the nest content, especially in Krykkjefjellet where the observation must be done from below, is physically demanding and sometimes very hard to see. Eggs or chicks could be overseen, and in some ledges, it is not easy to identify the nests. These data must therefore be handled with care.

A strong advantage of this study is the large amount of data available, especially from the diet samples. Nevertheless, the most important time window in which most of the changes

happened in Kongsfjorden might already have passed by 2012. The initiation of the transition of the fjord, manifested in changes in the water body, higher water temperatures, higher salinity but also first appearances of Atlantic species in diet samples of black-legged kittiwakes, probably happened around 2005-2006 (Griffith et al., 2019; Tverberg et al., 2019; Vihtakari et al., 2018). The results from this study might have been more meaningful, if the phase of the transition, as well as a period before was covered and diet samples used e.g., in Vihtakari et al., (2018) were available for caloric analysis. This might be helpful to explain the decline in breeding success and clutch size in 2002 – 2003. Initially, we thought we had diet samples of 2004 at our disposal. Those samples turned out to be heavily degraded. I tried the calorimetry analysis on these samples, but the values were much lower than the samples of the other years and we decided not to include them (see figure Appendix 2). If the diet sample collection had been done more consistently over the whole time since the colony has been monitored, the samples available from the larger period would probably have improved the quality of this study. Also, having only diet samples from the breeding period available, we might have missed important changes in the species compositions of the prey species, that happened during other periods of the years.

Another weakness of the project is the large number of unidentified fish in the species composition of the diet samples. Because fish pieces are in some cases heavily fragmented and sometimes no otoliths can be found, it becomes difficult to identify the item to taxa level. In 2017, the diet samples were not analyzed for their content at all. Perhaps stable isotope analysis could have been a method to avoid these unidentified items. Most of the fish species found in the samples are easily classifiable as Arctic or Atlantic, after Vihtakari et al. (2018), so the information about the species in the unidentified samples would have been of great value for this project. Further, using only the frequency of occurrence of prey species in diet samples, one risks creating a bias of how important the prey items are for the nutrition of the birds. It might have been wiser to also consider the weight and size of the items to be able to calculate a more veritable picture of the diet of the birds. Arising from the scope of this project, only a limited number of diet samples could be analyzed from each year. Since 10-15 randomly picked samples were used, it is possible that Arctic species could be overrepresented in Atlantic years and vice versa. Having the possibility to conduct a more extensive survey, it would be interesting to also analyze the remaining diet to increase the samples size and decrease the bias.

One of the most severe aspects to discuss is the lacking consideration of the stage of digestion of the samples. Clearly, some samples were more heavily degraded by the look of them. It could be worth considering developing a method with which the stage of digestion of the sample could be classified. I do not know for how long the bird had carried the content in its stomach before regurgitation, which might have had an impact on how much energy there is left in the sample. In 2016 (containing *Arctozenus risso*) and 2012 (containing polar cod and an unidentified crustacean), I found samples with unmatched high energy content of around 27 – 28 KJ/g DW. These large values could derive from the samples having been very fresh when being collected. Perhaps the birds only just came back from their foraging trip when caught and the prey items had not yet started to be digested. When comparing the samples where only polar cod was present however, it seems likely that the high value derives from the unidentified crustacean instead. The energy density in the samples with *Thysanoessa Inermis*, had a mean energy content of 22.78 KJ/g DW. Fresh samples from summer had however around 27 KJ/g DW (Nowicki et al. 2022, publication in progress), which enhanced the idea that the diet samples containing the species had already been heavily digested upon collection. Also, there were very low energy values, especially in 2019 and 2020. These could derive from the samples being already very digested when the bird was caught, because it's foraging already lay a long while back. This idea was also enhanced by the fact, that the discussed fresh samples did not corrode the different parts of the oxygen bomb as much as the diet samples did, which might result from stomach acid in the samples, that also could have altered the compounds of the diet. For all prey items contained in the samples, a freshly sampled counterpart from the same period and area would be interesting to analyze to find out about the effect of the digestion on the samples. This could give insight into interannual variation of the energy content in the prey species.

4.5 Future studies

To further understand the processes influencing the population development of the kittiwakes, it would be interesting to find out how the diet during non-breeding time influences the breeding success, as suggested by Hovinen et al., (2019) and Reiertsen et al., (2014).

Further, comparing the findings with similar results from other regions to see if similar processes happen elsewhere would be helpful for the understanding. Since the decline in population numbers of kittiwakes on Svalbard is nowhere near the trend on the mainland, it would be interesting to compare diet samples from Svalbard with diet samples of regions with a stronger decline in population numbers. This could help answering, if the qualitatively high

Arctic prey, the kittiwakes used to feed on almost exclusively, has been replaced by almost equally qualitatively high prey, the mainland population are now lacking. Because of northwards shifts of species ranges, the main populations could be exposed to less qualitative food, since the former prey shifted their ranges. If this was not the case, the mainland populations could be threatened by other circumstances, such as higher exposure to contaminants and pollution, less food in general due to higher fishing activities in the area, becoming bycatch themselves or increased predation (Acampora et al., 2017; CAFF, 2020). Having only the salinity as a physical proxy for the Atlantification available, only a limited amount of the variability could be explained by the Atlantification. In future studies, combining the salinity with other physical proxies, such as sea ice extent, could help to find a clearer correlation between the physical proxies and the energy content in the diet samples and explaining for example the outstanding values of 2016. Including also other factors that influence the population health of the kittiwakes in Svalbard, such as contamination, one could create a more complete picture of the effects on the population trends of seabirds (Hitchcock et al., 2019; Guzzo et al., 2014).

5. Conclusion

This study contributes to the understanding of how the Atlantification of the European Arctic influences the energy availability during breeding season for black-legged kittiwakes in Svalbard. The variability in the prey because of incoming boreal species is likely decrease the energy content in the diet and therefore also the energy transfer to the chicks, which could negatively affect the productivity. On the other hand, especially the Atlantic *Mallotus villosus* could be a possibility for the birds to meet their energy requirements, as the species has a similar energy density to the former main prey and Arctic species *Boreogadus saida*. Surprisingly, the clutch size seems to be a good proxy for the reproductivity of the birds and is significantly positively correlated with the energy content in the diet. Nevertheless, the Atlantification can explain the decline in the seabird population only to a moderate degree and more research is needed on the shifts in abiotic and biotic factors with increased climate change as well as other factors influencing the population health of black-legged kittiwakes.

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7. Appendix

Statistical analysis shows no significant trend of the water temperature at 35 m or 85 m over time (linear model, 35 m: adjusted $R^2 = -0.0003$, $p = 0.666$, 85 m: adjusted $R^2 = -0.0002$, $p = 0.558$). Daily medians of both depths are positively correlated (correlation coefficient = 0.834). Using statistical tests for the influence of the water temperature on the caloric content of the diet samples, the results remain highly statistically insignificant for both depths (linear model, 35 m: adjusted $R^2 = -0.157$, $p = 0.832$; 85 m: adjusted $R^2 = -0.133$, $p = 0.816$).

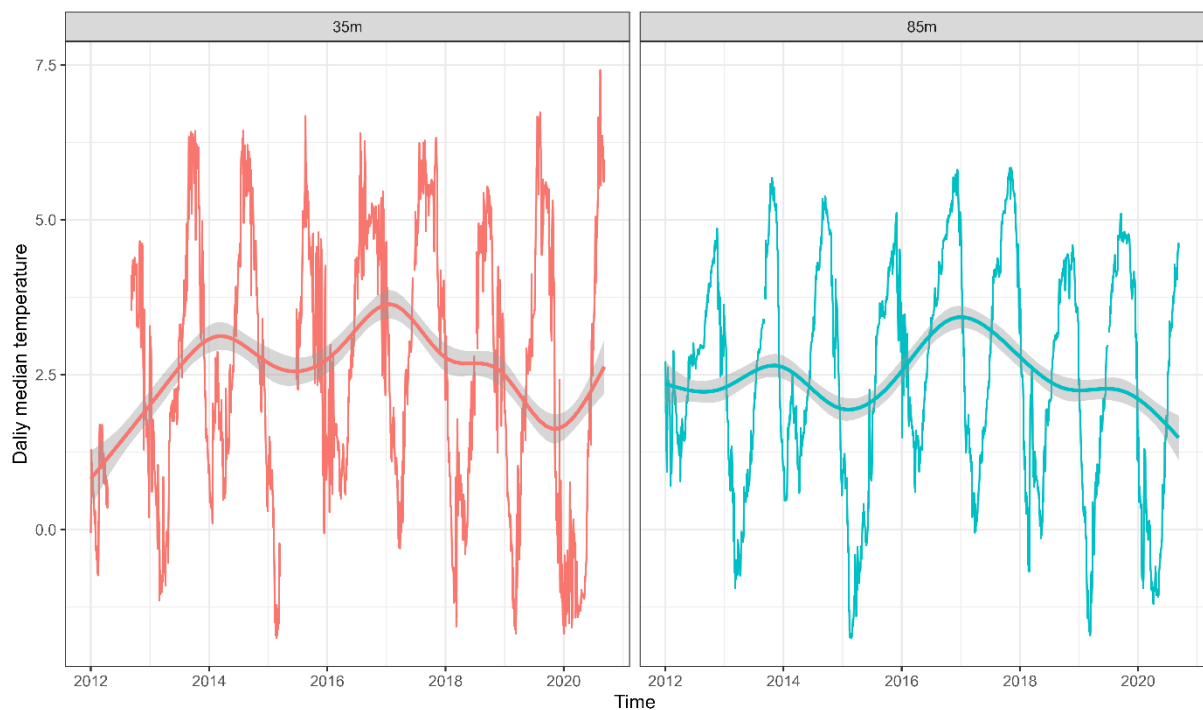


Figure Appendix 1: Daily median water temperatures in Kongfjorden over time with fitted values. Panel a: Temperature at 35 m depth, panel b: temperature at 85 m depth.

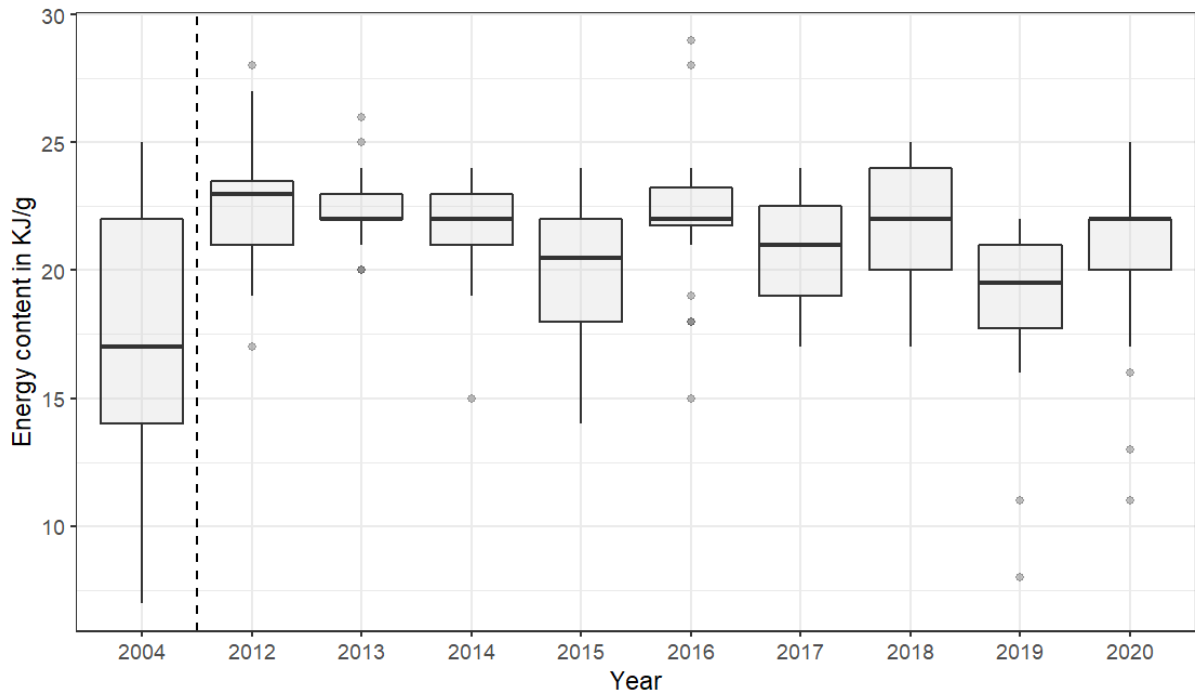


Figure Appendix 2: Distribution of energy content in diet samples over time in KJ/g DW, with 2004.

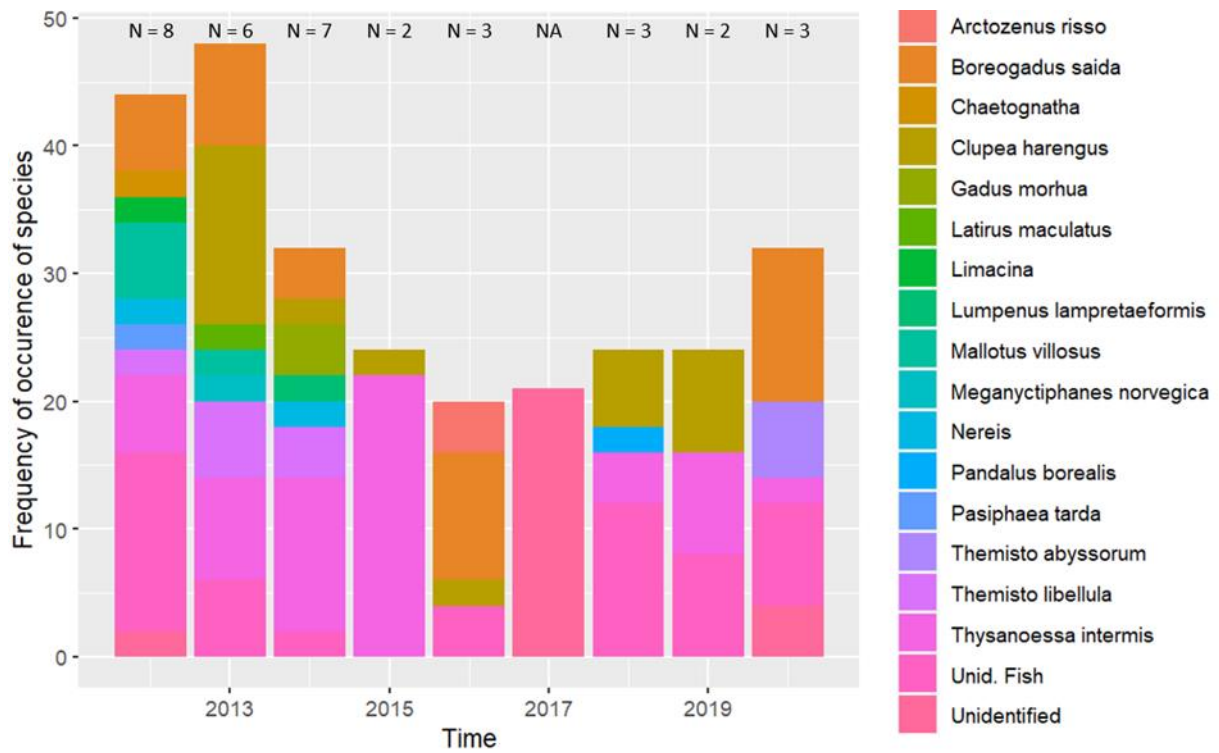


Figure Appendix 3: Frequency of occurrence of prey items per year and the number of species found. Weight or size of prey items are not considered.

Table Appendix 1: Number of observed nests in the colony Krykkjefjellet, with at least one egg, total number of three-egg clutches, and relative amount of three-egg clutches.

	2012	2013	2014	2015	2016	2017	2018	2019	2020
Number of observed nests with at least 1 egg	145	80	n.a.	n.a.	130	144	155	233	139
Absolut number of 3 egg-clutches	14	0	n.a.	n.a.	10	0	3	1	0
Relative amount of 3 egg-clutches	9.7%	0%	n.a.	n.a.	7.7%	0%	1.9%	0.43%	0%

Table Appendix 2: Overview the energy content of four prey species calculated in this study and compared to literature. Energy content as mean or range with standard error, shown in KJ/g DW of dry weight. Comments: important differences of publications compared to this study.figure

Species	This project: Energy content as mean with SE (KJ/g DW)	Finding from other publications: Energy content as mean with SE (KJ/g DW)	Reference	Comments
<i>Boreogadus saida</i>	22.4 ± 0.30	21.6 ± 0.48 - 22.2 ± 0.42	Harter et al., 2013	Canadian Arctic
<i>Thysanoessa inermis</i>	20.78 ± 0.34	27.06 ± 1.36	Robynne Nowicki, publication in progress	
<i>Clupea harengus</i>	20.39± 0.52	17.23 ± 0.43 - 19.05 ±1.01	Bernreuther et al., 2013	Herring in captivity
<i>Mallotus villosus</i>	22.43± 0.5	20.86 ± 0.29 - 21.86 ± 0.60	Hedeholm et al., 2011	Capelin in Greenland