

# Atlantification consequences on Svalbard seabirds



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## ***Sammendrag***

I dette studiet har vi sett på sammenhengen mellom oppvarmingen av Svalbard («Atlantifisering») og effekten dette har på næringsvalg og ungeproduksjon hos to av de mest tallrike sjøfuglartene på øygruppen, nemlig alkekonge og krykkje. Vi fant en sammenheng mellom økende sjøtemperatur (og redusert sjøisutbredelse) i Vest-Spitsbergenstrømmen og næringsvalget hos de to artene. Redusert sjøisutbredelse og/eller varmere sjøvann var assosiert med en lavere andel arktiske arter i dietten. Imidlertid er mekanismene bak disse storskala endringene i temperatur/sjøisutbredelse og næringsvalg hos sjøfuglene uklare, og det er behov for mer detaljerte studier på en finere skala. Vi fant ingen sammenheng mellom næringsvalg og ungeproduksjon; en diett bestående av atlantiske arter resulterte ikke i lavere ungeproduksjon enn en diett bestående av arktiske arter. Dette betyr imidlertid ikke at «atlantifisering» av Svalbard ikke kan ha alvorlige konsekvenser for sjøfuglene på øygruppen, men betyr trolig heller at effekten ikke gjør seg gjeldene gjennom redusert ungeproduksjon.

## ***Abstract***

Our study investigated the relationships between the warming of Svalbard and the diet and reproductive output of two common seabird breeding on Svalbard, the black-legged kittiwake and the little auk. We found some apparent relationships between the ocean warming (and decline in sea-ice extent) at a large spatial scale in the West Spitsbergen current and the diet of these two species. These relationships indicate that a lower sea-ice extent and/or a warmer sea surface temperature are associated with a lower proportion of Arctic prey in seabird diet. The mechanisms linking these large scale environmental changes and the diet of kittiwakes and little auks are unclear, and studies at a finer spatial scale are needed. We did not find any relationship between seabird reproductive output and their diet, and feeding on Atlantic prey does not lead to a lower reproductive success than feeding on Arctic ones. This does not mean that the Atlantification of Svalbard has no detrimental on Svalbard seabirds, but rather that these effects are likely not related to changes in seabird breeding success.

## ***INTRODUCTION***

The Arctic is warming faster than any other region on the planet (Serreze and Barry 2011, Intergovernmental Panel on Climate Change 2013). This Arctic amplification (Serreze and Barry 2011) is not spatially homogeneous and some regions within the Arctic like the Barents Sea have an even higher rate of warming (Screen and Simmonds 2010, Lind and Ingvaldsen 2012, Nordli et al. 2014). This rapid warming is predicted to strongly alter both the terrestrial and marine ecosystems (Parmesan 2006, Poloczanska et al. 2013) and to lead to an “Atlantification” or “borealization” of the Arctic environment (Kortsch et al. 2012, Fossheim et al. 2015, Vihtakari et al. 2018) . Indeed, boreal species that currently exist as outlier/border populations in the Arctic or at the edge of the Arctic are predicted to shift their distribution northward and/or increase in abundance (Callaghan et al. 2004, Parmesan 2006). Those changes might be leading to the replacement of key prey species for arctic seabirds (Vihtakari et al. 2018) such as the copepod *Calanus glacialis* or the polar cod *Boreogadus saida* by potentially less energy-rich temperate species, which has the potential to impact foraging and reproductive performances of ice-associated arctic seabird species (Ramírez et al. 2017).

Seabirds such as the black-legged kittiwake *Rissa tridactyla* (hereafter, kittiwake) and the little auk *Alle alle* can be used as messengers of Arctic ecosystem changes (Gremillet et al. 2015, Vihtakari et al. 2018). Kittiwake diet in Kongsfjorden, Svalbard has indeed shifted over the last years from a diet dominated by Arctic species (e.g. polar cod) to a more mixed diet with high contribution from Atlantic species (e.g. capelin *Mallotus villosus*, herring *Clupea harengus*, Vihtakari et al. 2018). After their first mention in kittiwake diets in 2005, the proportion of these Atlantic species varied extensively from one year to the next, despite the general increase in the fjord water temperature, suggesting that prey composition in seabird diet might not be predicted solely by warming temperature, but rather by a complex interaction of oceanographic conditions and individuals foraging decision.

Previous studies investigating seabird responses to prey shift in marine arctic ecosystems showed variable species responses, from no apparent effect in little auks in Greenland (Amélineau et al. 2016) or kittiwakes in Svalbard (Vihtakari et al. 2018) to a

decrease in reproductive performance in Brünnich's guillemots in Canada (Gaston et al. 2005). Many seabird species, including the little auk (e.g. Grémillet et al. 2012, Jakubas et al. 2017), demonstrated flexible foraging responses when facing less favorable conditions such as reduced prey availability and quality. Foraging compensation in sub-optimal conditions (e.g. longer commuting time between food sources and the colony, longer time to find and capture the prey...) might, however, have detrimental short- or long-term consequences on an individual fitness (Kitaysky et al. 2010, Harding et al. 2011). Responses of arctic seabird species to prey changes appear thus broad and complex, underlining the need for studies relating individual prey selection to individual reproductive performance across years and environmental conditions. Analyses integrating movement of seabirds, associated to prey selection would have the potential to unravel the relative costs and benefits of feeding choices, whether on polar or Atlantic species, and to lead to a deeper understanding of the future challenges imposed by climate changes on seabird community.

This project aimed to combine tracking, diet, demographic and environmental data to unravel the potential causal mechanisms linking oceanographic conditions in Svalbard to seabird population responses. For this, we focused on the black-legged kittiwakes in Kongfsjorden and the little auks in Isfjorden, two of the most common seabirds breeding in Svalbard. These two species differ in terms of habitat and diet, where kittiwakes are surface-feeders feeding on both fish and marine invertebrates, whereas the little auk, a diving seabird, feeds almost exclusively on copepods during the breeding season. Representing different components of the Arctic marine food webs, these two species were used in this study to test the following predictions (1) a warmer ocean and a lower sea ice extent are associated with a higher prevalence of Atlantic prey in seabird diet ; (2) individuals feeding on Arctic prey have different foraging patterns and achieve a higher breeding success than individuals feeding on Atlantic ones.

## ***MATERIAL AND METHODS***

### *Study sites and species*

The study took place in 2009-2018 (little auks) and 2014-2018 (kittiwakes) in two fjords (Kongsfjord and Isfjord) in west Spitsbergen, Svalbard (Fig. 1). Little auks were studied in Isfjorden (Bjørndalen ; 78°14'N 15°20'E) and black-legged kittiwakes mostly in two colonies within Kongsfjorden (Ossian Sarsfjellet, 78°56'N 12°26'E ; Observasjonsholmen, 78°56'N 12°17'E). Breeding success of kittiwakes was only obtained in years 2017 and 2018. Some additional diet data have been obtained for kittiwakes from two additional colonies (Krykkjefjellet, 78°54'N 12°11'E ; Blomstrandhalvøya, 79°00'N 12°07'E).

The little auk is a colonial alcid, which lays a single-egg in rocky crevices in talus slopes (Stempniewicz 1981), and feeds preferably on Arctic water associated copepods (especially *Calanus glacialis*, which represents on average >80 % of the chick diet in Bjørndalen colony, Hovinen et al. 2014b) potentially due to their high lipid content (Harding et al. 2009, Jakubas et al. 2012). Krill, amphipods and other copepod species (e.g. *C. finmarchicus*, the second most abundant prey in little auk summer diet) are also utilized (Rosing-Asvid et al. 2013, Hovinen et al. 2014b). Black-legged kittiwakes are colonial cliff-breeders, that generally lay 1 or 2 eggs on Svalbard (Strøm 2006). They feed mostly on fish and crustaceans (Gasbjerg 2010). In both species, females and males share the incubation and chick-rearing duties.



*Figure 1. Study sites in Svalbard.*

### *Kittiwake GPS tracking*

Bird captures occurred throughout breeding seasons, covering the incubation and chick rearing periods. Individuals were caught using noose pole. In total, five types of GPS were deployed with their mass ranging from 6.3-18.6g ( $\bar{x} \pm \text{SD}$ ;  $13.1 \pm 3.8$ ), representing approximately 1.5-5.5% of birds' body mass. Prior to use, GPSs were sealed in waterproof heat shrink tubing and then attached to the birds' back feathers using TESA tape.

Filtering of GPS data followed Harris et al. (Harris et al. 2019). Briefly, speed has been filtered for a maximum of  $80 \text{ km h}^{-1}$ , threshold above what measurements were assumed as emerging from location errors (Paredes et al. 2012, Christensen-Dalsgaard et al. 2018). Based on frequency histograms, trips were identified once the bird left and returned to the colony, which was determined as an area of 300 meters radius around it. Each trip needed moreover to last for at least one hour. Only complete tracks were considered. All tracks were

regularized, filling gaps to standardize every point collection to the programmed interval sampling procedure. In order to be comparable among years, all tracks were standardized using a locational interval of 10 minutes. Not all trips were foraging ones, but each individual trip was screened for the presence of an area restricted search. In total, the original 1038 trips were cut off to 955, representing ca. 92% of the original dataset. Distribution of sampled individuals and relative trips are shown in Table 1.

**Table 1.** Number of individuals sampled and associated trips as a function of year and breeding stage

<b>BREEDING STAGE</b>	<b>2014</b>	<b>2015</b>	<b>2016</b>	<b>2017</b>	<b>2018</b>
Incubation	33 (4)	52 (11)	128 (34)	88 (38)	46 (23)
Chick Rearing	12 (3)	83 (9)	159 (36)	226 (52)	114 (36)

#### *Nest monitoring*

At Bjørndalen, between 13 and 50 nests were monitored annually in period 2009-2018 (total of 440 monitored nests). These little auk nests were from unknown (unringed) individuals. In Kongsfjorden (Ossian Sarsfjellet and Observasjonsholmen colonies), 27 and 15 nests were monitored in years 2017 and 2018, respectively. At least one kittiwake breeding on these monitored nests was sampled for diet analyses. Nests were visited and their content (presence and number of egg or chicks) checked on average twice a week in each colony. Breeding success was determined when a chick survived until 15 days of age (fledging occurs when chick are approx. 30 days of age, but logistical constraints prevented us to monitor chick survival until that age).

#### *Diet analysis*

Diet samples were obtained from spontaneous food regurgitates (kittiwakes) or from food stored in the gular pouch (little auks). We considered only samples collected during the chick rearing period.

For black-legged kittiwakes, we assessed the proportion of Arctic and Atlantic prey using the definitions from Vihtakari et al (2018). Arctic prey were the polar cod and the crustacean *Temisto libellula*, while the Atlantic prey were the capelin *Mallotus villosus*,

herring *Clupea harengus*, Atlantic cod *Gadus morhua*, and the crustaceans *T. abyssorum* and *Pandalus borealis*. We considered the proportions of Arctic and Atlantic prey in terms of wet mass (i.e., average mass percentage) in 206 samples collected in period 2014-2018.

For little auks, we assessed the proportion of the main two prey that are the copepods *Calanus glacialis* (Arctic species) and *C. finmarchicus* (Atlantic species). We considered the proportions in terms of number of copepods in 245 samples collected in period 2009-2018.

#### *Environmental parameters*

We considered two environmental parameters that are expected to play a significant role in the Svalbard marine food webs and thus the diet of Svalbard seabird: the sea-ice extent and the sea temperature. More specifically, we considered in this study only large scale parameters, that are the maximum sea-ice extent and the maximum sea surface temperature in the Fram Strait, that is highly influenced by the West Spitsbergen Current data from <http://www.mosj.no/>.

#### *Movement analysis*

The use of glacier fronts was coded as a binary response, equal to 1 if a bird spends at least 30 consecutive minutes at the front (i.e., 3 locational points) and 0 otherwise. The front zone was depicted as a 800 m buffer around the average front line in period 2014-2018. This buffer was decided through bootstrap resampling (i.e., 999 iterations), investigating the magnitude of change of our response variable across the different diameters (i.e., 100m – 1200m). The optimal size was then selected based on the stabilization of our variable.

#### *Statistical analyses*

All data were analysed with R software (R Development Core Team 2016).

Diet data and average breeding success data (little auks) were analysed using linear models with a gaussian error distribution (*lm* function); breeding success of kittiwake (data at

the individual level) was analysed with linear models with a binomial error distribution and a logit link function (*glm* function).

We used a kernel density estimation (KDE) to investigate if the probability of occurrence at the fronts change as function of years. Using the bivariate normal kernel (function *kernelUD* from *adehabitatHR* package), we analyzed locations of birds coming from the Ossian Sarsfjellet and Observasjonsholmen colonies and compared their utilization distributions between 2017 and 2018. In accordance to the study objective, we focused on the 50% isopleth, defined as the “*core area*” of individuals’ home range (Soanes et al. 2013). The bandwidth (*h*) has been selected through the identification of the averaged scale of individual searching pattern, computed via first-passage time analysis or FPT (Fauchald and Tveraa 2003). Prior to the FPT analysis, all tracks were regularized in space, in order to account for potential speed bias (Fauchald and Tveraa 2006). Optimal step length was evaluated through a series of scenarios comparing the number of locations from original and rediscrretized tracks. We defined the “*optimal step length*” parameter as the one that minimized differences, in terms of numbers of relocations, with the original time-regularized tracks. FPT was processed on all tracks and we then identified the scale at which the maximal variance of the log(FPT) occurred. We thereafter averaged those scales across all trips and used this mean as the smoothing parameter of the kernel estimators. Grid size effect have been evaluated through sensitivity analyses (i.e., sizes: 500m-2000m), where the optimal size was selected based on the magnitude of change across the different scenarios.

## **RESULTS**

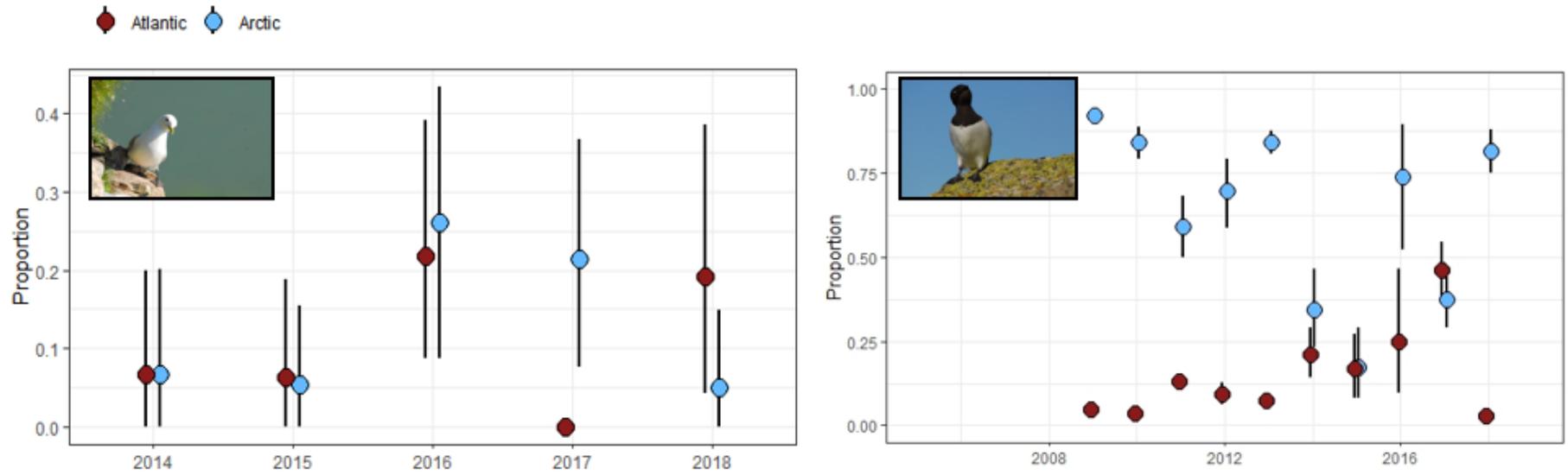
### *Environmental conditions and seabird diet*

The diet of both little auks (Isfjorden) and black-legged kittiwakes (Kongsfjorden) showed large inter-annual fluctuations in the proportion of Arctic and Atlantic prey but these changes seem to be independent from each others (Fig. 2). In little auks, the diet was almost exclusively made of *C. glacialis* and *C. finmarchicus* and the abundance of both species varied in opposite direction (Fig. 2). There was a significant decline in the proportion of

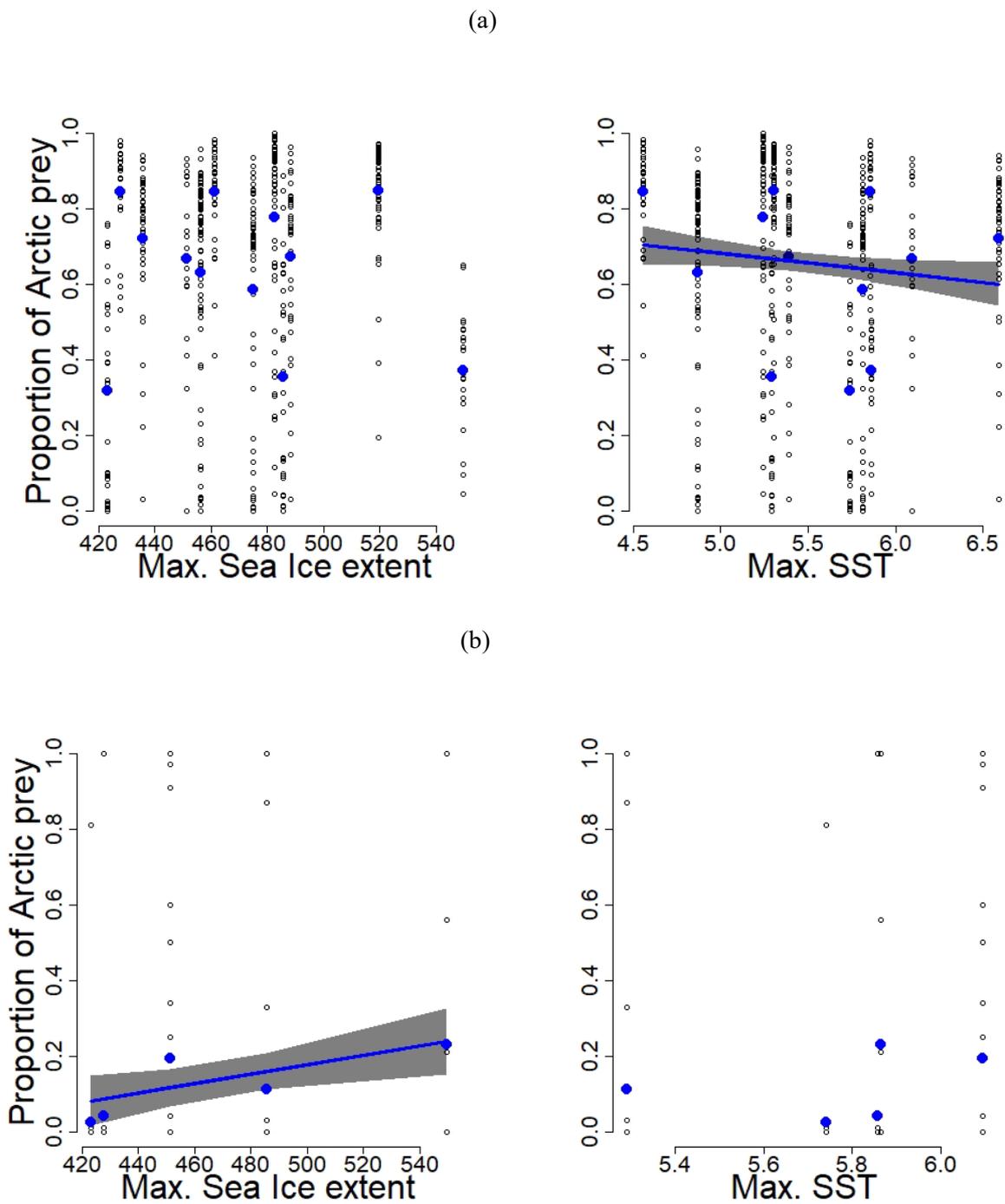
Arctic prey (*Calanus glacialis*) and a concurrent increase in the proportion of Atlantic one (*C. finmarchicus*) in little auk diet but only until 2017 (Fig. 2). In 2018, the proportion of *C. glacialis* was, however, very high again with almost no *C. finmarchicus* in little auk food samples.

In kittiwakes, there was no obvious linear change and the diet of kittiwakes was only partially made of “real” Arctic or Atlantic prey (Fig. 2). Indeed, the majority of the kittiwake diet was made of “intermediate species” that are neither truly Arctic or Atlantic (e.g. snake blenny *Lumpenus lampretæformis* and *Nereis spp*).

Only a small part of the observed changes in bird diet could be explained by changes in sea-surface temperature or sea-ice extent in the Fram strait (Fig. 3). A higher maximum SST had an apparent and significant negative effect on the proportion of Arctic prey in little auk diet (Fig. 3a ; effect of the SST:  $-0.05 \pm 0.02$ ,  $p=0.03$ ), while the maximum sea-ice extent had a positive and significant effect on the proportion of Arctic prey in kittiwake diet (Fig. 3b; effect of the sea-ice extent:  $0.0012 \pm 0.0005$ ,  $p=0.01$ ).



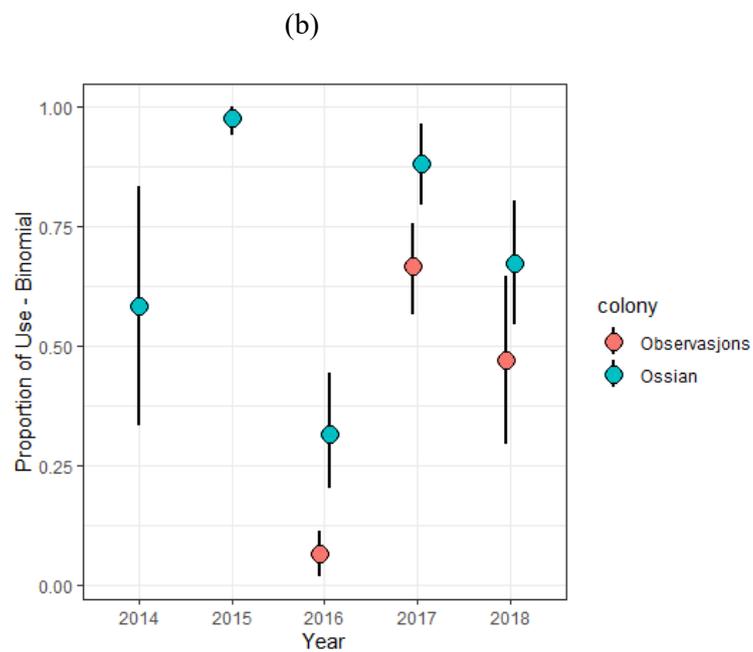
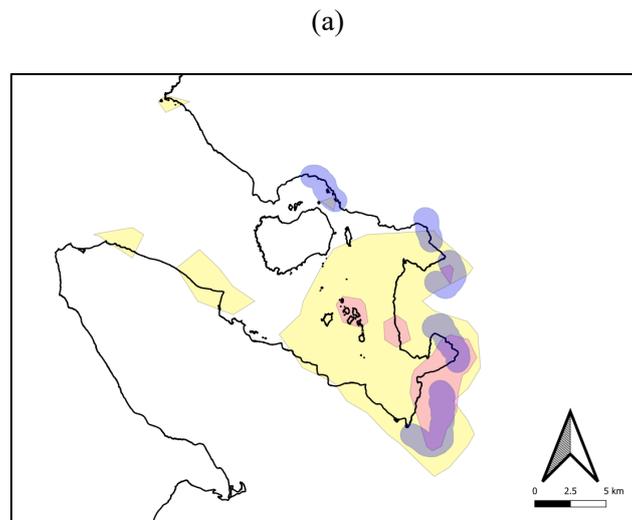
**Figure 2.** Proportion of Arctic and Atlantic prey in black-legged kittiwakes (left panel) and little auks (right panel) breeding respectively in Kongsfjorden (Observasjonsholmen and Ossian sarsfjellet) and Isfjorden, Svalbard. Results are from the chick-rearing period only.



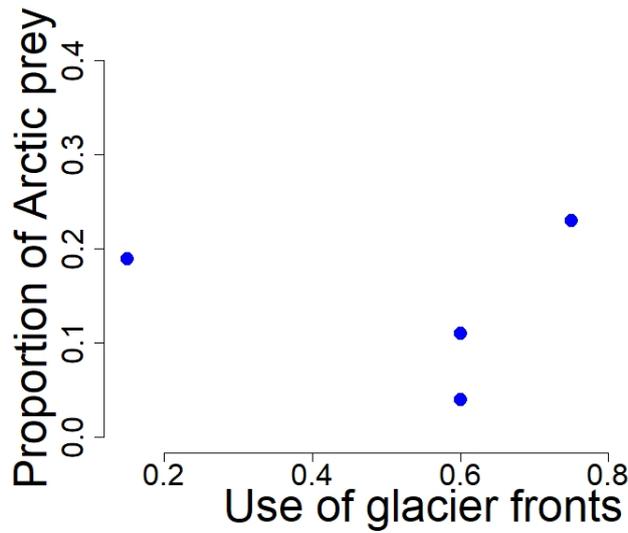
**Figure 3.** Relationships between the maximum sea-ice extent and the maximum sea surface temperature in the Fram strait and the proportion of Arctic prey in little auk (a) and black-legged kittiwake (b) diet. Data are from 2009-2018 for little auks and from 2004-2018 for kittiwakes.

### *Diet and foraging*

During the chick rearing period, kittiwakes breeding in Kongsfjorden forage mostly within the fjord. One significant feature of foraging kittiwakes in Kongsfjorden is the use of glacier fronts ( particularly the Kronebreen one ; Fig. 4a), and the use of glacier front varied greatly among years (Fig. 4a & b). Based on the FPT analysis, a smoothing parameter ( $h$ ) of 802.32 has been applied, with a grid size of 500m x 500m. The core area used during chick rearing period was approximately 7 times larger in 2018 than 2017 (i.e., area; 2017: 2,846 m<sup>2</sup>, 2018: 20,165 m<sup>2</sup>). Movement were much more restricted in 2017 and individuals were expected to be found for about 50% of their trips at the Kronebreen and Kongsvegen South fronts (Fig. 4a). However, contrary to our prediction, the proportion of Arctic prey in kittiwake diet samples was not related to the use of glacier fronts (Fig. 5).



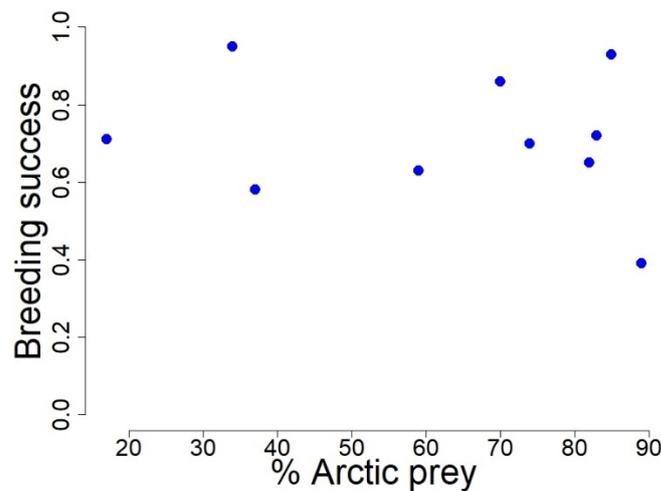
**Figure 4. a)** Kittiwake distribution in Kongsfjorden, during chick rearing, for 2017 (pink) 2018 (yellow) (# of bird trips: 2017  $n = 149$ ; 2018  $n = 80$ ). The five glacier fronts and their respective buffer are represented in blue **b)** Annual use of glacier front (95% CI) by foraging black-legged kittiwakes breeding in Kongsfjorden during the chick-rearing period (Observasjonsholmen:  $n = 229$ ; Ossian sarsfjellet:  $n=254$ )



**Figure 5.** Relationships between the use of glacier fronts by foraging kittiwakes and the proportion of Arctic prey in their diet. Data are from 2014-2018 and from several colonies in Kongsfjorden, Svalbard.

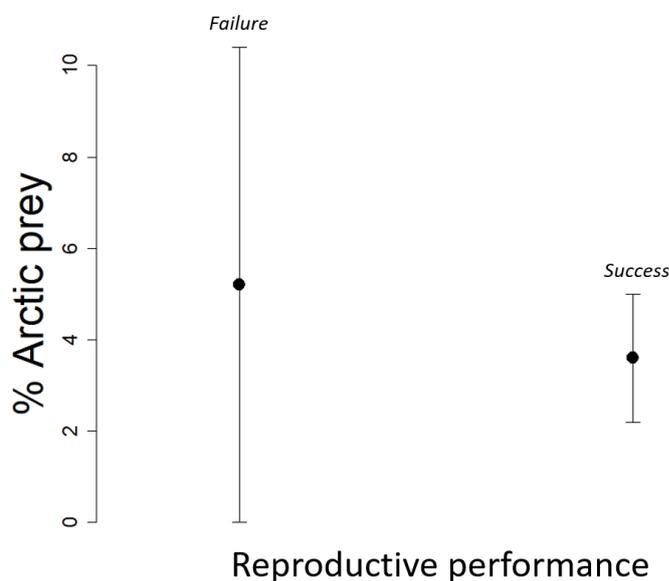
#### *Diet and reproductive performance*

We could not test for a relationship between diet and reproductive performance in little auk at the individual level as data from diet and breeding success were collected from different individuals. However, at the population level, we could not detect any relationship between the average breeding success and the average proportion of Arctic prey in the diet (Fig. 6).



**Figure 6.** Relationship between the proportion of Arctic prey (i.e. *Calanus glacialis*) in the diet of little auks breeding in Isfjorden, Svalbard.

In kittiwakes, the breeding success of individuals in 2017 and 2018 was independent of the proportion of Arctic prey found in their diet samples (n=42 nests where at least 1 diet sample from 1 parent has been analysed ; p-value>0.7; Fig. 7).



**Figure 7.** Average proportion ( $\pm$ SE) of Arctic prey in black-legged kittiwakes that successfully raised  $\geq 1$  chick until 15 days of age (right symbol) or not (left symbol)

## **DISCUSSION**

Using diet, tracking and demographic data from two seabird species breeding on Svalbard, this study aimed at testing the predictions that (1) a warmer ocean and a lower sea ice extent were associated with a higher prevalence of Atlantic prey in seabird diet and that (2) individuals feeding on Arctic prey had different foraging patterns and achieved a higher breeding success than individuals feeding on Atlantic ones.

Regarding the relationships between environmental conditions (sea-ice extent and sea surface temperature), our results supported our predictions. Indeed, we found that the maximum sea-ice extent in the Fram strait (i.e. sea-ice extent in April) was positively correlated to the proportion of Arctic prey in kittiwake diet. Similarly, the maximum sea-surface temperature in the Fram strait was negatively correlated with the proportion of Arctic prey (i.e. *Calanus glacialis*) in little auk diet. Both results support the prediction that the

warming of the Arctic ocean is leading to a change in seabird diet with more prominent Atlantic prey and thus to an Atlantification of Arctic food webs (Kortsch et al. 2012, Fossheim et al. 2015, Vihtakari et al. 2018). These observed relationships are based on large-scale environmental parameters (i.e. Fram strait/West Spitsbergen Current) and/or relatively short time-series (especially for kittiwakes). It is at that stage unclear how changes in large-scale sea-ice and/or surface temperature may explain the changes in seabird diet. Finer scale studies, using longer series would ideally be needed to unravel the mechanisms behind these relationships and to confirm that a warm ocean (and/or an ocean with less sea ice) is the main driver behind the observed changes in seabird diet.

In Kongsfjorden, black-legged kittiwakes may forage intensely in front of glaciers, where food availability is expected to be high and where prey are expected to be mostly Arctic species (Lydersen et al. 2014). The use of glacier fronts by foraging kittiwakes varied a lot among years as did the kittiwake diet. However, during the period of our study, these fluctuations were independent of each other and years where kittiwakes used intensely glacier fronts, the proportion of Arctic prey in their diet was not higher. It is possible that the relative proportion of Atlantic versus Arctic prey in their diet was mainly driven by the inflow of Atlantic water entering the fjord (Svendsen et al. 2002, Kubiszyn et al. 2014) rather by a variable use of glacier fronts. Information on the amount of Atlantic water on the west coast of Spitsbergen and its inter-annual variation would be needed to confirm such a potential relationship.

Different oceanographic processes are likely driving the proportion of *C. glacialis* and *C. finmarchicus* in little auk diet. Indeed, the inter-annual changes in these proportion are independent of the changes in the proportion of Arctic and Atlantic prey in kittiwake diet. Little auk foraging areas are virtually unknown in Isfjorden but little auk may forage far out of the fjords (Hovinen et al. 2014a, Ramírez et al. 2017). This thus suggests that changes in little auk and kittiwake diet are also, at least partly, driven by local, small-scale, factors and not only by large-scale changes in sea ice and/or sea temperature.

In none of the study species was the breeding success (i.e. probability to raise a chick successfully until 15 days of age) associated with the average diet of the parents. This does not support our prediction and several explanations can be proposed. First, this may indicate that these two species are capable to compensate for a lower availability of their preferred prey through foraging plasticity (e.g. Grémillet et al. 2012, Jakubas et al. 2017). Such behavioural plasticity may have some long term, cumulative costs and foraging on sub-optimal prey may at some point lead to a decrease in future reproductive performance and/or survival through carry-over and cumulative effects. Costs associated with a lower abundance of the preferred prey may also be apparent on other demographic traits such as the breeding propensity. It is possible that the proportion of birds starting to breed every year is lower when environmental conditions (i.e. availability of Arctic prey) are not optimal, which may strongly affect the population dynamics (Jenouvrier et al. 2005). However, seabird breeding propensity is a difficult parameter to assess. Multi-event capture-recapture modelling (Pradel 2005) may represent a useful method in this case and such approach should be explored.

Alternatively, our results may also indicate that Atlantic prey are not less profitable for seabirds. For example, it is often considered that *Calanus* species associated with Arctic water masses (e.g. *C. glacialis*) contain disproportionately larger lipid stores than their boreal congeners such as *C. finmarchicus* (Scott et al. 2000, Falk-Petersen et al. 2009). However, a recent study revealed that that lipid content is actually closely related to body size for these species (i.e. is not species-specific) and that there is considerable overlap in body size between them (Renaud et al. 2018). This indicates that the Atlantic species are not necessarily sub-optimal from an energetic point of view. Confirming this later hypothesis is necessary to fully understand the potential consequences for seabirds of a warming Arctic. There is now strong evidence that the marine ecosystems in the Arctic are changing with potential shifts in prey available to top predators. Whether or not these shifts will strongly affect seabird populations is dependent on the energetic value of the new “Atlantic” prey entering the systems (or more exactly on the balance between the cost of foraging on such prey and their

energetic benefits). Further studies evaluating these energetic costs and benefits associated with foraging on Arctic vs. Atlantic prey is urgently needed.

### ***MANAGEMENT IMPLICATIONS***

Our study investigated the relationships between the warming of Svalbard (and concomitant decline in sea-ice extent) and seabird diet and reproductive output. To understand how the warming of Svalbard effects seabird reproduction is of key importance to be able to predict how the populations will develop in the coming decades. By transporting nutrients from sea to land through guano and prey remains, seabirds constitute an important link between the marine and terrestrial ecosystems important for all land-living animals on the archipelago. While we found some apparent links between the ocean warming at a large spatial scale and the seabird diet, the mechanisms linking these two parameters are unclear. Moreover, there seems to be no consequence on seabird reproductive output: feeding on Atlantic prey does not lead to a lower reproductive success than feeding on Arctic ones. This suggest that, if the Atlantification of Svalbard has detrimental effects for (some) seabirds, these effects are likely not related to changes in breeding success.

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