



Consequences of Atlantification on a Zooplanktivorous Arctic Seabird

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Global warming, combined with an increasing influence of Atlantic Waters in the European Arctic, are causing a so-called Atlantification of the Arctic. This phenomenon is affecting the plankton biomass and communities with potential consequences for the upper trophic levels. Using long-term data (2005–2020) from a high Arctic zooplanktivorous seabird, the little auk (*Alle alle*), we tested the hypothesis that the Atlantification affects its diet, body condition and demography. We based our study on data collected in three fjords in West Spitsbergen, Svalbard, characterized by distinct oceanographic conditions. In all three fjords, we found a positive relationship between the inflow of Atlantic Waters and the proportion of Atlantic prey, notably of the copepod *Calanus finmarchicus*, in the little auk chick diet. A high proportion of Atlantic prey was negatively associated with adult body mass (though the effect size was small) and with chick survival (only in one fjord where chick survival until 21 days was available). We also found a negative and marginally significant effect of the average proportion of Atlantic prey in the chick diet on chick growth rate (data were available for one fjord only). Our results suggest that there are fitness costs for the little auk associated with the Atlantification of West Spitsbergen fjords. These costs seem especially pronounced during the late phase of the chick rearing period, when the energetic needs of the chicks are the highest. Consequently, even if little auks can partly adapt their foraging behaviour to changing environmental conditions, they are negatively affected by the ongoing changes in the Arctic marine ecosystems. These results stress the importance of long-term monitoring data in the Arctic to improve our understanding of the ongoing Atlantification and highlight the relevance of using seabirds as indicators of environmental change.

Keywords: *Alle alle*, borealization, copepod, *Calanus*, fitness costs, little auk, Spitsbergen

INTRODUCTION

The Arctic is warming faster than the rest of the globe (Cohen et al., 2020) and there is an increasing influence of warm and saline Atlantic waters entering the Arctic from the south (Pavlov et al., 2013; Skogseth et al., 2020). These changes strongly affect both the terrestrial and marine ecosystems (Parmesan, 2006; Poloczanska et al., 2013; Csapó et al., 2021) and are leading to shifts in biological communities with northern temperate species potentially replacing endemic Arctic species (Descamps and Strøm, 2021). This process is called “borealization”, or “Atlantification” in the marine Atlantic section of the Arctic (Ingvaldsen et al., 2021). Borealization has already been observed at different trophic levels, and in several regions of the Arctic, including the Barents Sea (see review in Ingvaldsen et al., 2021), Greenland (e.g., Møller and Nielsen, 2020), Canada (e.g., Ferguson et al., 2010; Tape et al., 2018) and the Chukchi and Beaufort Seas (e.g., Divoky et al., 2015; Gall et al., 2017).

In marine systems, the warming of the ocean is associated with changes in the distribution and/or abundance of key species. For example, the polar cod *Boreogadus saida* is a central species in Arctic marine food webs preyed upon by many different predators (Hop and Gjøsaeter, 2013). It has seen its distribution shrinking in the Barents Sea due to ocean warming and associated loss of habitat (Eriksen et al., 2015; Fosshem et al., 2015; Huserbråten et al., 2019), and is being gradually replaced by temperate species like the Atlantic cod *Gadus morhua* and capelin *Mallotus villosus*. Copepods from the *Calanus* genus are lipid-rich organisms (Hagen and Auel, 2001) that are key prey for fish, seabirds and mammals in the North Atlantic and Arctic ecosystems (Falk-Petersen et al., 2009). The proportion of the Arctic species, *Calanus glacialis*, has declined in the Barents Sea and West Greenland in the last decades while the proportion of the temperate species, *C. finmarchicus*, has increased (Aarflot et al., 2018; Møller and Nielsen, 2020; Tarling et al., 2022). Such a transition towards potentially smaller and less lipid-rich Atlantic copepods could affect the energy flow throughout the food web and have consequences on higher trophic levels (Falk-Petersen et al., 2009; Renaud et al., 2018). The ongoing borealization of Arctic food webs may also affect top- or meso- predators like seabirds (Descamps and Strøm, 2021; Stempniewicz et al., 2021b) through an effect on their foraging and thus reproductive performances (Ramírez et al., 2017) but very little is known about such consequences.

The little auk *Alle alle* is the most abundant seabird in the North Atlantic (Barrett et al., 2006) breeding almost exclusively at high latitudes (Descamps and Strøm, 2021; Wojczulanis-Jakubas et al., 2021). It has a strong influence on both marine and terrestrial ecosystem functioning and acts as an ecosystem engineer by consuming large amounts of zooplankton and by transporting vast amounts of nutrients from sea to land (Barrett et al., 2006; Zwolicki et al., 2016; González-Bergonzoni et al., 2017). In Svalbard during the breeding season, the little auk feeds primarily on the Arctic copepod, *C. glacialis*, but the Atlantic *C. finmarchicus* may also represent an important part of its diet (e.g., Karnovsky et al., 2003; Jakubas et al., 2011; Hovinen et al., 2014; Jakubas et al., 2016; Jakubas et al., 2020).

Along the west coast of Svalbard, the plankton communities are affected by the Atlantic water inflow (Kubiszyn et al., 2014; Gluchowska et al., 2016; Balazy et al., 2018; Hop et al., 2019). The influence of Atlantic water in this area has increased during the last decades (Muckenhuber et al., 2016; Nilsen et al., 2016; Tverberg et al., 2019; Skogseth et al., 2020; Bloshkina et al., 2021; Strzelewicz et al., 2022), which has contributed to an increase in the availability of North Atlantic prey such as *C. finmarchicus* (Aarflot et al., 2018; Hop et al., 2019). Little auks breeding in West Spitsbergen thus represent an ideal study system to assess the consequence of a shift from an Arctic to an Atlantic prey community on an endemic Arctic predator.

Several previous studies in western Svalbard fjords have suggested a link between the proportion of warm Atlantic Water (or more generally the sea temperature) and little auk foraging behaviour, chick diet and/or reproduction (Karnovsky et al., 2003; Jakubas et al., 2007; Kwasniewski et al., 2010; Jakubas et al., 2011; Kidawa et al., 2015). Results collectively indicate a negative effect of warm waters on little auk foraging (e.g. longer foraging trip duration, lower chick feeding frequency, lower energy value of the food delivered to the chick) and breeding performance (lower chick survival). However, all these studies were based on a limited time-scale (one to three years). Studies based on longer time-series are needed to unravel the potential consequences of the ongoing Atlantification. Such long-term data on little auk chick diet and life-history are now available from several western Svalbard fjords (Hornsund, Isfjorden and Kongsfjorden), characterized by distinct oceanographic conditions, with Kongsfjorden being most influenced by Atlantic Water, followed by Isfjorden and Hornsund (Gluchowska et al., 2016; Promińska et al., 2017).

Our study aimed primarily at testing for a relationship between the proportion of Atlantic Water in Svalbard fjords and the little auk chick diet composition and then to assess the consequences on their body condition and reproduction. More specifically, we hypothesized that an increase of the Atlantic Water inflow has detrimental effects on little auk body condition and reproduction. First, we predicted that the proportion of Atlantic prey in the little auk chick diet would be positively associated with the proportion of Atlantic Water in the fjord. Therefore the proportion would be highest on average in the fjords most influenced by the Atlantic Water (i.e. highest in Kongsfjorden, followed by Isfjorden and Hornsund) and higher in years of high Atlantic inflow. Second, we predicted that an increase in the proportion of Atlantic prey (in the chick diet) should be associated with a lower adult body condition as breeding birds may increase their foraging effort in such suboptimal foraging conditions (Kwasniewski et al., 2010; Karnovsky et al., 2011; Grémillet et al., 2012; Kidawa et al., 2015). This increased effort may lead to a sustained chick survival and/or growth rate (i.e. independent of the Atlantic water inflow), but a lower adult body condition (Harding et al., 2011). Alternatively, parents may not jeopardize their own condition by increasing their foraging effort to feed their chick when environmental conditions deteriorate and optimal food (i.e. Arctic prey) is less available (e.g., Welcker et al., 2009). In

such a case, an increase in the contribution of Atlantic prey in the diet should be associated with lower chick survival and/or growth rate (Jakubas et al., 2007; Kwasniewski et al., 2010; Kidawa et al., 2015) but without a strong effect on adult body condition.

MATERIAL AND METHODS

Study Sites and Species

The little auk is a high Arctic colonial seabird, weighing between 130 and 190 grams and laying a single-egg clutch, generally in early June on Svalbard with hatching occurring in early/mid-July (Stempniewicz, 2001; Ramírez et al., 2017). Chicks usually fledge when they are between 3 and 4 weeks of age (Gaston and Jones, 1998). Their life history is characterized by a high adult survival (Descamps et al., 2021) and delayed age at first breeding (Del Hoyo et al., 1996; Stempniewicz, 2001). On Svalbard, the population size is uncertain but may be as high as a million breeding pairs (Anker-Nilssen et al., 2015; Keslinka et al., 2019), and may be declining in some colonies (Descamps and Strøm, 2021). The little auk is a zooplanktivorous species, primarily utilizing the Arctic copepods, with *C. glacialis* generally representing its main prey on Svalbard during the breeding period (Stempniewicz, 2001).

From 2005 to 2020, a sample of adult little auks have been captured annually (see details in **Table 1**) in three different colonies during the chick-rearing period (Ariekammen colony in Hornsund, Bjørndalen colony in Isfjorden and Feiringfjellet colony in Kongsfjorden; **Figure 1**). Captures started every year when the first sign of chick feeding (i.e. birds with a full gular pouch) have been observed. These birds were captured either by hand in the nest chamber (Hornsund only) and/or using passive traps (noose carpets) deployed on rocks in the colony (all three fjords) or mist-nets (Hornsund only). Such captures with noose carpets or mist-nets could not target breeding birds specifically and it is possible that a few non-breeders (or failed breeders) were also captured. All these birds were ringed, and most were measured (total head length, to the nearest 0.1 mm) and weighed (to the nearest 5 g). Adults transport the food for their chick in a sublingual gular pouch and this food can thus be easily sampled at capture for further prey identification (details below). The diet

results presented in this study thus correspond to the chick diet (which is likely the same as adult diet, see Fort et al., 2010).

In Hornsund and Isfjorden, a group of nests (64 and 24 nests/year on average, with a range of [10, 155] and [9, 40], at Hornsund and Isfjorden respectively; **Table 1**) was monitored two to three times a week every season from approximately mid- (Isfjorden) or late- (Hornsund) incubation until the chicks were 15 (Isfjorden) or 21 (Hornsund) days old. At each visit, the status of the nest (egg, chick or empty) was recorded, and for a sample of nests at Hornsund, the chicks were weighed every 3 days.

Chick Diet Sample Analyses

Diet samples were analysed according to the procedures described in Harris et al. (2000). Organisms were enumerated and identified from subsamples until at least 300 individuals were counted. All *Calanus* specimens from copepodite stage (C1) to adult females (AF) were measured and identified on the basis of their prosome lengths, using size distribution tables that are established for Svalbard waters (Kwasniewski et al., 2003). Prey species were characterized as Arctic or Atlantic following the classification in Hop et al. (2019) and the total proportion of Atlantic and Arctic prey was calculated for each diet sample. A few species could not be clearly categorized as Arctic or Atlantic, but these species represented only approximately 5% of the little auk chick diet. Each diet sample was thus characterized by three proportions (i.e., % Arctic species, % Atlantic species and % species with undetermined distribution).

Atlantic Water Inflow

The Atlantic Water inflow was quantified as the percent contribution of Atlantic Water following the procedure introduced in Hop et al. (2019). Atlantic Water (AW) was defined as water with practical salinity at least 34.65 and potential temperature $\geq 3^{\circ}\text{C}$ following the definition from Cottier et al. (2005). Temperature-salinity data collected using onboard CTDs (i.e. instruments measuring conductivity, temperature and depth) in July-September were extracted from multiple sources. The UNIS Hydrographic Database was used as the main source for data up to 2019 (described in Skogseth et al., 2020). This dataset was complemented with data from the Norwegian Polar Institute, Institute of Oceanology Polish

TABLE 1 | Sample sizes of, and time periods covered by, the datasets on the Atlantic Water Index (AWI), proportion of Atlantic prey in little auk chick diet, adult body mass, chick survival and chick growth rate for three western Svalbard fjords (Hornsund, Isfjorden and Kongsfjorden).

Colony	AWI	Chick diet	Adult body mass ²	Chick survival (to 15 days)	Chick survival (to 21 days)	Chick growth rate
Hornsund	2006-2019	N=512 (2005-2020)	N=336 (2007-2020)	N=895 (2006-2013, 2015-2020)	N=695 (2006-2013, 2015-2020)	N=405 (2006-2013, 2015-2020)
Isfjorden	2005-2020	N=373 (2005-2007, 2009-2020)	N=214 (2005-2007, 2009-2020)	N=308 (2005-2007, 2009-2015, 2017-2020)	–	–
Kongsfjorden	2005-2020	N=264 (2006-2007, 2011-2020)	N=188 (2006-2007, 2011-2020)	–	–	–
Total		N=1149 ¹	N=738	N=1203	N=695	N=405

¹total sample size for the chick diet data differs here and in **Table 3** as data from **Table 3** only cover the years when the proportion of Atlantic Water can be estimated and thus only the period 2006-2019 for Hornsund.

²number of captured adults for which both the body mass and total head length were available.

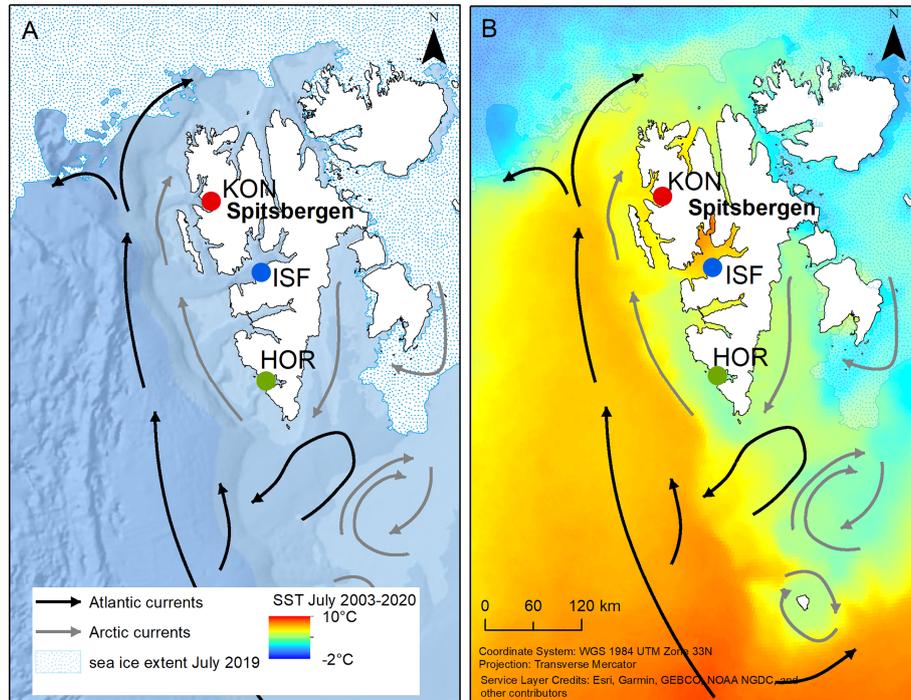


FIGURE 1 | Study sites on Svalbard. A map showing studied little auk colonies (KON – Kongsfjorden, ISF – Isfjorden, HOR – Hornsund), bathymetry (source: Arctic Ocean Base, https://services.arcgisonline.com/arcgis/rest/services/Polar/Arctic_Ocean_Base/MapServer) and July sea ice extent [example for July 2019; source: Multisensor Analyzed Sea Ice Extent - Northern Hemisphere (MASIE-NH), Version 1 with 4 km grid cell size (National Ice Center (NIC) and NSIDC, 2010)] **(A)** and SST in July in 2003-2020 (source: Moderate-resolution Imaging Spectroradiometer (MODIS) Aqua satellite data from Ocean Color Data webpage, <https://oceansci.gsfc.nasa.gov/MODIS-Aqua>) and the main Atlantic and Arctic currents in West Spitsbergen (after Loeng and Drinkwater, 2007) **(B)**.

TABLE 2 | Proportion of the ten main prey items in the little auk chick diet in three western Svalbard fjords (based on data from 2005-2020 for Hornsund and Isfjorden and from 2006-2020 for Kongsfjorden).

Prey	Hornsund	Prey	Isfjorden	Prey	Kongsfjorden
<i>Calanus glacialis</i> CV (Arc)	0.68	<i>Calanus glacialis</i> CV (Arc)	0.63	<i>Calanus glacialis</i> CV (Arc)	0.59
<i>Calanus finmarchicus</i> CV (Atl)	0.12	<i>Calanus finmarchicus</i> CV (Atl)	0.12	<i>Calanus finmarchicus</i> CV (Atl)	0.17
<i>Apherusa glacialis</i> (Arc)	0.06	<i>Themisto abyssorum</i> (Atl)	0.07	<i>Calanus hyperboreus</i> CV (Arc)	0.04
<i>Pagurus pubescens</i> (Arc)	0.04	<i>Thysanoessa inermis</i> (Und)	0.02	<i>Calanus hyperboreus</i> AF (Arc)	0.03
<i>Calanus glacialis</i> CIV (Arc)	0.02	<i>Euphausiacea</i> furcilia (Und)	0.02	<i>Thysanoessa inermis</i> (Und)	0.03
<i>Calanus glacialis</i> AF (Arc)	0.02	<i>Pagurus pubescens</i> (Arc)	0.02	<i>Themisto abyssorum</i> (Atl)	0.02
<i>Thysanoessa inermis</i> (Und)	0.02	<i>Calanus glacialis</i> CIV (Arc)	0.01	<i>Calanus glacialis</i> AF (Arc)	0.02
<i>Themisto abyssorum</i> (Atl)	0.01	<i>Calanus hyperboreus</i> CV (Arc)	0.01	<i>Calanus finmarchicus</i> AF (Atl)	0.02
<i>Calanus finmarchicus</i> CIV (Atl)	0.01	<i>Calanus glacialis</i> (Arc)	0.01	<i>Calanus glacialis</i> CIV (Arc)	0.01
<i>Themisto libellula</i> (Arc)	0.01	<i>Apherusa glacialis</i> (Arc)	0.01	<i>Euphausiacea</i> furcilia (Und)	0.01
% Arctic prey	0.83	% Arctic prey	0.72	% Arctic prey	0.71
% Atlantic prey	0.14 ^a	% Atlantic prey	0.20 ^a	% Atlantic prey	0.23 ^a

^adata differ slightly from the ones presented in the Result section as the averages presented in this table are based on all available years for each fjord while the ones presented in the text are based only on years where data are available in all three fjords.

Letters in brackets indicate whether the prey is an Arctic (Arc) or an Atlantic (Atl) species. "Und" stands for "undetermined distribution" and represents species that cannot be classified as Arctic or Atlantic. This classification is based on Hop et al. (2019).

Academy of Sciences, Joint Norwegian-Russian Ecosystem Survey for Barents Sea (Eriksen et al., 2018), the University Centre in Svalbard and UiT the Arctic University of Norway for 2019-2020. In total, these sources provided 945 (59.1 per year on average), 1156 (72.2), and 1085 (77.5) CTD casts to estimate an Atlantic Water Index (AWI) in the main basins of Kongsfjorden,

Isfjorden and Hornsund respectively, without side fjords and ending at the fjord mouth. Only one CTD cast from the same position, measured using the available coordinates, per day was included in the AWI estimation. Even though little auks do not always forage inside the fjords during chick rearing, they are regularly observed there (at least in Hornsund, Stempniewicz

et al., 2021a; Stempniewicz et al., 2021b) and generally do short trips to find food for their offspring and use areas located <50 km away from the colony (e.g., Welcker et al., 2009; Jakubas et al., 2020). We thus expect the within-fjord AWI to be representative of the level of “Atlantification” in the foraging areas used by breeding little auks for finding food for their chicks.

The Atlantic Water Index (AWI) was quantified as the average proportion of AW in CTD casts between July and September as:

$$AWI_s = \frac{\sum 1m \text{ bins with AW}}{\text{number of 1m bins in the cast}}$$

Annual AWI for a year y and region r was calculated as the average of all casts for the given year and fjord:

$$AWI_{y,r} = n^{-1} \times \sum_{i=1}^n AWI_s$$

Where n is the number of stations per year (y) and fjord (r). Casts to shallower depths than 100 m were excluded to reduce the bias surface waters would cause to the AWI. Data between July and September were used because these months are oceanographically comparable in the studied fjords (Cottier et al., 2005; Skogseth et al., 2020).

Statistical Analyses

All data were analysed with R software version 4.1.1 (R Development Core Team, 2021). Except when specified otherwise, visual inspection of model residual distributions indicated no heteroscedasticity and no auto-correlation for all models considered.

For analysing the inter-fjord and inter-annual variations in the proportion of Atlantic prey in the little auk chick diet ($n=1096$ diet samples when considering only the years where the AWI could be estimated in all the three fjords), we used beta regression mixed models (with the `glmmTMB` function of package `glmmTMB`, Brooks et al. (2017)) with a beta distribution and a logit link function. Year was included as a random factor in all models. Since the models require the dependent variable to be in the open interval (0,1), data were transformed as $\frac{y \times (n-1) + 0.5}{n}$ where y is the dependent variable (proportion of Atlantic prey in each little auk diet sample) and n total number of diet samples available (Smithson and Verkuilen, 2006; Cribari-Neto and Zeileis, 2010). We adopted a model comparison approach based on the Akaike’s Information Criterion or AIC (Burnham and Anderson, 2002) to determine whether or not the % of Atlantic prey varied among fjords and/or varied (linearly) with the AWI. We also considered the Fjord \times AWI interaction to test whether the relationships between % Atlantic prey and AWI varied among colonies. The most general model for this analysis was thus of the form: %Atlantic prey (in chick diet) \sim AWI + Fjord + AWI \times Fjord + (1|Year).

Then, we tested for an effect of the proportion of Atlantic prey in the chick diet on adult body mass. We considered the mass of adults weighed between mid-July and mid-August, which corresponds to chick rearing period ($n=738$). We used a two-

step approach: first, we considered the effect of the annual average proportions of Atlantic prey on individual body mass, and second, the effect of the proportion of Atlantic prey in individual diet samples on individual body mass. A significant effect of the proportion of Atlantic prey at both the inter-annual and inter-individual level would indicate that (i) seasons with high % Atlantic prey are associated with lower bird body mass on average, and that (ii) within a given year, individuals foraging more on Atlantic prey are characterized by a lower body mass. Such combined results would give support to a causal (i.e. mechanistic) relationship between the % Atlantic prey and bird body mass. To test these relationships, we used linear mixed models (`lmer` function of package `lme4`, Bates et al. (2015)) with a Gaussian error distribution and a random effect of the year. We also adopted a model comparison approach based on AIC (using maximum-likelihood estimation as all models had the same random structure) to assess if the bird body mass varied among fjords and/or varied (linearly) with the % Atlantic prey. We also considered the Fjord \times % Atlantic prey interaction to test if the relationships between % Atlantic prey and body mass varied among colonies. The body size (i.e. total head length of little auks) was included in all models so that results could be interpreted in terms of body condition (i.e. body mass independent of body size) as these two traits are significantly correlated in little auks (Wojczulanis-Jakubas et al., 2014a; Wojczulanis-Jakubas et al., 2014b). Preliminary analyses indicated that the date of capture had no effect on little auk mass (between mid-July and mid-August) and was thus not included in our models. The most general model for this analysis was thus of the form: Adult body mass \sim Body size (total head length) + % Atlantic prey (annual mean or individual level data) + Fjord + % Atlantic prey \times Fjord + (1|Year).

We then tested for an effect of the proportion of Atlantic prey on little auk chick survival (Hornsund and Isfjorden) and growth rate (Hornsund). Data on chick survival and growth rate could not be linked to the specific diet brought by their parents and we thus only tested for a relationship at the inter-annual level (i.e. tested for an effect of the annual average proportion of Atlantic prey on chick survival and growth rate). For analysing the chick survival, we considered mixed models with a binomial error distribution (the dependent variable following a Bernoulli distribution) and a logit link function using the `glmer` function of package `lme4` (Bates et al., 2015). In Hornsund, 39% of the monitored nests and 24% in Isfjorden had chick survival data for multiple years. However, this dependency (i.e. repeated measures of chick survival for some nests) did not affect our results; results were identical whatever the method used (e.g. randomly sampling only one measure per nest or including the nest identity, nested within fjord, as a random effect). Therefore, we only present results from simple mixed models with year as a random factor). We first considered the chick survival until 15 days of age (both fjords; $n=1203$) and then until 21 days of age (Hornsund only, $n=695$). For 15 day-survival analyses, we used AIC to compare models and to assess if the chick survival was affected by the chick diet and if this relationship was the same in both fjords. The most general model for this analysis was thus of the form: Chick survival to 15 days \sim % Atlantic prey (annual mean) + Fjord + %Atlantic prey \times Fjord + (1|Year). For the 21 day-

survival analysis, data were only available for Hornsund and we thus considered a single model $Chick\ survival \sim \%Atlantic\ prey + (1|Year)$.

The chick growth rates were calculated as the average gain in body mass per day. We only considered the first 16 days after hatching when the growth was linear (see **Figure SM-1**) and only chicks weighed at least twice during this period were included ($n=405$). Chick growth rates were analysed with a linear mixed model and a Gaussian error distribution. We used the *lmer* function (from the *lme4* package), and included the year as a random factor. Data were available for one fjord only and we considered a single model $Chick\ growth\ rate \sim \%Atlantic\ prey + (1|Year)$.

For each analysis, we assessed the proportion of variance in the data explained by the different models as the squared correlation between the observed and predicted values (Zheng and Agresti, 2000). To represent the uncertainty around the predicted relationships between the different variables considered, we calculated the 95% bootstrapped confidence intervals of the predicted values using the percentile method (i.e., using the 0.025 and 0.975 quantiles of 1000 replicates).

RESULTS

Inter-Fjord and Inter-Annual Variations in Little Auk Chick Diet

The average proportion of Atlantic prey in the little auk chick diet was $0.17 (\pm 0.18\ SD)$, $0.23 (\pm 0.19\ SD)$ and $0.23 (\pm 0.21\ SD)$ in Hornsund, Kongsfjorden and Isfjorden, respectively, when

considering only the years where data were available for all three fjords (2006, 2007, 2011-2020). The Atlantic prey was mainly dominated by *C. finmarchicus* (stage CV; **Table 2**) while the Arctic prey was dominated by *C. glacialis* (stage CV; **Table 2**). The differences in Atlantic prey among fjords were significant (even though they explained only a small fraction of the variance in diet; see **Table 3**) and Atlantic prey species were less present in Hornsund little auk diets while the difference between Isfjorden and Kongsfjorden was not significant (**Table 3**; results from model $\%Atlantic\ prey \sim Fjord$ with Isfjorden as the reference level: estimate of the difference between Kongsfjorden and Isfjorden on a logit scale: $0.11 \pm 0.08\ SE$, $z=1.39$, $p=0.16$, estimate of the difference between Hornsund and Isfjorden on a logit scale: $-0.20 \pm 0.07\ SE$, $z=-2.91$, $p=0.004$).

The proportion of Atlantic prey species showed large inter-annual fluctuations and these fluctuations were highly synchronous between Isfjorden and Kongsfjorden (Pearson's $r=0.93$, $p<0.001$), but not between Hornsund and Isfjorden or between Hornsund and Kongsfjorden (Pearson's $r<0.4$ and $p>0.2$ in both cases; **Figure 2**). Even though inter-annual changes in the proportion of Atlantic prey were not synchronized between Hornsund and the other fjords, some years were characterized by very high (e.g. 2014) or very low (e.g. 2018) proportions of Atlantic prey in all three fjords (**Figure 2**). The proportion of Atlantic species in the little auk chick diet has increased in all three fjords during the study period with no obvious difference in trend among fjords (**Figure SM-2**; **Table SM-1**).

The inter-annual changes in the proportion of Atlantic prey in the little auk chick diet were positively associated with the AWI (**Table 3**). This relationship varied among fjords and the slope of the AWI effect was steepest in Hornsund (**Table 3**; **Figure 2**). These relationships were independent of the long-term trends in AWI and in the % Atlantic prey (i.e. they remained the same, whether or not we kept a Trend \times Fjord interaction in the models; **Table SM-2**; **Figure SM-2**).

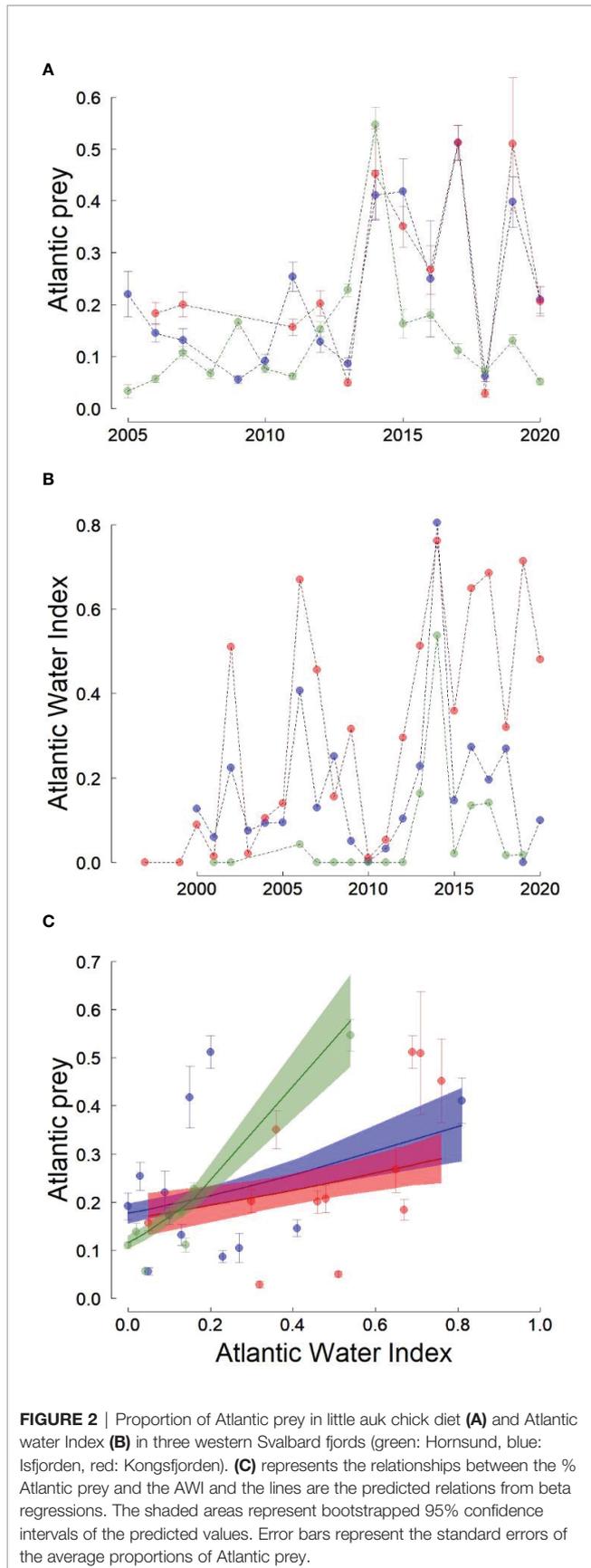
TABLE 3 | Effect of the Atlantic Water Index (AWI) in three western Svalbard fjords (Hornsund, Isfjorden and Kongsfjorden) on the proportion of Atlantic prey in the little auk chick diet.

(A)				
Model	np	AIC	ΔAIC	R^2
%Atlantic prey ~ 1	1	-1584.08	55.23	
%Atlantic prey ~ Fjord	3	-1604.13	35.18	0.32
%Atlantic prey ~ AWI	2	-1610.37	28.94	0.31
%Atlantic prey ~ AWI + Fjord	4	-1610.27	29.04	0.32
%Atlantic prey ~ AWI + Fjord + AWI \times Fjord	6	-1639.31	0.00	0.33
(B)				
Variables	Estimate	SE	z	p
Intercept-Hornsund	-1.85	0.11	-17.61	<0.001
Intercept-Isfjorden	-1.54	0.12	-13.00	<0.001
Intercept-Kongsfjorden	-1.88	0.19	-9.74	<0.001
AWI -Hornsund	3.22	0.54	5.99	<0.001
AWI -Isfjorden	1.02	0.38	5.64	0.007
AWI -Kongsfjorden	1.34	0.34	3.92	<0.001

Data ($n=1096$) are from 2005-2020 (with some years missing for each fjord). Results are from beta regression models with year included as a random factor (see methods for details). In (A), np represents the number of fixed parameters, AIC is the Akaike's Information criterion, ΔAIC is the difference between the AIC of a given model and the lowest AIC of all models considered and R^2 represents the proportion of explained variation by each model. Model in bold is the one with the lowest AIC. Table (B) represents the intercept and slope estimates of the AWI effect for each fjord for this best model (logit scale), along with the test statistics (z) and associated p-values.

Proportion of Atlantic Prey and Little Auk Body Mass

Body mass of adult little auks (controlled for body size) was similar among fjords but showed inter-annual variations that were negatively associated with the inter-annual fluctuations in the average proportion of Atlantic prey (slope of the effect: $-6.29 \pm 2.71\ SE$; **Table 4**; **Figure 3A**). This relationship was also significant when an individual body mass was linked to the proportion of Atlantic prey in its own chick diet (slope of the effect: $-5.61 \pm 1.85\ SE$; **Table 5** and **Figure 3B**). However, even though the effect of the proportion of Atlantic prey was significant, it explained only a negligible proportion of the inter-annual variations in little auk adult body mass (**Tables 4, 5**) and had a small effect size (i.e., an increase of 50% in the proportion of Atlantic prey only led to a decline in body mass of approx. 3 grams meaning ~2% of little auk body mass; **Figure 3**). The effect of the proportion of Atlantic prey was similar in all three fjords (i.e., the best models did not include a $\%Atlantic\ prey \times Fjord$ interaction; **Tables 4, 5**) but appeared weaker in Hornsund (**Tables 4, 5**; **Figure 3**). The relationship between the proportion of Atlantic prey and little auk body mass



was not confounded by any potential linear trend common in both variables (i.e. the effect of the proportion of Atlantic prey remained significant even if we included a *Trend × Fjord* interaction in the model; see **Table SM-3**).

Proportion of Atlantic Prey, Little Auk Chick Survival and Chick Growth Rate

The chick survival rate (until 15 days of age) averaged 0.92 ± 0.07 SD in Hornsund (2006-2020) and 0.84 ± 0.10 SD in Isfjorden (2005-2020) and the difference was significant (**Table 6**). Overall, there was no clear effect of the proportion of Atlantic prey in the diet on chick survival in either of the fjords, but this effect was much stronger (and marginally significant) in Hornsund than in Isfjorden (**Table 6; Figure 4A**).

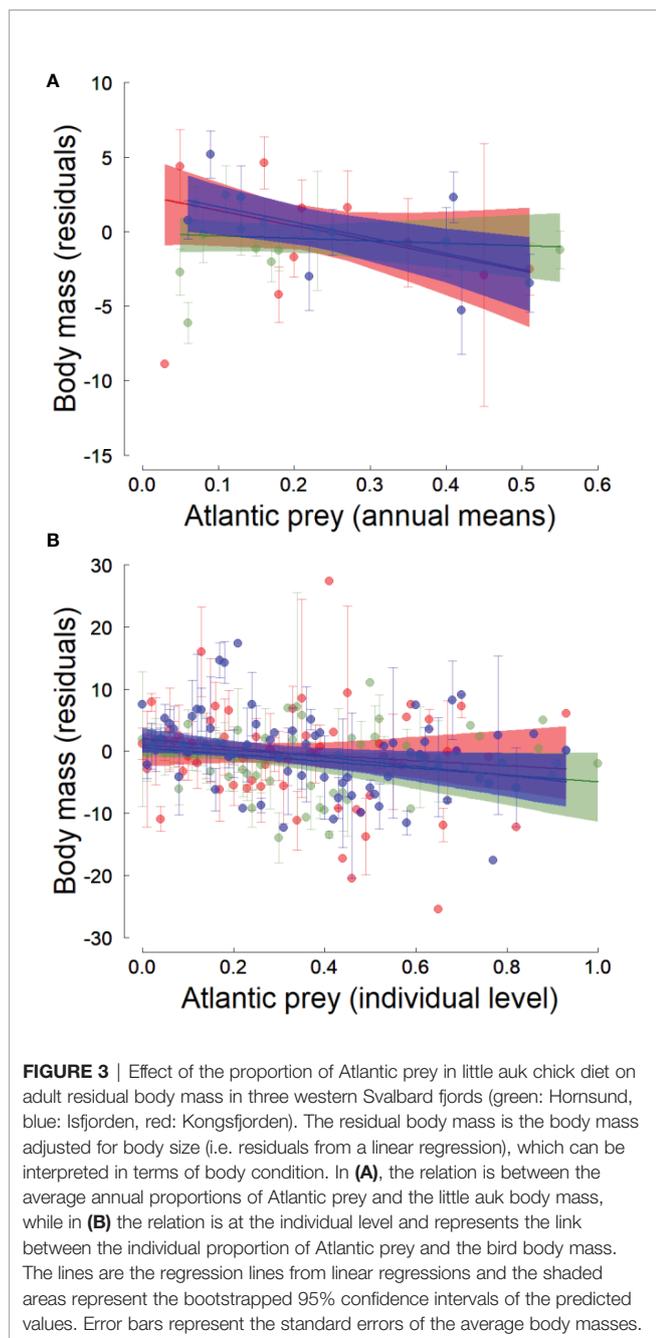
When considering the chick survival until 21 days (Hornsund only), the average chick survival dropped to 0.81 ± 0.25 SD and the effect of the proportion of Atlantic prey became highly significant even though it explained a small amount of variation in chick survival ($z = -3.51$, $p = 0.04$, $R^2 = 0.04$, slope \pm SE = -9.92 ± 4.95 ; **Figure 4B**).

During the first 16 days of life (linear phase of growth), chicks gained an average of 4.6 grams per day at Hornsund in 2006-

TABLE 4 | Effect of the mean annual proportion of Atlantic prey on body mass of adult little auks breeding in three western Svalbard fjords (Hornsund, Isfjorden and Kongsfjorden).

(A)				
Model	np	AIC	ΔAIC	R ²
Body mass ~ 1	1	5584.51	146.84	–
Body mass ~ Body size	2	5440.73	3.06	0.20
Body mass ~ Body size + Fjord	4	5443.42	5.75	0.20
Body Mass ~ Body size + %Atlantic prey (annual mean)	3	5437.67	0.00	0.20
Body Mass ~ Body size + %Atlantic prey (annual mean) + Fjord	5	5438.45	0.78	0.20
Body Mass ~ Body size + %Atlantic prey (annual mean) + Fjord + %Atlantic prey (annual mean) × Fjord	7	5439.91	2.24	0.20
(B)				
Variables	Estimate	SE	t	p
Intercept-Hornsund	-24.54	14.33	-1.71	0.09
Intercept-Isfjorden	-21.19	14.16	-1.50	0.13
Intercept-Kongsfjorden	-21.74	14.33	-1.50	0.13
Body size	3.49	0.26	13.20	<0.001
Annual mean %Atlantic prey -Hornsund	-2.06	3.83	-0.54	0.59
Annual mean %Atlantic prey -Isfjorden	-11.08	4.15	-2.67	0.009
Annual mean %Atlantic prey -Kongsfjorden	-11.03	5.38	-2.05	0.04

Data ($n = 738$) are from 2005-2020 (with some years missing for each fjord) and with body masses from the chick rearing period. Results are from mixed models based on a Gaussian error distribution (see Materials and Methods for details) and all models include year as a random effect. In **(A)**, np represents the number of fixed parameters, AIC is the Akaike's Information criterion, ΔAIC is the difference between the AIC of a given model and the lowest AIC of all models considered and R² represents the proportion of explained variation by each model. Model in bold is the one with the lowest AIC. Body size (i.e. total head length) has been included in all models so that results can be interpreted in terms of body condition (see Materials and Methods for details). Table **(B)** represents the intercept and slope estimates for the most general model (Body Mass ~ Body size + %Atlantic prey (annual average) × Fjord) along with the test statistics (t) and associated p-values.



2020. This growth rate was negatively affected by the average proportion of Atlantic prey in the chick diet; the effect was only marginally significant ($n=405$, $t=-1.89$, $p=0.08$, $R^2 = 0.25$, slope \pm SE = -11.53 ± 6.09 ; **Figure 5**).

The effects of the proportion of Atlantic prey on chick survival or growth rate at Hornsund were not confounded by any potential linear trend common in both variables (i.e. the effect of the proportion of Atlantic prey remained the same even if we include a *Trend* covariate in the model; see **Table SM-4**).

TABLE 5 | Effect of the individual proportion of Atlantic prey in the little auk (chick) diet on body mass of adult little auk breeding in three western Svalbard fjords (Hornsund, Isfjorden and Kongsfjorden).

(A)				
Model	np	AIC	Δ AIC	R^2
Body mass ~ 1	1	5584.51	150.49	–
Body mass ~ Body size	2	5440.73	6.71	0.20
Body mass ~ Body size + Fjord	4	5443.42	9.40	0.20
Body Mass ~ Body size + %Atlantic prey	3	5434.02	0.00	0.20
Body mass ~ Body size + %Atlantic prey + Fjord	5	5435.26	1.24	0.21
Body mass ~ Body size + %Atlantic prey + Fjord + %Atlantic prey \times Fjord	7	5438.10	4.08	0.20
(B)				
Variables	Estimate	SE	t	p
Intercept-Hornsund	-23.24	14.29	-1.63	0.10
Intercept-Isfjorden	-20.86	14.17	-1.47	0.13
Intercept-Kongsfjorden	-22.12	14.27	-1.55	0.12
Body size	3.47	0.26	13.15	<0.001
%Atlantic prey -Hornsund	-3.99	2.99	-1.33	0.19
%Atlantic prey -Isfjorden	-8.50	2.91	-2.92	0.004
%Atlantic prey -Kongsfjorden	-5.60	3.62	-1.55	0.12

Data ($n = 738$) are from 2005-2020 (with some years missing for some fjords) and from the chick rearing period. Results are from mixed models based on a Gaussian error distribution (see Materials and Methods for details) and all models include year as a random effect. In **(A)**, np represents the number of fixed parameters, AIC is the Akaike's Information criterion, Δ AIC is the difference between the AIC of a given model and the lowest AIC of all models considered and R^2 represents the proportion of explained variation by each model. Model in bold is the one with the lowest AIC. Body size (i.e. total head length) has been included in all models so that results can be interpreted in terms of body condition (see Materials and Methods for details). Table **(B)** represents the intercept and slope estimates for the most general model (Body Mass ~ Body size + %Atlantic prey \times Fjord), along with the test statistics (t) and associated p-values.

DISCUSSION

Our study adds to the growing body of evidence that the ongoing Atlantification impacts the Arctic environment and in particular the marine ecosystem in West Svalbard (e.g., Gluchowska et al., 2016; Vihtakari et al., 2018; Griffith et al., 2019; Hop et al., 2019). Using long-term data from three Svalbard fjords differing in environmental conditions, we show a positive relationship between the Atlantic Water Index, a proxy of Atlantic Water inflow, in all fjords and the amount of Atlantic prey in the little auk chick diet. These Atlantic prey items were generally more abundant in the more Atlantic Kongsfjorden and Isfjorden fjords as compared to the more Arctic Hornsund. While Arctic prey items were dominant in most years, little auk chick diet contained more Atlantic prey, and notably more *C. finmarchicus*, during years of high Atlantic Water inflow. The proportion of Atlantic prey had a significant negative impact on adult body mass, but the effect size was small resulting in only a few grams reduction in years with high AWI. Moreover, the proportion of Atlantic prey was negatively associated with the chick survival though only when considering the survival until 21 days of age (data available for Hornsund only). When considering the survival until 15 days of age (in Hornsund and Isfjorden), the effect was non-significant. Finally, the chick growth rate (data available for Hornsund only) was also

TABLE 6 | Effect of the individual proportion of Atlantic prey in the little auk (chick) diet on chick survival (to 15 days) in two western Svalbard fjords (Hornsund and Isfjorden).

(A)				
Model	np	AIC	Δ AIC	R ²
Chick survival ~ 1	1	656.77	16.15	–
Chick survival ~ Fjord	2	640.62	0.00	0.02
Chick survival ~ %Atlantic prey (annual mean)	2	652.20	11.58	<0.01
Chick survival ~ %Atlantic prey (annual mean) + Fjord	3	642.18	1.56	0.02
Chick survival ~ %Atlantic prey (annual mean) + Fjord + %Atlantic prey × Fjord	4	641.88	1.26	0.02
(B)				
Variables	Estimate	SE	z	p
Intercept-Hornsund	3.29	0.33	9.92	<0.001
Intercept-Isfjorden	1.85	0.29	6.31	<0.001
Annual mean %Atlantic prey -Hornsund	-4.47	2.65	-1.68	0.09
Annual mean %Atlantic prey -Isfjorden	<0.001	1.22	0.001	0.99

Data ($n=1203$) are from 2005-2020 for Isfjorden and 2006-2020 for Hornsund (no data in 2014). Results are from mixed models based on a binomial error distribution (see Materials and Methods for details) and all models include year as a random effect. In **(A)**, np represents the number of fixed parameters, AIC is the Akaike's Information criterion, Δ AIC is the difference between the AIC of a given model and the lowest AIC of all models considered and R² represents the proportion of variation explained by each model. Model in bold is the one with the lowest AIC. Table **(B)** represents the intercept and slope estimates for the most general model, along with the test statistics (z) and associated p -values.

negatively related to the proportion of Atlantic prey in the chick diet (though the effect was only marginally significant) with the growth rate decreasing from approximately 6 grams/day to less than 5 grams/day when the inflow increased from 5 to 25%. Our results thus indicate potential fitness costs associated with the Atlantification of the western Svalbard fjords. These costs seemed especially pronounced during the later part of the chick-rearing period (between 15 and 21 days of age) when the energetic needs of the chicks are at their highest (Konarzewski et al., 1993). It remains unknown, however, whether these costs were similar in all fjords. Even though our results indicate comparable relationship between the Atlantic Water inflow, the proportion of Atlantic prey in the chick diet and the decrease in adult body condition in all three fjords, this does not imply that similar effects on chick growth and survival, and thus similar fitness costs, should be expected. Additional data on chick growth and/or on chick survival in the later part of the chick rearing period would be needed in the other fjords to assess whether or not the Atlantification bears the same costs for all little auk colonies.

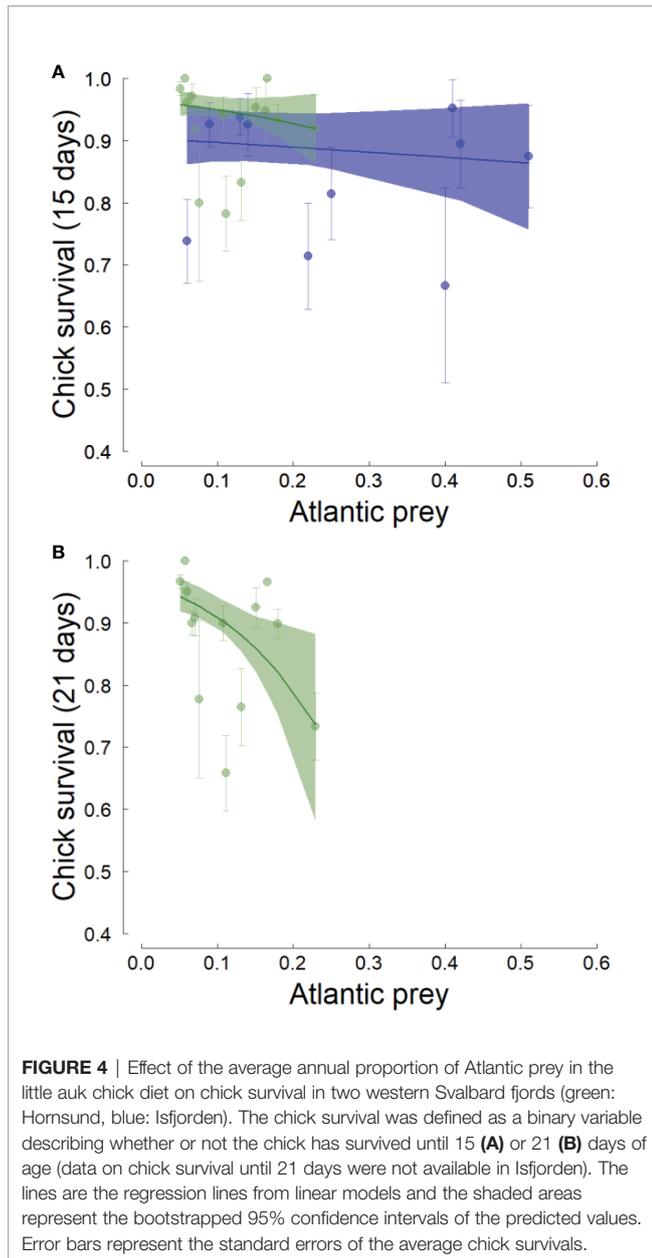
Our study identified negative relationships between the average proportion of Atlantic prey in chick diet in a given year and chick growth and survival. Testing for such relationships with diet data at the individual level (i.e. testing for a relationship between the diet of a given chick and its body condition or survival probability) could be potentially useful to confirm the potential mechanism linking the Atlantic Water inflow, the chick diet and their survival probability or growth rate. Such data would require sampling the food brought back to the chick by adults breeding in known nests and where chicks would be accessible.

Suboptimal Atlantic Prey

Our results confirm previous observations made in Svalbard fjords that were generally based on the comparison of two types of years (“warm” versus “cold”), or two types of fjords (one strongly influenced by the Atlantic Water inflow and one not). These earlier observations have shown that the proportion of *C. glacialis* in the chick diet is higher and the chick meals have higher energy content in Hornsund compared to Kongsfjorden (Karnovsky et al., 2011) and Magdalenefjorden, a fjord north of Kongsfjorden, largely influenced by Atlantic Water (Kwasniewski et al., 2010; Kidawa et al., 2015). Furthermore, the food loads delivered to the chicks are generally less energy-rich in Hornsund in warmer seasons (Jakubas et al., 2007; Kidawa et al., 2015; but see Wojczulanis-Jakubas et al., 2010) which in turn may be associated with a lower chick survival (Kidawa et al., 2015). All these results indicate that the little auk chick diet is more energy-rich when *C. glacialis* is more abundant (Kwasniewski et al., 2012). Chick diet composition of little auks from the main breeding colonies in Greenland and Svalbard shows that Atlantic prey, and more specifically *C. finmarchicus*, serve as a sub-optimal prey for little auks (Karnovsky et al., 2003; Frandsen et al., 2014) requiring a higher foraging effort from the parents (Karnovsky et al., 2010; Karnovsky et al., 2011). Our results support these findings and indicate that the adult little auks were in poorer condition when the Atlantic Water inflow was high, and that this may be a consequence of a higher foraging effort. Searching for the preferred prey, *C. glacialis*, among abundant but less favoured *C. finmarchicus*, may indeed require more time and energy (Jakubas et al., 2011; Karnovsky et al., 2011). Alternatively, the apparent negative effect of the Atlantic inflow on little auk body mass could be driven, at least partly, by changes in the proportion of non-breeders (including failed breeders) in our samples of captured birds. This would, however, assume that these birds have a lower body mass than breeders and that the proportion of non-breeders captured increased with a higher Atlantic inflow. We have no evidence for this and additional data on non-breeder body mass and on the probability to breed as a function of environmental conditions would be needed.

Adult Little Auks Prioritize Self-Maintenance

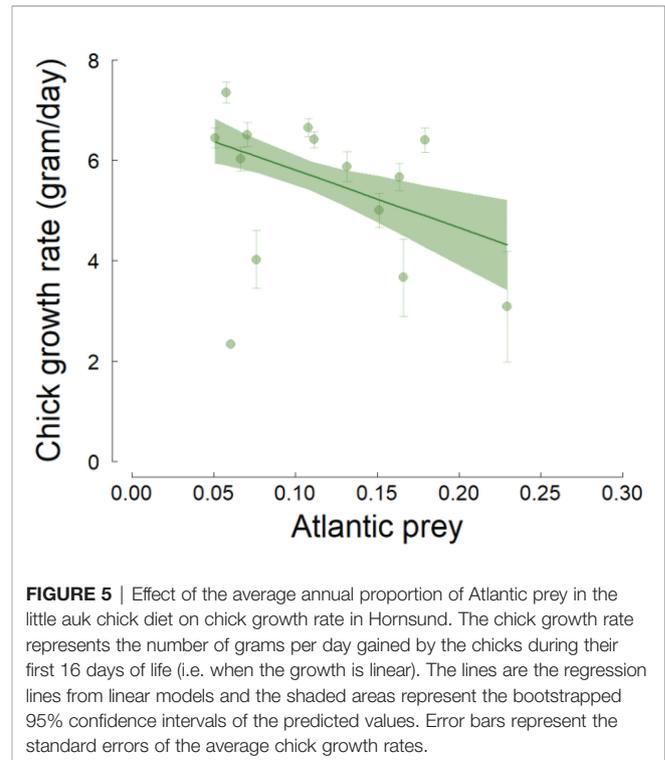
The potential increase in the little auk foraging effort when Atlantic waters, and thus Atlantic prey, are more prevalent is supported by the negative association between adult body mass and the proportion of Atlantic prey in the chick diet. However, even though this relationship was significant, the effect size was small and a large increase in the proportion of Atlantic prey in the chick diet only slightly decreased adult body mass. This indicates that, when foraging conditions deteriorate, even if there is a slight cost in terms of lower body condition, breeding little auks may prioritize their self-maintenance, and thus own condition, which could be at the cost of a lower chick growth and survival. This would represent the expected resource allocation strategy for such a long-lived species (Stearns, 1992) and fits with previous observations (Welcker et al., 2009; Kidawa et al., 2015). Therefore, little auks may increase their foraging effort to adjust to deteriorating environmental conditions (i.e. when the inflow of Atlantic Waters



increases) but they would do it only until a certain extent that is unlikely to jeopardize their own survival. The fitness costs of the Atlantification of Svalbard may thus be mostly paid by the chicks. Our results from Hornsund fit such interpretation but additional data would be needed to confirm such potential costs, and to better understand the shapes of such relationships between Atlantic inflow, foraging behaviour and reproductive investment, that are likely complex.

Conclusions

The Atlantification is not only influencing Svalbard, but similar changes are occurring in the other parts of the Arctic (Ferguson et al., 2010; Møller and Nielsen, 2020; Polyakov et al., 2020;



Ingvaldsen et al., 2021). Even though inter-annual variations have been very large, there has been a positive trend in the inflow of Atlantic Water into the Arctic in the last decades (Ingvaldsen et al., 2021). The little auk, an endemic Arctic species, is negatively affected by such Atlantification and even if they can be plastic and to some extent adapt their behaviour to new environmental conditions (e.g., Grémillet et al., 2012; Grémillet et al., 2015; Jakubas et al., 2017), they may still pay important fitness costs when the marine environment and associated prey become more “boreal” (i.e. north temperate). This may ultimately lead to population decline and local extinctions. The southernmost little auk population breeding in Iceland was extirpated at the end of the 20th century, possibly as a consequence of both ocean warming (that has affected the abundance and distribution of little auk prey) and human harvest (Jakubas et al., 2022). However, our work also showed that a large part of the inter-annual variations in little auk chick diet, body mass or chick growth/survival could not be accounted for by our Atlantic Water inflow index. Two explanations can be proposed to explain this low explanatory power.

First, this index was defined in our study as the proportion of Atlantic waters inside the fjords. However, little auk may also use areas outside the fjords to forage where oceanographic conditions and the influence of Atlantic water masses may be different. Creating an AWI index based on the actual foraging areas of the little auks for each specific colony would require identifying these foraging areas every year (through GPS-tracking for example). Although possible, this would be a very challenging study.

Second, the Atlantic Water inflow is only one among many factors that have the potential to affect little auk foraging and life-history. Other environmental parameters like the sea-ice

(Amélineau et al., 2016; Ramírez et al., 2017; Amélineau et al., 2019; Jakubas et al., 2020), or the weather conditions (Konarzewski and Taylor, 1989) also affect their foraging behaviour or chick growth rate. All these parameters may interact with each other and also have non-linear and complex effects. Disentangling their respective role should be a priority in future research, and this can only be achieved through the use of long-term data. Such data are essential to improve our understanding of the ongoing Atlantification, or borealization, and its consequences on Arctic endemic species like the little auk.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by Mattilsynet (Norwegian Food Safety Authority, in charge of animal welfare).

AUTHOR CONTRIBUTIONS

SD: conception, statistical analyses and draft the first version of the manuscript. SD, KW-J, DJ, HS, JW, KB-S, and PB: design of the study. MV: construction of the AWI index and contributed in data collection. KB-S and RB: diet data analyses. SD, KW-J, DJ, HS, JW, JH, AS, RS, NK, and DK: data collection. All authors revised the manuscript critically and had substantial impact on the final draft of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.878746/full#supplementary-material>

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