

# Relationships between isotopic ratios, body condition and breeding success in a High Arctic seabird community

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**ABSTRACT:** Predators such as seabirds are often used as bio-indicators of the marine environment. This is based on the assumption that changes in seabird populations are driven by changes in their prey. We tested this assumption in a High Arctic seabird community by assessing the relationships between the diet, body condition, and breeding performance of 4 ecologically different species: the little auk *Alle alle*, black-legged kittiwake *Rissa tridactyla*, Brünnich's guillemot *Uria lomvia*, and glaucous gull *Larus hyperboreus*, breeding in Svalbard, Norway. Interannual changes in seabird diet (2009–2015) were assessed by estimating their carbon and nitrogen isotopic ratios ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) during the breeding and non-breeding seasons (i.e. using blood and feather tissues). We found interannual variation in the isotopic ratios during both seasons in all 4 species. These variations differed among species, thus suggesting dietary changes, instead of changes in isotopic baselines, as the most plausible mechanism underlying such patterns. We also found that seabirds had a lower average hatching success when the average  $\delta^{15}\text{N}$  during the previous non-breeding season was higher. Our results suggest that changes in the average prey composition during the non-breeding season may partially explain changes in breeding performance of Svalbard seabirds.

**KEY WORDS:** Diet · Marine birds · Svalbard · Carry-over effects · Reproductive output · Stable isotopes · Trophic level · Nitrogen · Carbon

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## 1. INTRODUCTION

Food abundance and quality are key determinants of animal demography and population dynamics (Martin 1987, Zera & Harshman 2001, Ruffino et al. 2014, Louzao et al. 2015). Poor food availability or quality generally results in reduced breeding outcomes across species (e.g. snails, Martone & Micheli 2012; reindeer, Ballesteros et al. 2013; swallows, Winkler et al. 2014; water fleas, Choi et al. 2016). However, in many trophic systems, and especially in marine food webs, changes in resource availability

are very difficult to monitor due to the dynamic nature of primary and secondary production at large spatial scales (Nicol et al. 2000, Perry et al. 2010, Afán et al. 2015). The breeding performance of high-trophic level predators may respond to changes in the structure and function of an ecosystem, including the availability of the resources on which they rely (e.g. Furness & Camphuysen 1997, Thompson & Ollason 2001, Piatt et al. 2007, Parsons et al. 2008). This has led to the concept of bio-indicator species, which has been widely applied to seabirds (Bost & Le Maho 1993, Durant et al. 2009, Fort et al. 2016). How-

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ever, this concept does not always apply (Piatt et al. 2007), and relationships between food and reproduction may be more complicated than expected. Indeed, breeding performance per se may not be sufficient to infer changes in resource availability (Gremillet & Charmantier 2010), as predators may compensate for poor resource availability by increasing foraging effort, or by switching prey type or foraging area (e.g. Furness & Camphuysen 1997, Schwemmer & Garthe 2008, Erikstad et al. 2009). Thus, data on diet composition should also be incorporated to detect such changes.

The analysis of naturally occurring stable isotopes of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) constitutes an integrative tool that can be used to estimate the trophic niche (i.e. the portion of the ecological niche that describes the food resources and foraging habitat of a given consumer (Hobson & Bond 2012, Cherel et al. 2014, Swanson et al. 2015). The isotopic niche projects the n-dimensional trophic niche onto a reduced number of axes, e.g.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , and can be interpreted as an n-dimensional simplification of, and thus a proxy for, the trophic niche (Newsome et al. 2007). In the marine environment, a natural inshore-offshore gradient in  $\delta^{13}\text{C}$  may be used to identify the foraging area of marine predators (lower values often indicating more offshore foraging, but see Saupe et al. 1989, Dunton et al. 2006), while  $\delta^{15}\text{N}$  varies according to trophic position (higher values indicate higher trophic position; Newsome et al. 2007, Hussey et al. 2014). Stable isotopes integrate dietary information over different time scales depending on the tissue type (Bearhop et al. 2004, Newsome et al. 2007). Isotopic ratios from blood provide information for a period of 2 wk to 1 mo preceding the sampling event (Bearhop et al. 2002, Ogden et al. 2004), whereas isotopic ratios from body feathers reflect the diet of an individual during the period of feather growth (which can take place several months before the actual sampling event; Hobson & Bond 2012). Thus, by sampling different tissues, a consumer's isotopic ratios may provide insight into its foraging ecology at varying temporal scales.

Here, we tested whether interannual changes in the isotopic ratios were associated with variation in the body condition and breeding success of a High Arctic seabird community. We considered 4 seabird species breeding in Svalbard, Norway: the little auk *Alle alle*, black-legged kittiwake *Rissa tridactyla*, Brünnich's guillemot *Uria lomvia*, and glaucous gull *Larus hyperboreus*. These species are characterized by different foraging and feeding habits (see details

in Section 2 and Wold et al. 2011). The Arctic in general, and the Svalbard Archipelago in particular, are experiencing rapid and directional environmental changes (Nordli et al. 2014, Laidre et al. 2015, Descamps et al. 2017a), with changes in seabirds' diet and foraging habits already documented (Vihtakari et al. 2018). This area provides us with a unique opportunity to investigate how potential changes in seabird diet can affect their condition and breeding performance.

First, we assessed interannual changes in carbon and nitrogen isotopic ratios during the breeding and non-breeding seasons using 7 yr of data (2009–2015). We considered isotopic ratios from blood and feather samples to be representative of the average diet during part of the breeding and non-breeding seasons, respectively. Second, we tested the hypothesis that variation in seabird body condition and breeding performance can be explained by inter-annual changes in their isotopic ratios during the breeding and non-breeding seasons. Diet during the non-breeding season may potentially affect breeding performance indirectly through carry-over effects on individual body condition (e.g. Sorensen et al. 2009, Kowenbergh et al. 2013, Salton et al. 2015), whereas diet during the breeding season may influence breeding performance both directly via chick provisioning (Martin 1987) and indirectly through an effect on parent body condition, which could translate into lower feeding activity (Moody et al. 2012).

## 2. MATERIALS AND METHODS

### 2.1. Study sites and species

The study took place during 7 consecutive years (2009–2015) at 4 breeding sites in west Spitsbergen, Svalbard (Fig. 1), Norway, during incubation and chick-rearing, from mid-June to late July (little auks *Alle alle*, black-legged kittiwakes *Rissa tridactyla* and Brünnich's guillemots *Uria lomvia*) and from late May to late June (glaucous gulls *Larus hyperboreus*). Little auks and black-legged kittiwakes were caught in Isfjorden (Bjørndalen; 78° 24' N, 15° 34' E, and Grunantbyen; 78° 17' N, 15° 10' E, respectively), Brünnich's guillemots at the Ossian Sarsfjellet colony in Kongsfjorden (78° 93' N, 12° 44' E), and glaucous gulls at various locations in the Kongsfjorden area. However, not all species were caught in all 7 years of the study (see Supplement 1 at [www.int-res.com/articles/suppl/m613p183\\_supp.xls](http://www.int-res.com/articles/suppl/m613p183_supp.xls), Table S1). Maximum foraging distance to the breeding site ranges from

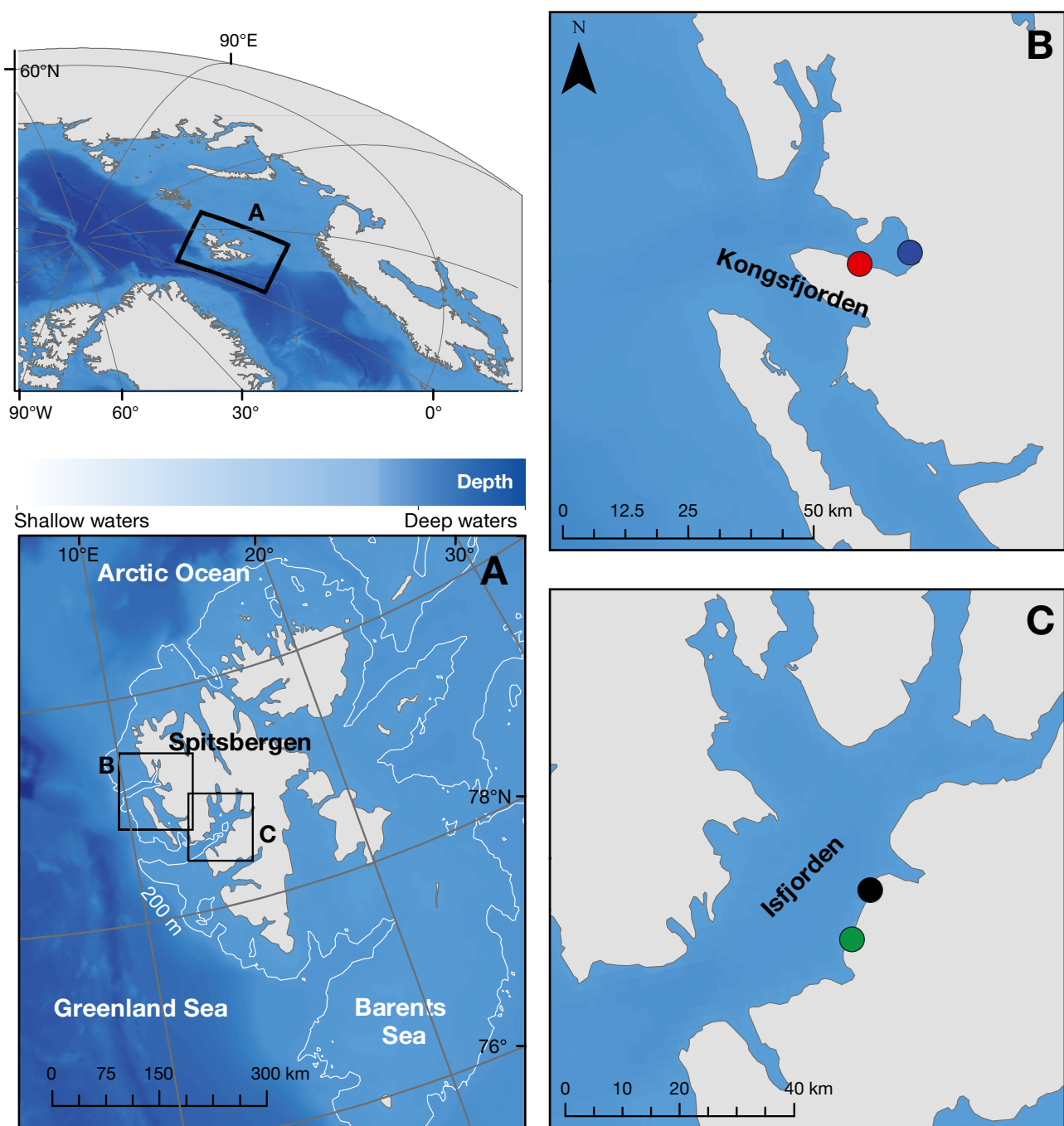


Fig. 1. Breeding sites of little auks *Alle alle* (black circle), black-legged kittiwakes *Rissa tridactyla* (green circle), Brünnich's guillemots *Uria lomvia* (blue circle), and glaucous gulls *Larus hyperboreus* (red circle) included in the study (Svalbard Archipelago). Glaucous gulls were all breeding within Kongsfjorden and not in a specific colony

<20 km in guillemots (Ramírez et al. 2017) to ca. 200 to 300 km in little auks (Jakubas et al. 2016) and kittiwakes (Goutte et al. 2014). No movement data were available for glaucous gulls, but they likely forage most of the time within fjords (S. Descamps pers. obs.). Spitsbergen guillemots spend the winter north

of Iceland and in southwest Greenland (Frederiksen et al. 2016), little auks in the Greenland Sea (Fort et al. 2013), kittiwakes on the Great Banks, east of Canada (Frederiksen et al. 2012), and glaucous gulls disperse widely over most of the northeast Atlantic (B. Moe pers. comm.).

The little auk is a colonial alcid, which lays a single egg in rocky crevices in talus slopes (Stempniewicz 1981), and preferentially forages on high-lipid copepods associated with Arctic waters (Harding et al. 2009, Jakubas et al. 2012), especially *Calanus glacialis*, which represents >80% of the chick diet in Bjørndalen (Hovinen et al. 2014). Black-legged kittiwakes are colonial cliff-breeders that typically lay 1 or 2 eggs in Svalbard (Strøm 2006). They feed mostly on fish, crustaceans, and other marine invertebrates (Reiertsen et al. 2014, Vihtakari et al. 2018). Brünnich's guillemots are colonial cliff-breeders and lay a single egg. Their diet consists mainly of fish and crustaceans (Anker-Nilssen et al. 2000). Glaucous gulls breed in or close to other seabird colonies, often on an elevated point at the top of a cliff or on rocks beneath the colony, and lay 1 to 3 eggs (Strøm 2006). Gulls are generalist feeders, and their diet consists of a wide variety of prey from both marine and terrestrial food webs: fish, mollusks, crustaceans, insects, offal, and eggs, chicks, and adults of other seabird species (Anker-Nilssen et al. 2000). Black-legged kittiwakes and glaucous gulls are surface feeders, while little auks and Brünnich's guillemots are divers. In all of our study species, females and males share the incubation and chick-rearing duties, and they molt their chest feathers during the non-breeding season (Dwight 1925, Gaston & Jones 1998, Coulson 2011). The molt pattern is not always known in detail, but there is typically a partial molt of body feathers during the pre-breeding season (Dwight 1901, Gaston & Jones 1998), and chest feathers of our 4 study species are therefore expected to have grown during this period (spring).

## 2.2. Bird captures

Birds were caught with a noose-carpet (little auks), a noose pole (black-legged kittiwakes and Brünnich's guillemots), or an air-propelled net or a noose triggered at a distance (glaucous gulls). All captured birds were marked with a combination of a stainless steel ring and plastic color ring(s). Birds were captured and sampled for feathers and blood only once annually during the breeding season (June–July). The annual number ( $\pm$ SD) of individuals caught averaged  $15 \pm 2$  for little auks,  $15 \pm 8$  for kittiwakes,  $14 \pm 7$  for guillemots, and  $18 \pm 4$  for glaucous gulls. A total of 4 little auks, 21 kittiwakes, 13 guillemots, and 1 glaucous gull were sampled more than once for stable isotopes during the study period (average number of replicates and their range: 2.3 [2, 3] for little

auks, 2.4 [2, 4] for guillemots, 3.3 [2, 5] for kittiwakes, and 2 replicates for 1 glaucous gull). Birds were weighed using a Pesola scale ( $\pm 1$  g for little auks,  $\pm 5$  g for kittiwakes and guillemots, and  $\pm 10$  g for glaucous gulls), and the length of their wing (i.e. length of the longest primaries) was measured with a wing rule (to the nearest mm). We defined bird body condition as the residual from a linear regression of individual body mass on individual capture date (in Julian days) and wing length (a proxy of body size; Jakob et al. 1996, Schulte-Hostedde et al. 2005; see Supplement 2 at [www.int-res.com/articles/suppl/m613p183\\_supp.pdf](http://www.int-res.com/articles/suppl/m613p183_supp.pdf), Fig. S1).

Feather and blood samples were collected for analyses of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Blood samples (0.2 to 0.5 ml) were collected from the brachial vein and stored in 70% ethanol, or frozen in Eppendorf tubes ( $-20^\circ\text{C}$ ; kittiwake blood only), until preparation for stable isotope analyses (70% ethanol does not alter the isotopic composition of tissues; Hobson et al. 1997). Five feathers were taken randomly from the chest (or from the head; little auk feathers in 2009 and 2011) and stored in sealed plastic bags. Little auk chest and head feathers had similar isotopic ratios (Wilcoxon rank sum test; carbon:  $W = 310.5$ ,  $p = 0.63$ ; nitrogen:  $W = 338.5$ ,  $p = 0.99$ ; compared when both feather types were collected in 2013 and 2014 from 27 individuals in total), and thus, the feather type used to infer the little auk's diet should not influence the interpretation of isotopic data.

## 2.3. Nest surveys

Nests were located and marked during the incubation period and monitored every 2 to 4 d from early/mid-incubation until hatching (glaucous gulls) or until the mid-chick rearing period (little auks, kittiwakes and guillemots) to estimate hatching success and chick survival until 15 d of age. The chick rearing period averages 27–30 d for little auks, 35–49 d for black-legged kittiwakes, and 16–30 d for Brünnich's guillemots (i.e. chicks leave the colony with 1 parent at 16–30 d of age but stay under 1 parent's supervision for another 4 wk at least; del Hoyo et al. 1996). Our nest survey thus allowed us to estimate the egg and early chick survival for little auks, kittiwakes, and guillemots. Monitoring stopped at hatching for glaucous gulls, and only hatching success was available to assess the breeding performance of glaucous gulls.

Light-burrow scopes (Moritex Europe; little auks only) or direct observations (other species) were used

to determine the presence of egg(s) or chick(s) in the nest. The annual number ( $\pm$ SD) of nests monitored averaged  $34 \pm 8$  for little auks,  $47 \pm 11$  for black-legged kittiwakes,  $52 \pm 11$  for Brünnich's guillemots, and  $36 \pm 11$  for glaucous gulls.

#### 2.4. Stable isotope analyses

Whole blood was used in the analyses, except in little auks (2011), guillemots (2010), and kittiwakes (2009–2015), for which the red blood cells (RBCs) were analyzed. Because whole blood is made up primarily of RBCs (in terms of dry mass, upon which isotopic measurements are made), we assumed that whole blood and RBCs have similar isotopic ratios. Removing these years (little auk data from 2011 and guillemot data from 2010) from the analyses did not change our results (see Supplement 3, Table S4).

Lipid content in tissues can strongly bias  $\delta^{13}\text{C}$  measurements (Post et al. 2007) and, therefore, their interpretation in trophic studies (Tarroux et al. 2010). Thus, feathers were washed in a 2:1 chloroform:methanol solution to remove surface lipids and were cut into small pieces with fine scissors before encapsulation. Because there can be a strong inter-feather variation in isotopic ratios (Jaeger et al. 2009), all feathers collected from the same individual in a given season were pooled together and feather pieces homogenized before proceeding with encapsulations. All blood samples (RBC and whole blood) included in the analyses had C/N ratios  $<3.9$ , and thus, there was no need to extract lipids (see Supplement 1, Table S1; Logan et al. 2008). The  $\delta^{13}\text{C}$  values of feather samples for which the lipid removal was deemed incomplete, based on their C/N ratios being  $\geq 3.9$ , were excluded from further analyses ( $N = 42$  of 281 samples). Their  $\delta^{15}\text{N}$  were maintained in the analyses as nitrogen isotopic ratios are only marginally affected by lipid concentration (Tarroux et al. 2010).

Each sample (0.7 mg) was encapsulated before combustion in a Flash HT Plus elemental analyzer coupled to a Delta-V Advantage isotope ratio mass spectrometer via a CONFLO IV interface (Thermo Fisher Scientific). All analyses were run at the Stable Isotopes Laboratory (LIE) at the Doñana Biological Station, Seville, Spain.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  are expressed in ‰ of the deviation from isotopic ratios of international standards, i.e. Pee Dee Belemnite carbonate (PDB) for carbon and atmospheric air (AIR) for nitrogen (DeNiro & Epstein 1978). The following internal standards were used, once calibrated with interna-

tional standards supplied by the International Atomic Energy Agency: EBD-23 (cow horn), LIE-BB (whale baleen), and LIE-PA (bird feathers). Replicate assays of standards routinely inserted within the sampling sequence indicated analytical measurement errors of  $\pm 0.1\text{‰}$  and  $\pm 0.2\text{‰}$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively. Consumer-prey discrimination factors were assumed to be similar for all seabird species. In addition, we did not compare the isotopic ratios among tissues, and all isotopic values presented throughout are thus uncorrected values.

Individuals were sampled only once during the breeding season at different time periods (most of them being sampled during chick-rearing). Previous studies found significant individual specialization in the diet of little auks, Brünnich's guillemots, black-legged kittiwakes, and glaucous gulls (Bustnes et al. 2000, Woo et al. 2008, Ceia & Ramos 2015, Bond et al. 2016), which is also confirmed by our own stable isotope data for Svalbard kittiwakes (see Supplement 4, Fig. S2). Such individual specialization supports the assumption that our single measures of individual isotopic ratios per individual during a breeding or non-breeding season are a good proxy of their diet.

#### 2.5. Statistical analyses

All data processing and statistical analyses were performed in R.3.2.4 (R Core Team 2016).  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  during the breeding season ( $\delta^{13}\text{C}_{\text{breeding}}$  and  $\delta^{15}\text{N}_{\text{breeding}}$ ) were adjusted for the sampling date to remove the intra-seasonal variation in these 2 variables during the breeding season (see Supplement 5, Figs. S3–S5), and the residuals were used in all models described below.

##### 2.5.1. Interannual variation in isotopic ratios, body condition and reproductive performance

To test for interannual variation in  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and body condition during the breeding and non-breeding seasons for each species, we ran generalized linear mixed-effect models using individual-level data (GLMM, with an identity link function and Gaussian error distribution) with year, species, and their interaction as fixed effects and bird identity as a random factor (to take into account non-independence in repeated measurements on the same individuals). We ran separate GLMMs for breeding (blood isotopic ratios) and non-breeding seasons (feather isotopic ratios) using the function *lmer* in

the package 'lme4' (Bates et al. 2011). To test for interannual differences in reproductive performance (hatching success and chick survival), we ran linear models using 1 randomly selected year per nest (among all years in which the nest was monitored) because mixed models including the nest as a random factor could not converge. The hatching success represents the probability of hatching at least 1 chick, while the chick survival represents the probability of keeping at least 1 chick alive until 15 d of age.

We performed model selection with the Akaike Information Criterion (AIC). If the difference in AIC (or AIC<sub>C</sub>, the AIC adjusted for small samples) values between 2 models was <2, we considered the models to have equal statistical support, and in the case of nested models, the simplest was preferred (Burnham & Anderson 2002).

### 2.5.2. Relationships between changes in isotopic ratios, body condition and breeding performance

We tested for the effect of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (during the breeding and non-breeding seasons) on seabird body condition, hatching success and chick survival by running GLMs (with an identity link function and Gaussian error distribution) for the breeding and non-breeding seasons separately, using the annual means. We included the species as a covariate. The best model was selected using the AIC following the procedure described above. We did not test for these relationships using individual level data because most birds sampled for blood and feathers were captured late in the season (during chick-rearing) and were thus mostly successful breeders. As a consequence, the breeding success of these sampled birds overestimated the average breeding success in each colony. Therefore, we considered the average annual hatching success and chick survival based on all nests

monitored within each colony (see details in Section 2.3).

All data are available in Supplement 1 (Tables S1–S3).

Table 1. Interannual variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopic ratios (during the breeding and non-breeding seasons), body condition and reproductive performance of Svalbard seabirds. For  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and body condition, results are from generalized mixed effect models that include bird identity as a random effect. For reproductive variables, results are from linear models; only 1 value per nest (among all available years) was randomly sampled to avoid pseudo-replication (mixed models could not be used due to convergence issues). Variables  $\delta^{13}\text{C}_{\text{breeding}}$  and  $\delta^{15}\text{N}_{\text{breeding}}$  have been adjusted for the sampling date (to remove the intra-seasonal variation in isotopic ratios during the breeding season). Body condition represents the body mass adjusted for capture date and body size (wing length). Hatching success represents the probability of hatching at least 1 chick, and the chick survival variable represents the probability of having at least 1 chick survive up to 15 d of age. df: degrees of freedom, AIC: Akaike Information Criterion,  $\Delta\text{AIC}$ : the difference in AIC from the model with the lowest AIC

Response variable	Fixed effects	df	AIC	$\Delta\text{AIC}$
$\delta^{13}\text{C}_{\text{breeding}}$ (n = 250 from 205 individuals)	Year × Species	20	−45.18	0.00
	Year + Species	10	43.19	88.37
	Year	8	50.32	95.50
	Species	4	210.52	255.70
	Null (intercept only) model	2	204.52	249.70
$\delta^{15}\text{N}_{\text{breeding}}$ (n = 251 from 205 individuals)	Year × Species	20	321.30	0.00
	Year	8	382.62	61.32
	Year + Species	10	384.99	63.69
	Null (intercept only) model	2	446.71	125.41
$\delta^{13}\text{C}_{\text{non-breeding}}$ (n = 239 from 212 individuals)	Year × Species	20	525.27	0.00
	Year + Species	10	526.01	0.74
	Species	4	534.27	9.00
	Null (intercept only) model	2	698.82	173.55
	Year	8	701.13	175.86
$\delta^{15}\text{N}_{\text{non-breeding}}$ (n = 281 from 224 individuals)	Year × Species	20	699.45	0.00
	Species	4	720.79	21.34
	Year + Species	10	725.89	26.44
	Year	8	920.29	220.84
	Null (intercept only) model	2	922.45	223.00
Body condition (n = 301 from 288 individuals)	Null (intercept only) model	2	2674.23	0.00
	Year × Species	20	2680.23	6.00
	Year	8	2680.29	6.06
	Species	4	2685.71	11.48
	Year + Species	10	2686.16	11.93
Hatching success (n = 305 from 305 nests)	Year × Species	21	799.37	0.00
	Year + Species	9	853.20	53.83
	Species	4	922.37	123.00
	Year	7	946.06	146.69
	Null (intercept only) model	1	985.58	186.21
Chick survival (n = 194 from 194 nests)	Year × Species	16	455.66	0.00
	Year + Species	9	506.73	51.07
	Species	3	526.59	70.93
	Year	7	565.66	110.00
	Null (intercept only) model	1	565.08	109.42

### 3. RESULTS

Isotopic ratios of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  during the breeding and non-breeding seasons varied among years, and these variations were generally not parallel among species (i.e. the interaction between year and species was selected for all variables considered with a  $\Delta\text{AIC} > 2$  compared to the null model or model with year only; Table 1; see Supplement 6 at [www.int-res.com/articles/suppl/m613p183\\_supp.pdf](http://www.int-res.com/articles/suppl/m613p183_supp.pdf), Fig. S6). Only values of  $\delta^{13}\text{C}$  during the non-breeding season indicated potential parallel variation among species (i.e. equivalent statistical support for the additive and interactive effect, Table 1; Supplement 6, Fig. S6). However, the amplitude of these interannual variations was limited (Fig. 2). The body condition of the

4 species considered did not vary among years (Table 1; Supplement 6, Fig. S6), while the hatching success and chick survival varied among years and not in parallel among species (Table 1; Supplement 6, Fig. S6).

Interannual variations in  $\delta^{13}\text{C}$  during both the breeding and non-breeding seasons and interannual variation in  $\delta^{15}\text{N}$  during the breeding season were not related to Svalbard seabird body condition or reproduction in our Svalbard seabird study system (Table 2). However, we found a negative relationship between the interannual variation in  $\delta^{15}\text{N}_{\text{non-breeding}}$  and the average seabird hatching success (slope of  $0.59 \pm 0.20$  SE; Table 2, Fig. 3). Interannual variation in  $\delta^{15}\text{N}_{\text{non-breeding}}$  explained more than a third of the interannual variation in hatching success ( $R^2 = 35\%$ ).

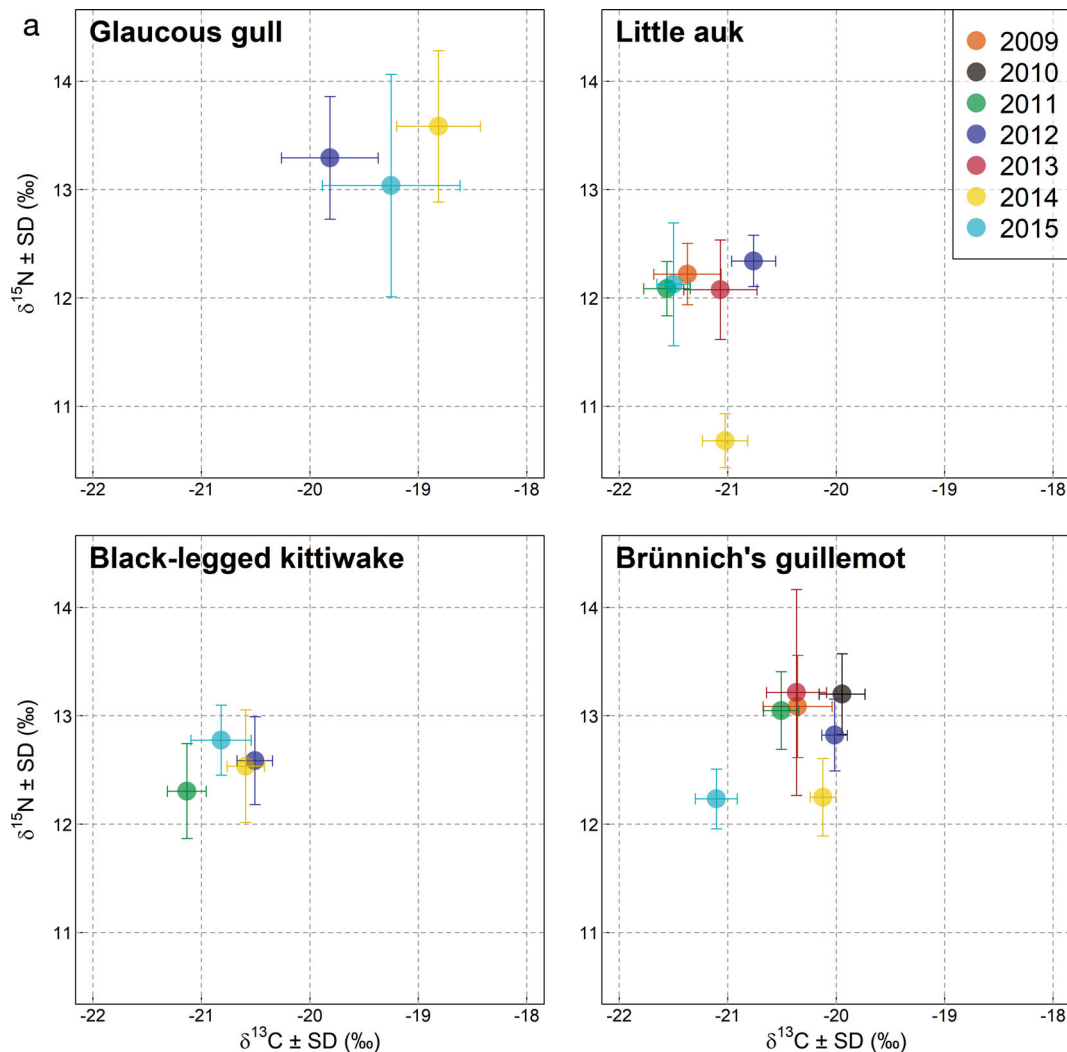


Fig. 2 (continued on next page). Average stable isotopic ratios ( $\pm 1$  SD) of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) in little auks, black-legged kittiwakes, Brünnich's guillemots, and glaucous gulls during (a) breeding and (b) non-breeding seasons in 2009 to 2015. Dots represent individual values for each species and year

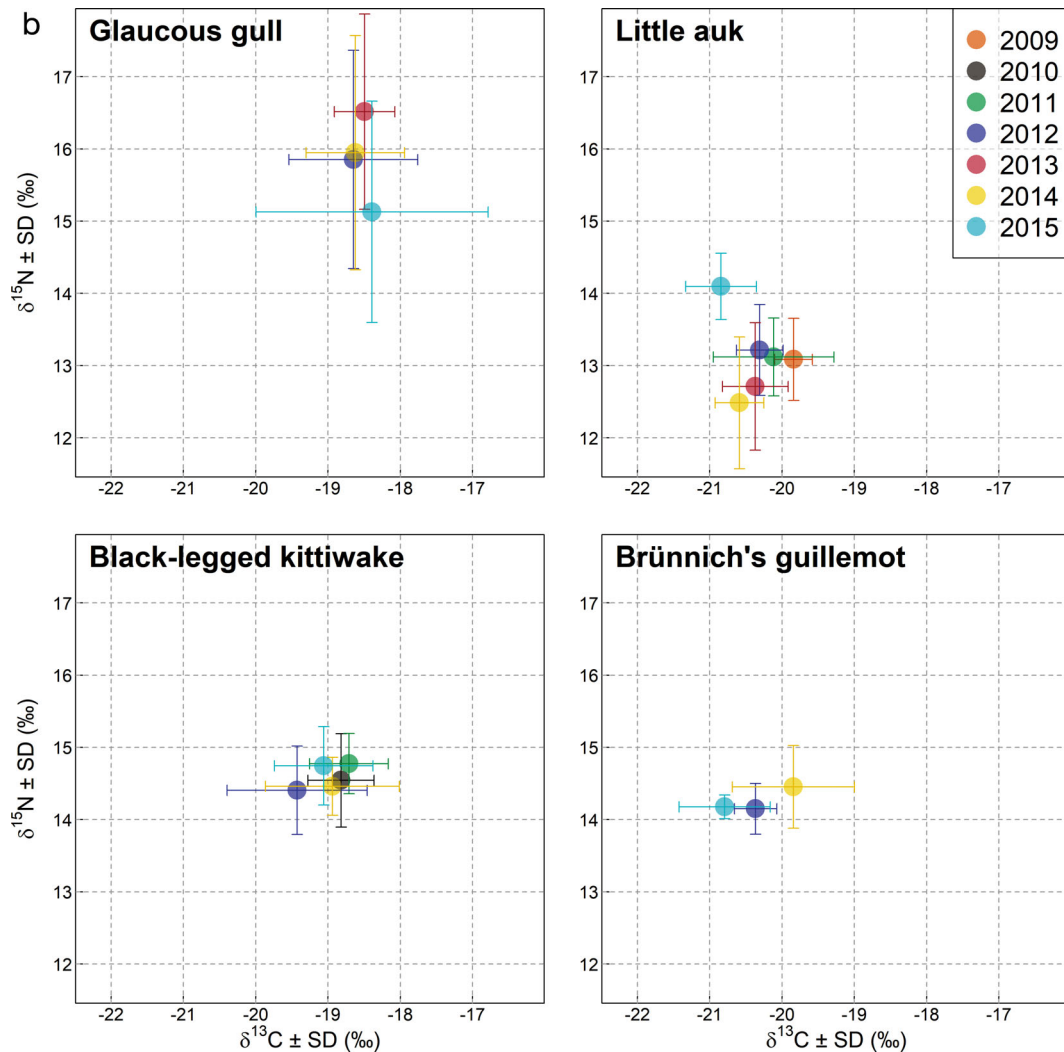


Fig. 2 (continued)

#### 4. DISCUSSION

We used 7 yr of isotope data ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) to investigate interannual dietary changes for 4 ecologically different seabird species from the High Arctic and their ultimate consequences in terms of breeding performance (hatching success and chick survival). The interspecific differences in feeding ecology likely explain the different variation in isotopic ratios we observed among species. Overall, the planktivorous, at-sea foraging little auks *Alle alle* had lower  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values than omnivorous glaucous gulls *Larus hyperboreus*, which forage both on land and at sea (Anker-Nilssen et al. 2000, Hovinen et al. 2014, Vihtakari et al. 2018). Intermediate  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in black-legged kittiwakes *Rissa tridactyla* and Brünnich's guillemots *Uria lomvia* likely reflect their diet, based on both fish and crustaceans, compared to that

of little auks (plankton) and glaucous gulls (from fish to birds). Although the feeding ecology of these 4 species may vary slightly between the summer and winter (Erikstad 1990, Gaston & Jones 1998), the similar isotopic patterns for both blood and feather samples suggested that the previous descriptions remain generally true independent of the season considered.

Isotopic composition also varied annually, although to a varying extent depending on the species, season, and isotope considered. For example, black-legged kittiwakes showed interannual variation of limited amplitude in  $\delta^{15}\text{N}$  during the breeding period (0.5‰), while  $\delta^{15}\text{N}$  values for little auks and Brünnich's guillemots for the same period showed larger variation ( $\geq 1.0\text{‰}$ ). In particular, the  $\delta^{15}\text{N}$  in summer was much lower in 2014 for little auks and in 2014 and 2015 for guillemots. The observed interannual variation in isotopic ratios of Svalbard seabirds may reflect



Table 2. Relationships between average annual carbon and nitrogen isotopic ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) during the breeding and non-breeding seasons and average seabird condition and reproductive performance in Svalbard. Results are from linear models, and all variables have been normalized (within species normalizing) so that models with only Species, 'Species +  $\delta^{13}\text{C}$ ' or 'Species +  $\delta^{15}\text{N}$ ' as fixed effects were not informative.  $\delta^{13}\text{C}_{\text{breeding}}$  and  $\delta^{15}\text{N}_{\text{breeding}}$  have been adjusted to the sampling date (to remove the intra-seasonal variation in these 2 traits during the breeding season). df: degrees of freedom, AIC<sub>C</sub>: Akaike Information Criterion corrected for small sample size,  $\Delta\text{AIC}_C$ : the difference in AIC<sub>C</sub> from the model with the lowest AIC<sub>C</sub>, and R<sup>2</sup>: the proportion of variance explained by the model

Response variable	n	Fixed effects	df	AIC <sub>C</sub>	$\Delta\text{AIC}_C$	R <sup>2</sup>		
Average body condition	17	Null (intercept only)	1	49.21	0.00			
		$\delta^{13}\text{C}_{\text{breeding}}$	2	51.17	1.96	<0.01		
		$\delta^{15}\text{N}_{\text{breeding}}$	2	50.64	1.43	0.12		
		$\delta^{13}\text{C}_{\text{breeding}} \times \text{Species}$	6	60.57	11.36	0.15		
		$\delta^{15}\text{N}_{\text{breeding}} \times \text{Species}$	6	62.61	13.40	0.43		
		$\delta^{13}\text{C}_{\text{non-breeding}}$	2	47.62	0.00	0.16		
	17	Null (intercept only)	1	47.95	0.33			
		$\delta^{15}\text{N}_{\text{non-breeding}}$	2	48.44	0.82	0.12		
		$\delta^{15}\text{N}_{\text{non-breeding}} \times \text{Species}$	8	69.38	21.76	0.45		
		$\delta^{13}\text{C}_{\text{non-breeding}} \times \text{Species}$	8	70.62	23.00	0.41		
		Average hatching success	17	Null (intercept only)	1	47.95	0.00	
				$\delta^{13}\text{C}_{\text{breeding}}$	2	49.80	1.85	0.04
$\delta^{15}\text{N}_{\text{breeding}}$	2			50.21	2.26	0.01		
$\delta^{15}\text{N}_{\text{breeding}} \times \text{Species}$	8			73.25	25.30	0.32		
$\delta^{13}\text{C}_{\text{breeding}} \times \text{Species}$	8			73.59	25.64	0.30		
$\delta^{15}\text{N}_{\text{non-breeding}}$	2			45.67	0.00	0.35		
19	Null (intercept only)	1	50.81	5.14				
	$\delta^{13}\text{C}_{\text{non-breeding}}$	2	53.36	7.69	<0.01			
	$\delta^{13}\text{C}_{\text{non-breeding}} \times \text{Species}$	8	75.85	30.18	0.23			
	$\delta^{15}\text{N}_{\text{non-breeding}} \times \text{Species}$	8	68.57	22.90	0.49			
	Average chick survival	15	$\delta^{15}\text{N}_{\text{breeding}}$	2	42.72	0.00	0.21	
			Null (intercept only)	1	43.53	0.81		
$\delta^{13}\text{C}_{\text{breeding}}$			2	45.89	3.17	0.02		
$\delta^{13}\text{C}_{\text{breeding}} \times \text{Species}$			6	56.46	13.74	0.38		
$\delta^{15}\text{N}_{\text{breeding}} \times \text{Species}$			6	59.68	16.96	0.24		
14			Null (intercept only)	1	40.68	0.00		
		$\delta^{13}\text{C}_{\text{non-breeding}}$	2	42.40	1.72	0.07		
		$\delta^{13}\text{C}_{\text{non-breeding}} \times \text{Species}$	6	58.08	17.40	0.26		
		$\delta^{15}\text{N}_{\text{non-breeding}}$	2	42.73	2.05	0.05		
$\delta^{15}\text{N}_{\text{non-breeding}} \times \text{Species}$		6	59.22	18.54	0.20			

changes in their trophic niche (i.e. prey) and/or changes in the isotopic composition of their prey driven by changes in isotopic baselines (Bond & Jones 2009). The  $\delta^{15}\text{N}$  of bulk tissues integrates the ratios from distinct amino acids reflecting either the baseline of a given food web (source) or the trophic level of the digested prey (Lorrain et al. 2009) and can indeed theoretically be affected solely by changes in baseline  $\delta^{15}\text{N}$ . Changes in baseline  $\delta^{15}\text{N}$  would probably have led to parallel and synchronous changes in the isotopic ratios of seabird species that feed within the same food chains, which was not the case (Supplement 6). Even though we cannot com-

pletely rule out this hypothesis, changes in baseline isotopic ratios of such amplitude seem less likely in the context of our study.

Our results support the hypotheses that some changes in diet occurred for all 4 species considered during both the breeding and non-breeding seasons and that the changes during the non-breeding season may have important consequences for seabird fitness. Indeed, we found that the average hatching success was negatively correlated to the average trophic level during the previous non-breeding season. This relationship was the same for all 4 species considered. All of these species winter in the North Atlantic but generally in different areas: north of Iceland and in southwest Greenland for Brünnich's guillemots (Frederiksen et al. 2016), in the Greenland Sea for little auks (Fort et al. 2013), on the Great Banks, east of Canada, for kittiwakes (Frederiksen et al. 2012), and over most of the northeast Atlantic for glaucous gulls (B. Moe pers. comm.). However, it is possible that they forage within the same area close to Svalbard in the spring when they come back to breed. They would thus be exposed to the same environmental conditions at the time of chest feather moult, which could explain the lack of inter-species variation in the relationship between  $\delta^{15}\text{N}$  and breeding success observed here.

This correlation does not necessarily imply a mechanistic relationship but may indicate that feeding on prey at

higher trophic levels during the non-breeding season has some negative carry-over consequences on the breeding performance of seabirds breeding in Svalbard. One potential explanation could be that in years with generally high productivity, the abundance and availability of lower trophic organisms is higher and thus represents a higher proportion of the diet in the upper trophic levels, including seabirds (Miller et al. 2010, 2011). This would lead to negative associations between overall food availability, average trophic level (and thus  $\delta^{15}\text{N}$ ) of seabirds, and their reproductive output. In such a case, the driver of the decreasing reproductive outputs would

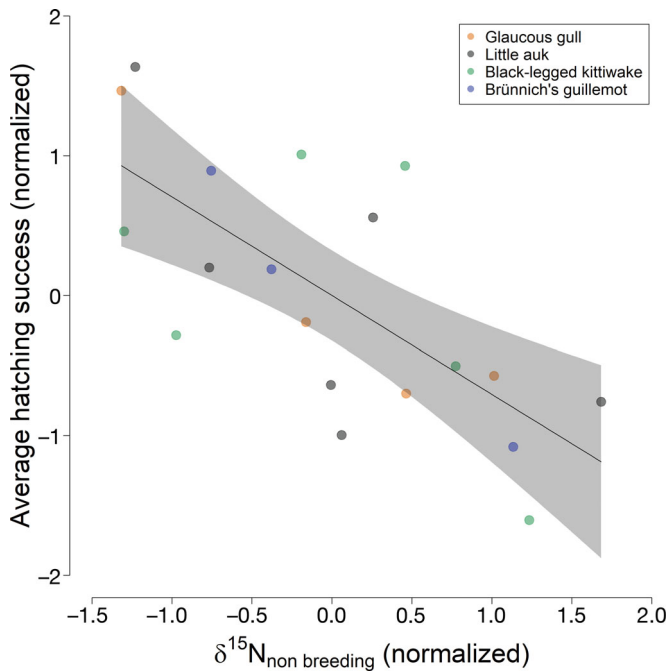


Fig. 3. Average hatching success of Svalbard seabirds in relation to nitrogen isotopic ratio during the previous non-breeding season. The line represents the prediction from a linear model and its associated 95% confidence interval (shaded areas)

not be the increase in average trophic level per se but rather the lower food availability for low productivity years. An alternative explanation would be that high  $\delta^{15}\text{N}$  is the consequence of birds using more of their endogenous reserves (Cherel et al. 2005). Low food availability during the non-breeding season could thus potentially lead to this negative association between  $\delta^{15}\text{N}$  and subsequent breeding success in Svalbard seabirds. These 2 alternative explanations remain speculative, and further studies examining the relationships between primary productivity, plankton and fish availability during the non-breeding season, seabird diet, and subsequent reproduction are needed.

The apparent correlation between reproductive success and average  $\delta^{15}\text{N}$  compared to the absence of a relationship between average  $\delta^{15}\text{N}$  and body condition may be indicative of a trade-off between a bird's own maintenance and reproduction. Indeed, in long-lived species like seabirds, individuals are expected to prioritize their own condition and thus survival, at the expense of the survival of their egg or chicks (Saether & Bakke 2000). Seabirds may maintain a relatively constant body condition even in years with limited food availability but at the cost of a lower reproductive investment and therefore a lower re-

productive success (Sæther et al. 1993, Mauck & Grubb 1995, Erikstad et al. 1998). This explanation fits well with the absence of clear interannual variation in seabird body condition. Alternatively, our proxy for body condition may not provide an adequate picture of bird physiological condition and health and/or an adequate picture of the average condition during the breeding season. We estimated bird condition only once per season and per bird, and thus, it may mostly reflect near-term environmental conditions and/or bird breeding status (i.e. the condition of a bird may be dependent on its offspring developmental stage). As a consequence, there could be some relationship between trophic level during the non-breeding season and bird body condition during pre-breeding or breeding, but that were not detected using our proxy of body condition. Obtaining measures of body condition during the pre-breeding period and/or repeated measures of condition during the breeding season may be necessary to reveal such relationships.

## 5. CONCLUSION

Food abundance is generally considered to be a key determinant of individual breeding performance in free-living populations (Martin 1987, Zera & Harshman 2001), but the importance of diet composition, in terms of prey species, is less clear. Here, we found that interannual variation in the average breeding performance of 4 Svalbard seabirds was negatively correlated with interannual variation in their average trophic level during the non-breeding season. This suggests that changes in the structure and functioning of marine food webs during the non-breeding season (resulting from changes in marine productivity) may have consequences for seabirds' reproductive performance. Several Svalbard seabird species are currently experiencing rapid changes (Descamps et al. 2013, 2017b, Petersen et al. 2015) and it has generally been assumed that changes in the food chain are a key driver. Our study supports the hypothesis that environmentally driven changes in seabird diet may affect their reproduction and, thus, that reproductive success of Svalbard seabirds may be used to some extent as bioindicators of their (non-breeding) marine environment. Our results are based on indirect measures of diet that have important limitations. Further studies identifying the prey consumed during the non-breeding season by seabirds and their inter-annual changes are now needed to move forward.

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