Species and spatial variation in the effects of sea ice on Arctic seabird populations

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Abstract

Aim: The Arctic is warming rapidly, and sea ice is disappearing. This is expected to have profound effects on Arctic wildlife. However, empirical evidence that this decline in sea ice is associated with a decline in Arctic wildlife populations is lacking.

Location: Svalbard Archipelago.

Methods: Using long-term time series data (1988–2018) from two fjords in West Spitsbergen (Svalbard), we tested whether or not sea ice concentration was associated with the population size of two of the most common Arctic seabirds, the Brünnich’s guillemot (Uria lomvia) and black-legged kittiwake (Rissa tridactyla).

Results: We found that the size of guillemot and kittiwake colonies has declined on Svalbard from the mid-1990s onwards, though the shapes of these trajectories were not linear and kittiwake colony size has stabilized or even increased in recent years. Sea ice concentration in West Spitsbergen also declined during the study period. Independent of these long-term trends, sea ice concentration was positively and significantly associated with seabird colony size with a 2-year lag, though variations in sea ice explained only a small proportion of the changes in colony size. One likely mechanism linking sea ice and seabird population size involves changes in the food chain, with poor sea ice conditions in a given year leading to low food availability 2 years later. This would affect breeding probability and hence colony size for kittiwakes and guillemots. This relationship between sea ice and colony size was the same in both fjords for guillemots. In the case of kittiwakes, it was not apparent in the fjord where productive glacier fronts, intensely used by kittiwakes to forage, may have buffered the effects of changes in sea ice.

Main conclusions: Our study provides evidence that the ongoing decline in Arctic sea ice plays a role in Arctic seabird population trajectories. However, sea ice disappearance on the breeding grounds was likely not the main driver of changes in seabird populations.

KEYWORDS
black-legged kittiwake, Brünnich’s guillemot, Rissa tridactyla, sea ice concentration, Svalbard Uria lomvia
The Arctic is warming faster than any other region on Earth (Screen & Simmonds, 2010; Serreze & Barry, 2011), and temperature increases in the Arctic (observed and projected) are more than twice the global average (AMAP, 2019). This warming underlies dramatic environmental changes and, in particular, changes in the cryosphere, resulting in a very rapid and pronounced reduction in sea ice extent, thickness and seasonal duration (Meredith et al., 2019). This decline in sea ice is expected to have profound effects on Arctic wildlife and ecosystems (Descamps, Aars, et al., 2017; Macias-Fauria & Post, 2018; Post et al., 2013), and several studies have indeed shown that sea ice decline negatively affects specific traits of some Arctic species (e.g. Brünnich’s guillemot Uria lomvia reproduction, Gaston et al., 2005; black guillemot Cepphus grylle manndti chick survival, Divoky et al., 2015; ringed seal Phoca hispida foraging behaviour, Hamilton et al., 2015). In contrast, positive effects of sea ice disappearance have also been observed in species considered ice-dependent (e.g. positive relationships between sea ice loss and body condition in the Bowhead whale Balaena mysticetus, George et al., 2015). The effects of sea ice loss may vary depending on the species trait and/or period of the year considered (e.g. Barbraud et al., 2012; Olivier et al., 2005). They can also vary spatially (Gaston et al., 2005) emphasizing the complexity of the mechanisms linking sea ice changes and wildlife population dynamics. Unfortunately, empirical evidence linking sea ice and Arctic wildlife population dynamics are relatively scarce (but see Regehr et al., 2007 for an example of sea ice effect on polar bear Ursus maritimus population size), and there is a clear need for additional studies to provide further insights into how populations, species and communities are responding to sea ice retreat.

Sea ice may affect vertebrate populations through different mechanisms (see Descamps, Aars, et al., 2017; Macias-Fauria & Post, 2018; Moline et al., 2008 for reviews) but most are linked to prey availability (or accessibility, e.g. Lovvorn et al., 2015), at least for predator species like seabirds. Such predators may indeed be dependent on the potentially abundant fauna associated with sea ice (Cusset et al., 2019; Hunt Jr, 1991; Mehlum & Gabrielsen, 1993; Mehlum & Isaksen, 1995), like the polar cod Boreogadus saida (Kohlbach et al., 2017), a key species of ice-associated ecosystems (Huserbråten et al., 2019). A decline in sea ice extent or concentration is thus predicted to negatively affect predator species that rely primarily on sea ice habitat for foraging. The potential negative effects of a sea ice decline on top predator population sizes may be complex and potentially delayed in time (Zador et al., 2013). This can happen if, for example, poor sea ice conditions affect the productivity of these predators (i.e. number of offspring) and consequently future recruitment into their population and thus their population size with some time-lags. Such lagged effects may also happen if changes in sea ice affect predator vital rates through an effect on their prey. Less sea ice can translate into a lower productivity of plankton or fish (e.g. Huserbråten et al., 2019), which can mean a lower abundance some years later and lower survival and/or reproduction of their predators. Alternatively, sea ice conditions may have a direct effect on predators’ specific traits (e.g. foraging efficiency) and affect the predator vital rates with no lag (see Watanabe et al., 2020 for an example on the Antarctic Adélie penguin Pygoscelis adeliae).

Seabirds have been globally declining in recent years or decades (Croxall et al., 2012; Paleczny et al., 2015), and this decline concerns many Arctic species (e.g. Descamps, Anker-Nilssen, et al., 2017; Descamps et al., 2013; Gilchrist & Mallory, 2005; Merkel et al., 2014; Petersen et al., 2015). However, very few studies have investigated the importance of sea ice disappearance in driving Arctic seabird population trajectories, despite a potential key role (Laidre et al., 2008). Our study, based on long-term monitoring data (1988–2018) for two of the most common Arctic seabird species, the Brünnich’s guillemot (U. lomvia, hereafter guillemot) and the black-legged kittiwake (Rissa tridactyla, hereafter kittiwakes), aims to partly fill this gap.

We focused on six and five colonies of guillemots and kittiwakes, respectively, from Svalbard, a high Arctic archipelago located between the Greenland and Barents Seas. This region has warmed much faster than the global rate and has shown some of the fastest rates of sea ice declines ever observed (Descamps, Aars, et al., 2017; Forland et al., 2011; Laidre et al., 2015). Both guillemots and kittiwakes seem to forage preferentially at sea ice edges and feed on ice-associated fish and crustaceans (Cusset et al., 2019; Hunt Jr et al., 1996; Mehlum & Gabrielsen, 1993; Mehlum & Isaksen, 1995), though the association between sea ice and kittiwakes appears weaker (Hunt et al., 1996; Mehlum & Isaksen, 1995). These two species thus offer an interesting study system to test the potential importance of sea ice conditions on the numbers of breeding individuals in two different study organisms, one strongly and one weakly associated with sea ice. First, we assessed the long-term trend in guillemots, kittiwakes and sea ice and tested whether or not these trends varied among species and “regions” (i.e. fjords). This should provide important insights about the scale of the main drivers affecting these species dynamics. We then looked for potential mechanistic links between sea ice and seabird dynamics by testing for an effect of sea ice concentration on colony size (independent of their long-term trends). We hypothesized that sea ice loss has a lagged effect on seabirds’ breeding propensity (the probability that sexually mature adults breed in a given year), and hence colony sizes (Jenouvrier et al., 2005), through changes in food availability (Zador et al., 2013). Specifically, considering that both kittiwakes and guillemots feed preferentially on polar cod (Mehlum & Gabrielsen, 1993; Vihtakari et al., 2018) and that the stock biomass of polar cod is affected by sea ice conditions with a lag of 2–3 years (Huserbråten et al., 2019), we predicted that kittiwake and guillemot colony size should be mainly affected by the sea ice conditions 2–3 years earlier. Alternatively, concurrent sea ice conditions may affect seabirds’ reproductive success by shaping food availability and/or accessibility and thus the population size 4–5 years later when kittiwake and guillemot offspring start to recruit (kittiwakes and guillemots start breeding generally at 4 and 5 years of age, respectively, Coulson, 2011; Gaston & Jones, 1998). Such an effect between sea ice and colony size through bird breeding success, and
then recruitment, is thus expected to be delayed by 6–8 years (i.e. lag of 2–3 years between sea ice conditions and prey availability and thus breeding success, and then additional lag of 4–5 years between breeding success and recruitment into the population). Considering the large-scale decline in sea ice and the inter-species differences in their association with sea ice, we predicted a similar effect of sea ice decline in both fjords but a stronger effect on guillemot than on kittiwakes.

2 | MATERIAL AND METHODS

2.1 | Model species and study area

The study took place between 1988 and 2018 at six bird colonies in west Spitsbergen, Svalbard (Figure 1). Kittiwakes were breeding in five of these six colonies, sympatrically with guillemots (Figure 1). Kittiwakes are colonial cliff-breeders that typically lay 1 or 2 eggs in Svalbard in early June (Strøm, 2006). They feed mostly on fish, crustaceans and other marine invertebrates (Reiertsen et al., 2014; Vihtakari et al., 2018), with polar cod being an important prey for Svalbard kittiwakes (Vihtakari et al., 2018). Guillemots are colonial cliff-breeders that lay a single egg in late May/early June. Their diet consists mainly of fish and crustaceans (Anker-Nilssen et al., 2000), like polar cod *B. saïda* and ice-associated crustaceans in the spring (Mehlum & Gabrielsen, 1993). Kittiwakes are surface feeders, while guillemots are divers. Spitsbergens guillemots spend the winter north of Iceland and in Southwest Greenland (Frederiksen et al., 2016) and kittiwakes on the Great Banks, east of Canada (Frederiksen et al., 2012). Both guillemots and kittiwakes are highly philopatric (i.e. breeding individuals come back to breed year after year to the same colony and very often use the same exact nest or location, Coulson, 2011; Gaston & Jones, 1998) and changes in their population size are therefore unlikely to be driven by emigration processes but rather by changes in their survival and/or reproduction.

2.2 | Colony monitoring data

In each of these six colonies, one to 11 plots were chosen in 1988 and then counted almost annually during the incubation period (June). These colonies ranged from approximately 1,000–40,000 pairs and plots represent 2%–100% of the colony. On average, colonies were counted 23 times during the study period (range 17–29 for kittiwakes and 17–30 for guillemots), leading to a total of 114 colony size estimates for kittiwakes and 136 for guillemots. Following standardized international procedures to monitor guillemot and kittiwake colonies (Walsh et al., 1995), we counted the total number of individuals present in each plot for guillemot and the total number of active nests for kittiwakes (with 10× binoculars). Active nests

![FIGURE 1](image-url) Study area at Spitsbergen (Svalbard, Norway). Symbols indicate colony locations for Brünnich’s guillemots (squares) and black-legged kittiwakes (triangles) in Isfjorden (red) and Kongsfjorden (blue). Shaded rectangle on the western coast of Spitsbergen represents the area from which the long-term time series (1988–2018) of sea ice concentration data was extracted to evaluate the relationship between sea ice conditions and seabirds’ population sizes. This rectangle includes a large-enough marine area encompassing the main foraging grounds for both species during the pre-breeding and breeding seasons. For illustrative purposes, we include background colours pinpointing the seasonal ice zone (taken from Ramírez, Tarroux, et al., 2017). Dark blue in cells along the coastline indicates no data on sea ice.
were defined as nests with incubating birds. Distinguishing between breeding and non-breeding individuals from a distance is not possible in guillemots, so all individuals present in each plot were counted. Our results thus report colony attendance rather than number of breeding individuals per se for guillemots. However, both parameters are highly correlated (see Figure SM1) so that our results can be interpreted in terms of changes in the number of breeding guillemots (even though non-breeders like immature birds may be present in the colony, Harris et al., 2016). The standard procedure was to visit each colony and plot several times per season (usually 3–4 times) during mid/late incubation (around mid-June typically), but due to logistical constraints some plots or colonies were visited only once per season. At each visit, the number of guillemot and/or number of kittiwake active nests present in each plot were counted two to three times by different observers. For each year, we then averaged the number of guillemot or kittiwake nests counted in each plot at each visit and for every count and summed these numbers to obtain a proxy of colony size per year and per colony.

2.3 | Sea ice data

Daily satellite remote sensing data on sea ice concentration were sourced online at the National Snow and Ice Data Center (Boulder, Colorado USA; https://nsidc.org/data/seaice_index/; accessed on April 2019). These images show the percentage of ice cover for each roughly 25-kilometre-square data cell that is covered more than 15 per cent by ice on a given day (Fetterer et al., 2002). Sea ice concentration data were extracted and averaged from a large-enough fixed marine area expected to encompass the main foraging grounds for both species during the pre-breeding and breeding seasons (Figure 1). The foraging grounds during the pre-breeding season are unfortunately unknown for the black-legged kittiwake and Brünnich’s guillemot on Svalbard, but tracking data during early breeding (incubation period) indicated that >85% and >95% of all foraging trips take place within 50 km from the colony for kittiwakes and guillemots, respectively (see details about the tracking data in Ramírez, Tarroux, et al., 2017; Harris et al., 2020, and in the Figure SM2). These results suggest that both species forage generally close to Svalbard and that our selected area should include most of their foraging grounds.

After smoothing the daily sea ice concentration time series using 10-day running means, we considered the annual maximum sea ice concentrations in the study area for each year (i.e. in the period September-August). This annual maximum sea ice concentration is strongly correlated with the maximum and average spring sea ice concentration (Pearson’s r = .92 and 0.88 with the maximum and average concentration in the period March-May, respectively) and to the total number of days with sea ice concentration >15% (Pearson’s r = .80). Moreover, the sea ice concentration extracted from this area is highly correlated with the maximum sea ice concentration extracted from larger areas and/or from areas centred around each colony specifically (see details in Figure SM3). All of these results indicate that the maximum annual sea ice concentration in the selected area (Figure 1) is a good proxy for the general sea ice conditions and their inter-annual variations in West Spitsbergen over the last decades. We tested for the effect of the maximum sea ice concentration on seabird colony size with and without a time-lag of 1–8 years.

2.4 | Statistical analyses

All analyses were done with R software (R Development Core Team 2010) and normalized time series was used in all cases. Although count data are often analysed with a Poisson or negative binomial distribution, we used a Gaussian distribution and normalized time series as this approach provides a simpler platform to model temporal autocorrelation and heteroscedasticity.

In a first step, we assessed the long-term trend in our sea ice metric and in kittiwake and guillemot colony size. We used linear models (lm function) to assess the trend in sea ice and generalized mixed-effect models with colony included as a random factor (see Descamps et al., 2013; Regular et al., 2010 for a similar approach) to assess the trend in bird colony size. We used the lm function (nlme package) in R, with a Gaussian distribution, and adjusted the variance structure to take into account residual heteroscedasticity (Zuur et al., 2009). We used an exponential variance structure (Zuur et al., 2009), which provided the lowest Akaike’s information criterion (AIC) values (Burnham & Anderson, 2002). Details about model residuals’ distribution are given in Figure SM2. To assess the shape of the trend and its potential variation among fjords, we compared different models with and without a fjord×trend interaction using AIC and maximum-likelihood estimation (as all models had the same random structure). If the difference in AIC values between two models was <2, the models had equal statistical support and in the case of nested models, the simplest was preferred. We considered linear, quadratic and cubic trends that allow the regression curves to have 0, 1 or 2 inflections. Preliminary analyses using additive models (GAMM) indicated that there was no need to consider a larger number of inflection points and thus polynomial regressions of higher degrees. We first performed a trend analysis for each species separately and then tested specifically in a second step whether or not the trend varied among species.

We used a similar approach to test for an effect of sea ice on guillemot and kittiwake colony size (with and without a time-lag of 1–8 years). We used generalized mixed-effect models (lm function) with colony included as a random factor, the fjord as a two-level fixed factor and an exponential variance structure (see Figure SM4 for details about residuals’ distribution). Model selection was done with AIC and we tested for the effects of sea ice on colony size while keeping variables describing the trend identified for each species in the first step (see Results and Table 1). This approach allowed us to test for a sea ice effect on colony size independent of the long-term trend. To estimate the amount of
variance in colony size explained by changes in sea ice, we pro-
vided the marginal $R^2$ using the r.squaredGLMM function from
the MuMIn package (Barton, 2009; Johnson, 2014; Nakagawa &
Schielzeth, 2013).

3 | RESULTS

3.1 | Long-term trends in sea ice and seabird colony
size

The maximum sea ice concentration in West Spitsbergen showed
large inter-annual fluctuations and has declined linearly in the last
three decades from about 40% to 15% in our study area between
1988 and 2018 (Figure 2, Table 1).

Both guillemots and kittiwakes started to decline rapidly in the mid-
- late 1990s (Figure 3). A cubic function was preferred for
describing the trend in both species, indicating that there was
more than one inflection in their trajectories (Table 1, Figure 3).
For kittiwakes, long-term trends had a similar shape in both fjords
but some differences existed (Table 1, Figure 3) and both the de-
cline in the 1990s and the increase in the 2000s occurred earlier
in Kongsfjorden than in Isfjorden (Figure 3). No such variation was
observed for guillemot, and trends were the same in both fjords.

### TABLE 1 Long-term trend in sea ice concentration and seabird colony size in Svalbard (1988–2018)

| Species                        | Fixed effects | Random factor | df  | AIC  | ΔAIC |
|--------------------------------|---------------|---------------|-----|------|------|
| Max. Spring Sea ice concentration | Quadratic     | Colony        | 3   | 374.25 | 0.00 |
| Linear                         | 2             | Colony        | 2   | 374.32 | 0.07 |
| Cubic                          | 4             | Colony        | 4   | 375.70 | 1.45 |
| Null                           | 1             | Colony        | 1   | 387.79 | 13.54|
| Brünnich’s guillemot           | Cubic         | Colony        | 6   | 145.70 | 0.00 |
| Cubic × Fjord                  | Colony        | 10            | 147.45 | 1.75 |
| Linear × Fjord                 | Colony        | 6             | 171.20 | 25.50 |
| Quadratic × Fjord              | Colony        | 8             | 173.79 | 28.09 |
| Linear                         | Colony        | 4             | 174.91 | 29.21 |
| Quadratic                      | Colony        | 5             | 174.95 | 29.25 |
| Null                           | Colony        | 3             | 384.53 | 238.83|
| Black-legged kittiwake         | Cubic × Fjord | Colony        | 10            | 290.85 | 0.00 |
| Cubic                          | Colony        | 6             | 298.31 | 7.46 |
| Quadratic × Fjord              | Colony        | 8             | 304.05 | 13.20 |
| Quadratic                      | Colony        | 5             | 308.77 | 17.92 |
| Linear                         | Colony        | 4             | 310.22 | 19.37 |
| Linear × Fjord                 | Colony        | 6             | 310.74 | 19.89 |
| Null                           | Colony        | 3             | 317.80 | 26.95 |

Note: We considered the maximum spring sea ice concentration that is the maximum sea ice concentration in the period September–August in West Spitsbergen (details in Methods). Seabird colony size data are from six colonies of Brünnich’s guillemot and five colonies of black-legged kittiwake. Colonies are distributed in two fjords (two-modality variable: Isfjorden and Kongsfjorden). For each variable and species, several models were compared to assess the shape of the long-term trend (linear, quadratic or cubic). For the colony size, we also tested whether or not the trend varied among fjords. Best models are indicated in bold. Colony count data were normalized (i.e. each colony time series has a 0-mean and unit SD).

aThe degrees of freedom for each model include one extra parameter used for estimating the exponential variance structure.

![FIGURE 2 Spring sea ice concentration in West Spitsbergen.](image)

The figure represents the maximum annual sea ice concentration (%) from September to August in West Spitsbergen. The line and shaded areas represent the estimated trajectory from a linear regression and its associated 95% confidence interval. The slope of this regression has been estimated at $-0.8\%/\text{year}$ ($\pm 0.2\ SE$).
3.2 | Relationships between spring sea ice and seabird colony size

We found no effect of maximum sea ice concentration with no lag or with a lag of one, three or ≥4 years on guillemot or kittiwake colony size (i.e. models including sea ice concentration with these lags did not provide a better fit than a model with a cubic trend only; Table 2). However, we observed a positive association between the maximum sea ice concentration with a lag of 2 years and both guillemot and kittiwake colony size (i.e. models including both sea ice with a 2-year lag and a cubic trend provided a better fit than models with a cubic trend only; Table 2; Figure 4). More specifically, the maximum sea ice 2 years earlier was positively associated with Brünnich’s guillemot colony size in both fjords, while it was only positively associated with kittiwake colony size in Isfjorden (Table 2; Figure 4; slopes in Isfjorden and Kongsfjorden for guillemots, respectively: $0.089 \pm 0.053$ SE and $0.121 \pm 0.054$; slopes in Isfjorden and Kongsfjorden for kittiwakes, respectively: $0.433 \pm 0.155$ and $-0.059 \pm 0.139$). These results indicate that, independent of any long-term trend, years with more sea ice 2 years earlier were also years with more breeding guillemots in both fjords and more breeding kittiwakes in Isfjorden but not in Kongsfjorden. However, these results also indicate that the maximum sea ice concentration explained very little of the inter-annual fluctuations in seabird colony size once the long-term trend was accounted for ($R^2 = 0.51$ and 0.53 for the models Colony Size ~ Cubic and Colony Size ~ Cubic + Sea Ice lag 2, respectively, for guillemots; $R^2 = 0.16$ and 0.19 for the models Colony Size ~ Cubic × Fjord and Colony Size ~ Cubic × Fjord + Sea Ice lag 2 × Fjord, respectively, for kittiwakes). Our results also indicated that the long-term trend in both guillemot and kittiwake colony size is not well explained by the long-term trend in sea ice concentration (i.e. models with only sea ice variables had a much higher AIC than models with a cubic trend and explain a small part of the variation in colony size: $R^2 = 0.04$ for the model Colony Size ~ Sea Ice lag 2 for guillemots; and $R^2 = 0.03$ for the model Colony Size ~ Sea Ice lag 2 × Fjord, respectively, for kittiwakes; Table 2).

4 | DISCUSSION

4.1 | Long-term changes in sea ice and seabird colony size

Based on some of the few existing long-term and continuous time series data on Arctic wildlife, our study provides evidence that ongoing changes in the Arctic cryosphere affect the population dynamics of inhabiting seabirds and that this impact varies both spatially and among species.

The maximum sea ice concentration has decreased linearly in West Spitsbergen, Svalbard, in the last decades. This trend broadly concurs with changes in sea ice in other Arctic regions (Parkinson & Cavalieri, 2008). Concurrently, the size of guillemot and kittiwake colonies has generally declined on Svalbard from the mid-1990s onwards. This is particularly true for the guillemot population, in line

continued to decline. When considering the entire dataset (1988–2018) and both species combined, we found a clear trend × species interaction (Table SM1), which is driven by variable trajectories in the later part of the study. Indeed, when restricting the data to the period 1988–2005 for example, differences among species were not apparent (Table SM1).

The positive trend in kittiwake colony size in recent years was especially pronounced in Kongsfjorden (Figure 3). When considering only data from 2005 to 2018, results confirmed that kittiwake colony size significantly increased (see Table SM2) but in Kongsfjorden only, with a slope (and associated SE) equal to $1.28 \pm 0.47$ in Kongsfjorden and $0.47 \pm 0.53$ in Isfjorden.

FIGURE 3  Long-term trend in Brünnich’s guillemot (top) and black-legged kittiwake (bottom) populations in West Spitsbergen (Svalbard archipelago) in the period 1988–2018. The solid lines and shaded areas represent the average estimated trajectories from cubic regressions and their associated 95% confidence intervals. There was no difference in fjord trajectory for guillemots but there was some for kittiwakes (see Table 1). Colony count data (number of breeding pairs for kittiwakes and number of individuals for guillemots) were normalized (i.e. each colony time series had a 0-mean and unit SD)
TABLE 2  Effect of the maximum sea ice concentration on Brünnich's guillemot and black-legged kittiwake colony size in Svalbard

| Species                  | Model (fixed effects)               | df  | AIC   | ΔAIC  |
|--------------------------|-------------------------------------|-----|-------|-------|
| Brünnich's guillemot    | Cubic + Sea Ice lag 2               | 7   | 141.90| 0.00  |
|                         | Cubic + Sea Ice lag 2 × Fjord       | 9   | 142.34| 2.91  |
|                         | Cubic                               | 6   | 145.70| 5.30  |
|                         | Cubic + Sea Ice                     | 7   | 147.02| 5.12  |
|                         | Cubic + Sea Ice lag 1               | 7   | 147.02| 5.12  |
|                         | Cubic + Sea Ice lag 8               | 7   | 147.13| 5.23  |
|                         | Cubic + Sea Ice lag 5               | 7   | 147.23| 5.33  |
|                         | Cubic + Sea Ice lag 4               | 7   | 147.54| 5.64  |
|                         | Cubic + Sea Ice lag 3               | 7   | 147.60| 5.70  |
|                         | Cubic + Sea Ice lag 6               | 7   | 147.69| 5.79  |
|                         | Cubic + Sea Ice lag 7               | 7   | 147.69| 5.79  |
|                         | Cubic + Sea Ice × Fjord             | 9   | 147.34| 7.73  |
|                         | Cubic + Sea Ice lag 5 × Fjord       | 9   | 148.13| 8.24  |
|                         | Cubic + Sea Ice lag 1 × Fjord       | 9   | 147.10| 8.68  |
|                         | Cubic + Sea Ice lag 8 × Fjord       | 9   | 150.80| 8.90  |
|                         | Cubic + Sea Ice lag 3 × Fjord       | 9   | 146.06| 8.94  |
|                         | Cubic + Sea Ice lag 7 × Fjord       | 9   | 151.27| 9.37  |
|                         | Cubic + Sea Ice lag 4 × Fjord       | 9   | 147.76| 9.43  |
|                         | Cubic + Sea Ice lag 6 × Fjord       | 9   | 151.34| 9.44  |
|                         | Sea Ice                             | 4   | 310.20| 168.30|
|                         | Sea Ice × Fjord                     | 6   | 314.09| 172.19|
|                         | Sea Ice lag 2                       | 4   | 317.96| 176.06|
|                         | Sea Ice lag 2 × Fjord               | 6   | 321.51| 179.61|
|                         | Sea Ice lag 1                       | 4   | 322.94| 181.04|
|                         | Sea Ice lag 1 × Fjord               | 6   | 326.86| 184.96|
|                         | Sea Ice lag 3                       | 4   | 336.89| 194.99|
|                         | Sea Ice lag 3 × Fjord               | 6   | 340.84| 198.94|
|                         | Sea Ice lag 4                       | 4   | 350.02| 208.12|
|                         | Sea Ice lag 4 × Fjord               | 6   | 353.92| 212.02|
|                         | Sea Ice lag 5                       | 4   | 357.43| 215.53|
|                         | Sea Ice lag 8                       | 4   | 357.82| 215.92|
|                         | Sea Ice lag 6                       | 4   | 360.17| 218.27|
|                         | Sea Ice lag 8 × Fjord               | 6   | 360.94| 219.04|
|                         | Sea Ice lag 5 × Fjord               | 6   | 361.04| 219.14|
|                         | Sea Ice lag 6 × Fjord               | 6   | 363.77| 221.87|
|                         | Sea Ice lag 7                       | 4   | 368.15| 226.25|
|                         | Sea Ice lag 7 × Fjord               | 6   | 372.13| 230.23|
|                         | Null                                | 3   | 384.53| 242.63|

| Black-legged kittiwake  | Cubic × Fjord + Sea Ice lag 2 × Fjord | 12  | 286.44| 0.00  |
|-------------------------|---------------------------------------|-----|-------|-------|
|                         | Cubic × Fjord + Sea Ice lag 2         | 11  | 290.42| 3.98  |
|                         | Cubic × Fjord                         | 10  | 290.85| 4.41  |
|                         | Cubic × Fjord + Sea Ice lag 4         | 11  | 291.04| 4.60  |
|                         | Cubic × Fjord + Sea Ice lag 5         | 11  | 291.51| 5.07  |
|                         | Cubic × Fjord + Sea Ice lag 8         | 11  | 291.56| 5.12  |
|                         | Cubic × Fjord + Sea Ice lag 1         | 11  | 291.99| 5.55  |

(Continues)
with previous studies that also identified a drop in population size (Descamps et al., 2013; Fluhr et al., 2017). The black-legged kittiwake population has also experienced an overall decline in Svalbard, which fits with the general decline observed on a circumpolar scale during the same period (Descamps, Anker-Nilssen, et al., 2017). However, the shape of its trajectory was clearly not linear, and the population began to increase (Kongsfjorden) or stabilize (Isfjorden) in the early or mid-2000s, partially recovering the maximum numbers recorded during the mid-1990s. As the kittiwake can be considered a more temperate or boreal species (i.e. also breeding in temperate environments) and Svalbard and the Barents Sea are undergoing an Atlantification or borealization process (Fosheim et al., 2015; Kortsch et al., 2012; Vihtakari et al., 2018), this may indicate that Svalbard now offers a rather favourable environment for this species despite a significant warming.

Our results emphasize the importance of considering both large-scale and more regional, or local, environmental processes in driving wildlife population dynamics. Indeed, while our results support a relationship between changes in sea ice on the breeding grounds and population dynamics of both guillemots and kittiwakes, it also indicates that such changes in sea ice explain only a small amount of the variance in colony size fluctuations and cannot alone explain

| Species                     | Model (fixed effects)                              | $df^a$ | AIC     | $\Delta$AIC |
|-----------------------------|----------------------------------------------------|--------|---------|--------------|
| Cubic $\times$ Fjord + Sea Ice lag 7 $\times$ Fjord | 12      | 292.43 | 5.99    |
| Cubic $\times$ Fjord + Sea Ice lag 6               | 11      | 292.52 | 6.08    |
| Cubic $\times$ Fjord + Sea Ice lag 5              | 11      | 292.61 | 6.17    |
| Cubic $\times$ Fjord + Sea Ice lag 7              | 11      | 292.75 | 6.31    |
| Cubic $\times$ Fjord + Sea Ice lag 8 $\times$ Fjord | 12      | 292.75 | 6.31    |
| Cubic $\times$ Fjord + Sea Ice + Fjord            | 11      | 292.84 | 6.40    |
| Cubic $\times$ Fjord + Sea Ice lag 4 $\times$ Fjord | 12      | 292.89 | 6.45    |
| Cubic $\times$ Fjord + Sea Ice lag 5 $\times$ Fjord | 12      | 293.32 | 6.88    |
| Cubic $\times$ Fjord + Sea Ice + Fjord            | 12      | 293.47 | 7.03    |
| Cubic $\times$ Fjord + Sea Ice lag 3 $\times$ Fjord | 12      | 293.82 | 7.38    |
| Cubic $\times$ Fjord + Sea Ice lag 1 $\times$ Fjord | 12      | 293.97 | 7.53    |
| Cubic $\times$ Fjord + Sea Ice lag 6 $\times$ Fjord | 12      | 294.09 | 7.65    |
| Sea Ice lag 2 $\times$ Fjord                       | 6       | 313.47 | 27.03   |
| Sea Ice lag 1 $\times$ Fjord                       | 6       | 314.77 | 28.33   |
| Sea Ice $\times$ Fjord                            | 6       | 315.41 | 28.97   |
| Sea Ice lag 1                                     | 4       | 315.98 | 29.54   |
| Sea Ice lag 2                                     | 4       | 317.41 | 30.97   |
| Null                                              | 3       | 317.80 | 31.36   |
| Sea Ice                                          | 4       | 318.04 | 31.60   |
| Sea Ice lag 6                                     | 4       | 318.14 | 31.70   |
| Sea Ice lag 8                                     | 4       | 319.36 | 32.92   |
| Sea Ice lag 3                                     | 4       | 319.44 | 33.00   |
| Sea Ice lag 7                                     | 4       | 319.57 | 33.13   |
| Sea Ice lag 5                                     | 4       | 319.70 | 33.26   |
| Sea Ice lag 4                                     | 4       | 319.75 | 33.31   |
| Sea Ice lag 7 $\times$ Fjord                      | 6       | 319.87 | 33.43   |
| Sea Ice lag 3 $\times$ Fjord                      | 6       | 320.17 | 33.73   |
| Sea Ice lag 6 $\times$ Fjord                      | 6       | 320.29 | 33.85   |
| Sea Ice lag 4 $\times$ Fjord                      | 6       | 320.83 | 34.39   |
| Sea Ice lag 5 $\times$ Fjord                      | 6       | 321.53 | 35.09   |
| Sea Ice lag 8 $\times$ Fjord                      | 6       | 322.53 | 36.09   |

Note: Colonies are from two fjords (Isfjorden and Kongsfjorden; see Figure 1). All models included the colony as a random effect. Different models with variable fixed effects were compared and each model was run using maximum likelihood (ML). “Cubic” represents the cubic trend in colony size. This trend (and its interaction with the fjord in the case of kittiwakes) has been included in some models to evaluate the effect of sea ice concentration independent of the common long-term decline in both sea ice and colony size (Table 1). Best models are indicated in bold.

$^a$The degrees of freedom for each model include one extra parameter used for estimating the exponential variance structure.
the long-term trend in these populations. This fits with a previous study on common eider (Somateria mollissima) in the Arctic where sea ice has been shown to affect inter-annual changes in population size (Hanssen et al., 2013) but where the long-term population trend (i.e. stable eider population) was apparently independent of the long-term decline in sea ice. Such results may seem paradoxical but simply indicate that sea ice changes were not the main driver of the dynamics of these populations, even though they played a significant role. These long-term trends in seabird populations might be better explained by larger scale changes in environmental conditions occurring on the wintering grounds (Frederiksen et al., 2016; Gaston, 2003). Indeed, the observed changes in seabird population trajectories in the mid-1990s are concordant with a large-scale environmental shift in the North Atlantic, related to a weakening of the sub-polar gyre or SPG (Hátún et al., 2005, 2009). The effects of the SPG on both guillemots and kittiwakes have already been documented (Descamps et al., 2013; Hátún et al., 2017) and the SPG strength is likely a key driver of seabird population dynamics in the North Atlantic. These results stress the potential importance of environmental conditions, including sea ice conditions, during the non-breeding season in driving marine wildlife dynamics. However, apart from a few studies in Antarctica (e.g. Jenouvrier et al., 2012), very little is known about the relative importance of sea ice conditions at different times of the year on ice-associated species and further studies are needed.

4.2 Spatial and species variations in sea ice effects

The effects of climate change are known to vary among species (Chen et al., 2011; Descamps et al., 2019; Moritz & Agudo, 2013) and spatially in parallel with the rate of warming (e.g. Deutsch et al., 2008; Ramírez, Afan, et al., 2017) or with the position of a given population within the species’ range (e.g. Gaston et al., 2005). Such spatial variations are expected to happen at a rather large spatial scale and closely situated populations of a given species are usually assumed to respond in the same way. Our results, however, indicate that even at a very small spatial scale (<100 km), different species and populations (or more precisely colonies) can respond differently to the same changes in their environment. Indeed, we found that the apparent effect of spring sea ice on seabird colony size was similar in both fjords for guillemots but not for kittiwakes, where this effect was observed in only one fjord. These two fjords (Isfjorden and Kongsfjorden) differ in size (Kongsfjorden being much smaller) and, while separated by less than 100 kms, differ in terms of oceanographic conditions and species (e.g. zooplankton) communities (Dalpadado et al., 2016; Gluchowska et al., 2016). Such differences can be explained by a different relative influence of the West Spitsbergen current (carrying warm Atlantic water) and Arctic-type coastal waters (Svendsen et al., 2002) but also by the role of tidal glaciers that largely affect the hydrography and functioning of Kongsfjorden (Hop et al., 2002; Lydersen et al., 2014). The fronts of these glaciers can affect the productivity of the entire fjord (Hop et al., 2002) and are intensely used by local kittiwakes but not guillemots (Lydersen et al., 2014; Urbanski et al., 2017). The large volume of melt water released by glaciers creates profitable feeding areas for surface-feeding species like kittiwakes (Nishizawa et al., 2020; Stott, 1936). The disappearance of sea ice may have occurred concurrently with faster glacier melting so that the loss of sea ice-associated foraging habitats may have been compensated for by the appearance of new foraging hot-spots at glacier fronts (see Gremillet et al., 2015 for concordant results in the Russian Arctic). This could explain why local kittiwake colonies in this fjord were apparently less affected by changes in sea ice and why their overall population dynamics differed compared to their conspecifics from Isfjorden (i.e. earlier and faster population growth).
increases in Kongsfjorden after the period of decline in the 1990s and the more ice-dependent guillemots (Hunt et al., 1996; Mehlum & Isaksen, 1995). The importance of tidal glacier fronts as foraging hotspots is not only relevant for seabirds and for Svalbard. Glacier fronts are important foraging areas for sea mammals (Hamilton et al., 2016; Vacquié-Garcia et al., 2018) and in other Arctic regions like the Canadian Arctic (McLaren & Renaud, 1982), the Russian Arctic (Gremillet et al., 2015), Greenland (Nishizawa et al., 2020) and Alaska (Arimitsu et al., 2016; Kuletz et al., 2003). Such local processes may affect the trajectories of some populations and induce some site- and species-specific variations in population responses even at a very small scale. Such variations need to be taken into account when predicting the consequences of climate warming on Arctic wildlife.

### 4.3 Mechanisms linking sea ice changes and seabird population size

Though climate change in general may affect seabird populations through a variety of mechanisms, these mechanisms seem to very often involve changes in the availability of food resources (Jenouvrier, 2013). Our results indicate that, independent of any long-term trend and for both species, years with more sea ice were associated with a larger colony size 2 years later. These larger colony sizes corresponded to a larger number of breeding pairs for kitiwakes and a larger number of individuals for guillemots (see Methods). The number of individual guillemots and the number of breeding pairs is highly correlated (see Figure SM1), and thus, our results may also indicate that sea ice positively influenced the number of breeders in guillemot colonies.

Our results and the 2-year time-lag observed between sea ice conditions and their effect on seabird colony size support the role of sea ice in seabird breeding propensity, and thus colony size, through an effect on the food availability (e.g. polar cod stock biomass, Huserbråten et al., 2019) 2 years later. It seems unlikely that sea ice may have affected seabird colony size through an effect on their productivity (i.e. breeding success and number of offspring produced) as this would have led to a 6–8-year time-lag between sea ice and colony size. It is, however, possible that natal dispersal (i.e. recruitment of birds in colonies other than their natal colony) introduced some noise into these relationships and thus prevented us from detecting any role for sea ice conditions on seabird productivity. Such natal dispersal is very limited in Brünnich’s guillemot (Steiner & Gaston, 2005) but can be more common in kitiwakes (Coulson, 2016). An assessment of natal dispersal in kitiwake would thus be needed to better understand the potential relationships between sea ice and kitiwake population dynamics and potentially confirm whether or not these relationships involve kitiwake productivity.

Interestingly, in the Bering Sea, black-legged kitiwake and Brünnich’s guillemot reproduction is associated with the timing of sea ice retreat (Zador et al., 2013), and this lagged relationship involves changes in the availability of age-1 walleye pollock Theragra chalcogramma. This fish is an important prey for both species in the eastern Bering Sea and its abundance in a given year is lower following warm years or years with earlier sea ice retreat (Hunt Jr et al., 2011; Zador et al., 2013). The timing of sea ice retreat is correlated with the sea ice extent (though the relationship may not be linear), as warm years generally show both an early ice break-up and a lower ice extent (e.g. Hochheim et al., 2010). The changes observed in the Bering Sea, and the potential mechanisms behind these changes, may thus be very similar to those observed on Svalbard with poor sea ice conditions in a given year leading to low recruitment of fish and thus lower availability of prey for kitiwakes and guillemots some years later. Kitiwakes and guillemots on Svalbard feed preferentially in the spring and summer on fish between 1 and 3 years of age, as well as invertebrates (Lønne & Gabrielsen, 1992; Mehlum & Gabrielsen, 1993; Vihtakari et al., 2018) and in particular on the polar cod (Mehlum & Gabrielsen, 1993; Vihtakari et al., 2018). The recruitment of polar cod in the Barents Sea is strongly associated with maximum sea ice cover and thus with the total stock biomass 2.5 years later (Huserbråten et al., 2019). A concordant relationship between sea ice and polar cod has been observed in the Canadian Arctic, where a decline in the proportion of polar cod delivered by guillemots to their chicks occurred approximately 2 years after a step change in sea ice conditions (Gaston et al., 2012). This supports the key role played by the polar cod in explaining the lagged relationships between sea ice and seabird colony size. Years with low sea ice extent led to a low recruitment of polar cod and then a low stock biomass approximately 2 years later. This lower availability of prey may have affected the condition of birds and their propensity to breed, leading to a lower number of breeding birds in colonies. The breeding propensity is known to be affected by pre-breeding environmental conditions (e.g. Jean-Gagnon et al., 2018; Madsen et al., 2007; Reed et al., 2004; Trathan et al., 1996) and to be an important determinant of population size (Jenouvrier et al., 2005).

Our results support the hypothesis that sea ice changes affect the number of breeding birds through an effect on the availability of their prey, but other mechanisms may also have played a role (e.g. changes in sea ice concentration may be associated with changes in the distance between the colonies and the sea ice edges and thus changes in the energetic costs of foraging, independent of the changes in the total food availability). Moreover, our study only focused on the decline in maximum sea ice concentration, used as a proxy for the general sea ice conditions in West Spitsbergen during the pre-breeding period, and which represents only one aspect of the ongoing cryosphere changes. Changes in sea ice concentration outside this period may also have played a role and, beyond the changes in sea ice concentration or extent, the physical characteristics (e.g. thickness) and dynamics (i.e. phenology) of the sea ice are also rapidly changing with potential important consequences for ice-associated species (Post, 2017; Ramirez, Tarroux, et al., 2017). Our results confirm that changes in spring sea ice concentration affect seabird populations but did not unravel all the potential consequences that changes in the cryosphere may have on seabirds. These
consequences may be numerous and complex and partially driven by site- and species-specific traits.

4.4 | Concluding remarks

Given that some climate models suggest that the Arctic Ocean could be seasonally ice-free within the next few decades (AMAP, 2019), it is important to better understand how Arctic wildlife is responding to the loss of sea ice. Our study provides some evidence that sea ice concentration affects seabird colony size on Svalbard and years with more sea ice are associated with higher seabird abundance 2 years later. The recent increase in kitiwake population size on Svalbard (Grémillet et al., 2015). This has important implications for the management of Arctic species and should be taken into account when projecting the fate of populations in relation to large-scale environmental changes like global warming.

ACKNOWLEDGEMENTS

This study was funded by the programmes MOSJ (www.mosj.no) and SEAPOP (www.seapop.no). FR institution received funding from the Spanish government through the ‘Severo Ochoa Centre of Excellence’ accreditation (CEX2019-000928-S). We thank F. Mehlum for initiating and leading the monitoring of Svalbards seabirds in the period 1988-1998, H. Strøm for leading it in the period 1999-2004 and H. Steen in the period 2005-2009. We also thank Sarah Young for English editing, S. Oppel and one anonymous referee for very valuable comments and all of the numerous field assistants, who helped in collecting these long-term monitoring data every summer on Svalbard, and in particular E. Lorentzen, D. Ruché, S. Svavarsdottir, B. Merkel, I. Lopez-Saraza, A. Vilches and M. Andersen for their long-term contribution.

CONFLICT OF INTEREST

Authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13389.

DATA AVAILABILITY STATEMENT

All data are available at https://data.npolar.no/dataset/c98f2f39-ef3a-4542-bc1b-eefc49a1267 (https://doi.org/10.21334/npolar.2021.c98f2f39).

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BIOSKETCHES

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Author contributions: SD and FR designed the study. SD analysed data and wrote a first draft; FR extracted the sea ice data and participated to the writing and editing of the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Descamps, S., & Ramírez, F. (2021). Species and spatial variation in the effects of sea ice on Arctic seabird populations. Diversity and Distributions, 27, 2204–2217. https://doi.org/10.1111/ddi.13389