


PRIMARY RESEARCH ARTICLE

Diverging phenological responses of Arctic seabirds to an earlier spring

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Abstract

The timing of annual events such as reproduction is a critical component of how free-living organisms respond to ongoing climate change. This may be especially true in the Arctic, which is disproportionately impacted by climate warming. Here, we show that Arctic seabirds responded to climate change by moving the start of their reproduction earlier, coincident with an advancing onset of spring and that their response is phylogenetically and spatially structured. The phylogenetic signal is likely driven by seabird foraging behavior. Surface-feeding species advanced their reproduction in the last 35 years while diving species showed remarkably stable breeding timing. The earlier reproduction for Arctic surface-feeding birds was significant in the Pacific only, where spring advancement was most pronounced. In both the Atlantic and Pacific, seabirds with a long breeding season showed a greater response to the advancement of spring than seabirds with a short breeding season. Our results

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emphasize that spatial variation, phylogeny, and life history are important considerations in seabird phenological response to climate change and highlight the key role played by the species' foraging behavior.

KEYWORDS

breeding phenology, climate warming, foraging strategy, phylogeny, spring onset

1 | INTRODUCTION

Climate change is affecting species and communities worldwide causing population declines (Descamps, Anker-Nilssen, et al., 2017; Jenouvrier, 2013) and species range shifts (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Tingley, Monahan, Beissinger, & Moritz, 2009). The timing of annual events such as seasonal migratory movements or breeding is critical to how organisms use their environment and respond to climate change (Socolar, Epanchin, Beissinger, & Tingley, 2017). The time window favorable for migration, reproduction, and/or growth is indeed often limited, especially at high latitudes. Outside this window, conditions may be suboptimal with harsher weather and/or lower food availability (Durant, Hjermmann, Ottersen, & Stenseth, 2007). Consequently, an inability to adjust phenology to environmental change may have important fitness consequences (Miller-Rushing, Høye, Inouye, & Post, 2010; Visser & Gienapp, 2019).

Wildlife responses, including phenological ones, can be phylogenetically structured, with some clades being more sensitive than others to ongoing climate change (Davis, Willis, Primack, & Miller-Rushing, 2010; Lavergne, Evans, Burfield, Jiguet, & Thuiller, 2013) due to phylogenetic signals in species' niche characteristics or life-history traits (Pearman et al., 2014). Understanding how phylogeny and species' traits influence phenological changes is needed to improve our understanding of climate change impacts on free-living organisms. Moreover, climate change is not a spatially uniform process and different populations of the same species may exhibit variable responses depending on the magnitude of change in their environment. In particular, Arctic ecosystems are disproportionately affected by climate warming, a phenomenon known as Arctic amplification (Serreze & Barry, 2011). This rapid warming has strongly altered the phenology of marine and terrestrial Arctic systems, changes that can have detrimental consequences for Arctic fauna through disruption of trophic interactions (Post et al., 2013). Indeed, considering the short time window at high latitudes within which living organisms can grow and reproduce, the reproduction of Arctic species strongly depends on how spring phenology matches their energetic requirements with resource availability (Ramírez et al., 2017). Keogan et al. (2018) demonstrated that seabird populations, when analyzed on a global scale, have not adjusted their reproductive timing in response to ocean warming in the last decades. However, considering the Arctic amplification process, responses of Arctic seabirds to ongoing climate change are expected to be more pronounced than seabirds breeding elsewhere. Here, using a large-scale, long-term and multispecies data set (Figure 1; Supporting Information S1), we investigated the phenological responses of Arctic seabirds to changes in the spring onset as a function of species phylogeny and life

history. The spring onset, that can be defined as the beginning of the growing season in terrestrial systems or the timing of spring bloom in marine ones, is an appropriate yardstick to study changes in the breeding phenology of Arctic species (Visser & Both, 2005) as it drives the entire food web dynamics that occur after the winter in Arctic ecosystems (Post et al., 2013; Søreide, Leu, Berge, Graeve, & Falk-Petersen, 2010). Seabirds generally share very similar life histories, with high survival, low fecundity and high philopatry, but they show variation in some traits that have the potential to affect their phenological response to changing environmental conditions. More specifically, the duration of seabird breeding season (i.e., time spent on the breeding grounds) is highly variable lasting from 25 days (e.g., common eider *Somateria mollissima*) to >100 days (e.g., Leach's storm petrel *Oceanodroma leucorhoa*; Del Hoyo, Elliott, & Sargatal, 1992, 1996). Species tied to nesting sites longer may be under greater selective pressure to match seasonal peaks in food abundance to times of greatest energetic needs in order to fledge their chicks before environmental conditions deteriorate. This may have led to a greater plasticity in reproductive timing in slow nesting species and their response to an advancement in spring should thus be more pronounced than fast nesting ones.

We also had a strong expectation concerning the role of foraging strategy (surface-feeding vs. pursuit-diving) as a driver of phenological response among species and two alternative hypotheses can be drawn. First, the environmental space used by surface feeders is narrower than the one used by pursuit-diving birds (two- vs. three-dimensional space). Surface feeders are thus often considered more sensitive to variations in food availability than divers (Furness & Tasker, 2000; Passuni et al., 2016), and their breeding phenology should be more tightly associated with environmental variations than that of pursuit-diving birds. Alternatively, surface feeders have lower energetic flight costs (Elliott et al., 2013) and may explore a larger (horizontal) environment to find their food at a lower cost than divers. Therefore, if cost of flight is the key parameter driving seabird phenological response to changes in environmental conditions, surface feeders should be less sensitive than divers to changes in environmental conditions. Nevertheless, for either hypothesis, species' phenological responses are predicted to show a strong relationship with foraging strategy, and thus with species phylogeny.

2 | METHODS

2.1 | Seabird phenology data

Data on seabird breeding phenology were gathered from the published literature using different sources and in particular Web of

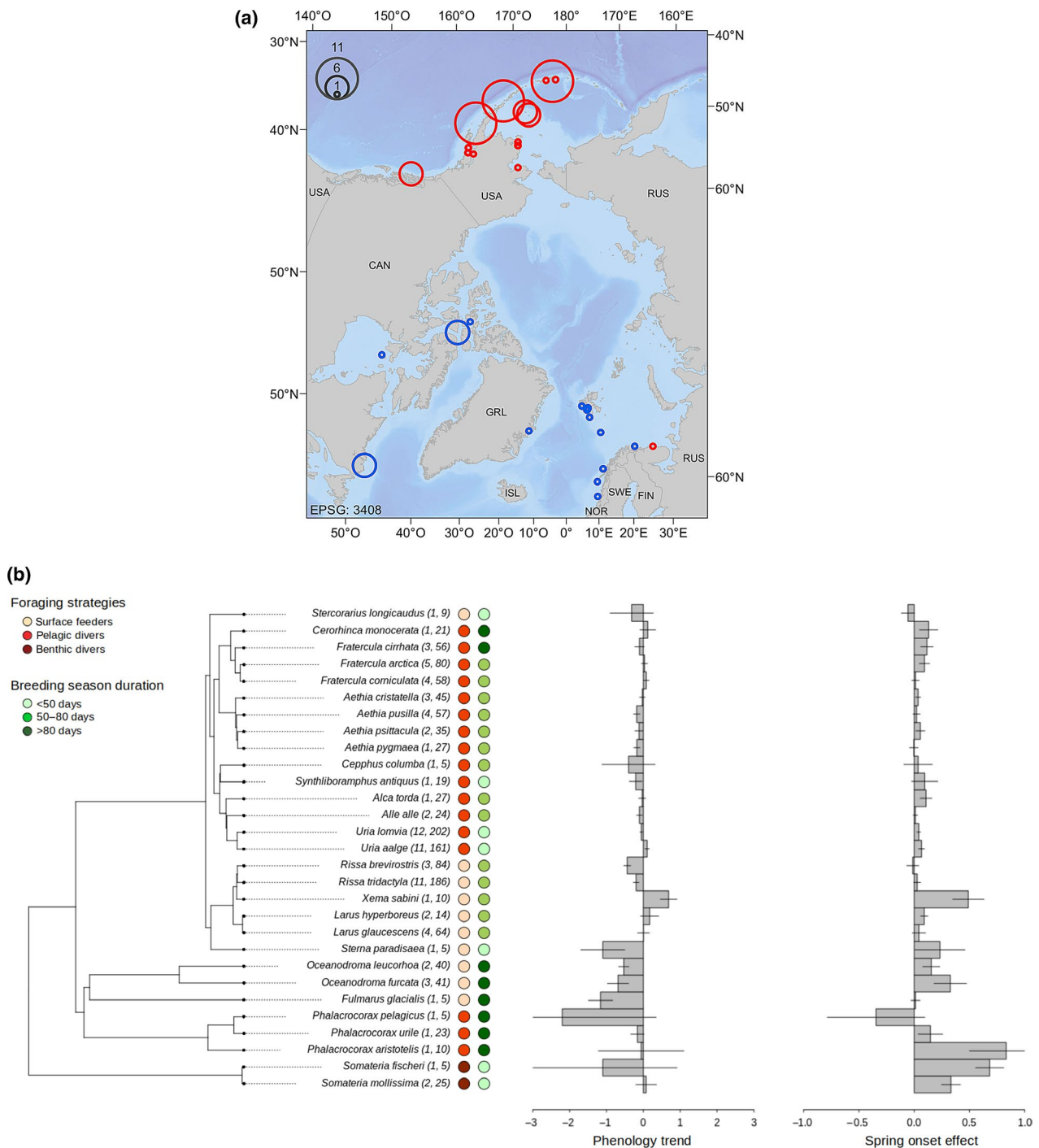


FIGURE 1 Trends in Arctic seabird phenology (hatching date). (a) Seabird breeding sites included in the study. In total, breeding phenology data ($n = 1,343$ estimates of annual mean hatching dates) have been collated from 36 breeding locations and 29 species between 1982 and 2016. The circle colors represent the two different clusters of colonies, that is, the Pacific (red circles) and Atlantic (blue circles) regions (see Section 2 section for details about how clusters have been identified). The size of the circles represents the number of species with available breeding phenology data at each breeding site. (b) Phylogenetic tree of all study species, their trend (and SE) in breeding phenology, and response to spring onset interannual variation (and SE). Numbers in brackets are the number of colonies and total number of years for each species where phenology data were available

Science and Google Scholar. We focused on the 64 seabird species defined as Arctic seabirds by the Conservation for Arctic Flora and Fauna or CAFF (Petersen et al., 2008) and used the English, American, and/or Latin names of the species as key words to look

for all published literature on that given species. We considered data from locations within the Arctic boundaries as defined by CAFF (http://library.arcticportal.org/1378/1/CAFF_Map_No_46_The_limits_of_the_Arctic_according_to_various_definitions_2001.JPG) as

well as a few additional colonies within the Gulf of Alaska. In total, 45 references mentioning seabird laying or hatching dates were gathered (Supporting Information S1). In most references, annual breeding dates were extracted directly from figures; in some others, annual breeding dates were explicitly reported. In a few cases, annual estimates of breeding dates slightly differed between publications for the same location and species; in such situations, we used the average of these different breeding dates.

Additional, unpublished breeding phenology data were provided directly by CBird, the Circumpolar Seabird Expert Group of CAFF (<https://www.caff.is/seabirds-cbird>). Data covered the period 1957–2016, but 99% were collected from 1975 onward. Furthermore, as one of our key objectives was to link changes in seabird phenology with changes in spring onset, we considered only the time period when data on spring onset were available (i.e., 1982–2016; see Section 2.3). Considering the period 1975–2016 or 1982–2016 led to the same results regarding temporal changes in seabird phenology and we only presented results based on the period 1982–2016. This allowed us to run all our models on the same data set and to make model comparisons more straightforward.

In total, data were collated from 36 locations and 29 species, corresponding to a total of 86 breeding phenology time series (we considered only time series ≥ 5 years). Most of the data (80%) were mean hatching dates, 8% were mean laying dates, 10% were median hatching dates, and 2% were median laying dates. Mean laying dates were transformed into mean hatching dates by adding the mean incubation length as reported in Del Hoyo, Elliott, and Sargatal (1992, 1996). Data on both mean laying dates and mean hatching dates were available from 13 colonies (13 different species) and were used to validate our approach (see details in Supporting Information S2). Moreover, we assumed that median hatching dates would represent good proxies of mean hatching dates. Indeed, data from 16 colonies and 10 species included both the mean and median hatching dates and supported this assumption (Supporting Information S2). Finally, we also estimated mean hatching dates using data on median laying dates by adding the incubation length as reported in Del Hoyo, Elliott, and Sargatal (1992, 1996). Both median laying dates and mean hatching dates were available from three colonies and two species and were used to validate our approach (see details in Supporting Information S2). In total, we obtained 1,343 annual estimates of mean hatching dates for the period 1982–2016 distributed from 52°N to 80°N (Figure 1). The average and median lengths of these phenology time series (i.e., number of years with data, not necessarily continuous) were respectively 16 and 14 years (range 5–36).

2.2 | Seabird foraging and duration of breeding season

We classified the 30 study species into three foraging categories, that are, surface-feeding, benthic diving and pursuit-diving (Supporting Information S1). Surface feeders take their prey within the upper 1–2 m of the water column, whereas divers forage at greater depths. The long-tailed skua (*Stercorarius longicaudus*) is not

a typical surface-feeding species as kleptoparasitism may be an important feeding strategy. However, we assumed that this species would be more sensitive to what happens at the sea surface rather than to what happens at deeper depths and thus classified it in the surface-feeding category. This did not affect our results and conclusions. We also considered the duration of the breeding season defined as the number of days between egg laying and chick departure from the nesting site (Supporting Information S1), using information from Del Hoyo, Elliott, and Sargatal (1992, 1996).

2.3 | Sea surface temperature and spring onset

We defined the spring phenology in the marine environment surrounding seabird colonies based on the changes in daily sea surface temperature (SST) within 120 km of each colony. These areas were expected to encompass most of the seabird foraging areas (e.g., Thaxter et al., 2012). Considering a different range (e.g., 60 km) led to the same results. We estimated the date at which SST started to increase between January and June and used this date as a definition of the spring onset. The procedure is detailed in Supporting Information S3. In the marine environment, temperatures are linked to sea ice dynamics (Steele & Dickinson, 2016), primary productivity (Holding et al., 2015) and the spring bloom (Lewandowska & Sommer, 2010). Changes in the timing of ocean warming (i.e., our definition of spring onset) are thus likely related to the entire food web dynamics.

Sea-surface temperature data were from the National Oceanic and Atmospheric Administration (high resolution data, 0.25° spatial resolution; NOAA/OAR/ESRL PSD, Boulder, Colorado, USA; sourced online at <http://www.esrl.noaa.gov/psd/>, accessed in July 2017). This product provides daily information on SST for 35 complete years (1982–2016) and uses Advanced Very High Resolution Radiometer (AVHRR) satellite data from the Pathfinder AVHRR SST data set when available for September 1981 through December 2005, and the operational Navy AVHRR Multi-Channel SST data for 2006 to the present day. The product also uses in situ data from ships and buoys, and includes a large-scale adjustment of satellite biases with respect to the in situ data.

Our spring onset proxy, based on SST dynamics, was significantly and negatively correlated with the average spring (i.e., April–May) SST ($n = 967$ data from the same 120 km colony range zones defined earlier: $\beta = -.005$, $p < .001$; Pearson's $r = -.37$) and was significantly and positively correlated with average spring sea ice concentration (for the areas with sea ice during the winter or spring; $n = 578$, $\beta = .49$, $p = .005$, Pearson's $r = .29$; daily sea ice concentration data from National Snow & Ice Center <http://nsidc.org/data/>, averaged over April and May). This indicates that an early spring (in terms of SST warming) is on average a warm spring and a spring with less sea ice. Moreover, based on spring chlorophyll-*a*, an early spring also tends to be a spring with higher average spring primary production ($n = 312$, $\beta = -.004$, $p = .06$; weekly chl-*a* data from Copernicus Marine Environment Monitoring Service, <http://marine.copernicus.eu/>, L4 product from GlobColour project, averaged over April and May for the period 1997–2016). Therefore, our

spring onset parameter was associated with interannual changes in the spring marine environment and had the advantage of being available for all years and colonies at a fine temporal scale (daily interval).

2.4 | Statistical analyses

All analyses were performed with R software (R Development Core Team, 2016). In all models, response and explanatory variables were centered on their mean for each colony separately (with colony defined as a group of conspecific individuals breeding at a single site). Results are presented as slope estimates $\pm 95\%$ credible intervals (CI). To assess the spatial variation in the trends in seabird hatching dates and spring onset, we used a hierarchical cluster analysis based on the Euclidian distance between colonies. Considering more than two clusters resulted in poorer fit (i.e., higher deviance information criterion [DIC]) irrespective of the model and response variable considered. More specifically, a model with three clusters (Pacific, East Atlantic, West Atlantic; Figure 1) indicated that the trends in spring onset and in seabird phenology, and the effect of spring onset on seabird phenology were the same in the East and West Atlantic (results not shown). We thus considered in subsequent analyses a variable *ocean* based on two clusters only, that is, the Atlantic and Pacific basins (Figure 1). The cluster analysis was performed with the functions *hclust* and *cutree* in R.

Our analyses were done in two separate steps. First, we aimed at estimating the phylogenetic signal in the temporal trend and in the response to changes in spring onset of seabird breeding phenology using classical measures of phylogenetic heritability. Second, we tested more specifically our initial predictions that Arctic seabird phenology would advance through time, be related to changes in spring onset, and vary as a function of the species' foraging strategy and duration of the breeding season.

We first determined whether closely related species were more similar to each other in terms of the two study variables: the temporal trends in hatching dates, and the spring onset effect on hatching date. To do so, we first calculated these two variables for each species as the slope (and standard error) of the regression of hatching date on year (linear effect) or spring onset using linear mixed models with colony defined as random factor (using the *lme* function). In case data for a given species were only available at a single colony, a linear model (function *lm*) was used instead to estimate the slope and associated standard error. We used two separate models for estimating the trend and the effect of spring onset, and we considered the detrended spring onset (i.e., the residuals from a linear regression of the spring onset over a linear trend). We then partitioned the variance of each of these two response variables between its phylogenetic components (σ_p) and its intraspecific component (σ_s), which we used to compute phylogenetic heritability (Housworth, Martins, & Lynch, 2004). These variance components were estimated as random effects using Bayesian *MCMCglmm* models (Hadfield, 2010) run separately on 100 phylogenetic trees, each model being run for 200,000 iterations, discarding the first 5,000 steps as burn-in and sampling model parameters every 1,000 iterations. Model outputs from

distinct trees were then merged together to obtain posterior distributions of each variance components σ_p and σ_s and of phylogenetic heritability $H^2 = \sigma_p / (\sigma_p + \sigma_s)$. To allow comparison with other studies, we also quantified the phylogenetic signal using a standard metric, namely Blomberg's *K* metric (Blomberg, Garland, & Ives, 2003). Hence we computed *K* for the same study variables while accounting for slope uncertainty, as developed by Ives, Midford, and Garland (2007). Blomberg's *K* indicates a low phylogenetic signal when close to zero, and a strong phylogenetic signal when close to (or above) one. The phylogenetic signal of the time before leaving nest was also estimated using Blomberg's *K*. As foraging strategies were discrete (dummy) characters, we estimated their phylogenetic signal using a metric we call *D'*, which equals to $1 - D$, where *D* is the metric developed by Fritz and Purvis (2010) for measuring the phylogenetic signal of binary characters. We did this simple transformation so that our *D'* metric indicates low phylogenetic signal when close to zero, and strong phylogenetic signal when close to one, thus in a comparable way than other metrics of phylogenetic signal for quantitative characters. To do so, we used packages *phytools* (Revell, 2012), *ape* (Paradis, Claude, & Strimmer, 2004), and *caper* (Orme et al., 2013).

Then, in a second step, to test formally whether or not seabird breeding phenology significantly advanced through time and was affected by changes in spring onset, we considered annual hatching dates at the colony level as the response variable and used linear mixed models taking into account the phylogenetic structure of our study species (Hadfield & Nakagawa, 2010). These phylogenetic relationships among our 29 species were based on 100 samples of the Jetz, Thomas, Joy, Hartmann, and Mooers (2012) species tree (www.birdtree.org) using the Hackett et al. (2008) backbone. We modeled hatching date as a function of intercept only, and variables *year*, *spring onset (detrended)*, *foraging strategy*, *duration of breeding season*, *ocean* and relevant two- or three-level interactions. Models were all of the form:

$$\text{Hatching date} = \mu + \beta x_1 + \dots + \beta x_2 + (1|\text{colony}) + (1|\text{species}) + \alpha + \epsilon,$$

where μ is the global mean response (intercept), βx_i represents the fixed effects, "colony" and "species" are random factors, α is the effect of phylogeny (i.e., non-independence among species due to their evolutionary history), and ϵ is the residual term.

To fit and compare these alternative models while taking the phylogenetic dependence into account, we used the *MCMCglmm* package (Hadfield, 2010). All models were run in parallel for 200,000 iterations on all phylogenetic trees, discarding the first 5,000 steps as burn-in and sampling model parameters every 1,000 iterations. Note that, in all analyses, we define a colony as a group of conspecific individuals breeding at a single site so that different species breeding at the same site would be characterized by a different "colony" level. Preliminary analyses indicated that models' goodness of fit and parameter estimates were not affected by the inclusion of an additional random effect for the year, and even deteriorated by the specification of random slopes instead of random intercepts only. These additional random effects were thus not included in our models. We then pooled the posterior distribution of parameters of each replicated runs of the same model, in order

to account for phylogenetic uncertainty in parameter estimation (Pagel & Lutzoni, 2002). Model selection was performed by comparing mean DIC (Spiegelhalter, Best, Carlin, & Linde, 2002) between alternative models (averaged across all phylogenetic trees for each model). Parameter expanded priors were used for all random effects. Plots of the mean and variance of the posterior distribution were examined to assess autocorrelation in the posterior samples. Our data also did not suffer from significant spatial autocorrelation and colonies close to each other within each ocean basin (Pacific and Atlantic) were not more likely to have similar trends in hatching dates than colonies farther away (Supporting Information S4).

3 | RESULTS

Over the 35-year study period, Arctic seabirds showed widely disparate temporal trends in their hatching dates, as well as very different estimated effects of spring onset (defined here as the date when SST starts to increase after winter, see Section 2) on their hatching

date (Figure 1). Despite this large interspecific variation, the temporal trend in hatching dates showed a strong phylogenetic signal, although estimated with a rather large CI ($H^2 = 0.52$, $CI = 0.09-0.94$). The estimated effect of spring onset on hatching date showed a similar phylogenetic signal ($H^2 = 0.62$, $CI = 0.19-0.92$). This was corroborated by Blomberg's K metric of phylogenetic signal (temporal trend: mean $K = 0.40$, mean $p = .004$; spring onset effect: mean $K = 1.42$, mean $p = .001$). These strong phylogenetic signals were consistent in both oceans, in the Atlantic (trend: mean $K = 0.80$, mean $p = .053$; spring onset effect: mean $K = 1.70$, mean $p = .020$) and the Pacific (trend: mean $K = 0.51$, mean $p = .005$; spring onset effect: mean $K = 1.93$, mean $p = .001$). This phylogenetic structure in species' phenological response seems to be linked to the phylogenetic structure in their foraging strategies and in the duration of the nesting period (Figure 1). We found a strong phylogenetic signal on the number of days before leaving the nest (mean $K = 1.0$, mean $p < .001$) and on foraging strategies (surface-feeding: mean $D' = 1.9$, mean $p < .001$; pursuit diving: mean $D' = 2.1$, mean $p < .001$; benthic diving: mean $D' = 2.5$, mean $p < .001$; see Section 2 for details).

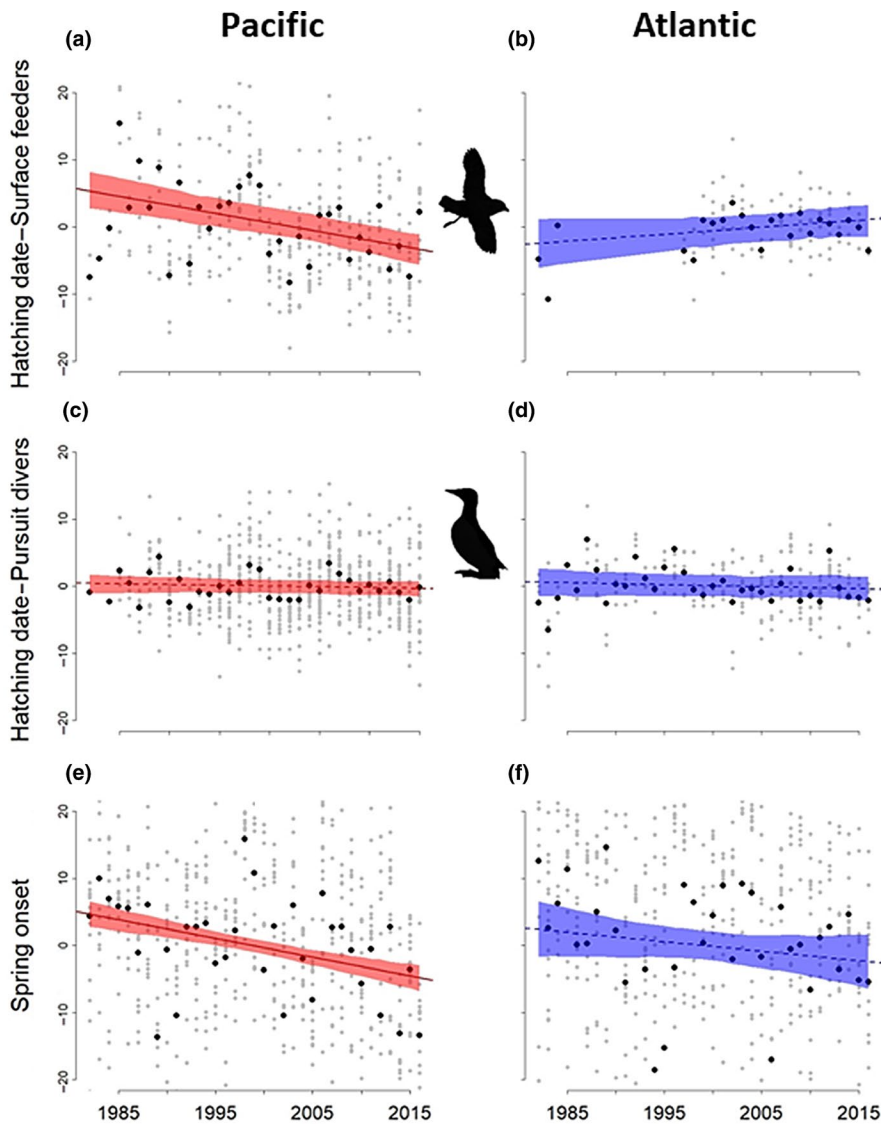


FIGURE 2 Trends in Arctic seabird phenology (hatching date, a–d and spring onset (e, f) as a function of the region (Pacific and Atlantic) and foraging strategy (surface feeders vs. pursuit divers). Benthic divers represent only 3% of the data ($n = 48$ hatching dates) and were not represented here (see Section 3 for details). Gray symbols represent the annual hatching dates (a–d) for all species and colonies or the annual spring onset (e, f) for all colonies; black symbols represent the mean hatching dates (a–d) averaged over all species and colonies and the mean spring onset (e, f) averaged over all colonies. These mean values are for visual representation only and analyses were done at the colony level (i.e., colony was included as a random factor in all models). The red (Pacific; panels a, c, and e) and blue (Atlantic; panels b, d, and f) lines and shaded areas represent the predicted linear temporal trends and their 95% credible intervals. Dashed lines represent slopes nonsignificantly different from zero

To confirm and quantify the relationships between life-history traits, temporal changes in hatching dates, and the effect of changes in spring onset, we considered annual average hatching dates for all years, species, and colonies (Supporting Information S5). We found that hatching of Arctic seabirds occurred on average 0.8 days earlier per decade (slope = -0.08 days/year, 95% CI = $[-0.12; -0.05]$) during the period 1982–2016. This pattern was primarily driven by Pacific colonies (Figure 2). In fact, in the Pacific region, hatching occurred on average 4 days earlier in 2016 than in 1982 (slope = -0.11 days/year, 95% CI = $[-0.16, -0.07]$) while hatching date did not significantly change in the Atlantic (slope = 0.004 days/year, 95% CI = $[-0.07, 0.07]$; Table 1b). Changes in breeding phenology not only varied among ocean basins but also among foraging strategies (Table 1b). In both oceans, hatching dates of pursuit diving species remained remarkably constant over time (slope = -0.02 days/year, 95% CI = $[-0.08, 0.04]$ for the Pacific and slope = -0.03 days/year, 95% CI = $[-0.11, 0.06]$ for the Atlantic; Figure 2c,d; Supporting Information S6). Hatching dates of benthic divers (eider spp.) were also constant over time in the Pacific (slope = 0.02 day/year, 95% CI = $[-0.49, 0.62]$) but very few data ($n = 30$) were available for these species (no data in the Atlantic). Two diving species apparently did not fit in the general pattern and showed rather strong temporal trends (Figure 1b): the pelagic cormorant (*Phalacrocorax pelagicus*) and the spectacled eider (*Somateria fischeri*), though these trends were associated with rather large standard errors (Figure 1b).

Contrary to diving species, hatching dates of surface-feeding species significantly advanced in the Pacific (slope = -0.26 days/year, 95% CI = $[-0.33, -0.19]$, Figure 1a). This was mostly due to four species (out of six with available phenology data in the Pacific): the black and red-legged kittiwake (*Rissa tridactyla* and *R. brevistris*, respectively) and the Leach's and Fork-tailed storm petrel (*O. leucorhoa* and *O. furcata*, respectively; Figure 1; Supporting Information S6). One species (glaucous-winged gull *Larus glaucescens*) did not show any significant change in hatching date. On average, Pacific surface feeders bred 10 days earlier in 2016 than in 1982. Changes in hatching dates of surface feeders were not significant in the Atlantic (slope = 0.10 days/year, 95% CI = $[-0.08, 0.29]$; Table 1b; Figure 1b). Very few data were available for Atlantic surface feeders before 1997 (Figure 2). However, results were the same when constraining our analyses to the period 1997–2016 (and also the same when adding in our sample of data time-series shorter than 5 years), indicating that the observed variation in phenological trends among oceans and foraging strategies is robust. Finally, we did not find any effect of the duration of the breeding season on seabird breeding phenology, neither in the Atlantic nor in the Pacific (Table 1a).

The spatial variation in the trends of hatching dates of surface-feeding species (i.e., significant advancement in the Pacific and no change in the Atlantic) fits with the spatial variation in the advancement of the spring onset. Indeed, spring advanced significantly during our study period by 0.21 days/year on average (95% CI = $[-0.32, -0.10]$), and, even if the effect was statistically not strong (Table 1b),

TABLE 1 Variation in spring onset and Arctic seabird breeding phenology. (a) Temporal changes in Arctic seabird breeding phenology. The mean hatching date is the response variable. Data ($n = 1,343$) were from 36 colonies, 29 species, and 35 years (1982–2016). The Pearson's correlation coefficient between the observed hatching dates and the ones predicted from the model with the lowest DIC was equal to 0.20, indicating that a relatively high proportion of the variation in hatching dates was explained by the linear trend, the ocean and the foraging strategy. (b) Temporal changes in spring onset, defined as the annual date between January and June when the sea surface temperature starts to increase after winter (see Section 2 for details). Data ($n = 1,260$) were from 36 colonies and 35 years (1982–2016) and all models include a colony random effect. (c) Effect of spring onset on Arctic seabird breeding phenology. Data ($n = 1,343$) were from 36 colonies, 29 species, and 35 years (1982–2016)

Predictors (fixed effects)	n	DIC	ΔDIC
(a) Trends in seabird breeding phenology			
Year × foraging strategy × ocean	13	8,589.97	0.00
Year × foraging strategy	9	8,596.43	6.46
Year × duration breeding season × ocean	11	8,606.00	16.03
Year × ocean	7	8,606.07	16.10
Year × duration breeding season	7	8,605.67	15.70
Year	5	8,608.31	18.34
Intercept only	4	8,624.27	34.30
(b) Trends in spring onset			
Year	4	11,159.45	0.00
Year × ocean	6	11,161.97	2.52
Intercept only	3	11,171.96	12.51
(c) Effect of spring onset on seabird breeding phenology			
Spring onset	5	8,600.88	0.00
Spring onset × duration breeding season	7	8,601.04	0.16
Spring onset × foraging	7	8,601.43	0.55
Spring onset × ocean	7	8,604.55	3.67
Spring onset × duration breeding season × ocean	11	8,608.96	8.08
Spring onset × foraging × ocean	11	8,607.60	6.72
Intercept only	4	8,624.31	23.42

Note: In (a) and (b), the year represents a linear trend. In (a), (b), and (c), the ocean corresponds to a two-modality (Pacific, Atlantic) variable; considering a higher number of modalities (i.e., clusters) resulted in poorer fit (see Section 2 for details about the clustering procedure). In (a) and (c), the foraging strategy corresponds to a three-modality variable (pursuit divers, benthic divers, and surface feeders) and all models take the phylogenetic structure into account and include a colony random effect. The duration of the breeding season represents the number of days between laying and when the chick(s) leave the nesting area. Slopes of most of these models and their 95% credible intervals are given in Supporting Information S5.

Abbreviation: DIC, deviance information criterion.

spring advancement was more pronounced in the Pacific than in the Atlantic (slope of -0.28 days/year, 95% CI = $[-0.44, -0.14]$ in the Pacific and of -0.14 days/year, 95% CI = $[-0.31, 0.02]$ in the Atlantic).

Spring onset in the Pacific was on average 10 days earlier in 2016 than in 1982, whereas there was no statistically discernible advance in the Atlantic (Figure 2e,f).

The (detrended) date of spring onset had a positive and significant effect on Arctic seabird hatching dates (Table 1c) although the effect size was small. Assuming a linear relationship between date of spring onset and seabird breeding phenology, this model suggests that a 10 day advancement in the spring onset would translate to less than a 1 day advancement (slope of 0.050 days/year, 95% CI = [0.032, 0.069]) in seabird hatching. As for the temporal trend, there was some variation among species in their response to the advancement in spring onset but for most species, the effect of spring onset was positive, though not significant for many when analyzed separately (Supporting Information S6). On average, this response was similar in the Pacific and Atlantic, and for surface-feeding and diving species (Figure 3; Supporting Information S5) but was slightly more pronounced for “slow breeding species” (Figure 3; Table 1c). Indeed, a 10 day advancement of the spring would be associated with a 1 day advancement in hatching for seabirds that have a breeding season lasting 100 days and with a 0.3 day advancement in hatching for seabirds that have a breeding season lasting 50 days. This difference in spring onset effect was mainly driven by species that have a very long breeding season (>80 days; Figure 3; slope for species with a breeding season <80 days: 0.04, 95% CI = [0.02, 0.06]; slope for species with a breeding season >80 days: 0.15, 95% CI = [0.08, 0.20]). Indeed, when removing species with a breeding season >80 days, there is no longer an effect of the breeding season duration (results not shown) and a model with an interaction between the spring

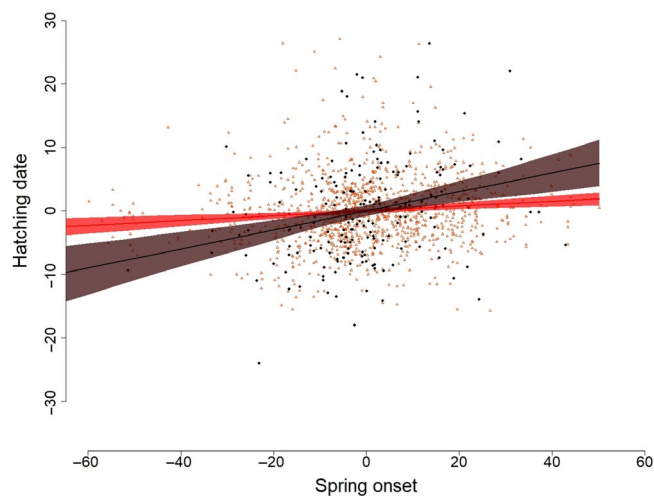


FIGURE 3 Effect of spring onset on Arctic seabird phenology (hatching date) as a function of the duration of the breeding season (i.e., number of days between laying and chick departure from nesting site). The duration of the breeding season was defined as a two-modality factor: species that stay >80 days (black line and symbols) or <80 days (red line and symbols) at the nesting site. The shaded areas represent the 95% credible intervals around predicted values, and the circles or dots represent the observed values (centered on their mean)

onset and a two-modality variable “Duration of breeding season > or <80 days” had a much better fit (DIC = 8,592.71).

4 | DISCUSSION

The seabird species in this study were not equally sensitive to climate change and only some exhibited a phenological response to a shifting climate. In particular, we found that surface-feeding species advanced their reproduction in the last 35 years while diving species showed a remarkably stable timing of breeding. Such changes in breeding phenology of surface feeders only appeared in the Pacific, where the spring advancement was more pronounced and thus where selective pressures were potentially greater. Moreover, seabirds with a longer breeding season had a stronger response to the advancement of spring.

Our results add to the mounting evidence that effects of climate change are often phylogenetically structured, as showed for a wide range of plants, animals, and terrestrial birds (Davis et al., 2010). Indeed, we found a significant phylogenetic structure in the species' trend in breeding phenology and in their phenological response to changes in spring onset. The strength of these phylogenetic signals is however difficult to evaluate as the CI around their mean were rather large. Our study is among the first to propose a key mechanism to these potential phenological signals and suggests that they are driven, at least partly, by the species' foraging strategy. Previous studies have emphasized the role of feeding strategies in structuring seabird responses to climatic fluctuations (Hyrenbach & Veit, 2003; Sandvik & Erikstad, 2008). While diving species exhibited stable breeding phenology over recent decades, reproduction of surface-feeding birds has advanced through time. This advancement was significant in the Pacific region only where surface-feeding species now breed on average 10 days earlier than 35 years ago. This result is driven by colonies located around the Aleutian Archipelago where most of the Pacific data came from (Figure 1). The 10 day advancement coincides with the observed 10 day advancement in spring onset in the Pacific. The northern Pacific (including the Bering Sea) has indeed changed drastically (Grebmeier et al., 2006) and previous studies support our findings of an earlier spring onset in the Pacific (Burrows et al., 2011; Stabeno & Overland, 2001). The Atlantic has also warmed in the last decades (Polyakov, Alexeev, Bhatt, Polyakova, & Zhang, 2010) but the spring onset proxy indicated that timing of ocean warming in the spring did not change much in the North Atlantic as compared with the North Pacific. Even if both regions experienced recent environmental changes and warming with important consequences on ecosystems (Descamps, Aars, et al., 2017; Kitaysky & Hunt, 2018), these changes likely had different patterns. The Atlantic Multidecadal Oscillation has been mostly positive in the last 20 years while the Pacific one was strongly negative (Steinman, Mann, & Miller, 2015). These modes are key drivers of SST variability (Steinman et al., 2015) so that we can expect that SST dynamics and environmental changes have been different. This would explain why Arctic phenology of seabirds did not change in the same way in the last decades in both oceans but

the exact mechanisms behind these changes remain unknown. Even if the advancement in spring onset paralleled the advancement in surface-feeding bird phenology in the Pacific (i.e., both share the same long-term trend), there was only a weak relationship between the interannual variation in spring onset and interannual variations in hatching dates. This suggests that either there are no causal relationships between sea surface temperature dynamics and breeding timing, or that these causal relationships are complex and involve a number of abiotic and biotic drivers. This would not be surprising as relationships between sea temperatures and marine organisms are complex (Poloczanska et al., 2016), and for seabirds involve several intermediate trophic levels and include food-related as well as nest-site and colony-related processes (Burr et al., 2016). These processes may also vary across Arctic regions; for instance, there are notably different sea ice dynamics in the Pacific and Atlantic. A considerably larger area is impacted by sea ice on the Pacific side, possibly leading to more pronounced biological changes in response to changing sea ice distributions and seasonality (Langbehn & Varpe, 2017).

Our study provides important additions to the recent conclusion that seabird breeding phenology is insensitive to shifting climate change on a global scale (Keogan et al., 2018). While their study did not identify a response based on biogeographical region, they identified variation in rates of phenological response to SST at the spatial scale of site, highlighting the need for additional studies at smaller geographical scales. Our study was limited to the Arctic, where more rapid and dramatic environmental changes are occurring (Serreze & Barry, 2011). At high latitudes we expect nesting seabirds to have evolved under the selective pressures of pronounced seasonal cycles, which impose (temperature-related) physical constraints on the temporal window for breeding. Therefore, our focus on this region where organisms may be sensitive to these physical constraints, and where there are amplified environmental changes, may explain why we detected a seabird response. The notably high rates of environmental change in the northern Pacific (Grebmeier et al., 2006), specifically, might explain why we detected regional change in seabird breeding phenology. Directional changes in seabird breeding phenology have also been observed in Antarctica (Barbraud & Weimerskirch, 2006; Descamps et al., 2016), where several species, but not all (e.g., Youngflesh et al., 2017), have actually delayed their reproduction in response to climate change (by approx. 1–2 days per decade). These studies indicated that climate warming may not always be associated with earlier breeding (Visser & Both, 2005) and emphasized the importance of spatial variation in phenology. Our work highlights the value of complementing large-scale phenological studies such as Keogan et al. (2018), with those on smaller geographic scales in order to identify at what spatial and taxonomic scales mechanisms for seabird breeding timing are acting.

Consistent with the overall conclusion in Keogan et al. (2018), we found that some species are insensitive to the spring advancement. Diving species, and most notably the Alcidae family (Figure 1), showed a remarkable lack of phenological change over the last decades, suggesting that breeding phenology changed very little in response to climate warming and spring advancement

in this group. This may suggest that pursuit-diving seabirds have access to a wider environmental space and/or show larger foraging plasticity and thus manage to get enough food and accumulate sufficient energetic reserves to start breeding independent of spring onset. Alternatively, breeding timing of divers may be primarily driven by specific environmental constraints (or cues) that have not changed over the last decades. As an example, being as early as possible at the breeding site may outweigh the importance of being synchronous with the environment in case there is a high competition for breeding sites (Kokko, 1999). Additional studies at the species and colony level are needed to unravel the environmental drivers of breeding dates in diving species and assess the life-history consequences of an earlier spring.

Given the potentially large consequences that phenological changes may have on reproductive success (e.g., Ramírez et al., 2017; Youngflesh et al., 2017) and population dynamics (McLean, Lawson, Leech, & Pol, 2016), assessing phenological change is essential especially in the Arctic where changes are among the fastest on Earth. Our results emphasize the importance of spatial variation and life history (more specifically, foraging strategy) in phenological response to climate change. Organisms unable to adjust their breeding phenology to climate change might be more prone to population decline (Møller, Rubolini, & Lehikoinen, 2008). Further studies linking population trends with breeding phenology are needed.

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AUTHOR CONTRIBUTION

The study was designed by S.D. and was part of the *Seatime* project led by Ø.V., Z.B. and S.D. S.D. and S.L. analyzed the data. S.D. wrote the manuscript with contributions from S.L., and M.L.M., G.J.R., Ø.V., F.R., T.A.N., R.T.B., Z.B., S.C.D., K.E.E., D.B.I., and S.H.L. commented on earlier drafts. S.B. collated the phenology data from the literature and F.R. gathered and organized the environmental data. The CBird/CAFF and SEAPOP groups (S.D., T.A.N, R.T.B., S.C.D., K.E.E., D.B.I., S.H.L., M.L.M., G.J.R., T.K.R., H.S.) provided additional phenology data.

DATA AVAILABILITY STATEMENT

Data are available in the Dryad data repository, <https://doi.org/10.5061/dryad.np92nm2>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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