

RESEARCH ARTICLE

Opposite, but insufficient, phenological responses to climate in two circumpolar seabirds: Relative roles of phenotypic plasticity and selection

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Abstract

1. The magnitude of climate change has been greatest in the Arctic, accelerating climate-induced shifts in phenology, but wildlife responses vary. Variation may be due to the relative importance of phenotypic plasticity or phenotypic selection.
2. Here, we examine and contrast the environmental drivers of plasticity in breeding phenology of two circumpolar seabirds at their receding summer range limit using unique datasets of marked individuals covering 25 and 30 years. Based on prior knowledge of the local ecosystems, we predicted that climate would generate opposing patterns of plasticity in the two populations.
3. Laying phenology of kittiwakes in the Gulf of Alaska was associated with a large-scale climate oscillation (Pacific Decadal Oscillation) while the Arctic-breeding murre adjusted laying to sea-ice conditions. Kittiwakes laid earlier after experiencing colder climate about 2 years prior and laying dates did not advance over the study, but murre laid earlier when warmer climate led to earlier spring sea-ice break-up, and murre laying dates advanced by 1 week since 1990. Selection favoured earlier laying in both species.
4. Both populations adjusted breeding phenology to environmental variation, but we anticipate opposing effects on phenology with continued climate change. Ice-constrained species can likely adapt to some extent because plasticity can provide the necessary shift to this physical barrier, although individuals were only able to adjust by ~1 week while ice conditions advanced by over a month. In more temperate regions, where phenology is driven by bottom-up effects, plasticity and selection counteract one another leading to limited adaptability. We provide insights into the likely adjustments by Arctic marine animals to an increasingly warmer and ice-less summer.

KEYWORDS

black-legged kittiwake, Brünnich's guillemot, clutch initiation date, Lande-Arnold equation, phenotypic plasticity, reaction norm, thick-billed murre, timing of breeding

1 | INTRODUCTION

Wildlife phenology is advancing in response to climate change, especially in the rapidly warming Arctic (Mallory et al., 2020; Panchen & Gorelick, 2017; Saalfeld & Lanctot, 2017; Shaftel et al., 2021; but see Kwon et al., 2018). Those advances will be constrained by populations' inherent phenotypic plasticity and their ability to adapt evolutionarily to such changes. While phenological advances could result from plasticity or selection, long-term monitoring studies indicate that individual plasticity accounts for much of the observed shifts in phenology (Bonnet et al., 2019; Charmantier et al., 2008; Nussey et al., 2005) and is necessary for rapid responses to climate, especially in long-lived organisms (Charmantier & Gienapp, 2014). Individual variation in either plasticity in response to climate (an interaction between individual and environment, I×E; Nussey et al., 2007; Dingemans & Dochtermann, 2013) contributes to further heterogeneity in some populations. Over longer time-scales, evolutionary processes may select for individuals with phenology that increases fitness, or even select for individuals with plastic responses that enhance fitness (Bonnet et al., 2019; Charmantier & Gienapp, 2014).

Several different mechanisms, not mutually exclusive, can produce climate–phenology relationships, and the consequences of climate change depend on which mechanism is at play. First, climate may drive prey phenology; therefore, predators integrate climate information via sensory and endocrine systems to match timing of breeding with prey availability. If climate change advances the phenology of both predators and prey at the same rate, the predator population may 'keep in step' with environmental change by integrating changing environmental cues; if climate change disrupts the predictive relationship between climate cues and prey availability, then breeding success may decline due to trophic mismatch (Thackeray et al., 2010; Visser et al., 1998). Second, climate may drive prey availability, so predators either integrate sensory information about prey abundance into endocrine responses and breeding decisions, or individual energetics directly influence phenology (Whelan et al., 2021). Under this mechanism, phenological shifts are a symptom of underlying changes in prey availability and, in the specific case where prey availability declines, are unlikely to rescue a population. Greater food availability almost always advances breeding phenology (Boutin, 1990; Ruffino et al., 2014); thus, if climate change decreases prey abundance, then predator breeding phenology may be delayed; if climate change increases prey abundance, then breeding phenology may advance. Third, climate may constrain breeding phenology independent of prey availability. For example, snowpack can block access to breeding sites (Sauve et al., 2019) and the absence of non-climate supplementary cues (e.g. nest sites) inhibits the endocrine cascade that leads to reproduction. If climate change relieves these constraints, breeding phenology may advance.

Globally, most populations are advancing spring phenology in response to climate change (Parmesan, 2006), but others have delayed (e.g. Dobson et al., 2017) or not shifted phenology in response to climate (e.g. Lewis et al., 2012). A recent global meta-analysis concluded

that seabirds—taxa with broad geographic distributions—are phenologically insensitive to sea-surface temperatures, implying that such variation may have little impact on seabird phenology (Keogan et al., 2018). However, numerous studies of seabirds have observed laying date plasticity in response to other environmental variables linked to temperature (incl. Gaston & Hipfner, 1998; Gaston, Gilchrist, & Mallory, 2005; Gaston, Gilchrist, & Hipfner, 2005; Reed et al., 2006; Brommer et al., 2008; Dobson et al., 2017; Sauve et al., 2019). Together, these studies suggest that (a) sea-surface temperature may not be the exclusive environmental variable integrated by seabirds to time spring phenology, (b) the spatial scale and identity of phenologically relevant environmental cues are population specific, and (c) since relationships between temperature and phenology are not always negative in seabirds, responses across these taxa may average to zero.

Here, we examine and contrast the environmental drivers of laying date plasticity in two populations of circumpolar seabirds in very different ecosystems: one with seasonal sea-ice and another without ice. Based on prior information about the local oceanography, we expected the two populations to respond very differently in the face of climate change. Most studies have been of a single population or of multiple species at a single site, and we wished to illustrate how two declining circumpolar species (Frederiksen et al., 2016; Hatch, 2013) can respond in an ice-bound and an ice-less system, respectively. Our study is complementary to that of Sauve et al. (2019) on a third Arctic seabird, the black guillemot *Cepphus grylle*, where the constraint was also a physical barrier: snowfall limiting access to breeding sites. We used longitudinal data for Pacific black-legged kittiwakes *Rissa tridactyla* (hereafter 'kittiwakes') on Middleton Island, Alaska (ice-free), and thick-billed murres *Uria lomvia* (hereafter 'murres') on Coats Island, Nunavut (seasonal sea-ice). Both species occur primarily in sub-Arctic and Arctic regions, and we studied both species near their southern range limit. Arctic ecosystems are characterised by strong seasonality and short summers, but also periods of high biological productivity.

Arctic-breeding seabird populations have experienced some of the greatest climate change in recent decades (Post et al., 2009; Post et al., 2019), but are simultaneously constrained by strong seasonality because the window of time when resources support breeding remains relatively narrow. Moreover, seabirds, like other air-breathing Arctic marine animals, face the physical constraint of sea-ice, limiting foraging opportunities. However, below the marginal ice zone—or once the sub-Arctic is ice-free—phenology will be constrained by food availability directly. In that situation, plasticity and selection might counteract one another with selection for earlier breeding but individuals constrained to breed later when they have greater reserves. Thus, the relative importance of plasticity and selection for changes in breeding date might be expected to be different for populations with and without ice. Furthermore, historical selection for plasticity would likely be very strong in the murre system with seasonal sea-ice, and this may erode genetic variation for plasticity and lead to high population-level plasticity, but result in low I×E. We test a set of hypotheses

regarding climate–phenology relationships in the two populations (Table 1), with broad aims to (a) identify climate drivers of laying phenology, (b) quantify population- and individual-level plasticity in response to annual variation in climate, (c) estimate the contributions to individual variation in laying phenology of climate and breeder experience, and (d) estimate selection on laying date. The overarching aim was to predict the impact of climate change on reproductive phenology for these two populations in contrasting environmental contexts.

2 | MATERIALS AND METHODS

2.1 | Study systems

We used individual-based reproductive data from black-legged kittiwakes breeding on Middleton Island, Alaska (1996–2019) and thick-billed murres breeding on Coats Island, situated in northern Hudson Bay, Nunavut (1990–2019; Figure 1). Middleton Island is situated in the Gulf of Alaska, approximately 100 km south of

mainland Alaska. It is surrounded by open water year-round, and black-legged kittiwakes arrive on the breeding grounds in March or April (Whelan et al., 2020). The climate of the island is strongly influenced by the Pacific Decadal Oscillation (PDO; Mantua & Hare, 2002). At this location, negative PDO indices are associated with cold sea-surface temperatures, high precipitation, capelin-rich fish stocks and high kittiwake breeding success, while positive PDO indices are associated with warm waters, low precipitation, low capelin availability and low breeding success in kittiwakes (Hatch, 2013). Climate change is expected to increase the frequency and intensity of marine heatwaves (Frölicher et al., 2018) and may even disrupt large-scale climate oscillations such as the PDO (Litzow et al., 2020).

In contrast, around Coats Island, sea-ice forms annually, with spring break-up typically occurring in May or June. In spring, thick-billed murres follow the receding ice edge from overwintering areas in the Labrador Sea to arrive on the breeding grounds during the ice break-up (Gaston et al., 2011; Patterson et al., 2021). The main prey item, Arctic cod *Boreogadus saida*, is typically consumed when associated with ice, but murres are unable to access this resource

	Middleton Island, Alaska	Coats Island, Nunavut
<i>Physical barrier?</i>	No	Yes (ice)
<i>Hypothesis</i>	<i>Prediction for kittiwakes</i>	<i>Prediction for murres</i>
Pre-breeding climate has strong effects on laying phenology in highly seasonal environments with high inter-annual variation in climate	Kittiwakes will adjust laying phenology to climate	Murre will adjust laying phenology to climate
Individual variation in plasticity (I×E) is greater in populations limited by climate-driven food supply, not by physical constraints	Kittiwakes will exhibit individual variation in response to climate	Murres will not exhibit individual variation in response to climate

TABLE 1 Hypotheses and predictions tested in this study.

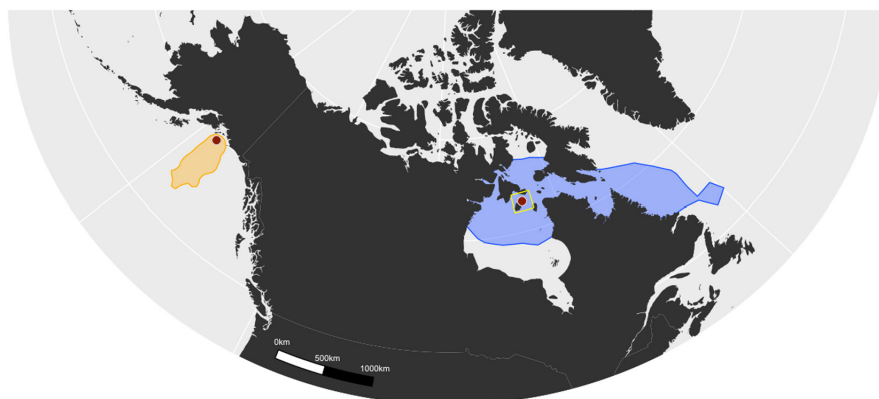


FIGURE 1 Pre-breeding utilisation distributions (95%) of black-legged kittiwakes (orange; April 30) and thick-billed murres (blue; May 1–31). Red points indicate locations of the breeding colonies on Middleton Island and Coats Island. Yellow box (200 × 200 km) in northern Hudson Bay indicates the scale at which sea-ice concentration best predicted murre laying phenology. Location estimates produced via geolocators deployed over multiple years (kittiwakes: 2010–2012; murres: 2018–2019).

when ice coverage is continuous (Gaston et al., 2011). Previous work in this system found that, at the population level, laying dates were generally earlier in years of early sea-ice break-up and warmer spring temperatures (Gaston, Gilchrist, & Hipfner, 2005; Gaston & Hipfner, 1998). During the decades since monitoring began in 1981, Arctic sea-ice extent has declined, and spring sea-ice break-ups have advanced (Hochheim & Barber, 2014; Mudryk et al., 2018; Serreze et al., 2007; Stroeve et al., 2007). As climate change continues to warm the Arctic, sea-ice extent is expected to continue its decline (IPCC, 2019).

2.2 | Reproductive monitoring

2.2.1 | Black-legged kittiwakes on Middleton Island, Alaska

The kittiwake colony, which breeds on a former radar tower modified as nesting habitat (described in Gill & Hatch, 2002), has been monitored for individual-level breeding phenology and breeding success every year since 1996, except 2014. Each adult kittiwake (whether hatched on the tower or immigrating into the tower population) was banded with a unique combination of colour bands and a metal band, and sexed via behavioural observations each year. While kittiwakes are generally monogamous and long-lived, individuals often have multiple mates over their lifetime due to divorce and mate mortality. We excluded observations from individuals of unknown sex and food-supplemented pairs (Gill & Hatch, 2002). Nest contents were checked twice daily to observe appearance/disappearance of eggs and chicks. Kittiwakes lay clutches of 1–3 eggs and will sometimes produce a second clutch if the first clutch is lost; we therefore defined laying date as the clutch initiation date for the first clutch. We defined fledging success as the number of chicks that reached fledging age (~45 days) or were still present in the nest at the end of the breeding season (range: 0–3).

2.2.2 | Thick-billed murres on Coats Island, Nunavut

The murres, which breed on a natural cliff in a colony of 15,000 breeding pairs, were monitored semi-continuously since the 1980s; plots (groups of 40–200 nests monitored each year and interspersed throughout the colony) were checked daily. Intensive monitoring of breeding phenology began in 1990 (the earliest year included in this study), but no laying phenology data were collected for 2012, 2015 or 2016. Individuals were marked with a numbered metal band and a cohort-specific colour combination (different for immigrant adults vs chicks). We sexed individuals via molecular techniques, pairing with birds sexed via molecular techniques and pairing with a former mate of a known-sex individual. We excluded observations where the identity of the female was unknown. Murres lay a single egg clutch and will often relay if the

first egg is lost; we therefore defined laying date as the date the first egg was laid. We defined hatching success as the number of eggs hatched (either 0 or 1).

It can be difficult to observe an egg or chick brooded by a cliff-nesting murre, and in most cases the timing of egg laying must be estimated based on the last date a bird was observed without an egg and the first date observed incubating. In some years, the field team arrived after eggs were laid, and laying dates were estimated based on hatching dates (based on the last date a bird was incubating an egg and the first date observed brooding a chick). In cases where both a laying window and a hatching window were observed, we used the estimated laying date from the narrower time window. If the windows were of equal duration, we used laying date window estimates rather than back-calculations from hatching date windows. We then calculated mean laying date for each year and excluded any eggs laid 14 days after the annual mean laying date, because these were mainly relay attempts misidentified as first attempts.

2.2.3 | Ethical approval

Research activities on Middleton Island, AK, were approved by the McGill Animal Care Committee (animal use protocol 2016–7814 and precursors) and permitted by the United States Fish and Wildlife Service (Migratory Birds Permit 33779 and precursors). Research activities on Coats Island, NU, were approved by the McGill Animal Care Committee (animal use protocol 2015–7599, 2016–7814 and precursors) and permitted by the Canadian Wildlife Service (Scientific Research Permit NUN-SCI-16-03 and precursors) and Nunavut government (Nunavut Wildlife Permit 2020-031 and precursors).

2.3 | Pre-breeding distributions

To describe pre-breeding distributions for each species, we used published location estimates for kittiwakes breeding on Middleton Island (Whelan et al., 2020) and murres breeding on Coats Island (Patterson et al., 2021). We used multiple years of location estimates for each colony (kittiwakes: 2010–2012; murres: 2018, 2019) and calculated 95% utilisation distributions during the month prior to when the population typically initiates laying (kittiwakes: April; murres: May) using *adehabitatHR* (Calenge, 2006).

2.4 | Environmental variables

We obtained environmental data at various spatial scales to use for sliding window analyses and subsequent models of laying date (Table S1). We used two region-specific indices for large-scale climate oscillations: the Pacific Decadal Oscillation (PDO) and the North Atlantic Oscillation (NAO). We extracted daily

mean sea-surface temperature at four spatial scales around each colony (50×50 km, 100×100 km, 200×200 km, kittiwakes: Gulf of Alaska, murre: 400×400 km), and daily mean sea-ice concentration around Coats Island at the same four spatial scales. We obtained local mean ambient temperatures for Middleton Island Airport. We used ambient temperature and snow depth from the weather station nearest to Coats Island (Coral Harbour, NU; 145 km from the colony).

The two climate indices, PDO and NAO, were available at a monthly resolution. We aggregated all other environmental data to a monthly scale by first taking the mean of hourly data and/or daily resolution data to produce comparable datasets at a monthly resolution for all climate variables and thus avoid spurious results due to differences in temporal resolution.

Sliding window analyses to determine the sensitivity of laying date to climate.

We used a sliding window approach (*climwin*, Bailey & van de Pol, 2016) to evaluate the potential environmental drivers of laying date. We used absolute windows that shifted (by 1-month increments in length and start date) over a period from zero to 24 months before the mean laying date of the population over the entire long-term study period (kittiwakes: 4 June; murre: 23 June). This approach allowed a test for both current and lagged effects of climate on laying phenology. Although we were concerned primarily in the effect of the physical barrier (ice), we wished to allow for lagged ecosystem-level effects as both species feed on a prey base of 2-year-old juvenile fishes and a 2-year lag in foraging response has been observed in kittiwakes (Osborne et al., 2020; Provencher et al., 2012). We used linear mixed effects base models (*lme4*, Bates et al., 2014) to test for linear effects of means for each climate variable on unscaled laying dates of each species. We included random effects of female ID, male ID and year for kittiwakes (laying date $\sim (1 | \text{female ID}) + (1 | \text{male ID}) + (1 | \text{year})$) but did not have sufficient data to include male ID in models of murre laying date (laying date $\sim (1 | \text{female ID}) + (1 | \text{year})$).

After identifying the windows that best predicted laying dates for each climate variable, we tested whether the climate window identified was a significant improvement over randomised climate windows (*randwin* function, repeats = 5) using a significance threshold of $p < 0.05$. To proceed with population- and individual-level plasticity analyses, we selected the environmental variable with the lowest AIC value among climate windows that were significantly different from randomised windows.

2.5 | Population-level plasticity and temporal trends

We calculated annual mean laying dates for each species. To examine population-level plasticity, we fitted Bayesian linear models of unscaled annual mean laying date in response to the climate variable selected through climate window analyses (kittiwakes: lagged PDO; murre: sea-ice concentration at 200 km scale). We tested whether

climate shifted over the study period via Bayesian linear models. To test for a shift in mean laying dates over the study period, we fitted Bayesian linear models of annual mean laying dates in response to study year (continuous covariate). Finally, to test whether laying date and breeding success were associated with the population level, we fitted Bayesian linear models of annual mean breeding success (kittiwakes: mean number of chicks fledged; murre: mean hatching success) in response to annual mean laying date.

2.6 | Individual-level plasticity analyses

We used all breeding records from first breeding attempts, including females with only a single nest record in the long-term dataset (Martin et al., 2011). To ensure that models were fitted to the same dataset, we excluded observations with missing data for the variables included in maximal models. For models that would account for individual variation in response to environmental conditions (I×E), we used the climate variable that best predicted laying dates in the sliding window analyses (kittiwakes: lagged PDO; murre: sea-ice concentration at 200 km scale). We also tested for individual variation in rate of change in laying date with age (I×Age; Appendix S1).

We fitted a series of Bayesian univariate linear mixed-effects models of laying date with varying levels of complexity in the random and fixed effects. We increased the complexity of the random structure by sequentially adding random effects of female ID, year, male ID (kittiwakes only) and an I×E term (random slope: female ID × climate). Random slopes of climate and female experience were mean centred (but not within-subject centred).

We fitted models of each random structure with an intercept only and then with fixed effects (breeding experience + environment) for each species. To account for nonlinear effects of parental age on laying date (Hipfner et al., 1997; Ratcliffe et al., 1998), we considered female breeding experience (number of years since the female was first observed breeding) as a proxy for age. We used within-subject centring to separate climate and female experience variables into within- and between-female components (van de Pol & Wright, 2009) and to test for quadratic effects of age (using equation 3b described in Fay et al., 2021).

2.7 | Selection on relative laying date

We estimated phenotypic selection on relative laying date using relative fledging success for kittiwakes and relative hatching success for murre. While reproductive success is more closely linked in time to reproductive phenology, survival may also be affected (such as via reduced time to moult prior to migration for late breeders). However, we did not use adult survival to examine selection due to low resighting rates. For both species, we included any offspring produced from second clutches because early breeding enhances the ability to produce a second clutch. We calculated relative laying date as the female's deviation from

the annual mean laying date, and relative fledging success as the pair's deviation from the annual mean number of fledglings (kittiwakes) or hatchlings (murre) produced. We obtained fledging data for all kittiwake nest records; however, we used a subset of murre records ($n = 573$) excluding observations of birds included in an egg-removal and wing-clipping experiment, where we only observed a hatching window (not laying window), and a year with only two observations (2003). Including records with only a hatching window would bias towards apparent reduced selection against late-laying females.

We fitted one univariate Bayesian linear mixed-effects model of relative fledging or hatching success per species, in response to linear and quadratic effects of relative laying date (Lande & Arnold, 1983). We mean-centred both fixed effect terms and scaled them by dividing each value by the standard deviation of the fixed effect variable. We used a random effects structure that included intercepts only (kittiwakes: female ID, male ID, and year; murre: female ID and year). We report the linear coefficient as an estimate of directional selection. To estimate the strength of stabilising or disruptive selection, we doubled the quadratic coefficient and confidence intervals (Lande & Arnold, 1983; Stinchcombe et al., 2008).

After finding directional selection for earlier relative laying dates in both species (but non-significant stabilising/disruptive selection; see below), we then fitted a univariate Bayesian mixed-effects model of either absolute number of fledglings (kittiwakes: Poisson with log link) or hatchlings (murre: categorical with logit link), in response to linear relative laying date. We used a random effects structure that included intercepts only (kittiwakes: female ID, male ID, and year; murre: female ID and year). This enabled visualisation of the relationship between relative laying date and breeding success.

2.8 | Statistical analyses

We followed the statistical methods of Sauve et al. (2019) to test for effects of climate and female age on laying phenology. With the exception of *climwin* analyses, we fitted all models with the R package MCMCGLMM (Hadfield, 2010) using parameter-expanded priors described in Sauve et al. (2019). We ran 50,000,000 iterations with a burn-in period of 5,000,000 and thinning interval of 5000. We evaluated the importance of random effects using DIC with and without fixed effects, where differences of 5 DIC were considered improvements in model fit (Spiegelhalter et al., 2002). We report estimates of variance components and confidence intervals <0.01 as 0. We calculated the proportion of variance due to each random effect for the best model (based on DIC) for each species, both for the intercept model and the model with fixed effects. We assessed significance of fixed effects via pMCMC values and Bayesian credible intervals. Finally, we calculated the proportion of total variance (V) due to each random component, including individual repeatability, using the random intercept model for each species (e.g. for female

kittiwake repeatability in laying date: $V_{\text{femaleID}}/[V_{\text{femaleID}} + V_{\text{maleID}} + V_{\text{year}} + V_{\text{residual}}]$).

3 | RESULTS

We obtained 2831 kittiwake laying dates from 1,000 females, 934 males, and 23 years. For murre, we obtained 1,099 laying dates from 395 females and 26 years. We used all of the kittiwake records and a subset of the murre records ($n = 573$ laying dates from 260 females and 13 years) to estimate selection on relative laying date.

3.1 | Pre-breeding distributions

Kittiwakes used pelagic, offshore locations near and south of the breeding colony before the breeding season (Figure 1; Figure S1). Most kittiwakes from the Middleton population were not actively migrating (Whelan et al., 2020) and were instead likely foraging on myctophids off the continental shelf (Hatch, 2013). Murre used a large area stretching from the Labrador Sea to Northern Hudson Bay before the breeding season. The relatively large area used by murre reflects their migratory movements from the Labrador Sea to the breeding colony, which follows the receding ice-edge (Gaston et al., 2011).

3.2 | Environmental drivers of laying date

Individual-level laying dates were associated with lagged PDO in kittiwakes; climate windows identified for ambient temperature at the colony and sea-surface temperatures at all four spatial scales were not significant improvements over randomised windows (Figure 2; Table S2). Laying dates of female kittiwakes were earlier in years of lower mean PDO index from July through September (20–22 months prior to laying).

Sea-surface temperature and sea-ice concentration were associated with murre laying dates at all four spatial scales (50, 100, 200 and 400 km), except sea-surface temperature at 400 km. As sea-surface temperature was closely correlated with sea-ice concentration, and we considered the latter to have a stronger physical mechanism (along with the lowest AIC), we completed subsequent analyses using only sea-ice concentration. Climate windows identified for ambient temperature, snow depth (which can limit access to certain murre sites) and North Atlantic Oscillation index were not significant improvements over randomised windows (Figure 2; Table S2). Laying dates of female murre were earlier in years of (a) lower mean winter and spring sea-ice concentration (January–June; 0–5 months prior to laying) and (b) warmer mean sea-surface temperatures in the month of laying (Jun; month of laying). Sea-ice break-up around the colony tends to follow a consistent pattern of complete ice coverage in winter, followed by a sharp decline

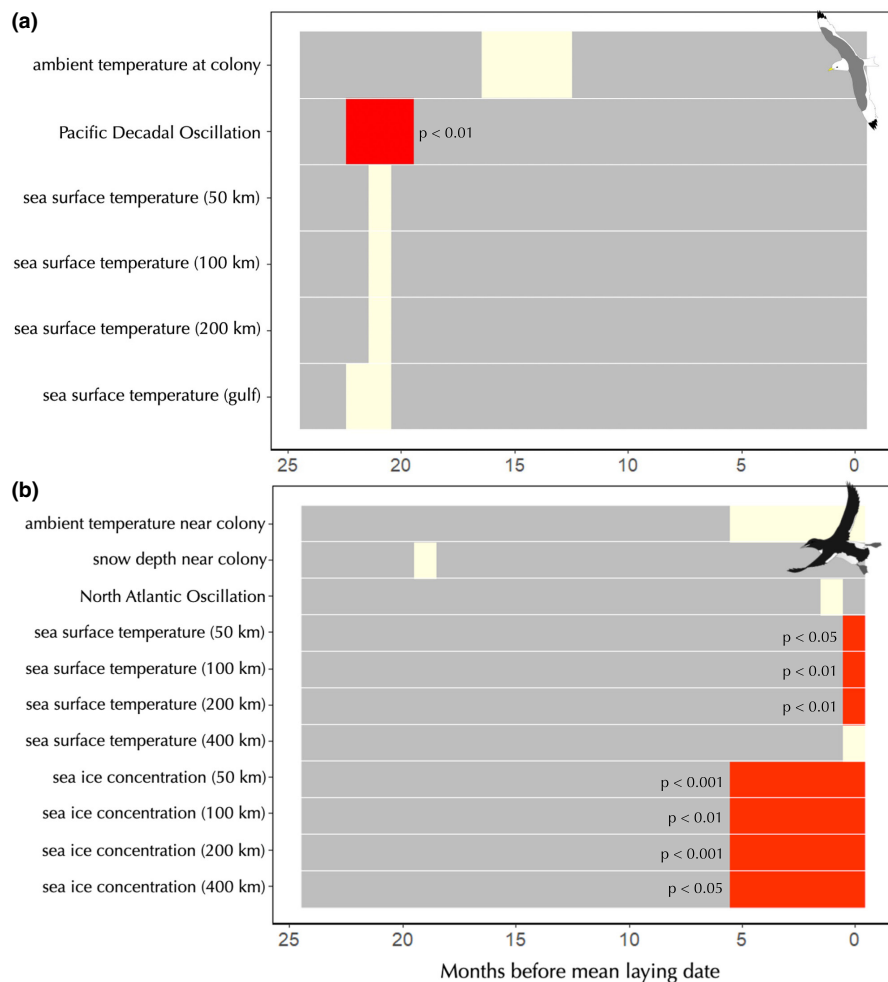


FIGURE 2 Results of climate window selection for prediction of laying dates in (a) black-legged kittiwakes and (b) thick-billed murre. Red and beige indicate the months identified as the best predictor of laying dates for the climate variable; red windows are significant improvements over randomised windows while beige windows are non-significantly different than random.

in concentrations beginning in May, then nearly complete open water by late July (Figure S2). Thus, the mean sea-ice concentration (and mean sea-surface temperature, which is highly correlated with sea-ice concentration during spring break-up; Figure S3) at this spatiotemporal scale correlates strongly with the timing of spring break-up (Figure S4).

We extracted annual mean PDO index and annual mean sea-ice concentration during the temporal windows identified via climate window analyses. We used these mean climate values in subsequent population- and individual-level models of laying date.

3.3 | Population-level phenology

3.3.1 | Black-legged kittiwakes

Mean laying dates of kittiwakes were earlier in years of lower lagged PDO (colder climate; Figure 3a; $\beta = 3.51$ CI [2.11, 4.88], pMCMC < 0.0001). Mean lagged PDO did not significantly change during the study period (Figure 3c; $\beta = -0.011$ CI [-0.082, 0.056], pMCMC = 0.74) and mean annual laying dates of kittiwakes did not significantly advance over the study period (Figure 3e; $\beta = -0.071$ CI [-0.413, 0.229], pMCMC = 0.66). On average, kittiwakes produced

fewer fledglings in years when the population laid late (Figure 3g; $\beta = -0.031$ CI [-0.054, -0.010], pMCMC < 0.01).

3.3.2 | Thick-billed murre

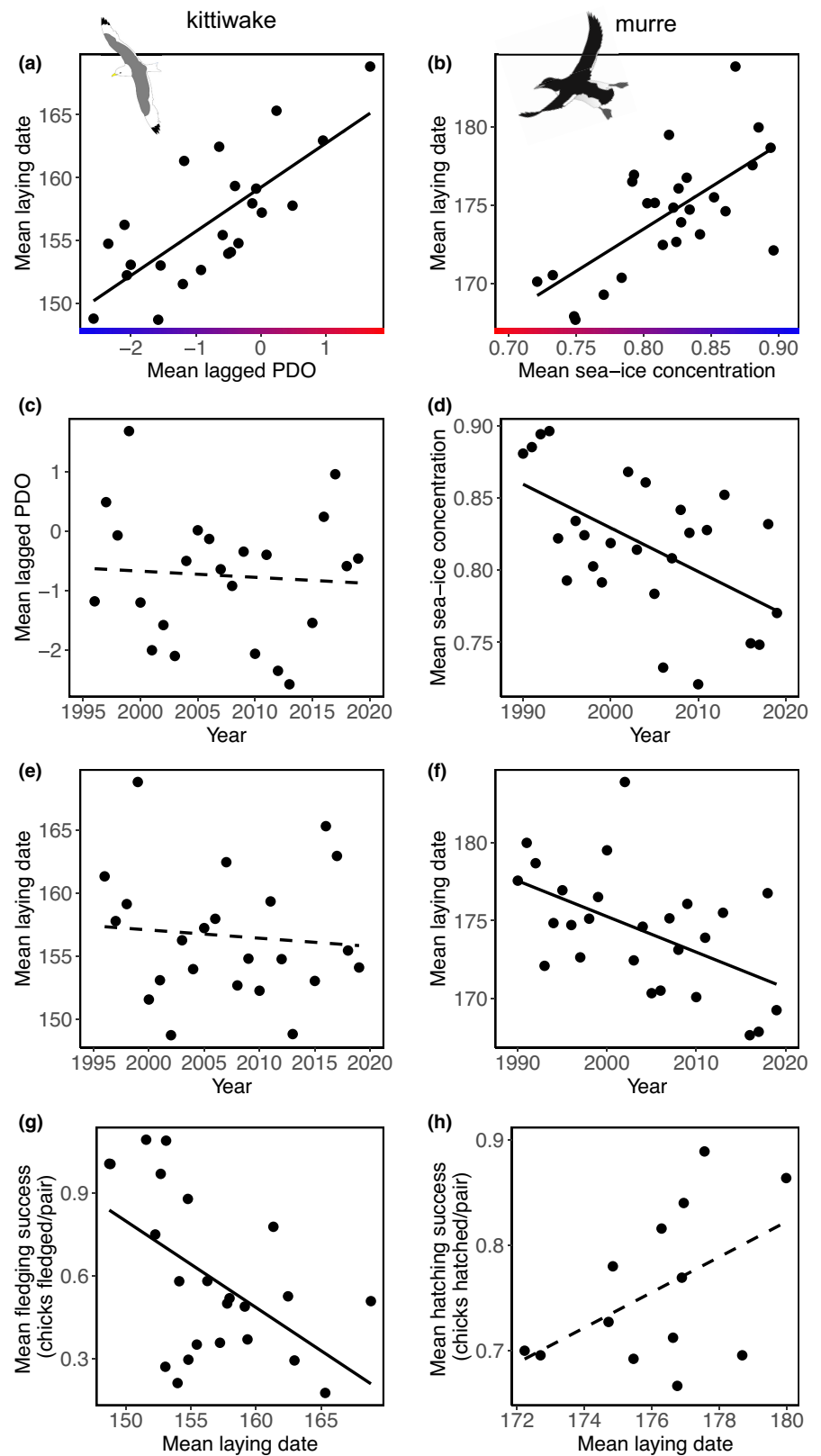
Mean laying dates of murre were earlier in years of lower winter and spring sea-ice concentrations (Figure 3b; $\beta = 54.02$ CI [27.92, 78.17], pMCMC < 0.001). Mean sea-ice concentrations declined during the study period (Figure 3d; $\beta = -0.0030$ CI [-0.0049, -0.0011], pMCMC < 0.01) and mean annual laying dates of murre advanced over the study period (Figure 3f; $\beta = -0.23$ CI [-0.39, -0.07], pMCMC < 0.01). We did not find an association between annual mean breeding success and mean annual laying date (Figure 3h; $\beta = 0.017$ CI [-0.003, 0.036], pMCMC = 0.08).

3.4 | Individual-level plasticity

3.4.1 | Black-legged kittiwakes

Female kittiwakes exhibited individual variation in laying date plasticity in response to lagged PDO ($I \times E$; Figure 4a; Table 2). Females

FIGURE 3 Population-level trends in laying date. (a) Annual mean laying dates of kittiwakes were earlier in years of lower lagged PDO index (cold/wet climate in July–September of year 2). Negative PDO indices are associated with colder climate in the Gulf of Alaska, while positive PDO indices are associated with warmer climate. The blue–red colour gradient on the x-axis shows a cold–warm temperature gradient. (b) Annual mean laying dates of murre were earlier in years of lower winter/spring sea-ice concentration (January–June at 200km scale around colony). Red–blue colours used on x-axis to show warm–cold temperature gradient. (c) Mean lagged PDO index (July–September of year 2) did not significantly change over the study period. (d) Mean sea-ice concentrations during winter/spring (200km) declined over the study period. (e) Mean laying dates of kittiwakes did not significantly advance over the study period (1996–2019). (f) Mean laying dates of murre advanced over the study period (1990–2019). (g) Kittiwakes produced more fledglings when laying dates were, on-average, earlier. (h) Murre hatching success was not higher when laying dates were earlier. Trendlines represent model predictions and dashed lines indicate non-significant trends; each point represents 1 year.



that consistently laid later also responded less strongly to PDO via plasticity (correlation between random intercept and random slope $I \times E$: -0.91 CI $[-1.00, -0.80]$). Female laying date was repeatable (0.18–0.22; Table 3; Table S3). All fixed effects predicted to influence laying date were significant except quadratic between-female

experience (Table S4). Females delayed laying date as lagged PDO increased (within-female lagged PDO), and females that experienced lower lagged PDO indices over their breeding lifetime laid earlier (between-female lagged PDO). Females laid earlier as they aged (within-female experience) and females with longer

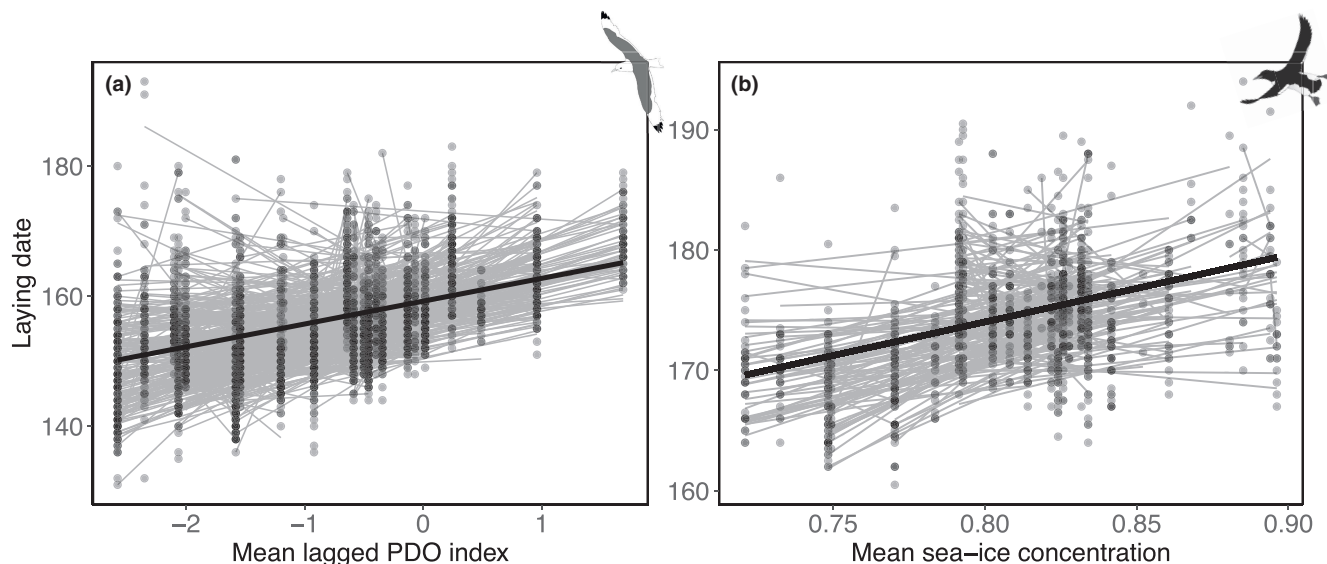


FIGURE 4 (a) Laying dates of kittiwakes in response to lagged PDO and (b) laying dates of murre in response to sea-ice concentrations. Grey lines represent individual-level responses to environment (raw slopes fitted for each female, not model predictions), and black lines represent model predictions for population-level plasticity. Note that the y-axes are on different scales due to less annual variation in murre laying phenology.

TABLE 2 Deviance information criterion (DIC) for models of black-legged kittiwake and thick-billed murre laying date with varying random and fixed effects structure.

Random effects structure	DIC (intercept only)	DIC (main + quadratic effects)
Black-legged kittiwake		
~ (lagged PDO female) + (1 male) + (1 year)	17,710	17,667
~ (1 female) + (1 male) + (1 year)	17,881	17,848
~ (1 female) + (1 year)	17,895	17,859
~ (1 female)	19,561	18,747
Thick-billed murre		
~ (sea-ice concentration female) + (1 year)	6,024	6,022
~ (1 female) + (1 year)	6,027	6,025
~ (1 female)	6,572	6,314

reproductive life spans tended to lay earlier on-average (between-female experience).

3.4.2 | Thick-billed murre

Female murre did not exhibit strong individual variation in laying date plasticity (no I × E; Figure 4b; Table 2). However, females showed consistent individual differences in laying date (I + E). We therefore report the results of the model that accounted for similarity among observations from the same females and years (random

intercepts of female ID and year, I + E; Table S5). Female laying date was repeatable (0.15–0.18; Table 3; Table S3). All fixed effects predicted to influence laying date were significant, except quadratic between-female experience (Table S5). Females advanced laying in years of low sea-ice concentrations (within-female ice) and females that, on-average, experienced lower sea-ice conditions laid earlier (between-female ice). Females laid earlier as they aged (within-female experience) and when they were, on-average, observed in years when they had more experience (between-female experience).

3.5 | Selection on laying date

Both species showed directional phenotypic selection for earlier laying dates (kittiwakes: $b = -0.13$, CI = $[-0.16, -0.10]$, pMCMC < 0.0001; murre: $b = -0.059$, CI = $[-0.099, -0.017]$, pMCMC < 0.01). It is important to note that we modelled different measures of annual breeding success for each population (fledging vs hatching success; about 1 L% of murre chicks die, thus hatching success is quite similar to fledging success; Gaston et al., 1983), so the strength of selection may not be comparable. We found little evidence for stabilising or disruptive selection in either population (kittiwakes: $\gamma = -0.031$, CI = $[-0.082, 0.024]$, pMCMC = 0.26; murre: $\gamma = -0.003$, CI = $[-0.081, 0.079]$, pMCMC = 0.86). Female kittiwakes that laid relatively early tended to produce more fledglings than late-laying females (Figure 5a; $b = -0.036$, CI = $[-0.044, -0.028]$, pMCMC < 0.0001). Similarly, female murre that laid relatively early tended to have greater hatching success than late-laying females (Figure 5b; $b = -5.2$, CI = $[-10.2, -0.7]$, pMCMC < 0.01).

TABLE 3 Estimates of the proportion of variance in laying date (day of year) due to each variance component in black-legged kittiwakes and thick-billed murre (95% credible intervals in brackets).

Model	Female ID (female repeatability)	Year	Male ID (male repeatability)
Black-legged kittiwake			
Intercept only	0.18 [0.12, 0.23]	0.42 [0.28, 0.57]	0.02 [0.00, 0.04]
Fixed effects	0.22 [0.16, 0.28]	0.26 [0.14, 0.39]	0.02 [0.00, 0.05]
Thick-billed murre			
Intercept only	0.15 [0.10, 0.22]	0.47 [0.32, 0.62]	—
Fixed effects	0.18 [0.12, 0.25]	0.31 [0.18, 0.45]	—

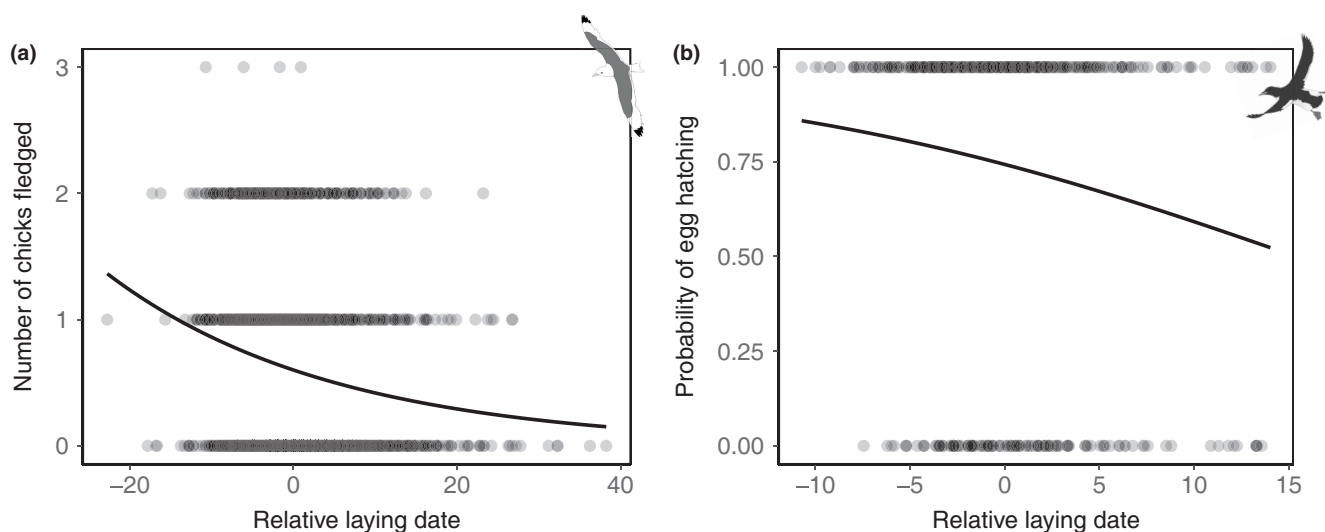


FIGURE 5 Females that laid earlier relative to the annual population mean (a) produced more fledglings in the kittiwake population and (b) were more likely to hatch an egg in the murre population. Lines represent model predictions from a Poisson GLMM (log link) of number of fledglings produced (0–3) in kittiwakes and a categorical GLMM (logit link) model of number of chicks hatched (0–1) in murre. Points show raw data and transparency is used to show density in areas of overlap.

4 | DISCUSSION

Climate had contrasting effects on the laying phenology of black-legged kittiwakes and thick-billed murre, although selection favoured earlier laying in both populations. Using a spatial window reflecting pre-breeding locations recorded by geolocators and a sliding time window approach, we identified key drivers for phenology in the two species. Kittiwake laying phenology was associated with lagged effects of a large-scale climate oscillation in the Pacific Ocean, where females laid earlier when preceded by a colder climate (negative PDO 20–22 months prior). Murre laid earlier in years of lower sea-ice concentrations and earlier spring break-up; as sea-ice concentrations declined in Northern Hudson Bay, murre laying dates advanced 7 days over the 30-year study. Although sea-surface temperatures in the North-East Pacific increased over the course of our study (Wills et al., 2018), we found no significant trend in kittiwake laying dates over the same period. This reflects the overriding influence of climate oscillating between warm and cold regimes in the North Pacific during the study period (Hatch, 2013; Wills et al., 2018).

The association between PDO and breeding phenology of Middleton Island kittiwakes was likely driven by time-lagged, bottom-up effects of climate on prey availability. The summer-autumn time period identified via climate window analysis coincides with the spawning phenology of several key forage fishes in the Gulf of Alaska (Doyle et al., 2019) and that cohort of juvenile fishes ultimately becomes the kittiwake prey base 2 years later (Hatch, 2013). Warmer climate may cause a phenological mismatch between some forage fish and their zooplankton prey (Anderson & Piatt, 1999) or decrease larval recruitment by depleting lipid reserves via increased metabolic rates (Piatt et al., 2020). Recent studies following an extreme marine heatwave in the region found cascading and lagged effects of the event on the Gulf of Alaska ecosystem, including forage fish and seabirds (Arimitsu et al., 2021; Osborne et al., 2020; Suryan et al., 2021). The Middleton Island kittiwakes increased foraging effort for at least 2 years after the heatwave (Osborne et al., 2020). Furthermore, breeding success in the population is positively associated with the presence of capelin in the diet (Hatch, 2013). Capelin abundance in the Gulf of Alaska (and in kittiwake diet) tends to be lower in warmer conditions (Anderson & Piatt, 1999; Hatch, 2013) and, intriguingly,

capelin mature at 2–3 years and their spawning occurs during the window identified as important for kittiwakes (summer-autumn, Doyle et al., 2019). Overall, as climate change warms the North Pacific (Fröllicher et al., 2018; Wills et al., 2018), we expect negative effects on kittiwake food supply at Middleton Island, which, in turn, will delay laying phenology and reduce breeding success.

Murres laid earlier as winter and spring sea-ice concentrations declined in Northern Hudson Bay over the past three decades. Sea-ice concentrations were strongly correlated with spring ice break-up and spring sea-surface temperature (which also predicted laying phenology, if not as strongly as ice) around the colony—taken together, this is strong evidence that murres cannot begin to breed until sea-ice break-ups enough for them to access prey around the colony. This concurs with movement studies that showed the timing of spring break-up constrains timing of migration and spring arrival to the breeding colony (Gaston et al., 2009; Gaston, Gilchrist, & Hipfner, 2005; Gaston, Gilchrist, & Mallory, 2005). The larger spatial distribution during pre-laying reflects these strong ice constraints; while kittiwakes spend 2 months around the colony waiting for foraging cues to breed, murres cannot enter Hudson Strait until the ice leaves and then breed within a few weeks (perhaps as soon as the ovaries can develop eggs). As climate change continues to advance the date of spring sea-ice break-up (Mudryk et al., 2018), murres will gain access to prey around the breeding colony earlier. Although sea-ice appears to be a strong constraint on timing of breeding for this population, it is likely that other environmental or intrinsic factors could influence breeding phenology in extreme low-ice years. We did not find evidence of lagged climate effects on murre laying phenology here, but an earlier study suggested that climate can have downstream effects on prey availability lagged by 2 years (Provencher et al., 2012) and this may become more important for murre phenology with Arctic warming.

Both murre and kittiwake populations are declining globally, and the reduced food supply during warmer, recent years provides a clear mechanism for kittiwake declines (Hatch, 2013). Indeed, the kittiwake population tends to have lower breeding success in warm phases of climate when breeding is late (this study; Hatch, 2013). For murres, the population declines are most rapid in the eastern Atlantic, which has been warming fastest (Frederiksen et al., 2016). Despite selection for earlier laying within years, murres did not, on average, produce more offspring during years of early laying. Murre chicks at Coats Island grow fastest when fed Arctic cod (*Boreogadus saida*), which are associated with cold water (Gaston & Elliott, 2014); as murres only advanced their lay date by 7–10 days while spring break-up advanced by 30 days, there is a phenological mismatch with their highest quality prey.

While both species showed clear responses to climate, only kittiwakes showed individual variation in laying date plasticity ($I \times E$). Kittiwakes were likely responding to variation in food availability, which might be perceived or accessed differently among individuals if they specialise on different resources. Murres, however, were responding to a physical barrier that might be expected to affect all individuals equally. Indeed, the predictable barrier of spring sea-ice

and short Arctic breeding season may have eroded genetic variation for plasticity (Brommer, 2013; Porlier et al., 2012). Throughout the study, the kittiwake population experienced highly variable and heterogeneous environmental conditions due to a large-scale climate oscillation, which could maintain variation in individual plasticity.

Reproductive success (our metric of 'fitness') declined with relative laying date for both murres and kittiwakes. Thus, both species may experience selection for earlier laying, although we do not report adult survival that could favour later breeding and lead to stabilising selection (Golet et al., 2004). At least in terms of reproductive success, the curve shape was slightly different between the two species, with kittiwakes decelerating and murres accelerating. Thus, selection was strongest for the earliest individuals in kittiwakes and against the latest individuals for murres. The trends may represent differences in age-specific reproductive success. Kittiwakes show little variation in reproductive success early in life but strong senescence late in life with the reverse true for murres (Elliott et al., 2014). Thus, selection on murre laying date may represent low breeding success in young birds, which tend to be very late layers, while the selection on kittiwakes may represent low success in senescent birds, which tend not to lay much later than middle-aged birds (Elliott et al., 2014).

5 | CONCLUSIONS

Our results do not support a recent meta-analysis of global seabird phenology that suggested seabirds are 'insensitive' to ocean temperature (Keogan et al., 2018). Ocean temperature clearly influences phenology in these two populations, albeit through very different mechanisms. Thus, although some seabird populations advance phenology in response to warm temperatures while others delay (and these responses may average to zero), this does not mean that populations are insensitive to ocean temperature. We suggest that ecological systems need to be understood in their local context (e.g. regional oceanography).

While climate change is global, the magnitude and mechanism of its effects on wildlife vary across ecosystems, species, populations and individuals. Thick-billed murres, as predicted by models of individual plasticity, advanced their timing of laying at Coats Island, while black-legged kittiwakes, for reasons peculiar to the dynamics of North Pacific marine oceanography, showed no such trend. The apparent plasticity of the kittiwakes is likely driven by bottom-up effects of climate on food supply, rather than direct effects of climate on phenology via sensory cues or physical constraints.

Although both populations showed considerable plasticity in response to variation in climate, such plasticity is unlikely to rescue the populations from climate change. Over 30 years, sea-ice break-up around Coats Island advanced more than 1 month (Figures S2 and S4) but the murre population only laid 7 days earlier. Thus, the realised changes in breeding date have not kept pace with climate change; furthermore, this may prevent murres from aligning chick-rearing with a peak in food availability (see Gaston

et al., 2009). In contrast, for the kittiwakes, no amount of phenological adjustment would rescue the population because the shifts in breeding date are not an adaptive adjustment to track climate changes, but rather a consequence of climate-driven reduced prey availability. Although we did not detect shifts the Pacific Decadal Oscillation index during the 25-year study, future warming will likely delay breeding in kittiwakes and lead to reduced reproductive success. In short, two declining, northern seabirds are unlikely to be able to adjust to rapid climate change through plasticity in timing of breeding.

AUTHORS' CONTRIBUTIONS

S.W. and K.H.E. conceived the ideas and designed the methodology; all authors collected data; S.W. analysed the data and drafted the manuscript; all authors contributed critically to interpretation and writing of the final manuscript, and gave final approval for publication.

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CONFLICT OF INTEREST

We do not have any conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data and code were uploaded for review. Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.9cnp5hqhg> (Whelan et al., 2022).

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REFERENCES

- Anderson, P. J., & Piatt, J. F. (1999). Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series*, 189, 117–123.
- Arimitsu, M. L., Piatt, J. F., Hatch, S., Suryan, R. M., Batten, S., Bishop, M. A., von Campbell, R. W., Coletti, H., Cushing, D., Gorman, K., Hopcroft, R. R., Kuletz, K. J., Marsteller, C., Pegau, S., Schaefer, A., Schoen, S., Straley, J., & von Biela, V. R. (2021). Heatwave-induced synchrony within forage fish portfolio disrupts energy flow to top pelagic predators. *Global Change Biology*, 27(9), 1859.
- Bailey, L. D., & Van De Pol, M. (2016). Climwin: An R toolbox for climate window analysis. *PLoS ONE*, 11(12), e0167980.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv:1406.5823*.
- Bonnet, T., Morrissey, M. B., Morris, A., Morris, S., Clutton-Brock, T. H., Pemberton, J. M., & Kruuk, L. E. (2019). The role of selection and evolution in changing parturition date in a red deer population. *PLoS Biology*, 17(11), e3000493.
- Boutin, S. (1990). Food supplementation experiments with terrestrial vertebrates: Patterns, problems, and the future. *Canadian Journal of Zoology*, 68(2), 203–220.
- Brommer, J. E. (2013). Phenotypic plasticity of labile traits in the wild. *Current Zoology*, 59(4), 485–505.
- Brommer, J. E., Rattiste, K., & Wilson, A. J. (2008). Exploring plasticity in the wild: Laying date–temperature reaction norms in the common gull *Larus canus*. *Proceedings of the Royal Society B: Biological Sciences*, 275(1635), 687–693.
- Calenge, C. (2006). The package adehabitat for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 516–519.
- Charmantier, A., & Gienapp, P. (2014). Climate change and timing of avian breeding and migration: Evolutionary versus plastic changes. *Evolutionary Applications*, 7(1), 15–28.
- Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E., & Sheldon, B. C. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, 320(5877), 800–803.
- Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: Mixed-effect modelling approaches. *Journal of Animal Ecology*, 82(1), 39–54.
- Dobson, F. S., Becker, P. H., Arnaud, C. M., Bouwhuis, S., & Charmantier, A. (2017). Plasticity results in delayed breeding in a long-distant migrant seabird. *Ecology and Evolution*, 7(9), 3100–3109.
- Doyle, M. J., Strom, S. L., Coyle, K. O., Hermann, A. J., Ladd, C., Matarese, A. C., Shotwell, S. K., & Hopcroft, R. R. (2019). Early life history phenology among Gulf of Alaska fish species: Strategies, synchronies, and sensitivities. *Deep Sea Research Part II: Topical Studies in Oceanography*, 165, 41–73.
- Elliott, K. H., O'Reilly, K. M., Hatch, S. A., Gaston, A. J., Hare, J. F., & Anderson, W. G. (2014). The prudent parent meets old age: A high stress response in very old seabirds supports the terminal restraint hypothesis. *Hormones and Behavior*, 66(5), 828–837.
- Fay, R., Martin, J., & Plard, F. (2021). Distinguishing within- from between-individual effects: How to use the within-individual centering method for quadratic patterns. *Journal of Animal Ecology*, 90, 1–12. <https://doi.org/10.1111/1365-2656.13606>
- Frederiksen, M., Descamps, S., Erikstad, K. E., Gaston, A. J., Gilchrist, H. G., Grémillet, D., Johansen, K. L., Kolbeinsson, Y., Linnebjerg, J. F., Mallory, M. L., McFarlane Tranquilla, L. A., Merkel, F. R., Montevecchi, W. A., Mosbech, A., Reiertsen, T. K., Robertson, G. J., Steen, H., Strøm, H., & Thórarinnsson, T. L. (2016). Migration and wintering of a declining seabird, the thick-billed murre *Uria lomvia*, on an ocean basin scale: Conservation implications. *Biological Conservation*, 200, 26–35.
- Frölicher, T. L., Fischer, E. M., & Gruber, N. (2018). Marine heatwaves under global warming. *Nature*, 560(7718), 360–364.
- Gaston, A. J., & Elliott, K. H. (2014). Seabird diet changes in northern Hudson Bay, 1981–2013, reflect the availability of schooling prey. *Marine Ecology Progress Series*, 513, 211–223.
- Gaston, A. J., Gilchrist, H. G., & Hipfner, J. M. (2005). Climate change, ice conditions and reproduction in an Arctic nesting marine bird: Brunnich's guillemot (*Uria lomvia* L.). *Journal of Animal Ecology*, 74, 832–841.
- Gaston, A. J., Gilchrist, H. G., & Mallory, M. L. (2005). Variation in ice conditions has strong effects on the breeding of marine birds at Prince Leopold Island. *Nunavut. Ecography*, 28(3), 331–344.

- Gaston, A. J., Gilchrist, H. G., Mallory, M. L., & Smith, P. A. (2009). Changes in seasonal events, peak food availability, and consequent breeding adjustment in a marine bird: A case of progressive mismatching. *The Condor*, *111*(1), 111–119.
- Gaston, A. J., & Hipfner, M. (1998). The effect of ice conditions in northern Hudson Bay on breeding by thick-billed murres (*Uria lomvia*). *Canadian Journal of Zoology*, *76*(3), 480–492.
- Gaston, A. J., Noble, D. G., & Purdy, M. A. (1983). Monitoring breeding biology parameters for murres *Uria* spp.: Levels of accuracy and sources of bias. *Journal of Field Ornithology*, *54*(3), 275–282.
- Gaston, A. J., Smith, P. A., Tranquilla, L. M., Montevecchi, W. A., Fifield, D. A., Gilchrist, H. G., Hedd, A., Mallory, M. L., Robertson, G. J., & Phillips, R. A. (2011). Movements and wintering areas of breeding age thick-billed murre *Uria lomvia* from two colonies in Nunavut, Canada. *Marine Biology*, *158*(9), 1929–1941.
- Gill, V. A., & Hatch, S. A. (2002). Components of productivity in black-legged kittiwakes *Rissa tridactyla*: Response to supplemental feeding. *Journal of Avian Biology*, *33*(2), 113–126.
- Golet, G. H., Schmutz, J. A., Irons, D. B., & Estes, J. A. (2004). Determinants of reproductive costs in the long-lived black-legged kittiwake: A multiyear experiment. *Ecological Monographs*, *74*, 353–372.
- Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, *33*(2), 1–22.
- Hatch, S. A. (2013). Kittiwake diets and chick production signal a 2008 regime shift in the Northeast Pacific. *Marine Ecology Progress Series*, *477*, 271–284.
- Hipfner, J. M., Gaston, A. J., & de Forest, L. N. (1997). The role of female age in determining egg size and laying date of thick-billed murres. *Journal of Avian Biology*, *28*, 271–278.
- Hochheim, K. P., & Barber, D. G. (2014). An update on the ice climatology of the Hudson Bay system. *Arctic, Antarctic, and Alpine Research*, *46*(1), 66–83.
- IPCC (2019). In H.-O. Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegria, M. Nicolai, A. Okem, J. Petzold, B. Rama, & N. M. Weyer (Eds.), *IPCC special report on the ocean and cryosphere in a changing climate*. In press.
- Keogan, K., Daunt, F., Wanless, S., Phillips, R. A., Walling, C. A., Agnew, P., Ainley, D. G., Anker-Nilssen, T., Ballard, G., Barrett, R. T., Barton, K. J., Bech, C., Becker, P., Berglund, P.-A., Bollache, L., Bond, A. L., Bouwhuis, S., Bradley, R. W., Burr, Z. M., ... Lewis, S. (2018). Global phenological insensitivity to shifting ocean temperatures among seabirds. *Nature Climate Change*, *8*(4), 313–318.
- Kwon, E., English, W. B., Weiser, E. L., Franks, S. E., Hodkinson, D. J., Lank, D. B., & Sandercock, B. K. (2018). Delayed egg-laying and shortened incubation duration of Arctic-breeding shorebirds coincide with climate cooling. *Ecology and Evolution*, *8*(2), 1339–1351.
- Lande, R., & Arnold, S. J. (1983). The measurement of selection on correlated characters. *Evolution*, *37*, 1210–1226.
- Lewis, S., Nussey, D. H., Wood, A. G., Croxall, J. P., & Phillips, R. A. (2012). Intrinsic determinants of a population trend in timing of breeding in the wandering albatross. *Oikos*, *121*(12), 2061–2071.
- Litzow, M. A., Hunsicker, M. E., Bond, N. A., Burke, B. J., Cunningham, C. J., Gosselin, J. L., Norton, E. L., Ward, E. J., & Zador, S. G. (2020). The changing physical and ecological meanings of North Pacific Ocean climate indices. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(14), 7665–7671.
- Mallory, C. D., Williamson, S. N., Campbell, M. W., & Boyce, M. S. (2020). Response of barren-ground caribou to advancing spring phenology. *Oecologia*, *192*(3), 837–852.
- Mantua, N. J., & Hare, S. R. (2002). The Pacific decadal oscillation. *Journal of Oceanography*, *58*(1), 35–44.
- Martin, J. G., Nussey, D. H., Wilson, A. J., & Réale, D. (2011). Measuring individual differences in reaction norms in field and experimental studies: A power analysis of random regression models. *Methods in Ecology and Evolution*, *2*(4), 362–374.
- Mudryk, L. R., Derksen, C., Howell, S., Laliberté, F., Thackeray, C., Sospedra-Alfonso, R., Vionnet, V., Kushner, P. J., & Brown, R. (2018). Canadian snow and sea ice: Historical trends and projections. *The Cryosphere*, *12*(4), 1157–1176.
- Nussey, D. H., Postma, E., Gienapp, P., & Visser, M. E. (2005). Selection on heritable phenotypic plasticity in a wild bird population. *Science*, *310*(5746), 304–306.
- Nussey, D. H., Wilson, A. J., & Brommer, J. E. (2007). The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology*, *20*(3), 831–844.
- Osborne, O. E., Hara, P. D., Whelan, S., Zandbergen, P., Hatch, S. A., & Elliott, K. H. (2020). Breeding seabirds increase foraging range in response to an extreme marine heatwave. *Marine Ecology Progress Series*, *646*, 161–173.
- Panchen, Z. A., & Gorelick, R. (2017). Prediction of Arctic plant phenological sensitivity to climate change from historical records. *Ecology and Evolution*, *7*(5), 1325–1338.
- Parnesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, *37*, 637–669.
- Patterson, A., Gilchrist, H. G., Gaston, A., & Elliott, K. H. (2021). Northwest range shifts and shorter wintering period of an Arctic seabird in response to four decades of changing ocean climate. *Marine Ecology Progress Series*, *679*, 163–179.
- Piatt, J. F., Parrish, J. K., Renner, H. M., Schoen, S. K., Jones, T. T., Arimitsu, M. L., Kuletz, K. J., Bodenstein, B., García-Reyes, M., Duerr, R. S., Corcoran, R. M., Kaler, R. S. A., McChesney, G. J., Golightly, R. T., Coletti, H. A., Suryan, R. M., Burgess, H. K., Lindsey, J., Lindquist, K., ... Sydeman, W. J. (2020). Extreme mortality and reproductive failure of common murres resulting from the Northeast Pacific marine heatwave of 2014–2016. *PLoS ONE*, *15*(1), e0226087.
- Porlier, M., Charmantier, A., Bourgault, P., Perret, P., Blondel, J., & Garant, D. (2012). Variation in phenotypic plasticity and selection patterns in blue tit breeding time: Between- and within-population comparisons. *Journal of Animal Ecology*, *81*(5), 1041–1051.
- Post, E., Alley, R. B., Christensen, T. R., Macias-Fauria, M., Forbes, B. C., Gooseff, M. N., Iler, A., Kerby, J. T., Laidre, K. L., Mann, M. E., Olofsson, J., Stroeve, J. C., Ulmer, F., & Virginia, R. A. (2019). The polar regions in a 2° C warmer world. *Science Advances*, *5*(12), eaaw9883.
- Post, E., Forchhammer, M. C., Bret-Harte, M. S., Callaghan, T. V., Christensen, T. R., Elberling, B., Fox, A. D., Gilg, O., Hik, D. S., Høye, T. T., Ims, R. A., Jeppesen, E., Klein, D. R., Madsen, J., McGuire, A. D., Rysgaard, S., Schindler, D. E., Stirling, I., Tamstorf, M. P., ... Aastrup, P. (2009). Ecological dynamics across the Arctic associated with recent climate change. *Science*, *325*(5946), 1355–1358.
- Provencher, J. F., Gaston, A. J., Hara, P. O., & Gilchrist, H. G. (2012). Seabird diet indicates changing Arctic marine communities in eastern Canada. *Marine Ecology Progress Series*, *454*, 171–182.
- Ratcliffe, N., Furness, R. W., & Hamer, K. C. (1998). The interactive effects of age and food supply on the breeding ecology of great skuas. *Journal of Animal Ecology*, *67*, 853–862.
- Reed, T. E., Wanless, S., Harris, M. P., Frederiksen, M., Kruuk, L. E., & Cunningham, E. J. (2006). Responding to environmental change: Plastic responses vary little in a synchronous breeder. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1602), 2713–2719.
- Ruffino, L., Salo, P., Koivisto, E., Banks, P. B., & Korpimäki, E. (2014). Reproductive responses of birds to experimental food supplementation: A meta-analysis. *Frontiers in Zoology*, *11*(1), 1–13.
- Saalfeld, S. T., & Lanctot, R. B. (2017). Multispecies comparisons of adaptability to climate change: A role for life-history characteristics? *Ecology and Evolution*, *7*(24), 10492–10502.
- Sauve, D., Divoky, G., & Friesen, V. L. (2019). Phenotypic plasticity or evolutionary change? An examination of the phenological response of an arctic seabird to climate change. *Functional Ecology*, *33*(11), 2180–2190.

- Serreze, M. C., Holland, M. M., & Stroeve, J. (2007). Perspectives on the Arctic's shrinking sea-ice cover. *Science*, 315(5818), 1533–1536.
- Shaftel, R., Rinella, D. J., Kwon, E., Brown, S. C., Gates, H. R., Kendall, S., Lank, D. B., Liebezeit, J. R., Payer, D. C., Rausch, J., Saalfeld, S. T., Sandercock, B. K., Smith, P. A., Ward, D. H., & Lanctot, R. B. (2021). Predictors of invertebrate biomass and rate of advancement of invertebrate phenology across eight sites in the north American Arctic. *Polar Biology*, 44, 237–257.
- Spiegelhalter, D. J., Best, N. G., Carlin, B. P., & Van Der Linde, A. (2002). Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 64(4), 583–639.
- Stinchcombe, J. R., Agrawal, A. F., Hohenlohe, P. A., Arnold, S. J., & Blows, M. W. (2008). Estimating nonlinear selection gradients using quadratic regression coefficients: Double or nothing? *Evolution: International Journal of Organic Evolution*, 62(9), 2435–2440.
- Stroeve, J., Holland, M. M., Meier, W., Scambos, T., & Serreze, M. (2007). Arctic Sea ice decline: Faster than forecast. *Geophysical Research Letters*, 34(9), L09501.
- Suryan, R. M., Arimitsu, M. L., Coletti, H. A., Hopcroft, R. R., Lindeberg, M. R., Barbeaux, S. J., Batten, S. D., Burt, W. J., Bishop, M. A., Bodkin, J. L., Brenner, R., Campbell, R. W., Cushing, D. A., Danielson, S. L., Dorn, M. W., Drummond, B., Esler, D., Gelatt, T., Hanselman, D. H., ... Zador, S. G. (2021). Ecosystem response persists after a prolonged marine heatwave. *Scientific Reports*, 11(1), 1–17.
- Thackeray, S. J., Sparks, T. H., Frederiksen, M., Burthe, S., Bacon, P. J., Bell, J. R., Botham, M. S., Brereton, T. M., Bright, P. W., Carvalho, L., Clutton-Brock, T., Dawson, A., Edwards, M., Elliott, J. M., Harrington, R., Johns, D., Jones, I. D., Jones, J. T., Leech, D. I., ... Wanless, S. (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, 16(12), 3304–3313.
- van de Pol, M., & Wright, J. (2009). A simple method for distinguishing within-versus between-subject effects using mixed models. *Animal Behaviour*, 77(3), 753.
- Visser, M. E., Noordwijk, A. V., Tinbergen, J. M., & Lessells, C. M. (1998). Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 265(1408), 1867–1870.
- Whelan, S., Hatch, S. A., Benowitz-Fredericks, Z. M., Parenteau, C., Chastel, O., & Elliott, K. H. (2021). The effects of food supply on reproductive hormones and timing of reproduction in an income-breeding seabird. *Hormones and Behavior*, 127, 104874.
- Whelan, S., Hatch, S., Gaston, A. J., Gilchrist, H. G., & Elliott, K. H. (2022). Data and code from: Opposite, but insufficient, phenological responses to climate in two circumpolar seabirds: relative roles of phenotypic plasticity and selection. *Dryad*, <https://doi.org/10.5061/dryad.9cnp5hqhg>
- Whelan, S., Hatch, S. A., Irons, D. B., McKnight, A., & Elliott, K. H. (2020). Increased summer food supply decreases non-breeding movement in black-legged kittiwakes. *Biology Letters*, 16(1), 20190725.
- Wills, R. C., Schneider, T., Wallace, J. M., Battisti, D. S., & Hartmann, D. L. (2018). Disentangling global warming, multidecadal variability, and El Niño in Pacific temperatures. *Geophysical Research Letters*, 45(5), 2487–2496.

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