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Geographic variation in the intensity of warming and phenological mismatch between Arctic shorebirds and invertebrates

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Abstract. Responses to climate change can vary across functional groups and trophic levels, leading to a temporal decoupling of trophic interactions or "phenological mismatches." Despite a growing number of single-species studies that identified phenological mismatches as a nearly universal consequence of climate change, we have a limited understanding of the spatial variation in the intensity of this phenomenon and what influences this variation. In this study, we tested for geographic patterns in phenological mismatches between six species of shorebirds and their invertebrate prey at 10 sites spread across ~13° latitude and ~84° longitude in the Arctic over three years. At each site, we quantified the phenological mismatch between shorebirds and their invertebrate prey at (1) an individual-nest level, as the difference in days between the seasonal peak in food and the peak demand by chicks, and (2) a population level, as the overlapped area under fitted curves for total daily biomass of invertebrates and dates of the peak demand by chicks. We tested whether the intensity of past climatic change observed at each site corresponded with the extent of phenological mismatch and used structural equation modeling to test for causal relationships among (1) environmental factors, including geographic location and current climatic conditions, (2) the timing of invertebrate emergence and the breeding phenology of

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shorebirds, and (3) the phenological mismatch between the two trophic levels. The extent of phenological mismatch varied more among different sites than among different species within each site. A greater extent of phenological mismatch at both the individual-nest and population levels coincided with changes in the timing of snowmelt as well as the potential dissociation of long-term snow phenology from changes in temperature. The timing of snowmelt also affected the shape of the food and demand curves, which determined the extent of phenological mismatch at the population level. Finally, we found larger mismatches at more easterly longitudes, which may be affecting the population dynamics of shorebirds, as two of our study species show regional population declines in only the eastern part of their range. This suggests that phenological mismatches may be resulting in demographic consequences for Arctic-nesting birds.

Key words: Arctic invertebrates; phenology; spatial gradient; structural equation modeling; timing of breeding; trophic interactions.

Introduction

Changes in phenology are one of the most common biological responses to recent climatic changes (Parmesan and Yohe 2003, Rosenzweig et al. 2008, Thackeray et al. 2012), but the magnitude of these shifts varies across functional groups and trophic levels (Parmesan 2007, Both et al. 2009, Thackeray et al. 2016, Cohen et al. 2018). Different rates of change in the phenology of organisms can lead to a decoupling of biological interactions resulting in a “phenological mismatch” (Visser et al. 1998, Durant et al. 2007; hereafter “mismatch”). Mismatches are widespread in all biomes (reviewed by Parmesan 2006, Thackeray et al. 2010). A recent meta-analysis demonstrated that asymmetric phenological shifts and the resultant asynchrony in interspecific interactions have increased since the 1980s, coinciding with the most dramatic climatic changes (Kharouba et al. 2018).

The original “Match-Mismatch Hypothesis” predicted that the growth rate of a consumer population should increase as its reproductive phenology becomes better matched with the phenology of their key food resources (Cushing 1990). The fast-growing literature on the topic now provides examples of the dissociation between producer–consumer and prey–predator populations, but also plant–pollinator populations, timing of gamete production, and species–habitat links resulting from climate change (Deacy et al. 2017, Ogilvie et al. 2017, Atmeh et al. 2018, Santangeli et al. 2018). Nevertheless, directly comparable replicates of ecological communities monitored for phenological mismatches at multiple geographic locations are rare (Pearce-Higgins et al. 2005, Bauer et al. 2009, Saino et al. 2009). Therefore, we have little understanding of the spatial variation in the frequency and strength of mismatches (Senner et al. 2018), even though the rate of climatic change is inconsistent across both latitudes and biomes (Loarie et al. 2009, Burrows et al. 2011).

Spatial variation found in the intensity of single-trophic-level responses to climate change, such as accelerated phenological shifts at higher latitudes (Both et al. 2004, Parmesan 2007, Post et al. 2018), predicts there should be geographic variation in the response of multi-trophic level interactions. Multiple studies have described mismatches across multiple sites (Pearce-Higgins et al. 2005, Bauer et al. 2009, Saino et al. 2009), but the cause of variation in the extent of mismatches was not a focus. Our understanding of spatial variation in the intensity of mismatch has largely been limited to a fine spatial scale (among breeding territories of Great Tits *Parus major*; Hinks et al. 2015) or to distinct breeding populations of a single species (Great Tits [Charmantier et al. 2008, Both et al. 2009], Hudsonian Godwits *Limosa haemastica* [Senner et al. 2017], Pied Flycatcher *Ficedula hypoleuca* [Both et al. 2006]). Recently, Burgess et al. (2018) examined the oak–caterpillar–passerine-bird food chain across eight degrees of latitude in the UK but found little variation in the degree of phenological mismatch.

Given the rarity of long-term, multi-trophic-level data in the North American Arctic, we examined the extent of phenological mismatches between six shorebird species and their invertebrate prey at 10 sites spread across the Arctic over the course of three years. The first part of our study employed a “space-for-time substitution” approach (Pickett 1989, Blois et al. 2013, Posledovich et al. 2018) and examined the relationship between the extent of climate change and the extent of mismatch that we estimated using three years of observational data as a snapshot at each of 10 sites. In the second part of our study, we examined latitudinal and longitudinal gradients in contemporary climatic conditions, as well as their relationship with the phenology of two trophic levels (Fig. 1).

The Arctic is characterized by a highly seasonal environment with a relatively simple food web (Gauthier et al. 2004, Liebezeit et al. 2014). The timing of pulses in invertebrate biomass in the Arctic has advanced from 2 to ≥10 d per decade (Høye et al. 2007, Tulp and Schekkerman 2008), and population-level studies have found that shorebirds can closely track annual changes in spring temperature and adjust the date of clutch initiation (Troy 1996, Liebezeit et al. 2014, Kwon et al. 2017, Saalfeld and Lanctot 2017). Low intra-individual repeatability in the timing of breeding, combined with generally low natal philopatry among shorebirds (Nol et al. 2010, Saalfeld and Lanctot 2017), suggests that variation in the timing of breeding is likely a flexible response to environmental change rather than an example of microevolution (Ghalambor et al. 2007). However, the capacity of shorebirds to make phenological shifts might be constrained because (1) many shorebirds migrate long-distances through heterogenous landscapes across which climate change may be occurring

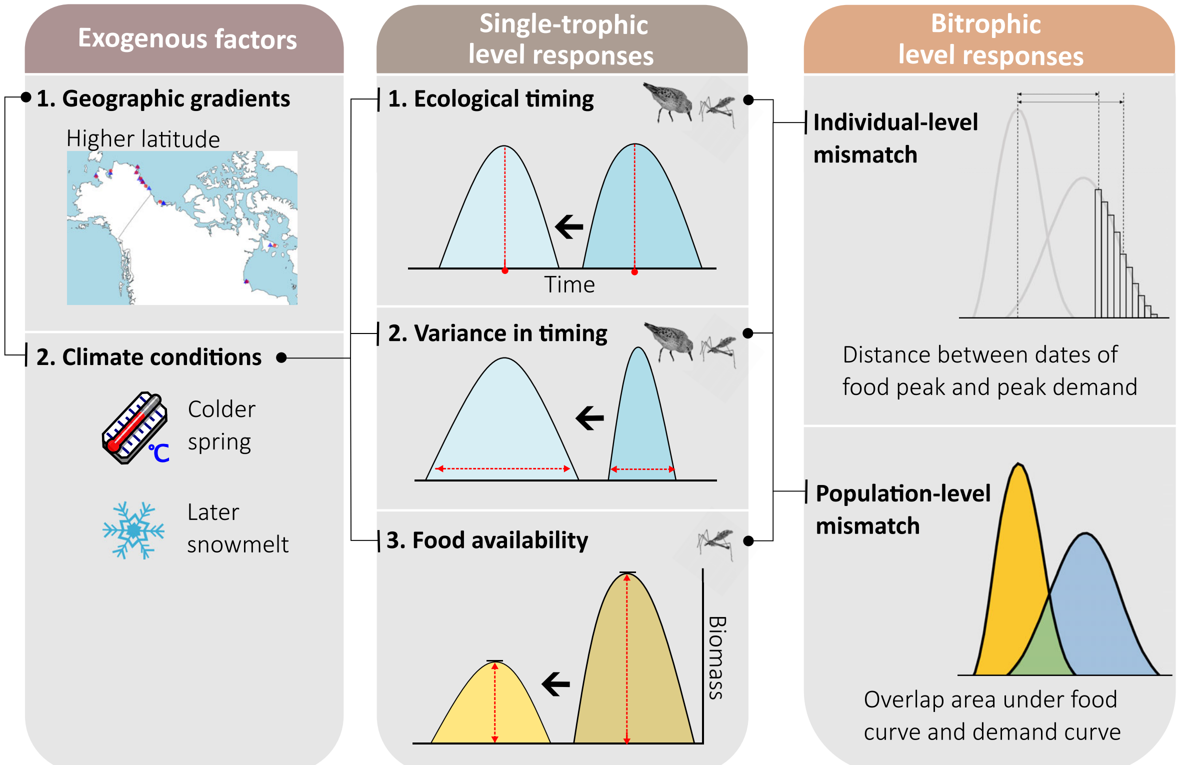

Fig. 1. Hypothesized causal relationships among geographic gradients, climate conditions, single-trophic level responses (or endogenous drivers), and bitrophic level responses.

at different rates (Senner 2012) and because (2) the timing of migration is affected not just by photoperiod but by predation risk, feather molt, and other events occurring throughout their annual cycle (O'Hara et al. 2002, Studds and Marra 2011, Conklin et al. 2013, Ely et al. 2018).

Long-term monitoring of model systems has documented negative impacts of mismatches on individual fitness and, in some cases, population growth (Clausen and Clausen 2013, Reed et al. 2013*b*, Plard et al. 2014, van Gils et al. 2016, but see Reed et al. 2013*a*, Dunn and Møller 2014, Franks et al. 2017). In Arctic-breeding shorebirds, phenological asynchrony with local food peaks is associated with lower nest survival, as well as reduced growth rates and offspring survival (McKinnon et al. 2012, Senner et al. 2017), although other studies have not found a negative effect on growth rates (McKinnon et al. 2013, Reneerkens et al. 2016). Furthermore, population declines among shorebirds in North America are of conservation concern, particularly among migratory species breeding in the eastern Canadian Arctic (Bart et al. 2007, Brown et al. 2010, Andres et al. 2012, Smith et al. 2012). Nonetheless, the potential role of phenological mismatches in explaining regional declines has not been previously studied due to the logistical challenges of working in remote Arctic habitats.

At 10 sites across the North American Arctic, we calculated the extent of the mismatch between the timing of the peak energetic demand of shorebird chicks and the peak biomass of their invertebrate prey. The timing of emergence in invertebrates and the timing of breeding in shorebirds in the Arctic are strongly correlated with spring temperature and the timing of snowmelt (Høye and Forchhammer 2008, Smith et al. 2010, Grabowski et al. 2013, Liebezeit et al. 2014). Therefore, we predicted close relationships among temperatures during the egg-laying period of shorebirds and the timing of snowmelt, peak invertebrate biomass, and shorebird clutch initiation (Fig. 1). We hypothesized a positive relationship between the slope of long-term changes in snow phenology and average temperatures during the laying period and the current extent of mismatches estimated from our 3-yr period of observations. Furthermore, we hypothesized that larger declines in eastern shorebird populations would be related to greater mismatches at more easterly longitudes.

It is not only the timing of hatch in relation to the food peak that matters to shorebird chicks, but also the shape of the food peak itself (Reneerkens et al. 2016; S. Saalfeld and R. B. Lanctot, *unpublished manuscript*). Incorporating into studies of phenological mismatches the topography of seasonal trends rather than simply pinpointing peak dates has been frequently suggested in theory (Durant et al. 2007, Both 2010, Miller-Rushing et al. 2010), but rarely applied in practice (Burr et al.

2016, Vatka et al. 2016; S. Saalfeld and R. B. Lanctot, *unpublished manuscript*). Therefore, we also tested the effects of spring temperature and the timing of snowmelt on the within-population synchronicity of shorebird hatching and invertebrate emergence using the width of the distribution curves, as well as the height of the food peak measured as daily maximum biomass (Fig. 1). Using structural equation modeling and our 3 yr of observational data, we then investigated the direct and indirect relationships among the geographic distribution of the sites and current climatic conditions on the extent of the phenological mismatch between breeding shorebirds and their invertebrate prey. Combined, our approach yielded direct insights into the interspecific and geographic variation in the strength of phenological mismatches that was heretofore impossible.

Methods

Study species

Our six study species were small to medium-sized shorebirds (F. Scolopacidae) with body masses ranging from 25 to 75 g (in ascending body mass): Semipalmated Sandpiper (*Calidris pusilla*), Western Sandpiper (*C. mauri*), Red-necked Phalarope (*Phalaropus lobatus*), Red Phalarope (*P. fulicarius*), Dunlin (*C. alpina*), and Pectoral Sandpiper (*C. melanotos*; Appendix S1: Table S1). These six species are long-distance migrants that share a modal clutch size of four eggs, an 18–23 d incubation period, and precocial young that are capable of self-feeding after hatch (Paulson 1993, Colwell 2010, Rodewald 2015). The six species differ in timing of breeding due to variation in their mating systems and nesting habitats (Pitelka et al. 1974; Appendix S1: Table S1). The monogamous species (small-bodied *Calidris* species) tend to nest earlier and in drier habitats than the polygamous species (phalaropes and Pectoral Sandpipers). Five of the six species (all but Pectoral Sandpipers) are currently exhibiting population declines, with Semipalmated Sandpipers and Red-necked Phalaropes declining more in the eastern parts of their ranges in North America (Thomas et al. 2006, Brown et al. 2010, Andres et al. 2012; Appendix S1: Table S1).

Optimally, the hatch of shorebird chicks coincides with the peak abundance of emerging small invertebrates on the Arctic tundra (Tulp and Schekkerman 2008, McKinnon et al. 2012). The precocial young begin foraging for themselves within a few hours after hatch and feed mostly on adult dipteran flies from the surface of the tundra vegetation until they start probing for chironomid larvae 1–2 weeks post-hatch (Holmes and Pitelka 1968). Daily survival rates of chicks are typically lowest during the first week of hatch (Ruthrauff and McCaffery 2005, Senner et al. 2017), and growth rates of newly hatched chicks are strongly dependent on prey availability (Schekkerman et al. 2003, Tjørve et al. 2007).

Study sites

We relied on data from the Arctic Shorebird Demographics Network (ASDN) to conduct this study. The ASDN is a research consortium comprised of 16 sites distributed along the Arctic coast of Alaska, Canada, and Russia with the shared objective of understanding why Arctic-breeding shorebirds are declining (Brown et al. 2017, Weiser et al. 2018). A coordinated monitoring effort with standardized methodology of the ASDN provided a rare opportunity to examine phenological mismatches at a broad geographic scale. Field data for our study were collected at 10 field sites from 2010 to 2012. However, additional data on the timing of clutch initiation in shorebirds from 2003 to 2014 were available from some sites and included in analyses where appropriate. The network of sites spanned ~13° of latitude (58–71° N) and ~84° of longitude (−164 to −81° W), with the two most distant sites separated by 3,850 km (Fig. 2; Appendix S1: Table S2). The community of shorebird species varied among our study sites but showed broad overlap in species composition (Fig. 2). We monitored up to 300+ shorebird nests per year at each site (Lanctot et al. 2015) and restricted our analyses to shorebird species for which we had a minimum sample of >15 nests within each site and year (Appendix S1: Table S3).

Data collection

Long-term shifts in temperature and snow phenology.— We estimated the long-term change in timing of snowmelt using remotely sensed snow cover data available for the Northern Hemisphere at a spatial resolution of $0.05° \times 0.05°$ (~5.5 km) from 2001 to 2014 (Peng et al. 2013, Chen et al. 2015). In this data source, the end date of snow cover (snow end date, SED) is defined as the last continuous 5-d period when snow cover was observed in the spring of the year (Peng et al. 2013, Chen et al. 2015). We extracted the SED for 10 grid cells, each of which included one of our study sites. Following the methods of Chen et al. (2015), the *snowmelt period* for each site was then defined as a 30-d window prior to the median SED for a given site from 2001 to 2014. In addition, we created a separate snow cover data set at a finer resolution of 4-km for the years from 2010 to 2012 in which the annual timing of snowmelt was defined as the first date when each site was snow-free to use in our structural equation models (see *Structural equation modeling*; Weiser et al. 2018).

Mean daily temperature data for each site were compiled from the nearest available meteorological station (distances from study sites ranging from 10 to 143 km with a mean of 47 km; Fig. 2; Appendix S1: Table S2). To quantify long-term trends in temperature, we examined the 25-yr period from 1990 to 2014 at nine sites and the 17-yr period from 1998 to 2014 at IKP; earlier data were not available at this site. To calculate long-term temperature changes, we fit a linear model to the mean daily

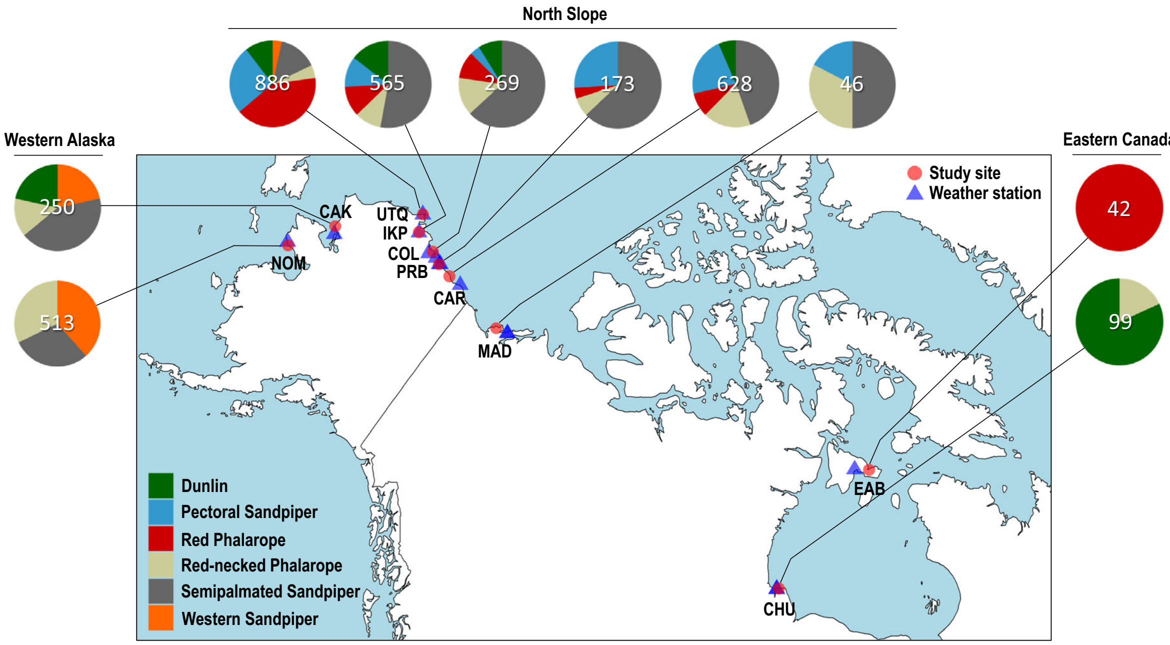

Fig. 2. Locations of study sites for shorebird population studies (red dots, 2010–2012) and weather stations where daily temperature data were collected (blue triangles, 1990–2014). Study sites, listed from left to right, include Nome (NOM), Cape Krusenstern (CAK), Utqiaġvik (formerly Barrow; UTQ), Ikpikpuk (IKP), Colville (COL), Prudhoe Bay (PRB), Canning River (CAR), Mackenzie Delta (MAD), Churchill (CHU), and East Bay (EAB). Pie charts show the proportion of monitored nests at each site (total sample size in circles) for the six shorebird species included in this study.

temperature for each day of the year as the response variable and the calendar year as the predictor. We used the slope of the model as an index of long-term temperature change for each Julian date at each site. Because the availability of temperature (25 yr) and snow data (14 yr) differed for our study, we used appropriate subsets of temperature data when examining the relationship between temperature and snow phenology.

Invertebrate biomass.—To determine the timing of peak availability and seasonal abundance of shorebird food resources, we sampled terrestrial invertebrates beginning with the onset of snowmelt and ending with the completion of shorebird hatch. Two line transects were deployed at each study site where breeding shorebirds were monitored: one transect in a dry habitat and the second in a mesic habitat. Each transect consisted of five modified Malaise pitfall traps placed 15 m apart. Individual traps consisted of a 38 × 5 × 7 cm plastic container buried at ground level that captured walking invertebrates, and a 36 × 36 cm mesh screen placed perpendicularly above the container to capture low-flying invertebrates that hit the screen and fell into the trap (Appendix S1: Fig. S1). Trap stations were visited every three days and the accumulated samples were stored in 50-mL whirl packs with 70–100% isopropanol or 100% ethanol. In the laboratory, invertebrate samples were sorted, identified to order or family, and their body lengths measured. Biomass was estimated from the measured body lengths using taxon-specific conversion coefficients (see Appendix S1: Table S4 for references). We excluded invertebrates >20 mg, as these prey items were likely too large for shorebird chicks to consume. Total daily biomass was then calculated as the total biomass of all taxa collected in a trap station on each sampling occasion divided by the number of days in the given sampling interval. Our invertebrate samples included a total of 77 taxa, nine of which collectively make up 90% of the total biomass. The nine main taxa were, in descending order of occurrence, spiders (Araneae), beetles (Carabidae), higher flies (Brachycera), parasitoid wasps (Hymenoptera), nonbiting midges (Chironomidae), crane flies (Tipulidae), bees (Hymenoptera, less than < 20 mg), fungus gnats (Mycetophilidae), and other small Hymenopterans. All nine taxa have been identified as major prey source for chicks from analyses of stomach contents or using genetic barcoding (Holmes 1966, Holmes and Pitelka 1968; S. F. MacLean, *unpublished data*; D. Gerik, *unpublished data*).

Shorebird nests.—We located shorebird nests by observing distraction displays of attending parents or by rope-dragging to flush incubating birds. Arctic-breeding shorebirds usually lay one egg every 1–2 d (Sandercock 1998, Colwell 2006). For nests found during laying, we estimated the date of clutch initiation by subtracting one day for each egg initially found from the date the nest was found. Nests were followed until the clutch was completed and then the predicted hatch date was calculated by adding the number of days for the species-specific incubation period to the date when the last egg was laid (Brown et al. 2014). For nests found during incubation, we floated eggs in warm water and estimated the flotation angle. We predicted the hatch date from the flotation angle using a species-specific regression equation with estimated error rates ranging from 1.7–3.8 d for our six study species (Liebezeit et al. 2007). The use of predicted hatch dates instead of actual hatch dates allowed us to include failed nests in our analyses. For each species at a given site and year, we defined the *egg-laying period* as the mean date of clutch initiation ± 2 SD (i.e., 95% of all nests).

Defining the phenological peaks

To identify the timing of peak invertebrate biomass, we fitted a quadratic function (date + date^2) to the daily total biomass obtained at each site and year (Tulp and Schekkerman 2008). We defined the date of the food peak for each site and year as the date when the first derivative of each model was closest to zero or the date on which an increasing trend of daily abundance turns to a decreasing trend (Appendix S1: Fig. S2). Studies of phenological mismatches with birds often assume that the peak energetic demand of offspring occurs at the time of hatching. However, for nidifugous shorebirds, food availability is likely the most critical to chick survival sometime after hatch due to the presence of an invaginated yolk sac that young use for nutrition during the first few days after leaving the nest (Williams et al. 2007). For our analysis, we used the chick age when their body mass reached 25% of adult body mass as a proxy for the timing of peak energetic demand in chicks. We chose this body mass because the basal metabolic rate of developing shorebirds peaks when chicks attain 25% of adult mass and then decreases rapidly thereafter (Ricklefs 1973). Growth curves were available for four of our six study species: Western Sandpiper (Ruthrauff and McCaffery 2005), Dunlin (Williams et al. 2007, McKinnon et al. 2013), Pectoral Sandpiper, and Red Phalarope (S. Saalfeld, *unpublished data*). We used the growth curve of Western Sandpipers as a model for Semipalmated Sandpipers and Red-necked Phalaropes based on their similar body sizes. From the available growth curves, we determined that the age when chicks attain 25% adult body mass varied from 3 to 9 d post-hatch among our study species (3 d for Semipalmated and Western Sandpipers, 4 d for Red-necked Phalaropes, 6 d for Dunlin and Red Phalaropes, and 9 d for Pectoral Sandpipers). For the four species with known growth curves, the peak metabolic rate also coincided with the steepest rate of mass gain during post-hatch development.

Parameterization of phenological mismatch

The extent of the mismatch for individual nests (M_{ind}) was calculated as the number of days between the date of peak invertebrate biomass (denoted as x_{food}; Fig. 3) and date of estimated peak demand for the chicks from each nest (denoted as x_{n}; Fig. 3). To estimate the extent of the mismatch at the population level, we identified the amount of invertebrate biomass and the number of shorebird broods at their peak energetic demand for each day of a field season. Daily values of total invertebrate biomass and the number of broods at the age of peak demand were converted into percentiles of the season's total value to standardize scales for direct comparison between the two distributions. At 9 of 10 sites, invertebrate sampling was discontinued 3–21 d before the last nest was estimated to hatch. To project invertebrate biomass during the period after sampling ceased, we fitted a natural cubic spline to each food distribution and substituted missing values with projected values. A smoothing curve was then fit separately to the seasonal variation in available food and shorebird demand using the gam and predict functions in the mgcv package of the R environment (Wood 2000, R Core Team 2019). Hereafter, these two curves are called the food curve and the demand curve, respectively. We overlaid the food curve with a smoothed demand curve for each shorebird species at each site and year. The area of overlap between the two curves (M_{pop}, Fig. 3) represented the extent of phenological match at the population level and was calculated using the integrate.xy function in the R

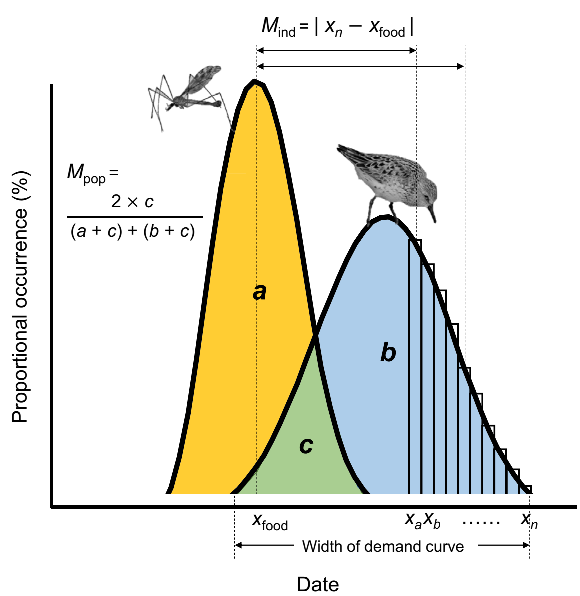

FIG. 3. Theoretical illustration of phenological mismatch at an individual-nest level (M_{ind}) and at a population level (M_{pop}). M_{ind} is calculated as the number of days between the date of peak invertebrate biomass (X_{food}) and the date of estimated peak demand for chicks within each nest (with individual nests indicated by X_a to X_n). M_{pop} is calculated as the overlapped area (*c*, green) under curves of available food (*a*, yellow) and peak shorebird demand (*b*, blue) multiplied by 2 and divided by the sum of areas under the two curves.

package sfsmisc (Maechler 2015). We then calculated an overlap coefficient for each shorebird species for each unique combination of site and year as follows:

$$\text{Overlap coefficient}_{i,j,k} = \frac{2 \times \text{overlap area under two curves}}{\text{total area under food curve}_{i,j} + \text{total area under demand curve}_{i,j,k}}$$

where i is the site (n = 10), j the year (n = 3), and k the shorebird species (n = 6). The overlap coefficient describes how much of the food is available to shorebird chicks, as well as how much of their demand could be met by that food. Complete phenological match with an overlap coefficient of 1 occurs when both curves match exactly.

Statistical analyses

To examine the relationship between temperature and snow phenology from 2001 to 2014, we fitted simple linear models with year as a predictor variable to (1) daily mean temperatures from 2001 to 2014 for the defined snowmelt period, (2) the snow end date (SED), and (3) daily mean temperatures from 2001 to 2014 for the egg-laying period, defined pooling years and species for each site. We considered the regression coefficients as a proxy of the long-term trend in each variable for a given site. We also fitted a linear model with average daily mean temperature during the snowmelt period to the SED and considered its coefficient value to be a proxy for the sensitivity of SED to temperature. For the sensitivity of the timing of clutch initiation to snowmelt and temperature, we regressed the clutch initiation dates of shorebirds monitored from 2003 to 2014 as the dependent variable with the SED and daily mean temperature during snowmelt and egg-laying periods of corresponding years as predictor variables.

Using the 25-yr (1990–2014) temperature slope for each day of the year, we calculated the mean slope for the snowmelt period at each site and the mean slope for the egg-laying period at each site for each species. We then used the temperature slopes during the snowmelt and egg-laying periods as well as the annual shift in SED, calculated for 2001–2014, as fixed effects in our linear mixed-effect models to separately explain variation in the extent of the mismatch at the individual and population levels (R package lme4; Bates et al. 2015). Each model included shorebird species as a random effect. Because we predicted that delayed snowmelt or cooling temperatures would be as disadvantageous as advancing snowmelt or warming temperatures for the optimal timing of breeding, we first compared a linear effects model to a quadratic effects model for each variable. The final model then only included the more significant term for each variable. We standardized the variables by subtracting the mean and dividing by the SD. Statistical significance of each variable was determined based on the 95% confidence intervals.

In addition, we present descriptive statistics to compare the size of phenological shifts between food peak and the demand peak of shorebirds observed from 2010 to 2012 and to show a correlation between our measures of individual- and population-level mismatch.

Structural equation modeling

We used structural equation modeling (SEM) to identify important exogenous and endogenous drivers of the extent of mismatches at the individual-nest and population levels (Fig. 1). SEM provides an effective way to dissect complex ecosystem functions, especially when multiple collinear variables are being considered (Whalen et al. 2013, Mortensen et al. 2016, Ogilvie et al. 2017). We used piecewise SEM, which estimates a separate variance–covariance matrix for each portion of the model and then pieces together the path estimates to construct a causal model (Shipley 2009, Lefcheck 2015). Due to the geography of the North American Arctic, the longitudes and latitudes of our study sites were collinear, with western sites located at higher latitudes. However, using SEM, we estimated the partial regression coefficients for latitude and longitude separately while holding the other variables constant.

Our four exogenous variables were: the latitude and longitude of our study sites, average daily mean temperature during the egg-laying period, and timing of snowmelt estimated at a 4-km resolution during our 3-yr study (Fig. 1). Our five single-trophic-level responses were dates of the food peak and clutch initiation, width of the food and demand curves, and the maximum invertebrate biomass. All variables were natural-log-transformed prior to analysis so that we could directly compare the strengths of different causal relationships (Grace 2006). We selected our final path models in four steps. First, we compared three candidate models (Appendix S2: Fig. S1) in which the four exogenous factors had different pathways to affect both the single-trophic level and bitrophic-level responses (Fig. 1). We chose the best model structure based on the information theoretic approach using the AIC_c estimates and the sem.-fit function in the R package piecewiseSEM (Lefcheck 2015). Second, retaining the best model structure from step 1, we compared models with all possible combinations of the four exogenous factors and chose the best model based on the AIC_c estimates. Third, we compared all possible combinations of the five single-trophic level responses and chose the best model while retaining the exogenous factor(s) chosen from step 2. Last, we added important missing paths with $P < 0.05$ to the reduced model until there was no important path missing. We repeated the same modeling procedure separately for individual-nest- and population-level mismatches. In the final model, each path was a linear mixed-effect model (LMM) with year and shorebird species as random effects. We used Shipley's test of directional separation (d-sep test) to evaluate overall model fit (Shipley 2013). We summarize the full model set and the results of model comparison in Appendix S2. We report the standardized regression coefficient for each path derived from the final model. Indirect effects of latitude and longitude on the extent of mismatch were calculated as the product of all beta coefficients in a given path (Mitchell 2001). The total indirect effects of latitude or longitude were then calculated as the sum of the indirect effects for all possible paths from latitude or longitude to the mismatch. All statistical analyses were conducted in an R environment (version 3.5.2; R Core Team 2019).

Results

Geographic variation in climate change

Over the past 25 yr (1990–2014), the greatest amount of warming occurred during autumn and winter at our 10 field sites (Fig. S3). Daily mean temperatures during the snowmelt period have decreased over the past 25 yr at two of our western sites (NOM, CAK), as well as at PRB (Fig. S3). The rate of temperature change during the egg-laying period of shorebirds varied depending on the species; in general, the rate of change was greater at more northerly and easterly sites (Wilcoxon signed rank test; $P = 0.008$ for both latitude and longitude).

The relationship between temperature and the timing of snowmelt was not consistent across sites, nor was there consistent warming across our large range of latitudes and longitudes. From 2001 to 2014, only the northernmost site (UTQ) experienced a statistically significant warming during both the snowmelt and egg-laying periods (Table S5). At UTQ, however, warming was not associated with an advancement of SED (Table S5; Fig. 4). By contrast, the SED has significantly advanced at two sites on the Alaskan North Slope (IKP and CAN), although the temperature increase was not statistically significant for either during the snowmelt or egg-laying periods (Table S5, Fig. 4). Four of our southernmost sites excluding NOM (CHU, EAB, CAK, MAD), showed opposite trends of temperature change between the snowmelt and egg-laying periods (2001–2014), whereas the five sites on the Alaskan North Slope showed consistent warming for both periods (Table S5).

Timing of egg-laying

A total of 7,943 shorebird nests from our six study species were monitored across our ten sites from 2003 to 2014 (Appendix S1: Table S3). The median date of clutch initiation for each site and year covaried with the SED ($\beta = 0.16$, SE = 0.07, $P = 0.031$) but not with the average daily mean temperature during snowmelt ($\beta = -0.66$, SE = 0.37, $P = 0.081$) or egg-laying periods ($\beta = 0.49$, SE = 0.36, $P = 0.175$; Fig. 4).

Climate change and the extent of phenological mismatch

Of the 7,943 shorebird nests, 3,148 were monitored from 2010 to 2012, during which time we also collected a total of 3,860 invertebrate samples at 3-d intervals. Inter-annual phenological variation within our three-year study was ~2 × greater for peak invertebrate biomass than for peak demand of shorebird chicks (absolute mean shift between consecutive years = 7.1 vs. 3.0 d; $t = 2.97$, $P = 0.006$; Appendix S1: Fig. S4). Our two parameters of phenological mismatch showed significant quadratic relationships, and the population-level match, measured as the extent of overlap between the food and demand curves, increased as more broods met their peak food demand ($M_{\text{pop}} = 0.51 - (0.002 \times M_{\text{ind}}) - (0.0004 \times M_{\text{ind}}^2)$, $P = 0.001$; Fig. S5). However, only 12% of the variation in population-level mismatch was explained by the individual-level mismatch (adjusted $R^2 = 0.123$).

For sites experiencing a more rapid advancement of SED between 2001 and 2014, the mean food demand peak of chicks occurred further away from the food peak, and this pattern was consistent among different shorebird species ($\beta = -5.50$, SE = 0.22, $t = 25.33$; Table 1, Fig. 5a). The overlap between the food and demand curves tended to be smaller at sites where the SED has either advanced or been delayed, but this negative quadratic effect of snow phenology was not statistically significant ($\beta = 0.09$, SE = 0.06, $t = 1.48$; Table 1, Fig. 5d). Greater long-term (1990–2014) warming or cooling during the snowmelt period was strongly correlated with a decrease in the overlap between the food and demand curves ($\beta = -0.06$, SE = 0.02, $t = -3.22$; Table 1, Fig. 5e). Furthermore, greater long-term warming during the egg-laying period was correlated with a decrease in the overlap between the food and demand curves (Fig. 5f) and exhibited a significant quadratic effect on the individual-nest-level mismatch, although the effect varied greatly among species (Table 1, Fig. 5c).

Proximate drivers on the extent of phenological mismatch

Based on our final structural equation models, sites at higher latitudes and more easterly longitudes experienced later snowmelt within our three-year observation, which was correlated with later clutch initiation, shorter width of the chick demand curve (meaning that there was less variation in the timing of the demand peaks among different broods) and dampened maximum measures of invertebrate biomass (Fig. 6a, b). At the individual-nest level, delayed clutch initiation significantly increased the temporal mismatch between the food and

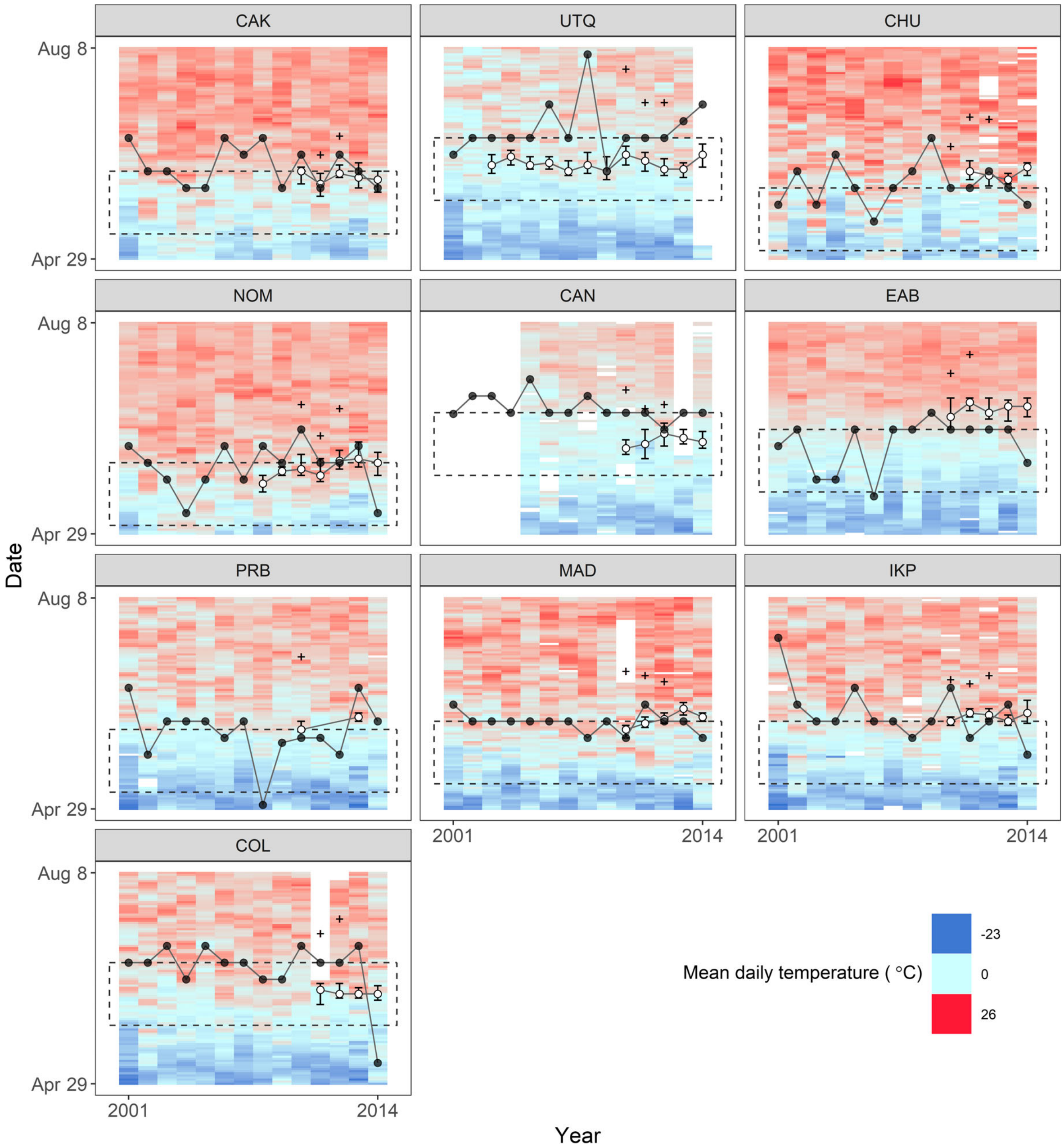

Fig. 4. Observed daily mean temperature for each day from 29 April to 8 August of 2001–2014 (ranged from −23°C to 26°C) indicated by colored tiles separately for 10 study sites. Overlaid data are the snow end date (or SED, solid dot), snow-melt period defined as a 30-d window prior to the median SED for a given site (dash-line box), median date of clutch initiation (white dot) ± 2 SD, and the observed local food peak (plus symbol). See Fig. 2 for site acronyms. The availability of data varied among sites, and blank tiles indicate missing information on daily mean temperatures.

demand peaks ($\beta = 6.75$, $P > 0.001$, Fig. 6a). At the population level, the overlap between the food and demand curves increased with protracted demand curves ($\beta = 0.64$, $P < 0.001$, Fig. 6b) or dampened peak maximum biomass ($\beta = -0.03$, $P = 0.001$, Fig. 6b). Peak maximum biomass was also negatively correlated with the width of the demand curve ($\beta = -0.21$, $P < 0.001$, Fig. 6b), which means that the timing of demand peaks among different broods was more synchronous when the food peak was higher. Combining three possible pathways between the timing of snowmelt and the overlap between curves, later snowmelt was strongly correlated with the reduced overlap between the food and demand curves ($\beta_{sum} = -0.26$, Fig. 6b).

Table 1. The 95% confidence intervals for the effect sizes of three climate change covariates (a) annual shifts of snow end date (SED) during 2001–2014, (b) 25-yr (1990–2014) trend of temperature change during snow-melt period ($\mathrm{TSlope}_{\mathrm{snowmelt}}$) and (c) during egg-laying periods ($\mathrm{TSlope}_{\mathrm{laying}}$) tested on the amount of phenological mismatch at the individual-nest and population levels.

	Individual-nest-level mismatch		Population-level match	
Covariate	LCI	UCI	LCI	UCI
(Intercept)	−0.091	7.904	0.295	0.533
Shifts in SED				
Linear	**−5.928**	**−5.076**	−0.120	0.029
Quadratic			−0.032	0.217
$\mathrm{TSlope}_{\mathrm{snow\text{-}melt}}$				
Linear	−0.919	0.079	−0.198	0.001
Quadratic			**−0.091**	**−0.021**
$\mathrm{TSlope}_{\mathrm{laying}}$				
Linear	−0.719	0.117	**−0.105**	**−0.019**
Quadratic	**1.372**	**1.915**		

Notes: Covariates were standardized and tested for their quadratic and linear effects. Upper (UCI) and lower (LCI) confidence intervals are shown only for terms included in the final model. Bold fonts indicate effects where 95% confidence intervals did not overlap zero.

Direct and indirect effects of breeding location on phenology and mismatch

Breeding site explained 46× more of the variation than shorebird species for mismatches at the population level (ratio of the marginal R^2_{site} : marginal $R^2_{\mathrm{species}} = 46$), and 1.7× more variation than shorebird species for mismatches at the individual-nest level (ratio of the marginal R^2_{site} : marginal $R^2_{\mathrm{species}} = 1.70$). Latitudinal variation in the extent of mismatches at both the individual-nest and population levels was explained by latitudinal variation in the timing of snowmelt and the narrower width of the demand curve at more northerly sites (all $P < 0.001$, shown as red arrows in Fig. 6a, b). However, our final structural equation models also included a direct path between longitude and the extent of the mismatches at both levels, indicating that factors not included in our model partly contributed to the observed longitudinal variation in mismatches. Overall, however, the latitudinal location of a breeding site, which varied by 13° in our study (58–71° N), had a stronger effect on the extent of mismatch than the longitudinal location (Table 2).

Discussion

Our Nearctic-wide study revealed that the rate of temperature increase over the past 25 yr was stronger at northerly and easterly sites, although most warming occurred during the cooler parts of the year. The long-term trend in temperature change during the snowmelt period was neither a reliable indicator of shifts in snow phenology nor the long-term temperature change during the egg-laying periods of shorebirds. Furthermore, the timing of clutch initiation in shorebirds was closely correlated with the timing of snowmelt, and changes in the timing of snowmelt coincided with a greater extent of phenological mismatch between shorebirds and their invertebrate prey at both the individual and population levels. Finally, our study also found that the site-specific timing of snowmelt had a strong correlation with the height of invertebrate peaks and the shape of food demand curves, which in turn, determined the extent of phenological mismatches at a population level. Thus, changes in snowmelt dynamics may be as important, or more important, as rates of temperature change per se, in determining the ability of Arctic-breeding birds to adequately respond to global climate change.

Geographic gradient of phenological mismatch

During our study, invertebrate phenology varied, on average, about two times more than the breeding phenology of shorebirds at the same sites. Our results therefore agree with previous studies showing that homeothermic consumers at higher trophic levels shift their phenology to a lesser degree than poikilothermic species at lower trophic levels (Parmesan 2006, Høye et al. 2007, Thackeray et al. 2010, 2016, Gienapp et al. 2014). We hypothesized that more substantial climatic change would result in greater mismatches and that larger population declines in eastern shorebird populations would be related to greater mismatches at more easterly longitudes. Our results generally matched these predictions: greater amounts of warming from 1990 to 2014 occurred at more northerly and easterly sites, and greater amounts of warming during either snowmelt or the egg-laying period corresponded with a greater extent of phenological mismatch between shorebirds and their invertebrate prey (see Fig. 5). For instance, one of our northernmost sites, Ikpikpuk (IKP), provides a good example, as it had the largest temperature increase (0.2°C increase per year from 1990 to 2014), which was coupled with the most rapid advancement in snowmelt out of all 10 sites (advancing 1.7 d per year from 2001 to 2014) and, hence, had the greatest mismatch at both the individual and population levels from 2010 to 2012.

Dissociation of climatic cues

The large geographic span of our study also led to variable climatic conditions among sites and complicated relationships. For example, at the northernmost site, Utqiaġvik (UTQ), there was a significant trend for increasing temperatures in both snowmelt and the egg-laying period from 2001 to 2014 (see Table S5), whereas there was no significant trend in temperatures during the 25-yr period from 1990 to 2014 (see Fig. 3), indicating that the rate of climate change may have recently accelerated at the site. Despite this recent warming, however, the timing of snowmelt at Utqiaġvik did not show any trend from 2001 to 2014. On the other hand, the Canning River (CAN) and Colville (COL) experienced no

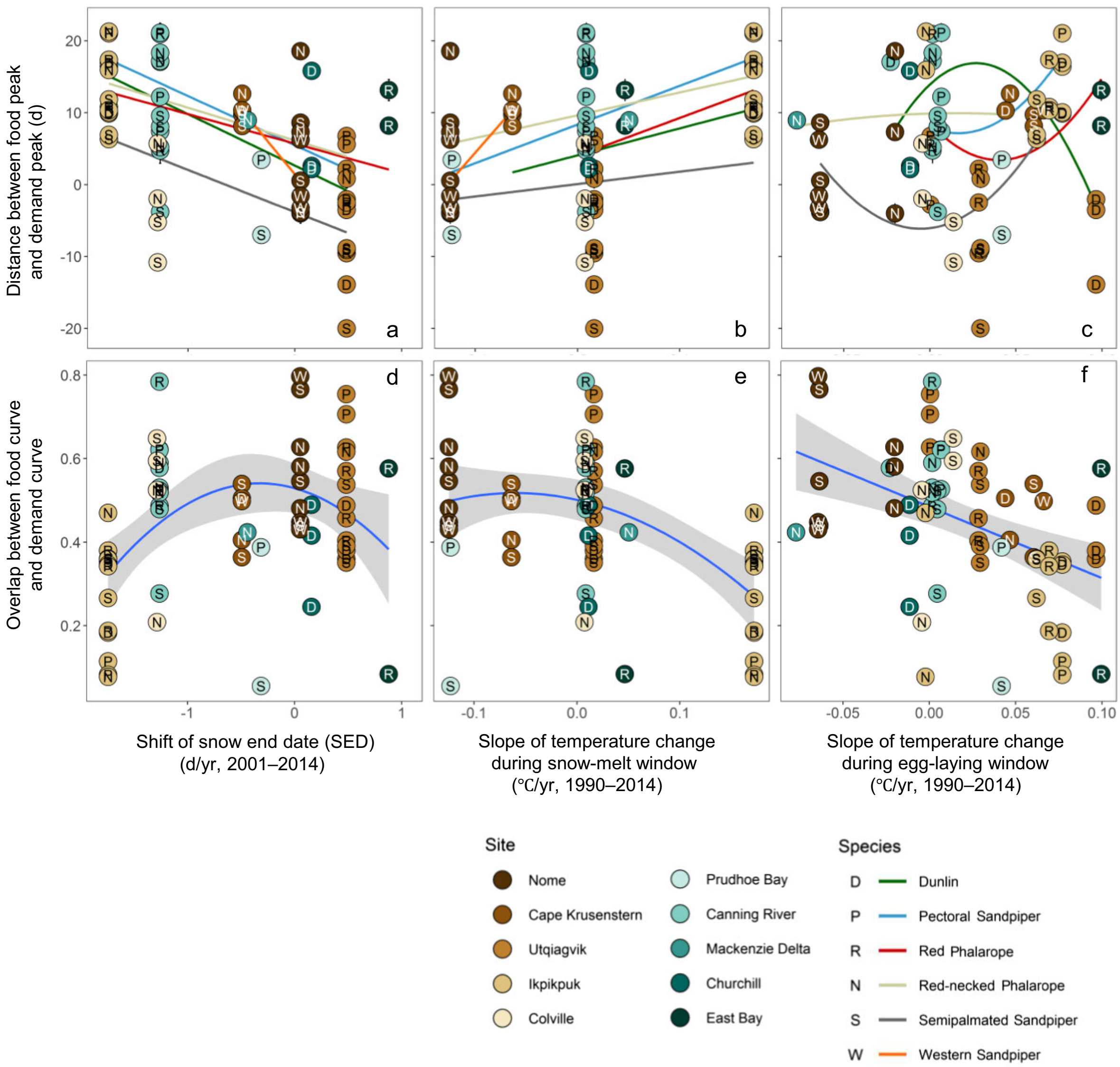

FIG. 5. Relationship between the current extent of phenological mismatch observed during 2010–2012 and three indices of climate change: (a, d) the rate of phenological shifts in SED from 2001 to 2014, (b, e) the slope of temperature change during the snow-melt period, (c, f) and egg-laying period between 1990 and 2014. Negative values on the *x*-axis represent either advancement of SED (a, d) or cooling trends (b, c, e, f). Points are mean values of individual-nest-level mismatch (±SE, top) and population-level mismatch (bottom) specific to each site, year, and shorebird species. For individual-nest level, 0 indicates a perfect match and negative vs. positive values indicate hatching being "earlier vs. later" than the food peak. Linear or polynomial regression lines are fitted depending on which term explained more variation in mismatch. For individual-nest-level mismatch, regression lines were fitted to show the random effect of species with 95% CI omitted.

significant warming across any time period yet showed an advancement in the timing of snowmelt. And, finally, in Nome (NOM), the extent of the phenological mismatch was relatively small, despite the consistent cooling observed over the past 25-yr during both snowmelt and the egg-laying period, possibly because the timing of snowmelt did not show a directional shift. This apparent dissociation of long-term snow phenology and changes in temperature agrees with recent findings that the predicted response of snow condition to climate change is complex (Mudryk et al. 2017, Musselman et al. 2017) and may have contributed to the variable responses of shorebirds that we found at these sites.

Our two easternmost sites, East Bay (EAB) and Churchill (CHU), exhibited another example of potentially dissociating climatic cues: the decoupling of the rate of temperature change between snowmelt and the egg-laying period. Despite overall greater warming occurring in winter at these two sites (see Fig. S3), average daily mean temperatures during the snowmelt period

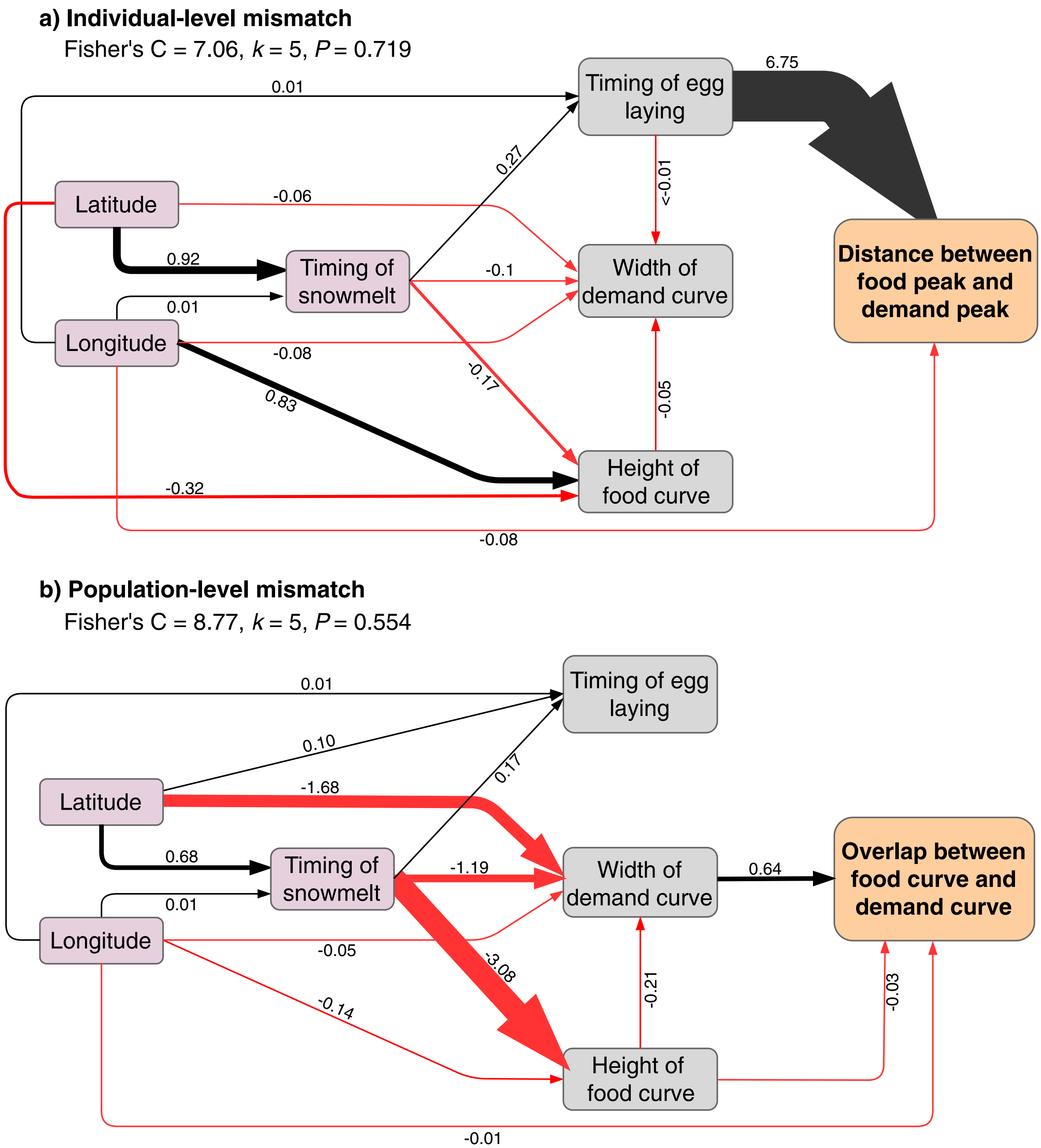

FIG. 6. Final paths from structural equation models showing relationships among geographic gradient, ecological timing, and the extent of phenological mismatch at an (a) individual-nest level and (b) a population level. Arrow widths are proportional to standardized path coefficient values (all $P < 0.05$). Red arrows indicate negative correlations whereas black arrows indicate positive correlations. N = 2,996 nests.

have slightly cooled from 2001 to 2014, leading to a delay in snowmelt. East Bay and Churchill are located within the Hudson Bay lowlands, where a continental climate creates colder and drier winters than sites at similar latitudes on either the Atlantic or Pacific coasts. The extent of snow cover across North America has generally decreased over the past 35 yr (Déry and Brown 2007), but these changes have been most pronounced in areas characterized by maritime climates (Brown and Mote 2009). Because East Bay and Churchill are also located at lower latitudes than all other sites, it is possible that either their low latitude, continental climate, or even the behavior of polar vortex (Zhang et al. 2016), have caused the decoupling of climatic change during

Table 2. Effect sizes of different pathways predicting the extent of phenological mismatch at the individual-nest and population levels.

Alternative pathways	Pathway-specific effect sizes	Total effect sizes of latitude and longitude
Individual-nest-level mismatch		
Latitude → snow → laying timing → distance	+1.68	+1.68
Longitude → snow → laying timing → distance	+0.02	−0.06
Longitude → distance	−0.08	−0.06
Population-level match		
Latitude → snow → demand width → overlap	−0.52	−1.53
Latitude → snow → biomass → overlap	+0.06	−1.53
Latitude → demand width → overlap	−1.08	−1.53
Longitude → snow → demand width → overlap	−0.01	−0.04
Longitude → snow → biomass → overlap	+0.001	−0.04
Longitude → demand width → overlap	−0.03	−0.04
Longitude → biomass → overlap	+0.01	−0.04
Longitude → overlap	−0.01	−0.04

Notes: Path coefficients were estimated from the best fit structural equation model. Pathway-specific effect sizes are the product of consecutive coefficients for each path. Total effect sizes of latitude and longitude were calculated as the sum of pathway-specific effect sizes. Demand width is the width of demand curve.

snowmelt and the egg-laying period. Regardless of the cause, however, it has likely led the shorebird populations at these sites to experience greater phenological mismatches (see also Senner et al. 2017), and this may help explain the observed regional population declines among shorebird species that use the East Atlantic Flyway (Bart et al. 2007, Brown et al. 2010, Andres et al. 2012, Smith et al. 2012).

What does a decoupling of spring temperatures and snowmelt potentially mean for shorebirds? The timing of clutch initiation in Arctic-breeding shorebirds is generally determined by the availability of snow-free habitats (Saalfeld and Lanctot 2017). Although the emergence of Arctic invertebrates is strongly tied to the snowmelt as well, sustained warmer ambient temperatures can shorten the period between the emergence and peak abundance of invertebrates (Høye and Forchhammer 2008). Previous studies have also shown that warming can decrease the abundance of soft-bodied, soil-dwelling Arctic invertebrates such as Collembolan, one of the main prey items of shorebird chicks (Sjursen et al. 2005, Dollery et al. 2006). In total, our study included three sites (UTQ, CHU, EAB) where the snow phenology has been delayed since 2001 despite a warming climate during the shorebird egg-laying period. These three sites also exhibited greater mismatches than did our other sites. Shorebirds breeding under such dissociated climatic conditions may therefore face as great a risk, or potentially an even greater risk, of phenological mismatch than shorebirds breeding in fast-warming climates (such as our IKP site).

Proximate mechanisms of phenological mismatches

Our analyses of the variation in the single-trophic level responses both within and across sites using structural equation models revealed potential mechanisms that can help explain the extent of mismatches between the hatching of shorebird young and their invertebrate prey. Our final SEM results revealed that across sites and years, later snowmelt reduced the duration of the demand curves of shorebirds and dampened the peaks in invertebrate abundance. More compact demand curves can indicate greater synchronicity in the timing of breeding, which can arise as organisms adapt to later snowmelt and, subsequently, narrower optimal breeding windows (Burr et al. 2016). However, the narrower the demand curve becomes, the higher the probability that broods will miss the food peak unless the peak in demand is timed precisely with the food peak (see the arrow connecting "width of demand curve" and "overlap between food curve and demand curve" in Fig. 6b). At 9 of our 10 sites, the cumulative number of degree-days and daily mean temperatures best predicted the daily mean biomass of invertebrates within each year (Shaftel and Rinella 2017). Therefore, we can hypothesize that late snowmelt delayed invertebrate emergence and ultimately dampened invertebrate peaks at our sites.

In our final SEM, the latitudinal and longitudinal gradient in the extent of mismatches was largely driven by the timing of snowmelt. This result agrees with our observation that the rate of long-term changes in snow phenology (2001–2014) had the strongest effect on the individual-nest-level mismatch (see Table 1). The observed significant effect of the timing of snowmelt on the phenology of Arctic communities is also similar to results from previous studies at selected arctic sites (e.g., National Petroleum Reserve of Alaska; Liebezeit et al. 2014). Our SEM results indicated that later snowmelt was correlated with greater mismatches, which is seemingly the opposite of what the traditional mismatch hypothesis predicts (i.e., warming climate leads to early snowmelt, which then leads to a mismatch across trophic levels). Our results are most likely driven by the fact that the northernmost site (Utqiaġvik) and easternmost sites (East Bay and Churchill), where we found greater mismatches, have also experienced delays in snowmelt, and more importantly, warming climates during the egg-laying period.

Our final SEM also included a direct path from longitude to the magnitude of mismatch at both the individual and population levels, suggesting the existence of additional drivers that were not included in our models. Future investigations should therefore consider a broader array of environmental and ecological factors that potentially exhibit longitudinal gradients. For example, longitude often corresponds to the flyway used by a migratory population (Boere and Stroud 2006, Senner 2012). In turn, the use of different migration routes and nonbreeding locations can affect the extent of the mismatch in a population by (1) determining the timing of arrival at breeding sites, and hence the timing of clutch initiation (Myers 1981, Both and Visser 2001, Schekkerman et al. 2002, Both et al. 2006, Gienapp and Bregnballe 2012), and (2) affecting the climate change regimes encountered throughout the annual cycle (Ahola et al. 2004, Senner 2012).

Species effects on phenological mismatches

Simultaneously monitoring multiple species at each site highlighted the strong effects of breeding location on the extent of phenological mismatches. Our six species exhibit diverse migration strategies and wintering distributions, which vary even within a species across different sites (see Brown et al. 2017). Despite the variation in ecological and physical environments to which these species are exposed outside of the breeding season, our study indicates that most species responded to commonly experienced conditions at breeding sites in similar ways. For instance, at those sites where snowmelt now occurs later than in the past, all of the species breeding at those sites are experiencing greater mismatches than they do at their other breeding sites (see Fig. 5a, b). Although the responses of our study species to those conditions uniquely experienced by each species, e.g., the rate of change in temperature during each species" specific egg-laying period, differ more dramatically (Fig. 5c), our results generally fail to support predictions that differences in life-history traits among species may be as strong predictors of the degree to which species are mismatched as the breeding location (Kerby and Post 2013). Instead, our results add to the growing literature suggesting that there are common ecological principles, such as the occurrence of contrasting climate change regimes, that determine the severity of phenological mismatches across sites and species (Visser and Both 2005, Senner et al. 2018).

Mismatches at the individual vs. population levels

The development of a metric to determine the extent of phenological mismatches that is easily applicable and directly comparable is key to making comparisons among sites and species. Previous studies have measured the interval between the date of a resource peak and the date of peak food demand for predators (Visser et al. 1998, Gaston et al. 2009, Senner et al. 2017), compared rates of temporal shifts at different trophic levels (Pearce-Higgins et al. 2005, Nielsen and Møller 2006, Charmantier et al. 2008, Bauer et al. 2009, Both et al. 2009, Saino et al. 2009, Reneerkens et al. 2016), and developed their own study-specific metrics to evaluate fitness consequences in relation to the timing of breeding (Both and Visser 2001, Sanz et al. 2003). Recently, Reed et al. (2013*b*) used separate metrics to define mismatches at both the individual and population levels. Our population-level metric improved on past work by incorporating the different shapes of the phenological curves at the two trophic levels instead of simply averaging the mismatch measures at an individual level (see also Vatka et al. 2016). We suggest that our method is more effective because it incorporates the daily fluctuations in the density of shorebird hatchlings as well as invertebrate biomass.

Across our 10 study sites, the width of the food curve was on average 2.7× wider than that of the demand curve (Appendix S1: Fig. S6). However, wider food curves did not lead to greater overlap with the shorebird demand curves and, hence, did not affect the degree to which populations were mismatched. A perfect match with the food curve at the population level is only achieved when the curves of food availability and offspring demand are identical, not when the entire population is hatched around the food peak. Therefore, our population-level metric is most representative of a situation in which offspring survival is at least partly determined by density-dependent competition among conspecific or heterospecific individuals over a limited resource, such as invertebrate prey. Because the emergence of invertebrate prey in the Arctic occurs highly synchronously but yields high abundances (Braegelman 2015), direct resource competition among broods is unlikely. Therefore, our population-level metric may be less informative for the bitrophic system of shorebirds and their invertebrate prey in the Arctic. As such, the 30-yr population trends of the six species in our study were correlated better with our individual-level mismatch metric than with the population-level metric (Kwon et al., *unpublished data*). Nonetheless, the ability of the curves to differ in shape can be critical to accurately identifying the degree to which species are mismatched, especially when the timing of development and peak abundance are highly variable among different invertebrate taxa (Høye and Forchhammer 2008, Bolduc et al. 2013, Shaftel and Rinella 2017). We thus encourage further testing of this population mismatch metric, especially with study systems where reduced competition over resources among species could compensate for the fitness cost of suboptimal breeding timing.

Fitness costs of phenological mismatches

Studies of mismatches in species and communities of conservation concern face an inevitable question: what level of mismatch will affect fitness? For Arctic-breeding shorebirds, efforts to identify the costs of mismatches have been limited to estimating how mismatches affect the post-hatch growth rate and survival of chicks prior to their first southward migration (McKinnon et al. 2012, 2013, Dinsmore et al. 2017, Senner et al. 2017) and has rarely been extended to assess the effects of mismatches on recruitment success or population growth because strong natal dispersal hampers the estimation of juvenile survival rates (but see van Gils et al. 2016). Our study was broad scale but focused on the relationship between invertebrate and shorebird reproductive phenology and not fitness costs per se. However, complementary studies undertaken at our study sites suggest that the mismatches we documented are having significant consequences for some of our study species. For instance, the growth rates of shorebird chicks at our study site in Utqiaġvik (S. Saalfeld and R. B. Lanctot, *personal communication*) and the post-hatch survival rates of chicks in Churchill depended on when young are hatched in relation to fluctuations in daily invertebrate biomass (Senner et al. 2017). Such studies thus provide a plausible link between our observations of greater trophic mismatches at more easterly longitudes and ongoing declines of eastern shorebird populations (Brown et al. 2010, Andres et al. 2012, Smith et al. 2012).

Projected climate conditions and unpredictable ecosystem responses

Since the mid-1960s, the timing of snowmelt in northern Alaska has advanced by ~8 d due to reduced winter snowfall and warmer spring temperatures (Stone et al. 2002). Consequently, the duration of snow cover in this region is decreasing by 2–4 d per decade (AMAP 2017). Climate change projections under high-emission scenarios indicate that the duration of snow cover will decrease by an additional 10–20% and that the area covered by near-surface permafrost will decrease by ~35% across much of the Arctic by mid-century (AMAP 2017). The linear relationship we found between the slope of past climatic change and the current extent of mismatches across the Arctic implies that continued warming will likely exacerbate trophic mismatches for shorebirds breeding across the Arctic. Our study also suggests that the extent of mismatch may increase in the eastern Arctic, where the shorebird breeding phenology is inherently delayed as a result of the continental climate, but spring temperatures are still warming rapidly. Nonetheless, estimating the predicted future extent of mismatches between shorebirds and their invertebrate prey is inherently difficult.

We thus suggest that there are four key issues for producing meaningful predictions for shorebirds and other Arctic species. (1) Reduce the uncertainty in current climate projections regarding the extent and duration of snow cover (Brown and Mote 2009, Bokhorst et al. 2016, Musselman et al. 2017). (2) Improve our understanding of both short- and long-term demographic responses of Arctic invertebrates to changes in climatic conditions (Danks 2004, Rall et al. 2010, Amarasekare and Sifuentes 2012, Moquin et al. 2014). (3) Identify the critical drivers of population dynamics that are occurring during other stages of the annual cycle but leading to reversible state effects that carry over to affect shorebirds during their breeding season in the Arctic (Studds and Marra 2011, Lameris et al. 2018, Murray et al. 2018). (4) Explore the indirect effects of ecosystem-level processes on Arctic species. The complex responses of tundra vegetation to climate change in the Arctic will undoubtedly impact the reproductive phenology of shorebirds, as well as all aspects of invertebrate ecology. Invertebrate ecology therefore needs to be more fully incorporated into future modeling efforts (Bjorkman et al. 2015, Wheeler et al. 2015, Wauchope et al. 2017).

Conclusions

We have shown that sites widely distributed across the Arctic have experienced different patterns of climate change and potential dissociation between snow cover and temperature during snowmelt and the egg-laying periods of shorebirds over the past 25 yr. Our space-for-time substitution approach revealed a linear relationship between the slope of past climatic change and shifts in snow phenology and the current extent of phenological mismatches between the hatching of shorebird young and the emergence of their invertebrate prey. Our continent-wide comparisons also indicate that shorebird populations are experiencing greater trophic mismatches at higher latitudes and more easterly longitudes, which may be contributing to regional population declines in several species of shorebird migrating along the East Atlantic Flyway. Failure to match changes in prey phenology may indicate inherent limitations in the ability of shorebirds to adapt to climate change and has implications for the conservation status of these species. Our results also highlight the important role of the timing of snowmelt on the initiation of nests and the subsequent hatching of shorebird young. Additionally, we show that the timing of snowmelt can shape the demand curve of shorebird young as well as the magnitude of the peak in invertebrate abundance and, in turn, the extent of phenological mismatches between these two groups. Finally, our study demonstrates the importance of understanding phenological mismatches as a complex process involving both environmental and ecological factors, as well as broad geographic drivers.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecm.1383/full

Data Availability

All data used in our analyses are available online at the NSF Arctic Data Center (https://arcticdata.io/catalog/#view/doi:10.18739/A2CD5M) except data on the historical snow phenology, which is available from Peng et al. (2013).