Research

Trophic matches and mismatches: can polar bears reduce the abundance of nesting snow geese in western Hudson Bay?

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Climate change driven advances in the date of sea ice breakup will increasingly lead to a loss of spring polar bear foraging opportunities on ringed seal pups creating a phenological trophic 'mismatch'. However, the same shift will lead to a new 'match' between polar bears and ground nesting birds. This new match will be especially prevalent along the Cape Churchill Peninsula of western Hudson Bay where both polar bears and nesting snow geese are abundant. Easily foraged goose eggs will provide at least some of the earlier arriving polar bears with compensation for the energy deficit accrued through lost seal hunting opportunities. We examine the potential impact of changes in the extent and pattern of polar bear egg predation on snow goose abundance using projection models that account not only for increases in the temporal overlap of the two species but also for autocorrelation and stochasticity in the processes underlying polar bear onshore arrival and snow goose incubation. Egg predation will reduce reproductive output of the nesting lesser snow geese and, under all but trivial rates, will lead to a reduction in the size of their nesting population on the Cape Churchill Peninsula. Stochasticity associated with the asymmetrical advances in polar bear onshore arrival and the snow goose incubation period will lead to periodic mismatches in their overlap. These, in turn, will allow snow goose abundance to increase periodically. Climate driven changes in trophic matches and mismatches may reduce snow goose numbers but will not eliminate this over-abundant species that poses a threat to Arctic landscapes.

Global climate change has led to shifts in the phenology of numerous species of plants and animals (Parmesan and Yohe 2003). Owing to inherent differences among species in their physiological tolerances, reaction norms and life histories, it is not surprising that their responses to even similar trends in climate change are not the same (Both et al. 2009). When the species affected are also ones that occur at different trophic levels in the same or linked ecosystems, mismatches in their normal trophic interactions may develop (Both et al. 2009). As many of those trophic interactions involve the transfer of nutrients and/or energy, these mismatches can reduce the success of one or more of the interacting species, reduce biodiversity and destabilize ecosystems (Visser and Both 2005).

One interesting climate related mismatch that spans trophic levels is the case of polar bears *Ursus maritimus* and their primary prey, the ringed seals *Phoca hispida* (Stirling and Parkinson 2006). Advances in the spring breakup of sea ice are believed to reduce the ability of polar bears to consume ringed seal pups during a time when this resource is especially critical to the polar bears (Stirling and Derocher 1993). This is particularly problematic for polar bears living in western Hudson Bay, near the southern limit of the species, where impacts of global change are expected to be felt more immediately (Skinner et al. 1998). Recent analyses of

polar bears in that region have reported declines in the body condition, reproductive success, survival and population size that coincide with an advance in spring sea ice breakup (Stirling et al. 1999, Regehr et al. 2007).

Ironically, the same climate-based shift and mismatch that is potentially depriving polar bears of their ability to hunt ringed seals on the sea ice is also bringing polar bears ashore on the Cape Churchill Peninsula, near Churchill, Manitoba, at a time when a large population of lesser snow geese *Chen caerulescens caerulescens* (henceforth snow geese) is incubating its eggs (Rockwell and Gormezano 2009). Polar bears have increasingly been observed eating snow goose eggs when their onshore arrival overlaps the incubation period. Similar goose egg predations have been observed on Southampton and Coats Islands (Smith et al. 2010), Akimiski Island in southern James Bay (K. F. Abraham pers. comm.) and on Svalbard (Madsen et al. 1998, Drent and Prop 2008). Although this new match to a different prey species could provide a substantial nutritional resource to at least part of the local polar bear population, the situation is so new that neither the extent of future predation nor its impact on the nesting snow goose population are yet known. While polar bears have also been observed capturing and consuming flightless goslings and adults after the

incubation period (Rockwell et al. unpubl.), we chose to focus on the impact of their nest predation given the comparatively low energy expenditure and high caloric reward associated with their eating eggs (Rockwell and Gormezano 2009).

Madsen et al. (1998) and Drent and Prop (2008) report that polar bear egg predation on Svalbard is sufficient that it is negatively impacting the resident goose populations. If egg predation in the Cape Churchill Peninsula region leads to a similar decline in the nesting population of snow geese, it would add a second irony to this climate-based 'mismatch becomes new match' situation. The mid-continent population of snow geese has grown to such an extent that it is severely degrading much of the Hudson Bay Lowlands (Jefferies et al. 2003). While the Canadian and US governments initiated a management program in 1997 to reduce the numbers of snow geese, those attempts have not yet been successful (Alisauskas et al. 2010). Increased climate-driven polar bear predation could actually aid in attempts to lower snow goose abundance and reduce local habitat damage.

Although the extent of egg predation and its impact on the snow goose population depends to some degree on the foraging behavior of polar bears and the reaction of snow geese to that predation, they ultimately depend on the dynamics of temporal overlap between polar bears and incubating snow geese. The processes underlying overlap – onshore arrival of polar bears and timing of snow goose incubation – are stochastic, partially independent and driven by autocorrelated climatic factors (e.g. the sea ice-albedo climate feedback mechanism: Curry et al. 1995). While deterministic linear analyses indicate the processes are advancing at different rates and suggest that overlap will increase (Rockwell and Gormezano 2009), such analyses may not accurately capture the joint dynamics of stochastic processes that are also influenced by feedbacks, time lags and increasing variability in the physical processes underlying climate change (Salinger 2005, Cryer and Chan 2008).

In this paper we examine the potential impact of increased polar bear egg predation on the Cape Churchill Peninsula population of snow geese. We first estimate advances in the incubation period of nesting snow geese and spring sea ice breakup (a surrogate for onshore arrival of polar bears, Stirling et al. 1999) using a series of models that account for autocorrelation and stochasticity in the underlying processes. We then use parameter estimates and stochastic projections from those analyses in combination with matrix population models to examine the increasing overlap and potential impact of polar bear egg predation on the nesting population of snow geese. Being mindful of the international management goal to reduce numbers of snow geese, we focus initially on models incorporating catastrophic levels of egg predation and evaluate its maximum potential impact. Since many factors related to both polar bears and snow geese could change this maximum potential impact (Discussion), we also examine the sensitivity of snow goose population dynamics under a complete range of constant and changing egg predation intensities.

We show that under the advances in overlap anticipated from global climate change, the abundance of snow geese in the Cape Churchill Peninsula will decline under all but near-trivial predation rates. However, even under the most extreme rate of predation, the snow goose colony on the Cape Churchill Peninsula should persist in the near term (25 year time span) and, as such, could continue to provide a nutritional subsidy for a portion of the local population of polar bears. Interestingly, the impact of polar bears on geese is less severe when stochastic variation in the underlying processes is accounted for than when it is ignored, as when using deterministic projections. We examine our findings in light of what is known about the interacting behaviors of polar bears and snow geese. Finally, we discuss the importance of our findings to management and conservation of snow geese and polar bears, and to general considerations of the impact of climate change and variation on trophic interactions and ecosystem stability.

Methods

Study site

This study makes use of data on snow geese and polar bears found in and around Wapusk National Park, approximately 30 km east of Churchill, Manitoba, Canada (Fig. 1). The snow geese are part of the mid-continent population (Abraham and Jefferies 1997) and the polar bears are part of the Western Hudson Bay (WH) population (Aars et al. 2006). Nesting snow geese are associated with more than 150 km of coastline on the Cape Churchill Peninsula and can be found up to 15 km inland although most occur within 5 km of the coast (Rockwell and Gormezano 2009).

Polar bears also occupy this nesting area as they move onshore in response to the breakup of sea ice in Hudson Bay (Rockwell and Gormezano 2009). During the ice-free period they occupy all of Wapusk National Park and much of the adjacent land to the west (Derocher and Stirling 1990). The advance of sea ice breakup in the spring will increasingly lead to the two species occurring in the same area at the same time. This joint use has already begun and has led to increasing predation of snow goose nests by polar bears (Rockwell and Gormezano 2009).

Data

Assessing the dynamics of temporal overlap between polar bears and incubating snow geese and projecting the potential impact of any resulting egg predation on the snow goose population requires annual timing data on both the snow goose incubation period and the on-shore arrival of polar bears. Clearly, the more years of overlap, the better are the chances of correctly capturing and projecting joint effects. Data on lesser snow goose nesting phenology have been collected since 1968 as part of a comprehensive, long-term study on the Cape Churchill Peninsula. Methodological details are given in Cooke et al. (1995) and a preliminary deterministic linear analysis of those data, using mean hatching date as an indicator for the incubation period, is presented in Rockwell and Gormezano (2009).

The date of sea-ice breakup in the portions of Hudson Bay that are relevant to the WH polar bear population has

Figure 1. Snow geese nest in coastal and near-coastal habitat of Wapusk National Park. As sea ice breaks up in the spring, the onshore movement of polar bears takes them into the nesting habitat of snow geese. During the ice-free period, polar bears are found throughout the Park and the areas north and west towards the Churchill River. Coastal concentrations of polar bears are high from Cape Churchill to Rupert Creek with the highest concentrations usually located north of the Broad River.

been used as a surrogate for the onshore arrival date of WH polar bears (Stirling and Parkinson 2006). Four studies have used deterministic linear analyses to examine the advance in sea ice breakup and its potential effect on polar bears of the WH population (Stirling et al. 1999, 2004, Stirling and Parkinson 2006, Regehr et al. 2007) and deterministic linear analyses of the data produced comparable estimates for the advance in the date of breakup (Rockwell and Gormezano 2009). More recently, Lunn (2008, Lunn pers. comm.) summarized a long continuous data series of sea ice breakup dates that extends those reported in Stirling et al. (1999). They are also based on Etkin's (1991) 50% ice cover criteria and are estimated with methods detailed in Stirling et al. (1999). Because those data cover nearly the same time span as our data on snow goose nesting phenology, we have used the Lunn (2008) data to model potential changes in the onshore arrival of polar bears. These two data sets are depicted in Fig. 2.

Statistical analysis of advancement in nesting phenology and sea ice breakup

While deterministic linear analyses demonstrated advances in both the incubation period of snow geese and the onshore arrival of polar bears (Rockwell and Gormezano 2009), failure to account for autocorrelation in time series data could lead to biased estimates of trend and stochastic variation associated with the underlying processes (Cryer and Chan 2008); parameters that are central to the rest of our analyses. To accomplish this with both snow goose nesting and sea ice breakup data, we first examined plots of the sample (partial) autocorrelation functions ('acf' and 'pacf' procedures in the TSA package of R 2.8.1). This provided some insight into plausible degrees of auto-regressive (AR) and moving-average (MA) signals in the data.

We then developed a set of stochastic regression models with AR and MA orders between 0 and 5 ('arima' procedure
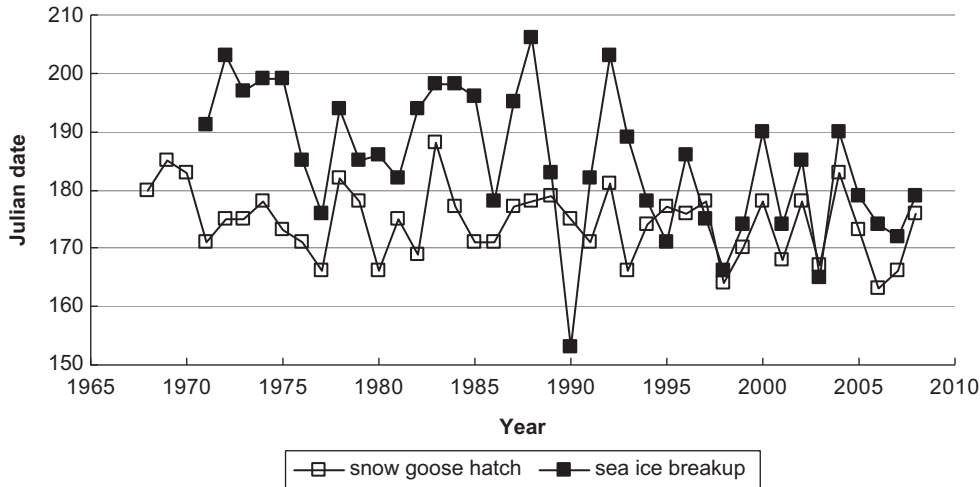
Figure 2. Time series for the mean Julian dates of lesser snow goose hatch in the Cape Churchill region (□), and Julian dates of sea ice breakup in the portions of Hudson Bay that are relevant to the WH polar bear population (■) (after Lunn 2008).

in the TSA package of R 2.8.1 and, henceforth ARMA models). Because time series data often exhibit high-order ARMA signals without displaying significant low-order signals, we also developed models with high-order ARMA terms and fixed the parameters for some low-order terms to 0 (i.e. the low-order terms were not estimated; Cryer and Chan 2008). In addition to the ARMA parameters, each stochastic regression model contained parameters for non-stationary trends in the respective time series (intercept and slope parameters, as opposed to differencing) and stochastic variation (i.e. 'white noise'; Cryer and Chan 2008).

Thus, the general form of our stochastic regression model was:

$$Y_t = \text{trend model} + \varphi_1 Y_{t-1} + \ldots + \varphi_5 Y_{t-5} + e_t$$
$$+ \theta_1 e_{t-1} + \ldots + \theta_5 e_{t-5} \quad (1)$$

where Y denotes the response variable (date of snow goose hatching or onshore arrival of polar bears), e is a standard normal deviation from the deterministic component of the model, and φ and θ denote the AR and MA parameters respectively.

We used Akaike's information criterion adjusted for sample size (AIC_c; Akaike 1973) to determine which model(s) served as the best approximation(s) to the data (Burnham and Anderson 2002). Precision of estimated model parameters was assessed based on standard errors and the extent to which 95% confidence intervals overlapped zero (Graybill and Iyer 1994).

Projections of the advancement of snow goose incubation period and polar bear onshore arrival

We used our best stochastic regression models for dates of sea ice breakup and hatching, along with their associated parameter estimates (including variance), to project both snow goose incubation period and polar bear onshore arrival for 25 years into the future. Projections based on global circulation models were not used to model advances in sea ice breakup because they do a poor job of predicting localized phenomena, especially in the regions of Hudson Bay relevant to the

WH population of polar bears (Gough and Wolfe 2001, Gagnon and Gough 2005). We believe 25 year projections provide insight into future dynamics but serve as a reasonable near-term time horizon for projections that do not overstep the length of the observed non-stationary time series (Fig. 2). Values of e_t (Eq. 1) were drawn from a normally distributed random variable e ~ $N(0,\sigma^2)$, where σ^2 denotes the estimated stochastic variation (i.e. white noise) in the time series attained from the focal model. We generated 1000 random realizations of the 25 year projections to obtain a representative sample for each of the two stochastic processes (hatching date and onshore arrival date) using R. These are referred to throughout as the ARMA projection set.

Because we were also interested in examining the possible effect of increasing levels of stochastic variance on the overlap of polar bears with the incubation period and its potential impact on the nesting snow goose population, we generated three additional projection sets using 25%, 50% and 100% inflation of the stochastic variance in the best ARMA models. These are referred to throughout as the 'added variance series', and serve as a numerical sensitivity analysis to increased temporal stochasticity.

For comparison with past studies that did not account for AR, MA or stochasticity in these two time series (Stirling et al. 1999, 2004, Stirling and Parkinson 2006, Regehr et al. 2007, Rockwell and Gormezano 2009), we also evaluated our data with simple linear regression models and evaluated their support with AIC_c (Appendix 1).

Projecting the overlap of polar bears and the snow goose incubation period

Nest initiation by snow geese on the Cape Churchill Peninsula spans a 7-day period with an average of 0.06, 0.11, 0.18, 0.30, 0.18, 0.11 and 0.06 of the females initiating on day one through seven (Cooke et al. 1995, Rockwell unpubl.). Eggs are laid one per day, and given a 24 day incubation period from the time the modal clutch of four is laid, the total incubation period averages 33 days (from the time the earliest initiating geese lay their first egg until the latest initiating females hatch their eggs; Rockwell and Gormezano 2009). We assumed that

all nests being actively incubated when polar bears arrived onshore were available for predation and we measured the extent of that potential by the overlap of onshore arrival with the incubation period. We estimated the overlap as match = last incubation date – arrival date + 1 and computed its change over our 25 year projection intervals.

We computed the match for each of the 25 years in the 1000 realizations of model projections; then linearly scaled the match values such that the mean match value across the 1000 realizations for year = 1 was match = 2. This corresponds to the best mean empirical estimate we have for current overlap of the end of the incubation period (Julian 175) and first onshore arrival of polar bears (Julian 174) in the Cape Churchill Peninsula (Rockwell and Gormezano 2009). To provide a point of reference for these stochastic models, we also projected the match for 25 years using a deterministic linear model in which the value increased annually from match = 2 by 0.426 days year^{-1}, the difference between our best deterministic estimates of annual advances in the snow goose incubation period (0.145 days year^{-1}) and the onshore arrival of polar bears (0.571 day year^{-1}).

Projecting the snow goose population in the face of overlap and potential predation

We used a baseline projection model modified from the one originally developed by Rockwell et al. (1997) for management of the mid-continent population of snow geese. The basic demography of the Cape Churchill Peninsula population is summarized by the 5-stage (1, 2, 3, 4 and 5+ age class categories), pre-breeding census, Lefkovitch projection matrix **A**, parameterized from data in Rockwell et al. (1997) and updated from Dufour et al. (2010) as:

$$\begin{matrix} 0 & 0.079 & 0.201 & 0.223 & 0.238 \\ 0.833 & 0 & 0 & 0 & 0 \\ 0 & 0.833 & 0 & 0 & 0 \\ 0 & 0 & 0.833 & 0 & 0 \\ 0 & 0 & 0 & 0.833 & 0.833 \end{matrix} \qquad (2)$$

The first row of the matrix provides stage-specific measures of reproductive success (including breeding propensity and juvenile survival) while the remaining elements correspond to adult survival. Estimates of adult survival incorporate the minor impact that conservation-order harvest regulations have had since 1998 (Alisauskas et al. 2010), whereas estimates of reproductive success were made prior to any evidence of polar bear predation on nests and include a nest failure rate of 0.085 resulting from predation primarily by arctic foxes *Vulpes lagopus*, herring gulls *Larus argentatus* and parasitic jaegers *Stercorarius parasiticus* (Cooke et al. 1995). Given these vital rates, the projected population growth rate is much greater (λ = 1.003) than the management goal (0.85 to 0.95 per year, Rockwell et al. 1997). The associated stable stage distribution is **w** = [0.169 0.141 0.117 0.097 0.477]. We used our most recent estimate of population size, distributed according to **w**, to initiate all projections and this included 58 798 females of which 48 855 were nesting birds of at least age class 2 (Rockwell unpubl.).

When snow goose numbers in a localized area of the Cape Churchill Peninsula increase in numbers and degrade that habitat, they disperse to adjacent, more intact habitat and thus avoid density-dependent population regulation (Cooch et al. 2001, Jefferies et al. 2003). In similar fashion, analyses have failed to detect any evidence of negative density-dependent effects on adult survival and, in fact, increases in adult survival are the most likely cause of increases in snow goose abundance (Alisauskas et al. 2010). Density-dependent effects are also lacking for both survival and reproductive success of the closely related greater snow goose *C. c. atlanticus* (Menu et al. 2002, Morrissettte et al. 2010). As such, our projections of overall snow goose abundance were independent of population density and pertain to the Cape Churchill region rather than specific locations that geese have moved into or away from.

In projecting the snow goose population under stochastic egg predation by polar bears, we had to account for the proportion of the nesting colony that would still be incubating when the polar bears arrived onshore. We determined this from our match value (estimated from the joint stochastic projection sets described above) and from the staggered initiation distribution of nesting birds, also given above. When match = 1, 94% of the nesting birds would have hatched their clutches, leaving only the 0.06 proportion of the population that initiated latest available for potential predation. When match = 2, the proportion available would be 0.06 + 0.11 = 0.17, etc., through match = 7 or higher, when the entire nesting population would be available. Clearly, when match = 0 or less, none of the nests are available for egg predation. The proportion of the population available for predation is termed p. We use the terminology 'total match' for situations when match $\geq$ 7, 'partial match' when 0 < match < 7 and 'mismatch' when match $\leq$ 0.

For simplicity we kept adult survival and reproductive success variables not related to egg predation constant because previous studies have found the population's dynamics are robust to environmental variability and that low levels of stochasticity in these variables have little effect on projected population dynamics (Rockwell et al. 2010).

The Cape Churchill Peninsula snow goose population was represented by the five age class vector **n** and was projected as:

$$\mathbf{n}_{t+1} = \mathbf{A} \times (1-p_t) \times \mathbf{n}_t + \mathbf{A}_{0,t} \times p_t \times \mathbf{n}_t \qquad (3)$$

where $\mathbf{A}_{0,t}$ is a modification of **A** wherein the baseline nesting success (1 – 0.085) is reduced by a scalar ranging from 0 for catastrophic, worst-case (maximum) predation by polar bears to 0.9 for low level predation. We examined the entire range of possible constant annual predation rates ($\mathbf{A}_{0,t} = \mathbf{A}_{0,t+1}$) on snow goose dynamics to establish both the worst case potential impact and to evaluate what level of predation would lead to a decline of any sort in the nesting population. These model realizations assume that a sufficient number of polar bears are ashore to achieve the specified predation rate, independent of their numbers (Rockwell and Gormezano 2009).

To provide a point of reference for the stochastic models, we projected the population under constant annual predation rates using the deterministic linear model for advancement

of 'match' explained above. We also projected the population under the maximum predation rate using the 'increasing variance series' amidst ARMA processes to examine the sensitivity of snow goose population dynamics to increasing stochasticity.

Finally, because it is possible that predation rates may change (either increasing or decreasing) over the 25 year projection period, we explored the effects of monotonic annual increases or decreases in the predation rates leading to $A_{0,t} \neq A_{0,t+1}$. We used a range of increasing and decreasing changes in the annual rates of predation but since the results were qualitatively the same, we report only those based on the projected annual decline in the polar bear population (Regehr et al. 2007), as it is the most realistic potential value of which we are aware. Assuming, for example, that predation rate is simply proportional to the size of the WH population, one could anticipate an annual decline in the predation rate of 0.986. Symmetrically, we used the compliment of this rate, 1.015, as an exemplar of the various scenarios that could lead to an increase in annual predation. Although we examined the effects of annual decreases and increases for the entire range of initial predation rates, we report only those for the maximum, medium and minimum initial rates.

All population projections were conducted using MAT-LAB 7.1.0.246 (R14).

Results

Advancement in nesting phenology and sea ice breakup

Our best stochastic regression model for snow goose nesting phenology (Table A1a) indicated a small but statistically significant advance in the mean date of snow goose hatch (and thus the incubation period) over the 41 years of study ($\beta_0 = 177.92$, SE = 1.75; $\beta_1 = -0.16$, SE = 0.07). In addition, hatch date displayed a negative autoregressive pattern with lag 3 ($\varphi_3 = -0.32$, SE = 0.17), and deviates from the linear advancement exhibited a substantial amount of stochastic variation ($\sigma^2 = 18.06$) as well as a positive moving average with lag 5 ($\theta_5 = 0.86$, SE = 0.29). Positive ARMA terms in a stochastic regression model imply that, independent of the deterministic trend, previous values (AR) or deviations (MA; Eq. 1) are carried over and remembered by the system. Negative ARMA terms, however, indicate a tendency for the time series to oscillate around the deterministic trend with values above the trend followed by values below the trend with a lag-order of x (Cryer and Chan 2008). Thus, on top of the linear advancement over time (β_1) and substantial random variation (σ^2), variation in snow goose nesting phenology also displayed a complex autoregressive-moving average pattern (a 3rd-order oscillatory signal and a 5th-order memory in the deviates). The next-best model also fit the data well ($\Delta AIC_c = 0.69$); however, these two models differed by only one AR parameter, and substantially out-performed all other candidate models including the simple linear regression model (equivalent to the one reported by Rockwell and Gormezano 2009; details in Table A1).

Our best stochastic regression model for sea ice chronology over 38 years (Table A1b) indicated that although

snow geese and polar bears did not overlap very often in the past ($\beta_0 = 196.79$, SE = 1.02), the advancement in date of WH ice breakup (and thus onshore arrival of polar bears) has occurred 3.7 times more rapidly than the advancement in snow goose nesting phenology ($\beta_1 = -0.59$, SE = 0.05). Deviates from this trend exhibited a large amount of stochastic variation ($\sigma^2 = 70.26$) as well as a negative moving average with 2nd and 3rd order lags ($\theta_2 = -0.51$, SE = 0.13; $\theta_3 = -0.47$, SE = 0.12). Thus, dates of WH ice breakup have advanced rapidly but are also highly stochastic and somewhat oscillatory (Fig. 2). This model was a much better fit to the data than the next-best model ($\Delta AIC_c = 2.76$), which differed by only one MA parameter (Table A1b). Relative to the simple linear regression model that has been used in the past (Stirling et al. 1999, 2004, Stirling and Parkinson 2006, Regehr et al. 2007, Rockwell and Gormezano 2009), the top-ranking stochastic regression model for WH sea ice with MA parameters was superior (Table A1b).

Projections of future overlap between polar bears and the snow goose incubation period

Starting from the recent two-day 'match' between first polar bears and the snow goose incubation period in the Cape Churchill Peninsula region (Methods), we used the best stochastic regression models (ARMA) described above to simulate 1000 projections of future joint advancement in snow goose nesting phenology and WH ice breakup (and thus onshore arrival of polar bears). These simulations indicate that, on average, the number of match days should increase to approximately 12 in 25 years because of the more rapid advancement in breakup of the WH icepack (~0.59 days per year) relative to the timing of snow goose nest initiation and hatch (~0.16 days per year) (Fig. 3, Table 1a). Phenologies of goose nesting and onshore arrival of polar bears are nevertheless highly stochastic (Fig. 2), and thus so is the projected degree of overlap between polar bears and nesting snow geese (Fig. 3). Now and in the near future, there will still be years when snow goose nests are not exposed to polar bear predation. Yet, the chance of such a mismatch will become smaller as climate change progresses and match years become more common (Fig. 3). Projections made with added temporal stochasticity and a deterministic model produced very similar 'mean match' results, but estimates of variance differed greatly (Table 1a).

Projections of the snow goose population in the face of overlap and potential predation

For the most severe predation scenario possible, we assumed all of the nests available when polar bears arrive onshore would be consumed annually – 91.5% by the bears and the remaining 8.5% by other, more traditional predators. We modeled the snow goose population's dynamics under this maximum predation scenario using our best-fitting, stochastic ARMA projection set. Twenty realizations of the model are depicted in Fig. 4a and the mean along with upper and lower 2.5 percentiles of 1000 such ARMA realizations are presented in Fig. 4b. The result for the deterministic projection of the same maximum predation scenario is included
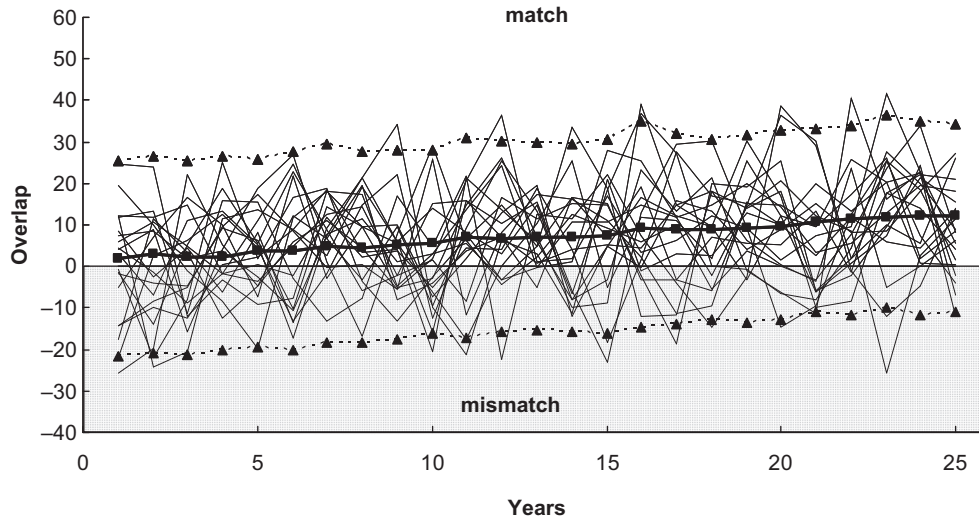
Figure 3. The extent of onshore overlap of polar bears and incubating snow geese is expected to increase over time given projections from our best fitting models for nesting phenology and advancement of sea ice breakup (and thus the arrival of bears on shore). The fine lines depict 20 realizations of the joint projections while the squares (■) and triangles (▲) depict the mean and upper and lower 2.5 percentiles of 1000 such realizations, respectively.

in Fig. 4b for comparison. Both the deterministic and stochastic projections begin with match = 2 when only 17% of the nesting population would be available for predation. The deterministic projection remains in this partial match state until year 12. During that time period, increasing proportions of the population are still incubating when polar bears

Table 1. The (a) extent of overlap (match) expected between the onshore arrival of polar bears and the snow goose incubation period at 25 years based on projections of the best stochastic regression models (ARMA), and (b) the estimated annual growth rate from 25 year projections of the snow goose population. For the stochastic projections the means and lower and upper 2.5 percentiles of 1000 independent trials are given. The added variance series examines the effect of increased stochastic variance in the joint ARMA projections on population growth rate, and the linear deterministic model serves as a baseline for comparison. (See text for additional details.)

(a)

	Days of match at t = 25			
Models used for projection	lower	mean	upper	variance
ARMA stochastic	−10.9048	12.1526	34.1390	141.60
Added variance series				
ARMA stochastic + 25%	−14.2245	12.2572	40.5758	179.4664
ARMA stochastic + 50%	−15.5873	12.3421	41.8071	210.0555
ARMA stochastic + 100%	−20.9797	12.1343	43.2671	287.3697
Linear deterministic		12.2240		0

(b)

	Lambda		
Models used for projection	lower	Mean	upper
ARMA stochastic	0.8824	0.9058	0.9293
Added variance series			
ARMA Stochastic + 25%	0.8827	0.9069	0.9289
ARMA stochastic + 50%	0.8862	0.9095	0.9321
ARMA stochastic + 100%	0.8882	0.9122	0.9349
Linear deterministic		0.8633	

arrive onshore. After year 12, match ≥ 7 and the entire nesting population is available annually for predation. From that point on, the rate of population decline due to egg predation in the deterministic model is maximized.

The population's dynamics under the ARMA stochastic projection are quite different. Early in the 25 year time span, some realizations include total matches (Fig. 3) and the entire nesting population would be exposed to predation. As a result, the initial mean rate of decline is greater than that found for the deterministic projection (Fig. 4b). Midway through the 25 year time span the situation changes. Unlike the case with the deterministic projection, both partial matches and mismatches are still possible after year 12 under stochastic ARMA projections (Fig. 3). As such, predation is periodically reduced or even absent in some realizations and the mean rate of population decline is lower than that expected under the deterministic projection (Fig. 4b).

Because of these differences, the overall annual growth rate of the snow goose population, estimated across the 25 years using the Heyde-Cohen equation (Caswell 2001), is higher under the stochastic ARMA projection than under the deterministic projection (Table 1b) and the anticipated population size at year 25 is more than three times higher (Fig. 4b). With stochasticity, there are periodic years of partial match and mismatch after year 12 that allow the snow goose population to successfully reproduce and rebound to some extent. The relationship between stochasticity in the match of polar bears and snow geese and the growth rate of the nesting colony is clearly seen in the added variance series of projections (Table 1). Increasing the stochastic variance of both the snow goose incubation period and polar bear onshore arrival under ARMA projection resulted in no change in the mean overlap at 25 years but substantially increased its variance (Table 1a). Increasing variance in the match raises the likelihood of periodic mismatches later in the projection period that, in turn, increasingly allows the snow geese to periodically reproduce and offset to some extent the cumulative effects of predation (Table 1b).
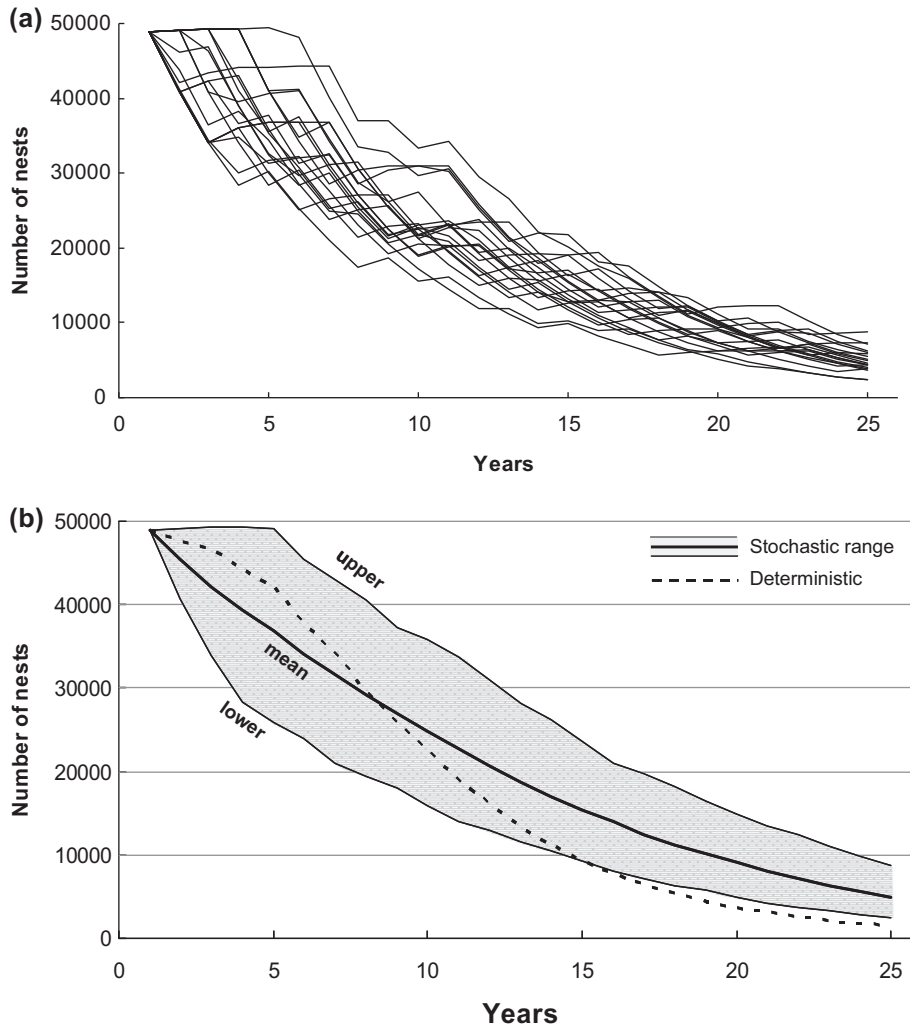
Figure 4. The nesting population of snow geese is expected to decline under growing polar bear egg predation stemming from increased overlap of the two species on the Cape Churchill Peninsula. The upper panel (a) depicts 20 realizations of stochastic projections using our best fitting models for advancement of nesting phenology and onshore arrival of the bears and the worst-case scenario of maximum polar bear nest predation. The lower panel (b) depicts the mean as well as upper and lower 2.5 percentiles of 1000 such realizations and also includes a deterministic projection based on a model using the mean rate of increasing overlap and maximum predation. Stochastic variation in the overlap process leads to a less severe rate of decline of nesting snow geese over the 25 years. At 25 years, the stochastic model projects 4939 nests while the deterministic model projects only 1489 nests, a more than three-fold difference.

Under the most severe predation scenario and projections of our best fitting stochastic models, the Cape Churchill Peninsula population of nesting snow geese is expected to decline to 4939 nesting pairs in 25 years, a nearly 90% reduction. Not surprisingly, as the rate of constant annual predation is reduced, reproductive output is increased and the nesting snow goose population does not decline as rapidly (Fig. 5). Importantly, however, the population would still decline as long as polar bears annually predated at least an additional 2.7% of the available nests during the climate driven increase in overlap of the two species. The number of nesting pairs at the 25 year mark would range from 4939 (at the absolute maximum predation rate) to 42 753 (at the minimum predation rate depicted in Fig. 5). In all cases, 25 year population sizes and growth rates were higher under stochastic than deterministic projections.

While projections using constant annual predation rates set the boundaries for the potential impact of polar bear predation on the nesting snow goose population, projections involving annual changes in those rates may provide a more realistic depiction of population dynamics of the nesting snow geese. Annual changes in the initial predation rates alter snow goose population dynamics in anticipated directions and displace the projected 25 year population size and growth rate to extents that depend on both the initial predation rate and the rate of annual change (Fig. 5). For example, a 1.4% annual decline in the maximum predation rate slowed the snow goose population decline by 2.1% while a 1.4% annual increase in the minimum predation rate depicted increased the snow goose decline by less than 0.3%. Annual 1.4% changes in the medium predation rate changed the population's growth rate by 0.9% and 1.3% (for decline and increase respectively). More extreme annual changes in the initial predation rate lead to greater impacts but follow the same pattern. None of the annual changes in predation rates examined (ranging

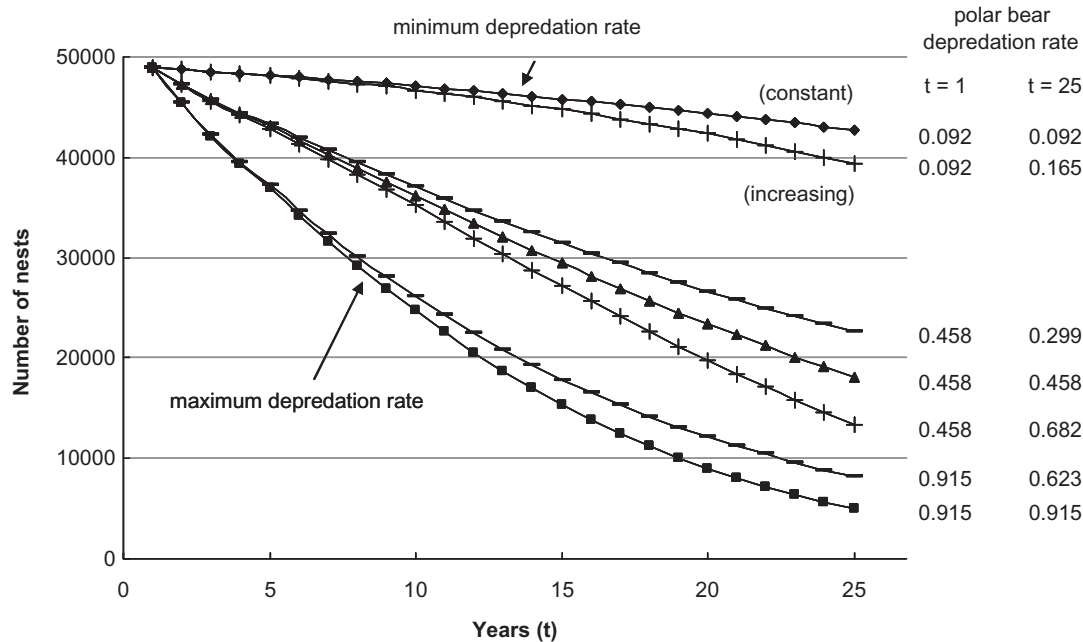|	minimum depredation rate	polar bear depredation rate	
		t = 1	t = 25
	(constant)	0.092	0.092
	(increasing)	0.092	0.165
		0.458	0.299
		0.458	0.458
	maximum depredation rate	0.458	0.682
		0.915	0.623
		0.915	0.915

Figure 5. The number of snow goose nests on the Cape Churchill Peninsula is projected to decline under all but trivial levels of polar bear predation. Projections assuming a constant rate of predation (solid symbols (◆, ▲, ■) set the boundaries of possible outcomes. Projections allowing increases (+) or decreases (–) in the initial predation rate over the projection interval lead to enhanced or reduced rates of decline. (Increases in the maximum initial rate and consistent decreases in the minimum initial rate are not possible). The projected rates of increase (1.015) or decrease (0.986) are based on estimates of decline in the WH polar bear population from Regehr et al. (2007). For clarity, only the means of sets of 1000 realizations are presented. The depiction for the 'maximum predation rate' is the same as shown as the mean of the stochastic projection in Fig. 4b. Its upper and lower 2.5 percentiles are the same as depicted there and those of the other means depicted in Fig. 5 are of similar magnitude. See text for details.

from the 1.4% depicted to 10%) resulted in 25 year population sizes that were outside the boundaries set by the constant annual rate projections depicted in Fig. 5. Importantly, and consistent with the constant annual predation scenario, the anticipated annual growth rates and 25 year population sizes were higher under stochastic than deterministic projections.

Discussion

Assuming global climate change continues as anticipated, polar bears will increasingly overlap the incubation period of lesser snow geese on the Cape Churchill Peninsula. At anything higher than trivial rates, polar bear nest predation should result in a decline of the nesting snow goose colony. However, even the most catastrophic predation rate is not expected to eliminate the local nesting population in the near term because climate driven mismatches in onshore polar bear arrival and snow goose incubation will allow for periodic years of low predation and temporary increases in nesting snow goose abundance. Eggs of the persisting snow geese would serve as a supplemental terrestrial food source for a portion of the local population of polar bears that could offset spring nutritional shortfalls during the ice-free season. In the following, we discuss our findings in greater detail and relate them to climate change and the limited information currently available on interactions between polar bears and geese. We end by examining how our work relates to general issues of climate-based matches and mismatches in the phenology of species occupying different trophic levels.

Stochastic ARMA models clearly provide better fit to changes in the snow goose incubation period and the spring disappearance of sea ice (the surrogate for onshore arrival of polar bears) than do simple linear regression models (Table A1). Like those models, they also predict that onshore polar bear arrival will increasingly overlap the incubation period of snow geese on the Cape Churchill Peninsula, setting the stage for increased nest predation. Our analyses reveal the presence of autocorrelation in both processes although they do not identify underlying causes. For snow geese, such autocorrelation is likely related to the fact that the geese are long-lived and as such, the same individuals or cohorts, perhaps with similar nesting tendencies and reactions to autocorrelated climate conditions, may predominate for short strings of years (Stenseth et al. 2002). For sea ice breakup, the "sea ice-albedo climate feedback mechanism" (Curry et al. 1995) suggests a positive momentum in breakup and as such the autocorrelation we detected may actually increase over time.

The stochastic ARMA models provide not only a more accurate projection basis for the joint processes underlying the increasing overlap but also generate different population dynamics for nesting snow geese than do deterministic linear models, and this is true for all rates and patterns of predation. Theory suggests that environmental stochasticity has a negative impact on population growth (Lewontin and Cohen 1969) but this is not necessarily true for inhomogeneous systems (Caswell 2001) or when species interactions

9

are considered (Chesson 2000). As shown in detail for the maximum rate of predation, snow geese fare better under stochasticity because mismatches allow periodic annual growth spurts to augment population abundance. Similar effects of stochasticity have been shown in maintaining coexistence in competitive systems (Adler and Drake 2008), arctic fox interactions with rodents (Henden et al. 2008), and in modifying the recovery potential of threatened species (Jenouvrier et al. 2009).

The beneficial effect of stochasticity on snow goose dynamics appears to be enhanced when the variance in mismatches is higher (Table 1). This suggests that if environmental stochasticity affecting the underlying processes increases, the snow goose decline should be less than projected. This is especially interesting in light of Salinger (2005) who indicates that environmental variation will increase as global change progresses. Combined with the work of Rockwell and Gormezano (2009), this suggests that while the climate-change-based advance in sea ice breakup leads to a new match and gives an advantage to polar bears over the snow geese, a related climate-change-based increase in environmental variation driving mismatches should diminish the edge.

The projected decline in numbers of snow geese nesting on the Cape Churchill Peninsula depends on not just overlap but also on the rate of predation by the increasingly matching polar bears. This, in turn, depends on factors related both to the numbers, arrival patterns and foraging behavior of polar bears and to the reaction of snow geese to the bears and their predation. Since the consumption of goose and other migratory waterfowl eggs is a relatively new phenomenon, information on these factors is quite limited and we summarize what is available and discuss its potential impact on our projections in the following.

Given an opportunity to forage on waterfowl eggs, polar bears will often consume large numbers of them (Madsen et al. 1998, Drent and Prop 2008, Rockwell and Gormezano 2009). Individual polar bears and their offspring have shown fidelity to new and abundant land-based food sources in the Churchill region where, for example, the same individual bears and their offspring were observed annually foraging near the Churchill landfill (Lunn and Stirling 1985). Similar habitual behavior has developed in polar bears foraging on goose and eider eggs on Svalbard where polar bears were also observed eating eggs while seals were still available on the ice, perhaps even advancing their annual onshore arrival to do so (Madsen et al. 1998, Drent and Prop 2008). Given these types of behaviors, it is possible that as individual bears begin foraging on eggs, their efficiency and rate of predation in subsequent years will increase as they become more familiar with snow goose nests, the nesting area and nesting phenology.

The spring onshore movement of polar bears is a gradual process in which the numbers of bears ashore increases as sea ice continues to disappear. As the date of breakup advances in response to climate change and the extent of overlap with the snow goose incubation period increases, larger numbers of bears, that may be more nutritionally stressed, are expected to be found on the nesting colony while there are eggs. Combined with the potentially changing foraging behaviors discussed above, these factors suggest that the

average rate of polar bear egg predation could increase over time. Our projections of increasing annual predation rate (Fig. 5) show that although this would reduce the numbers of nesting geese more rapidly, it could not exceed the decline associated with the maximum constant predation rate indicated in Fig. 5 that projects a lower bound of 4939 pairs of nesting snow geese in 25 years.

At the same time, there is evidence from Regehr et al. (2007) that the number of WH polar bears is declining at an average of $\lambda = 0.986$. If that rate of polar bear decline remained constant for 25 years, the current WH population would be reduced to 653 polar bears. Assuming that nest predation is simply dependent on the number of bears and that we began at the maximum predation rate (the worst-case scenario), 25 years of decline in the numbers of available bears would only lead to a 2.1% reduction in the average rate of annual snow goose population decline from 0.909 to 0.928 (Fig. 5). However, Rockwell and Gormezano (2009) reported that a single polar bear consumed the eggs of 206 common eider nests (with clutch and egg size nearly identical to those of snow geese) in 96 h before being chased away as a safety precaution. At such a consumption rate, it would take only 237 bears to consume the eggs from all the nests of the current 48 855 pairs of snow geese (in 96 h) and, of course, fewer each subsequent year as the snow goose population declined. While a reduction in the decline of snow geese due to declines in the local polar bear population is possible, we feel it is unlikely.

It is not yet known how snow geese will react to polar bear predation, especially if they are annually exposed to increasing levels of it. It is possible, for example, that snow geese might shift nesting sites away from core areas and this could reduce the effective rate of polar bear predation. However, studies of dark-bellied brent and greater snow geese, *Branta bernicla bernicla* and *C. c. atlanticus*, indicate that continued nesting at the same site did occur in years following heavy predation by arctic foxes (Spaans et al. 1998, Bêty et al. 2002). Further, Madsen et al. (1998) found that light-bellied brent geese *B. b. hrota* on Svalbard continued nesting annually at the same sites despite periodic polar bear predation that led to total nesting failure for a large portion of the colony and substantially reduced overall reproductive success of the entire colony. It is important to note, though, that geese can shift in response to some environmental pressure as evidenced by the initiation of two new southern nesting colonies of barnacle geese *B. leucopsis* (van der Jeugd et al. 2009).

On the Cape Churchill Peninsula, there was complete reproductive failure in 2009 resulting in part from heavy predation by a variety of predators including polar bears. Nesting density in 2010 was unchanged from its previous five year average suggesting that a single year's failure does not result in mass exodus (Rockwell unpubl.). A pilot study of marked snow geese at La Pérouse Bay showed that more than half of females whose nests were totally predated by arctic foxes and/or herring gulls changed their nest location in the subsequent year by up to 15 km (Rockwell unpubl.). Such a local geographic shift is well within the range over which polar bears are known to move and forage (D. Hedman pers. comm.) so it is unlikely that regional movement within the Cape Churchill Peninsula would substantially

reduce the impact of polar bears. Two such scenarios, starting at the maximum and a medium initial predation rate are depicted in Fig. 5. In both cases, the impact of 1.4% annual reductions in predation rates is not substantial. Unless the reaction of the geese virtually eliminated polar bear predation on the Cape Churchill Peninsula, the local snow goose population is expected to decline under global climate change.

The eggs of snow geese nesting on the Cape Churchill Peninsula are a nutrient resource that can be used by arriving polar bears to offset energy shortfalls related to earlier sea ice breakup and onshore arrival (Rockwell and Gormezano 2009). As the nesting population declines under increased overlap and predation, it might be expected that the available nutrient resource would also decline. However, since overlap and predation would occur earlier during the incubation period, a larger proportion of nests would still be available and the nutritional value of their eggs would be higher (Rockwell and Gormezano 2009). As a point of reference, our best data indicate there is currently a two day overlap between arriving polar bears and incubating snow geese. The eggs of the 17% of the snow goose population still incubating would provide 4.34×10^6 kilocalories of energy (Rockwell and Gormezano 2009).

Under anticipated climate change, the overlap of polar bears and the snow goose incubation period increases to a projected 12 day overlap in 25 years. On average, the entire nesting population (rather than just 17%) would still be incubating eggs and those eggs would have a 49% higher average caloric value than the near-hatching embryos encountered with the current two-day match (Rockwell and Gormezano 2009). In 25 years under the maximum predation rate (0.915), the expected 4,939 nests would provide 3.77×10^6 kilocalories. Under a medium predation rate (0.458), the expected 18 110 nests would provide 13.81×10^6 kilocalories. And under the minimum polar bear predation rate depicted in Fig. 5 (0.092), the expected 42 753 nests would provide 32.61×10^6 kilocalories. Except for near-maximum predation rates, the anticipated energy reserve from snow goose eggs after 25 years of predation is actually higher than what is currently available. This simply reflects the facts that earlier arriving bears would encounter a higher proportion of the nesting population and that the eggs of those geese would be more nutritionally valuable.

These energy reserves must be viewed as supplements that could be used by a portion of the population to offset deficits accrued through lost seal hunting opportunities related to climate change. Since increased overlap in arrival and incubation period would result from earlier sea ice breakup, that deficit could be larger unless polar bear foraging behavior prior to onshore arrival changed (e.g. increasing their daily rate of seal capture prior to or during breakup, Rockwell and Gormezano 2009). Such behavioral changes along with nutrient supplements from snow geese and other terrestrial and open-water sources (Dyck and Kebreab 2009, L. J. Gormezano unpubl.) are necessary if the region's polar bears are to maintain their current energy intake in the face of projected climate-mediated decreases in spring seal hunting opportunities. Research will be needed to document how polar bear foraging behavior changes as the climate warms.

The snow geese both nesting and rearing their young on the Cape Churchill Peninsula are partly responsible for the extreme habitat degradation of both coastal and near-coastal marshes since the mid 1980s (Jefferies and Rockwell 2002). The explosive growth of the local and mid-continent population of snow geese was in part a response to an increased nutrient subsidy across linked ecosystems that reduced potential bottom–up regulation of the herbivores in their summer habitat and helped initiate an apparent trophic cascade that continues to threaten the region (Jefferies et al. 2003, Abraham et al. 2005). Increased polar bear predation of snow goose eggs would serve as a novel form of 'top–down' regulation, operating to reduce the local snow goose population. As shown here, nearly any level of increased polar bear predation would begin reducing the numbers of nesting snow geese on the Cape Churchill Peninsula. Preliminary work (Rockwell unpubl.) suggests that if snow goose numbers were reduced there would be some recovery of some types of degraded habitat (e.g. fresh water sedge fen meadows). Such a situation represents a case where differential changes in phenologies across trophic levels (a greater advance in polar bear arrival than snow goose incubation period) lead to something other than destabilization of an ecosystem (cf. Visser and Both 2005).

The standard pattern to emerge when climate change affects phenologies differentially across trophic levels is that the mismatch reduces the success of one or both of the focal species (Both et al. 2009). We agree fully with Visser and Both (2005) that studies of the differential impacts of climate change on phenologies should address the extent of such mismatch and develop a yardstick to measure its effects. However, while the mismatch of polar bears and ringed seals, forced by advancing sea ice breakup, appears to be negatively impacting the polar bears, the new match with nesting snow geese may offset some of those losses. As such, the work here suggests that the valid quest for a mismatch yardstick needs to span a larger portion of single or linked ecosystems than just historically interacting species and traditional prey.

The work here also suggests that mismatches are not all 'bad'. In the short term, while periodic mismatches between polar bear arrival and snow goose incubation may restrict the nutrient supplement for bears in a single year, the same mismatch helps the geese by allowing periodic reproductive success and promoting pulses of population growth. In the longer term, such mismatches, especially when affected by stochasticity in the underlying climatic drivers, lead to a more persistent population of geese and a more sustained energy resource for the polar bears. Continuing the previous theme, the yardstick measuring the impact of mismatches must also integrate both near- and long-term dynamics with potentially increasing environmental stochasticity.

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Appendix 1

To compare our stochastic regression approach to past studies of the advancement in snow goose nesting and onshore arrival of polar bears that used simple, linear correlation or regression and did not account for autoregressive moving averages or stochasticity in these two time series (Stirling et al. 1999, 2004, Stirling and Parkinson 2006, Regehr et al. 2007, Rockwell and Gormezano 2009), we also evaluated our data with simple linear regression models and evaluated their support with AIC_c following Burnham and Anderson (2002) (Table A1). Because the top-performing stochastic regression (ARMA) models were a better fit to the time series data than simple linear regression models ($\Delta AIC_c > 2$), we focused on the ARMA models in the main text.

Nevertheless, we also projected future dates of snow goose hatch, onshore arrival of polar bears, and the match between the two processes using the simple linear regression models with and without a variance (σ^2) component (referred to as the linear projection sets). These provide for comparison to past studies but with updated data. Both the ARMA and linear projections assumed that dates of snow goose hatch and onshore arrival of polar bears vary independently over time. While there is some evidence that land- and marine-based climate processes are coupled (Gagnon and Gough 2005, Varvus 2007), there are also physical processes and evidence suggesting that any such coupling will likely not be complete (Curry et al. 1995, Skinner et al. 1998). The data used here have a Pearson product-moment correlation of r = 0.46 between dates of hatching and sea ice breakup. Such a correlation could reflect some common ecological drivers for annual changes in the dates or could be spurious, resulting from both time series having a negative non-stationary trend. To include the possibility that the correlation is meaningful in our evaluations, we generated projections for incubation period and onshore arrival under both ARMA and linear models using a multivariate random normal distribution that incorporated the observed estimate of correlation. These are referred to as the correlated ARMA and correlated linear projection sets. Details of the projections were conducted as described in the main text.

Estimates of 'mean match' were similar across the various projection sets, but estimates of variance differed greatly (Table A2). Higher levels of variance in the dynamics of overlapping phenologies provide periodic relief to the snow goose population and the resulting snow goose population growth rate is higher than other projections with lower variance (Table A3).

Given that the ARMA models were a much better fit to the data (Table A1), near-term projections made with these models should be more accurate than those made without parameters accounting for underlying autoregressive moving-average signals in the data (e.g. linear projections; Burnham and Anderson 2002).

Table A1. The best approximating stochastic regression models for the time series of (a) lesser snow goose hatch dates in the Cape Churchill region and (b) WH ice breakup based on Akaike's information criterion adjusted for sample size relative to that of the top model (ΔAIC_c). Each of these models contain an intercept and linear slope parameter (found to be a superior fit relative to nonlinear models), as well as a parameter for stochastic variation (white noise); the auto-regressive (AR) and moving average (MA) order of each model is denoted with an X. K denotes the total number of estimated parameters in each model, and the last model indicated is a simple linear regression model that does not account for temporal autocorrelation and is equivalent to the deterministic one reported in Rockwell and Gormezano (2009). Other models were considered but only those performing better than the linear regression model (last model in the list) are reported. Weight of evidence for a model is inversely related to its ΔAIC_c with $\Delta AIC_c = 0$ having the best fit.

(a) Snow goose hatch dates

Model

AR1	AR2	AR3	AR4	MA1	MA2	MA3	MA4	MA5	K	ΔAIC_c
		X						X	5	0.00
								X	4	0.69
				X	X	X	X	X	8	9.40
				X	X	X			6	9.68
X	X	X	X	X	X				9	9.77
X	X			X	X	X			8	9.81
X	X	X		X	X				8	9.88
X				X					5	10.15
									3	11.48

(b) WH ice breakup

Model

AR1	AR2	AR3	MA1	MA2	MA3	MA4	K	ΔAIC_c
			X	X			5	0.00
		X	X	X	X		6	2.76
X	X						5	4.30
X			X	X			6	4.95
X			X	X	X		7	5.61
			X	X	X	X	7	5.64
							3	6.01

Table A2. The extent of overlap (match) expected between the onshore arrival of polar bears and the snow goose incubation period at 25 years under our four stochastic projection sets and a linear deterministic model. For the stochastic projections the means, lower and upper 2.5 percentiles and variances of 1000 independent trials are given.

Models used for projection	Days of match at t = 25			
	lower	mean	upper	variance
ARMA stochastic	−10.9048	12.1526	34.1390	141.60
Linear stochastic	−12.0850	11.8139	34.0789	137.84
Correlated ARMA stochastic	−6.9960	11.8992	31.3447	97.45
Correlated linear stochastic	−5.8567	11.6247	29.6552	79.63
Linear deterministic		12.2240		0

Table A3. The estimated annual growth rate from 25 year projections of the snow goose population using our four stochastic projection sets and a linear deterministic model (under the worst-case scenario of polar bear nest predation). For the stochastic projections the means and lower and upper 2.5 percentiles of 1000 independent trials are given.

Models used for projection	Lambda		
	lower	Mean	upper
ARMA stochastic	0.8824	0.9058	0.9293
Linear stochastic	0.8730	0.9059	0.9372
Correlated ARMA stochastic	0.8798	0.9042	0.9275
Correlated linear stochastic	0.8735	0.9027	0.9334
Linear deterministic		0.8633	