

Climate change threatens polar bear populations: a stochastic demographic analysis

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Abstract. The polar bear (*Ursus maritimus*) depends on sea ice for feeding, breeding, and movement. Significant reductions in Arctic sea ice are forecast to continue because of climate warming. We evaluated the impacts of climate change on polar bears in the southern Beaufort Sea by means of a demographic analysis, combining deterministic, stochastic, environment-dependent matrix population models with forecasts of future sea ice conditions from IPCC general circulation models (GCMs). The matrix population models classified individuals by age and breeding status; mothers and dependent cubs were treated as units. Parameter estimates were obtained from a capture–recapture study conducted from 2001 to 2006. Candidate statistical models allowed vital rates to vary with time and as functions of a sea ice covariate. Model averaging was used to produce the vital rate estimates, and a parametric bootstrap procedure was used to quantify model selection and parameter estimation uncertainty. Deterministic models projected population growth in years with more extensive ice coverage (2001–2003) and population decline in years with less ice coverage (2004–2005). LTRE (life table response experiment) analysis showed that the reduction in λ in years with low sea ice was due primarily to reduced adult female survival, and secondarily to reduced breeding. A stochastic model with two environmental states, good and poor sea ice conditions, projected a declining stochastic growth rate, $\log \lambda_s$, as the frequency of poor ice years increased. The observed frequency of poor ice years since 1979 would imply $\log \lambda_s \approx -0.01$, which agrees with available (albeit crude) observations of population size. The stochastic model was linked to a set of 10 GCMs compiled by the IPCC; the models were chosen for their ability to reproduce historical observations of sea ice and were forced with “business as usual” (A1B) greenhouse gas emissions. The resulting stochastic population projections showed drastic declines in the polar bear population by the end of the 21st century. These projections were instrumental in the decision to list the polar bear as a threatened species under the U.S. Endangered Species Act.

Key words: climate change; demography; IPCC; LTRE analysis; matrix population models; polar bear; sea ice; stochastic growth rate; stochastic models; *Ursus maritimus*.

INTRODUCTION

Climate change is projected to have significant effects on population dynamics, species distributions and interactions, food web structure, biodiversity, and ecosystem processes (Convey and Smith 2006, Parmesan 2006, Grosbois et al. 2008, Keith et al. 2008). The climate is changing faster in the Arctic than in other areas (Serreze and Francis 2006, Walsh 2008). For Arctic marine mammals, the most critical of these changes involve the sea ice environment (Laidre et al. 2008). The extent of perennial sea ice in the Arctic has been declining since 1979 at an average rate of 11.3% per

decade (Stroeve et al. 2007, Perovich and Richter-Menge 2009). The summer minimum sea ice extent in 2005 set a new record, which was broken again in 2007; the ice extent in 2008 was the second lowest on record. This trend has led to concerns about Arctic species with strong associations with sea ice. The polar bear is one of the most ice-dependent of all Arctic marine mammals (Amstrup 2003, Laidre et al. 2008). As a top predator, it is also an important indicator of effects on the Arctic ecosystem (Boyd et al. 2006).

Arctic sea ice changes have been associated with negative effects on individuals and populations of polar bears (Stirling et al. 1999, Obbard et al. 2006, Regehr et al. 2006, 2009, Rode et al. 2010). Such observations alone, however, provide few insights into future impacts of climate, which can be assessed only by linking population growth models, environmental effects, and

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forecasts of the future environment. Although challenging, such assessments are necessary to forecast future trends and to inform policy debates and legal decisions. The U.S. Endangered Species Act, for example, requires an assessment of extinction risks within the “foreseeable future” (16 U.S. Congress 1531, 1973).

In this paper, we examine the current and projected future effects of climate change on a population of polar bears (*Ursus maritimus*; see Plate 1). Our approach is to develop stage-structured demographic models that incorporate the observed responses of the stage-specific vital rates to sea ice conditions. We then present a novel approach to connecting these demographic models to forecasts of future sea ice conditions from IPCC global circulation models (GCMs). The results reveal effects of climate on short-term transient dynamics, long-term population growth rates (deterministic and stochastic) and environment-dependent stochastic growth in the nonstationary environment created by climate change.

This study of climate effects was motivated by the need for an evaluation of polar bear population viability, following a petition to list the polar bear as a threatened species under the U.S. Endangered Species Act (Center for Biological Diversity 2005). The Act requires an evaluation of current conditions and a prediction of future risks to the population. This analysis was a contribution to those goals. The final listing decision concluded that declines in sea ice in polar bear habitat, both currently and in the future, pose a threat to the species, which is likely to become endangered in the foreseeable future. As a result, the polar bear was listed as a threatened species in May 2008 (U.S. Fish and Wildlife Service 2008).

Polar bears and sea ice

Polar bears occur in most Arctic areas that are ice covered for much of the year. They depend on sea ice for access to their primary prey (ringed seals *Phoca hispida* and bearded seals *Erignathus barbatus*) and for other aspects of their life history (Stirling and Oritsland 1995, Stirling et al. 1999, Amstrup 2003). Polar bears prefer habitat on the continental shelf where they have greater access to prey. The retreat of sea ice beyond the continental shelf, and longer ice-free periods during the summer, are expected to reduce foraging success, increase nutritional stress, and increase the distances polar bears must travel between seasonal use areas (Bergen et al. 2007). In some Arctic regions, the sea ice melts completely each year and polar bears are forced to spend the summer on shore. During this time they are largely food deprived, relying on body fat accumulated during the previous year. Longer movements over rougher sea ice and more open water could also increase the risks of injury or death (Monnett and Gleason 2006), especially for cubs.

Reductions in sea ice extent and/or duration have been associated with shifts toward more land-based denning, evidence of nutritional stress, reduced body

condition, reproduction, survival, and body size for polar bears in parts of their range (Stirling et al. 1999, Obbard et al. 2006, Stirling and Parkinson 2006, Fischbach et al. 2007, Regehr et al. 2007, Cherry et al. 2008). In recent years in the southern Beaufort Sea there have also been more numerous observations of unusual predation attempts and of drowned, emaciated, and cannibalized polar bears (Amstrup et al. 2006, Monnett and Gleason 2006, Stirling et al. 2008).

The study population

We analyzed the population of polar bears in the southern Beaufort Sea, one of the 19 regions defined by the IUCN Polar Bear Specialists Group (Aars et al. 2006). This population has previously been studied by Amstrup et al. (1986, 2001, 2006) and Regehr et al. (2006). Population size in 2006 was estimated as 1526 (95% confidence interval 1211–1841; Regehr et al. 2006). The study area (Fig. 1) lies on the northern coast of Alaska and adjacent Canada, extending from Wainwright, Alaska in the west to Paulatuk, Northwest Territories, in the east (for details see Amstrup et al. 1986, Regehr et al. 2009). A mark–recapture study of this population was conducted by the U.S. Geological Survey and the Canadian Wildlife Service from 2001 to 2006. During this period, polar bears were located using helicopters in the spring, and captured for marking or identification. The data set consisted of 818 captures of 627 tagged or radio-collared (approximately 6% of captures) individuals. A detailed statistical analysis of these data using multistate mark–recapture methods (Regehr et al. 2009) provided estimates of the vital rates used in our models.

Demography and climate change

In this study, we approach the demographic analysis of climate change effects using a sequence of models, of increasing sophistication, to explore different aspects of the problem (cf. Caswell 2001:644). We begin with a deterministic analysis of population growth in constant environments characterized by specific amounts of sea ice. Then we construct a stochastic model with which we analyze population growth in response to specified statistical patterns of sea ice fluctuations. Finally, we link the stochastic models to forecasts of sea ice fluctuations obtained from the output of a selected set of GCM climate models. This sequence of models proceeds from a constant environment, to a fluctuating but stationary environment, to a fluctuating and nonstationary environment.

It is well known that demographic analysis can influence policy decisions. Policy, however, can also dictate the direction of demographic analyses. In the case of the Endangered Species Act, classification as a threatened species requires a finding that the species is at risk of extinction “in the foreseeable future.” In the case of the polar bear, the foreseeable future was interpreted by the U.S. Fish and Wildlife Service as 45 years from

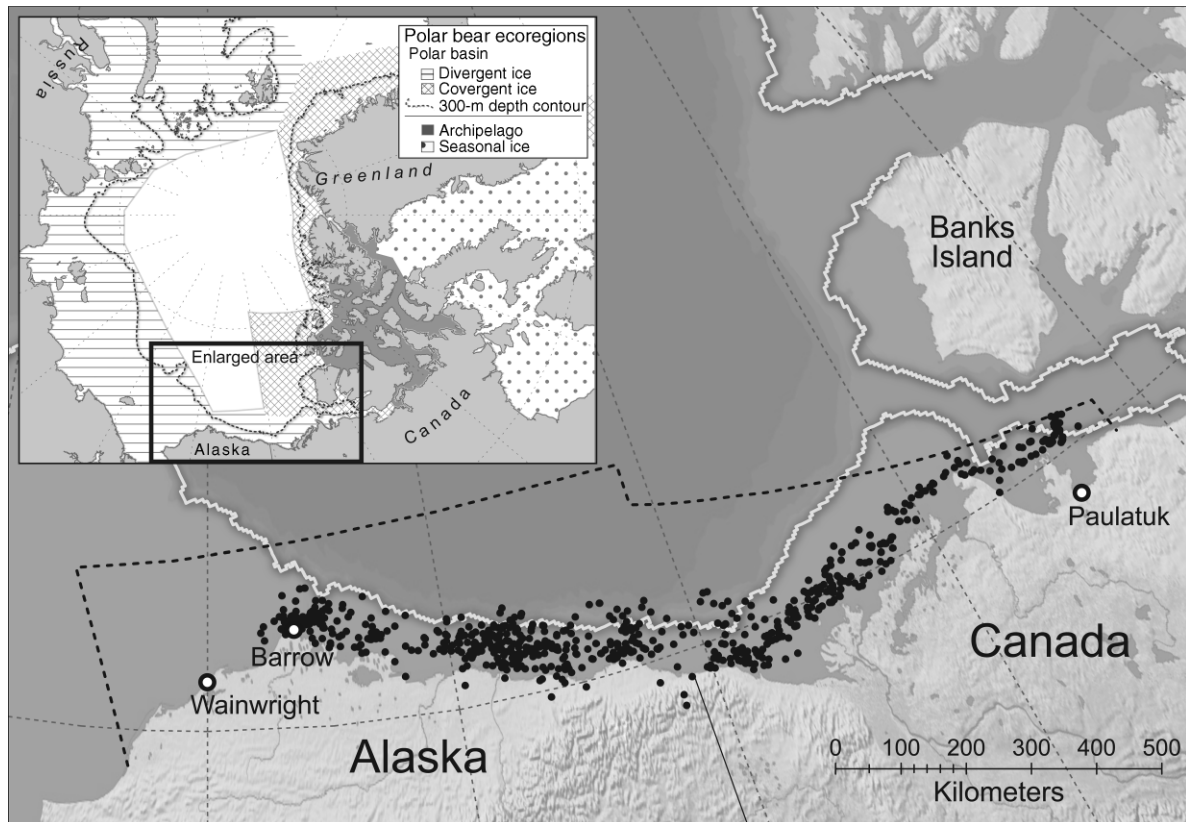


FIG. 1. The southern Beaufort Sea study area, showing locations of polar bears captured from 2001 to 2006. The dashed line is the population boundary, established by the International Union for the Conservation of Nature and Natural Resources (IUCN) Polar Bear Specialist Group. The white line is the 300-m bathymetry contour. The inset shows the four circumpolar ecoregions defined for polar bears by Amstrup et al. (2008). The figure is modified from Regehr et al. (2009).

2007 (U.S. Fish and Wildlife Service 2007). Asymptotic analyses using population growth rates, either stochastic or deterministic, may not properly address this question, so our analyses include transient projections with a particular focus on 45 years, but also longer time periods to 100 years. Comparisons of conclusions based on projections of 45 years with those based on asymptotic population growth rates may be instructive in future listing decisions.

DEMOGRAPHIC MODEL STRUCTURE

The life cycle

The polar bear is the largest extant ursid. Survival is relatively high; females as old as 32 years and males as old as 28 years have been reported (Stirling 1988). Females become pregnant for the first time in their fourth or fifth year, and give birth for the first time in their fifth or sixth year (Cronin et al. 2009). Females produce litters of one to three cubs in a winter den. Dependent young remain with their mothers from birth through the spring of their second year (Stirling 1988, Amstrup 2003), so the inter-birth interval for females successfully weaning young is at least 3 years.

Our life cycle model included six stages, based on age and reproductive status (Fig. 2). Stages 1, 2, and 3 contain nonreproductive females aged 2, 3, and 4 years, respectively. Stage 4 comprises adult females available to breed (i.e., without dependent young). Because mothers and cubs are not independent during the parental care period, we included these stages as mother-cub units; stage 5 comprises females accompanied by one or more cubs of the year, and stage 6 contains females accompanied by one or more yearling cubs.

This life cycle (Fig. 2) corresponds to a stage-structured matrix population model:

$$\mathbf{n}(t + 1) = \mathbf{A}_t \mathbf{n}(t) \tag{1}$$

where the vector $\mathbf{n}(t)$ gives the number of individuals in each stage and the matrix \mathbf{A}_t projects the population from t to $t + 1$. The projection interval extends from April to April, to coincide with sampling, which occurs in spring when females emerge from the den with their cubs. The entries in \mathbf{A}_t are defined in terms of lower-level vital rates: survival, $\sigma_i(t)$; breeding, conditional on survival, $\beta_i(t)$; cub-of-the-year litter survival, $\sigma_{L0}(t)$; and yearling litter survival, σ_{L1} . The survival probabilities, $\sigma_i(t)$, are the probabilities of surviving from time t

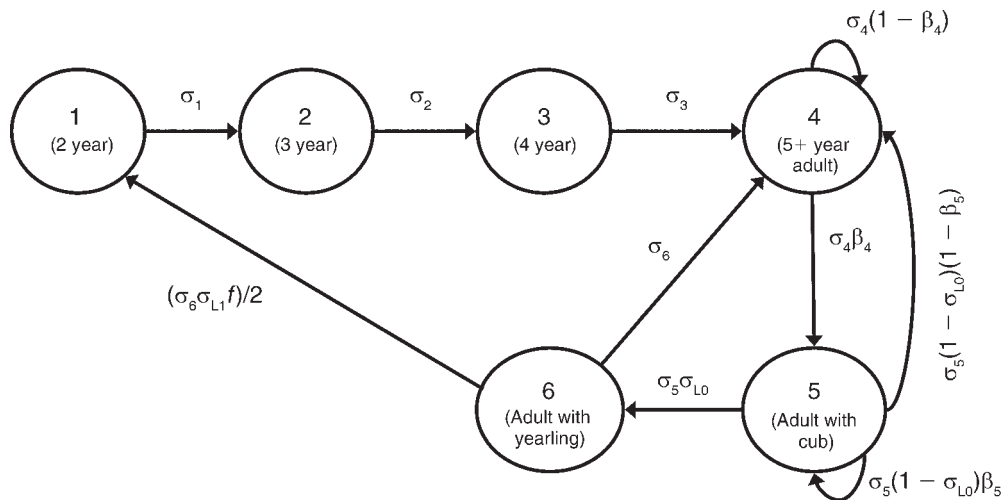


FIG. 2. Polar bear life cycle graph; σ_i is the probability an individual in stage i survives from time t to $t + 1$, σ_{L0} and σ_{L1} are the probabilities that at least one member of a cub-of-the-year or yearling litter, respectively, survives from time t to $t + 1$, f is the expected size of a yearling litter that survives to 2 years, and β_i is the conditional probability, given survival, of an individual in stage i breeding and thereby producing a cub-of-the-year litter with at least one member surviving until the following spring.

to $t + 1$ of an individual in stage i . The breeding probabilities are defined conditional on survival and are the probability of breeding, given survival, of an individual in stage i . Because we modeled stages 5 and 6 as mother–cub units, transitions from these two stages include litter survival probabilities. Litter survival is the probability that at least one member of a cub-of-the-year litter survives (σ_{L0}) or at least one member of a yearling litter survives (σ_{L1}).

Fertility in this model appears on the arc from stage 6 to stage 1. It depends on three quantities: survival of the mother (σ_6), survival of at least one member of a yearling litter (σ_{L1}), and the average number of 2-year-olds in a surviving yearling litter (f). Details of these calculations are given in Appendix B. The sex ratio of surviving offspring is assumed to be 1:1.

Demography and the sea ice environment

The southern Beaufort Sea is covered with annual sea ice from October through June, and partially or completely ice free from July through September when the sea ice retreats northward into the Arctic basin (Comiso 2006, Richter-Menge et al. 2006). To quantify sea ice availability to polar bears, Regehr et al. (2007, 2009) developed an index, $\text{Ice}(t)$, that measures the amount of time in year t during which polar bears are confronted with a lack of ice in their preferred habitat. We defined $\text{Ice}(t)$ as the number of days during year t in which the mean ice concentration was less than a threshold of 50%. Previous studies suggest that polar bears abandon sea ice below this threshold (Stirling et al. 1999, Durner et al. 2004). Because polar bears strongly prefer to forage over the continental shelf, $\text{Ice}(t)$ was calculated for waters on the continental shelf less than 300m in depth (see Regehr et al. 2009 for details). The index $\text{Ice}(t)$ has been referred to as “ice-free days”

(Regehr et al. 2007, 2009), and we will be consistent with this, but a more accurate description might be “low-ice days.” Note, however that increases in $\text{ice}(t)$ are decreases in the amount of sea ice available to polar bears, and vice-versa.

Parameter estimates

Our models are based on parameter estimates obtained from a multistate mark–recapture analysis (Regehr et al. 2009). That analysis evaluated a set of candidate statistical models for the vital rates, based on the life cycle structure. Those models were defined by constraining some or all survival or breeding probabilities to be equal across stages, and by specifying possible forms of temporal variation [time-invariant rates, time-varying rates, and rates dependent on sea ice conditions as measured by $\text{Ice}(t)$]. The results were model-averaged estimates (AIC-weighted) obtained using multi-model inference (Burnham and Anderson 2002, Anderson 2007). See Regehr et al. (2009) for a complete description of the model sets and parameter estimation methods. As is usual for mark–recapture estimation, survival probabilities estimated using these methods cannot distinguish true mortality from permanent emigration.

Our parameter estimation procedure produced two model-averaged estimates to describe the effect of sea ice on polar bear vital rates. One set was obtained as an AIC-weighted average of all models, including those with parametric dependence of survival probabilities on the covariate $\text{Ice}(t)$. We refer to this as the parametric model set, and it is the most well-supported by the data. However, the results of any parametric model reflect, to some degree, the choice of a parametric function, and it would have been desirable to explore alternative functional forms. This was impossible because of the

short duration of the study. To examine the possible effects of the functional form used, we also analyzed a set of AIC-weighted estimates from which the models with parametric covariate dependence were excluded. We refer to this as the non-parametric model set. Comparison of projections from the parametric and non-parametric model sets provides a check on the influence of the particular functional dependence on $\text{Ice}(t)$ (Regehr et al. 2009).

We concluded that survival probabilities (σ_1 – σ_6 , and σ_{L0}) depended on both $\text{Ice}(t)$ and time, while breeding probabilities (β_4 , β_5) were time dependent, decreasing in 2004 and 2005 (Regehr et al. 2009), when the number of ice-free days was particularly high (Table 1).

Confidence intervals, standard errors, and sampling distributions were obtained using a parametric bootstrap procedure (details in Regehr et al. 2009). To generate a bootstrap sample, we first chose a model with probability proportional to its AIC weight. A vector of mark–recapture parameters was then drawn from a multivariate normal distribution with the estimated mean and covariance matrix. This procedure was repeated for a specified number of times (usually 10 000) to obtain the bootstrap sample set. The mark–recapture parameters were transformed as necessary, into demographic parameters, projection matrices, growth rates, and so on, as appropriate. Confidence intervals were calculated using the percentile method. The bootstrap sample contains both model uncertainty (determined by the AIC weights associated with the models) and parameter estimation uncertainty (determined by the covariance matrix of the estimates).

The only parameters not directly estimated from the mark–recapture analysis were the survival of yearling litters (σ_{L1}) and fertility (f). Given an estimate of σ_{L0} from the mark–recapture estimation and an independent estimate of the frequency of one-cub and two-cub litters, it is possible to estimate individual cub survival and subsequently yearling litter survival, individual yearling survival, and the average number of two-year olds in a surviving yearling litter, f . Details of these calculations are given in Appendix B.

DETERMINISTIC DEMOGRAPHY

Deterministic analysis

We used both the parametric and non-parametric model-averaged estimates to construct year-specific projection matrices, \mathbf{A}_t , for each year, 2001–2005. We calculated the long-term population growth rate under the conditions in year t as the dominant eigenvalue, λ_t , of \mathbf{A}_t . The stable stage distribution and reproductive value distribution were calculated as the right and left eigenvectors \mathbf{w} and \mathbf{v} , respectively, corresponding to λ . Life table response experiment (LTRE) methods were used to quantify the contributions of each of the vital rates to the differences in population growth rate among years (Caswell 1989, 2001). To do so, we collected the vital rates (survival, litter survival, breeding) into a

TABLE 1. Deterministic population growth rate λ_t , with 90% confidence intervals, standard error, proportion of bootstrap samples <1 , and number of ice-free days [$\text{Ice}(t)$].

Year (t)	λ_t	Lower CI	Upper CI	SE	Proportion < 1	$\text{Ice}(t)$ (days)
Time-invariant model						
all	0.997	0.755	1.053	0.105	0.57	
Parametric model set						
2001	1.059	0.083	1.093	0.269	0.24	90
2002	1.061	0.109	1.094	0.265	0.24	94
2003	1.036	0.476	1.107	0.207	0.41	119
2004	0.765	0.541	0.932	0.120	1.00	135
2005	0.799	0.577	0.959	0.122	0.99	134
Nonparametric model set						
2001	1.017	0.810	1.088	0.092	0.43	90
2002	1.022	0.836	1.088	0.084	0.40	94
2003	1.075	0.903	1.129	0.077	0.19	119
2004	0.801	0.549	1.000	0.135	0.95	135
2005	0.895	0.446	1.020	0.185	0.88	134

Notes: Results are shown for the parametric model set, including parametric dependence of vital rates on $\text{Ice}(t)$, and for the nonparametric model set, which permits time variation, but does not impose the parametric functional form.

parameter vector θ , and chose the year 2001 as a reference condition. The difference in λ between the reference year and year t is decomposed into

$$\lambda_t - \lambda_{2001} \approx \sum_i \left(\theta_i^{(t)} - \theta_i^{(2001)} \right) \frac{\partial \lambda}{\partial \theta_i} \quad (2)$$

where the sensitivity term is calculated at the mean of the vital rates for the reference year and year t . Each term in the summation is the contribution of one of the vital rates to the difference in λ between the reference year and year t . A parameter may make a small contribution if it does not differ much among years or if λ is not very sensitive to differences in that parameter.

To examine transient effects, we projected population growth for 45, 75, and 100 years, using Eq. 1 and an initial population structure obtained from estimates of the southern Beaufort Sea population from 2004 to 2006 (Regehr et al. 2006):

$$\mathbf{n}_0 = (0.106 \quad 0.068 \quad 0.106 \quad 0.461 \quad 0.151 \quad 0.108)^\top. \quad (3)$$

Deterministic results

Estimated population growth rates were greater than 1 under the conditions experienced in 2001–2003 and less than 1 under the conditions experienced in 2004–2005 (Table 1). Confidence intervals were wide, but only a small proportion of the bootstrap samples for years with more ice-free days (i.e., 2004 and 2005) projected positive population growth (for complete bootstrap distributions, see Appendix C, Fig. C2).

Including parametric dependence on sea ice makes survival higher at low values of Ice, and lower at high values of Ice, compared to the nonparametric model set

TABLE 2. Life table response experiment (LTRE) analysis for population growth rate (λ), measured relative to the year 2001 for the nonparametric model set.

Parameter	Contribution to the difference between λ_t and λ_{2001}				Proportional contribution			
	2002	2003	2004	2005	2002	2003	2004	2005
σ_1	0.000	0.002	-0.007	-0.003	0.03	0.04	0.03	0.03
σ_2	0.000	0.002	-0.007	-0.003	0.03	0.04	0.03	0.03
σ_3	0.000	0.002	-0.007	-0.003	0.03	0.04	0.03	0.03
σ_4	0.001	0.008	-0.091	-0.045	0.25	0.15	0.42	0.36
σ_5	0.001	0.007	-0.049	-0.017	0.12	0.12	0.23	0.14
σ_6	0.000	0.004	-0.018	-0.008	0.09	0.07	0.08	0.06
σ_{L0}	0.001	0.012	-0.021	-0.013	0.21	0.22	0.10	0.10
β_4	0.001	0.011	-0.006	-0.025	0.15	0.19	0.03	0.20
β_5	0.000	0.002	-0.001	-0.001	0.02	0.03	0.00	0.01
f	0.000	0.006	-0.003	-0.002	0.06	0.10	0.01	0.02
σ_{L1}	0.000	0.002	-0.007	-0.003	0.03	0.03	0.03	0.03

Note: Values are expressed as contributions to the difference between λ_t and λ_{2001} and as a proportion of the total, where σ_i is the probability that an individual in stage i survives from time t to $t + 1$, σ_{L0} and σ_{L1} are the probabilities that at least one member of a cub-of-the-year or yearling litter, respectively, survives from time t to $t + 1$, f is the expected size of a yearling litter that survives to 2 years, and β_i is the conditional probability, given survival, of an individual in stage i breeding and thereby producing a cub-of-the-year litter with at least one member surviving until the following spring.

(Regehr et al. 2009). This amplifies the effect of reduced sea ice on survival, and carries over to the effect of Ice on population growth rates (Table 1). In our stochastic models, in which the severity of the impacts of reduced sea ice play a critical role, we will focus primarily on the results from the nonparametric model set.

The LTRE results (Table 2) show that the decline in λ during the low sea ice years (2004 and 2005) was primarily due to reduced survival of adult females (σ_4 , σ_5 , and σ_6), and secondarily to reduced breeding probability (β_4). Thus, the estimated reductions in survival and breeding in years with more ice-free days translated into dramatic reductions in population growth rate.

Fig. 3 shows λ as a function of $\text{Ice}(t)$, based on the AIC model-weighted parameter estimates, and the time-specific λ_t values from the nonparametric weighted model. The two agree well; population growth rate is relatively insensitive to sea ice for $\text{Ice}(t) < 127$ days, but longer ice-free seasons lead to a steep decline in λ (Fig. 3). Of course, extrapolation of the response of λ beyond the observed range depends entirely on the logistic parametric form assumed for the covariate dependence, and is unreliable. None of our analyses used such extrapolation.

Transient projections achieved exponential growth quickly, because the observed population vector (Eq. 3) is close to the stable stage distribution. Because these models are linear, population size at time t in the future relative to initial population size can be interpreted in terms of the proportional increase or decrease in population size. To display the transient dynamics and

their uncertainty, we use area plots (Fig. 4 and later). These plots show the proportion of simulations at any time falling in a set of categories from drastic population decline (relative size < 0.001) to large increases (relative size > 2). The proportion of simulations can be interpreted as the probability of outcomes, over the space defined by model uncertainty, parameter uncertainty, and, in our stochastic analyses, uncertainty about future environmental conditions.

STOCHASTIC DEMOGRAPHY

The deterministic growth rate for a given year describes the consequences of maintaining those conditions permanently. To construct a stochastic model that accounts for variation in conditions, we require a stochastic model for the sea ice environment. To this end, we classified sea ice conditions as “good” or “poor,” depending on whether they would lead to a value of λ greater or less than one. This corresponds to a threshold value of $\text{Ice} \approx 127$ days. Consider an environment in which good and poor years occur independently, with probability q of a poor year and $1 - q$ of a good year. In a poor year, the projection matrix is selected randomly from the matrices for 2004 and 2005; in a good year, the projection matrix is selected randomly from the matrices for years 2001–2003. The population grows according to Eq. 1 with

$$A_t = \begin{cases} A^{(2001)} & \text{with probability } (1 - q)/3 \\ A^{(2002)} & \text{with probability } (1 - q)/3 \\ A^{(2003)} & \text{with probability } (1 - q)/3 \\ A^{(2004)} & \text{with probability } q/2 \\ A^{(2005)} & \text{with probability } q/2. \end{cases} \quad (4)$$

This algorithm treats the variability within the good years, and within the poor years, as crude estimates of the variation in the vital rates within these categories

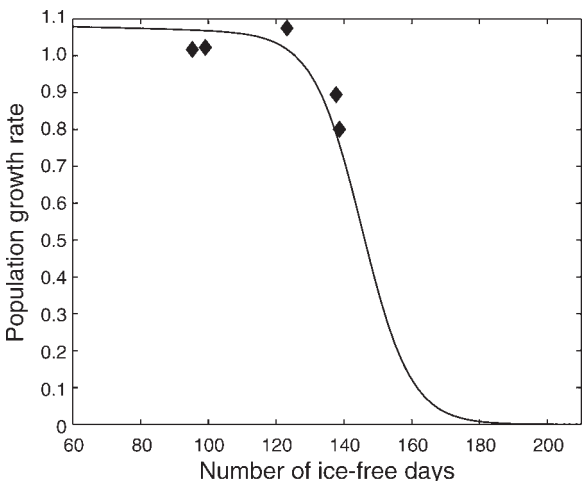


FIG. 3. Deterministic population growth rate, λ , as a function of the number of ice-free days, $\text{Ice}(t)$. Diamonds are deterministic population growth rates for 2001–2005 parameter estimates from the nonparametric model set.

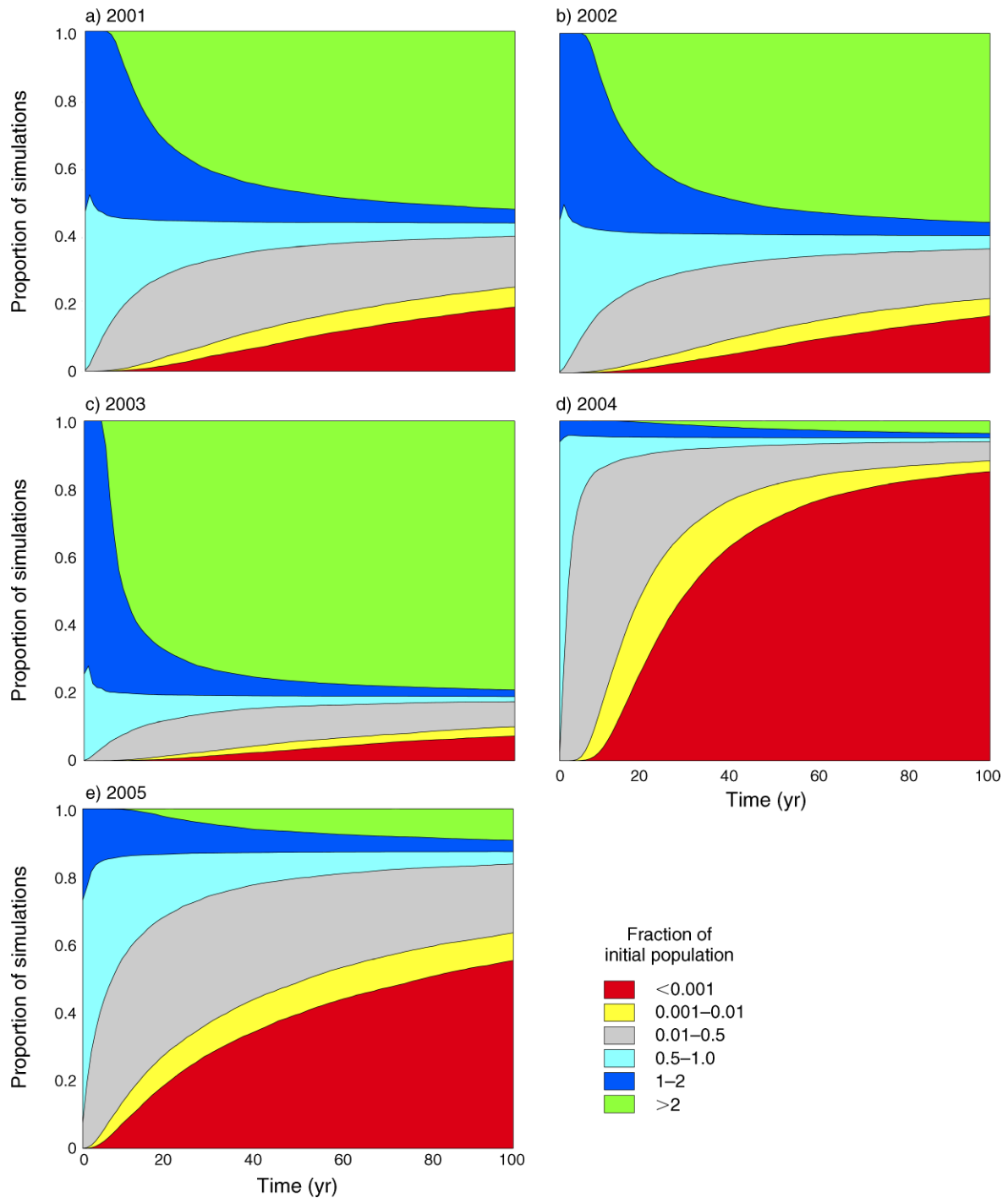


FIG. 4. Uncertainty analysis of transient deterministic projections. The population is projected forward for 100 years using the vital rates estimated for the specified year in the parametric model set. Area plots show the proportion of 10 000 simulations in which the projected population size increased or declined to the specified fraction of the initial population. Simulations were sampled from the bootstrap distribution of parameter values.

(see Caswell and Kaye 2001 for a similar approach in a fire model).

This stochastic model abstracts a continuous environmental factor into a finite set of discrete environ-

mental states. Such models have been used frequently, as in studies of fire (Silva et al. 1991, Caswell and Kaye 2001) and hurricanes (Pascarella and Horvitz 1998). A discrete environment model sacrifices some detail, but in

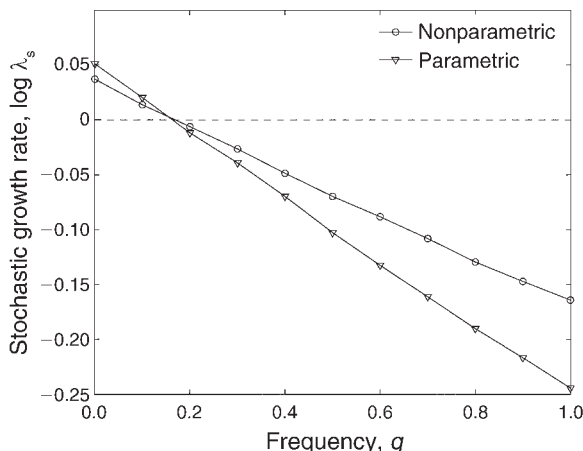


FIG. 5. The estimated stochastic growth rate, $\log \lambda_s$, as a function of the frequency q of years with poor ice conditions: $\log \lambda_s > 0$ indicates positive population growth; $\log \lambda_s < 0$ indicates negative population growth.

our case it avoids errors that would result from extrapolating the response of the vital rates to Ice beyond the observed range of Ice. Instead, our construction assumes that conditions at any value of $\text{Ice} > 127$ days are no worse than those observed in 2004–2005, and thus our model provides a lower bound on the effects of future climate change.

Stochastic analysis

The stochastic population growth rate is

$$\log \lambda_s = \lim_{T \rightarrow \infty} \frac{1}{T} \log \|\mathbf{A}_{T-1} \cdots \mathbf{A}_0 \mathbf{n}_0\| \quad (5)$$

where $\|\cdot\|$ is the 1-norm and \mathbf{n}_0 is an arbitrary initial population vector (e.g., Tuljapurkar 1990). We estimated $\log \lambda_s$ by Monte Carlo simulation with $T = 10,000$. To evaluate short-term transient population responses, we generated stochastic projections for 100 years, using the initial population in Eq. 3. To evaluate the effects of parameter uncertainty on stochastic growth, we repeated the calculations using models generated by sampling from the parametric bootstrap distribution of the vital rates. Both the long-term growth rates and the short-term projections include sampling uncertainty, model uncertainty, and environmental stochasticity.

Stochastic results

The stochastic growth rate declines nearly linearly as the frequency of poor years increases (Fig. 5). There exists a critical frequency of poor years ($q \approx 0.165$ for the parametric model set; $q \approx 0.17$ for the nonparametric model set) above which $\log \lambda_s < 0$ and the population will decline in the long run (Fig. 5). As expected, the results from the parametric model set respond to sea ice conditions more strongly than those from the nonparametric model set.

This critical frequency, about one poor ice year out of six, is exceeded by the frequency of poor ice years observed between 1979 (when satellite imagery began) and 2005 ($6/28 = 0.21$), by the frequency of poor years between 2001 and 2005 ($2/5 = 0.4$), and by the frequency predicted by IPCC climate models between now and the end of the century (Fig. 6).

Uncertainty plots of stochastic transient projections are shown in Fig. 7. At the $t = 45$ year time horizon, the probability of a major decline (to less than 1% of current size) increases from 0.17 to 0.82 as the frequency of a poor ice year increases from $q = 0.1$ to $q = 0.8$. The situation at $t = 100$ years is more dire; when $q = 0.1$ the probability of major decline is 0.24, increasing to 0.96 when $q = 0.8$.

DEMOGRAPHIC PROJECTIONS UNDER CLIMATE CHANGE FORECASTS

Models and analysis

The stochastic model (Eq. 4) describes stochastic population growth in a stationary environment characterized by a specified frequency of poor ice years. The Arctic environment is not stationary, however, so we now connect that model to forecasts of future sea ice conditions in response to climate change. Forecasts were obtained from each of a set of 10 IPCC Fourth Assessment Report (Solomon et al. 2007) fully coupled GCMs. The list of models is given in Appendix A: Table A1. The 10 GCMs were selected on the basis of the agreement of their 20th-century simulations with observed sea ice extent from 1953 to 1995 (see DeWeaver 2007 for details). All GCM forecasts were based on the “business as usual” greenhouse gas forcing scenario (SRES-A1B). Other forcing scenarios, some more optimistic and some more pessimistic, exist, but the A1B scenario is most appropriate for our purposes because it mimics recently observed emissions patterns and invokes neither societal changes that might increase emission rates nor conscious mitigation efforts that might reduce them.

Predictions of sea ice extent were obtained from the GCM output for an area including the southern Beaufort Sea and the surrounding divergent ice ecoregion (the Barents, Beaufort, Chukchi, Kara, and Laptev Seas; see Amstrup et al. 2008, Rigor and Wallace 2004). Sea ice trends in recent decades have followed a similar pattern throughout this region (Stroeve et al. 2007), justifying our application to the southern Beaufort Sea.

Obtaining forecasts of the frequency of poor ice years from the GCM output proceeded in three steps. First, we calculated $\text{Ice}(t)$ from the output, obtaining the number of “ice-free” months in each year from 2005 to 2100. These were transformed to ice-free days by multiplying by 30. To standardize the starting points, we additively adjusted the output of each GCM so that $\text{Ice}(2005) = 114.4$ days, the mean of $\text{Ice}(t)$ during 2000–

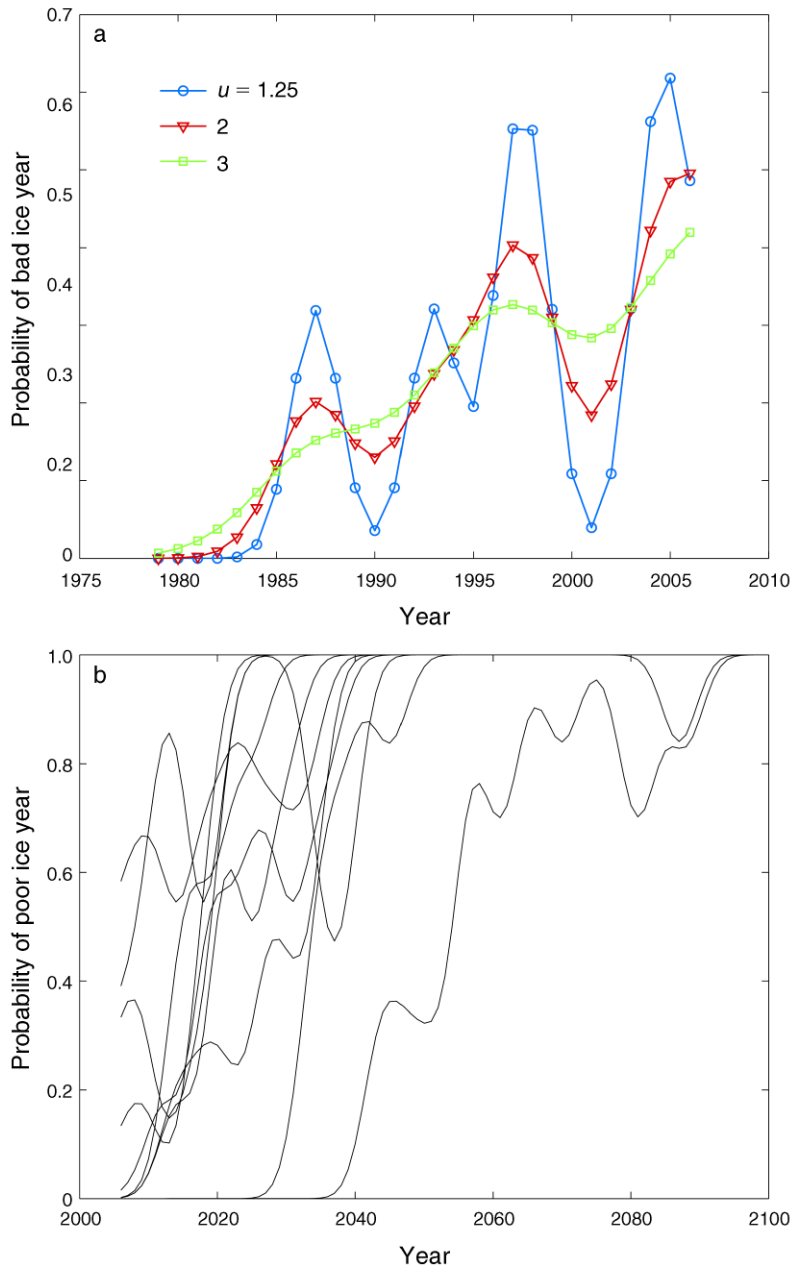


FIG. 6. (a) Frequency of poor ice conditions from 1979 to 2006, smoothed with a Gaussian kernel smoother with standard deviation $u = 1.5, 2,$ and 3 (see Copas 1983). Data are from Fig. 3 in Regehr et al. (2007). (b) The projected probability of a poor ice year, from 2005 to 2100, from 10 general circulation model (GCM) climate models. Kernel standard deviation = 2.5.

2005. Second, we transformed the value of $\text{Ice}(t)$ to a binary environmental state, classifying year t as good if $\text{Ice}(t) > 127$ days, or poor if $\text{Ice}(t) < 127$ days. The third step was to extract trends in the frequency of poor years from the sequence of binary outcomes. Such calculations always require some smoothing; we applied a Gaussian kernel smoother as described by Copas (1983; see Smith et al. 2005 for an ecological application similar to this one). The kernel standard deviation (2.5 years) was

chosen, as suggested by Copas (1983), as a subjective compromise between smoothing and variation.

Each of the 10 GCMs thus produced a time series of forecast values of $q(t)$ from 2005 to 2100. We used these frequencies to project the polar bear population, with $\mathbf{n}(0)$ given by Eq. 3 and \mathbf{A}_t chosen randomly at each time step with probabilities given by Eq. 4 and the forecast value of $q(t)$. To evaluate the effects of uncertainty, we repeated the calculations with each GCM using 1000

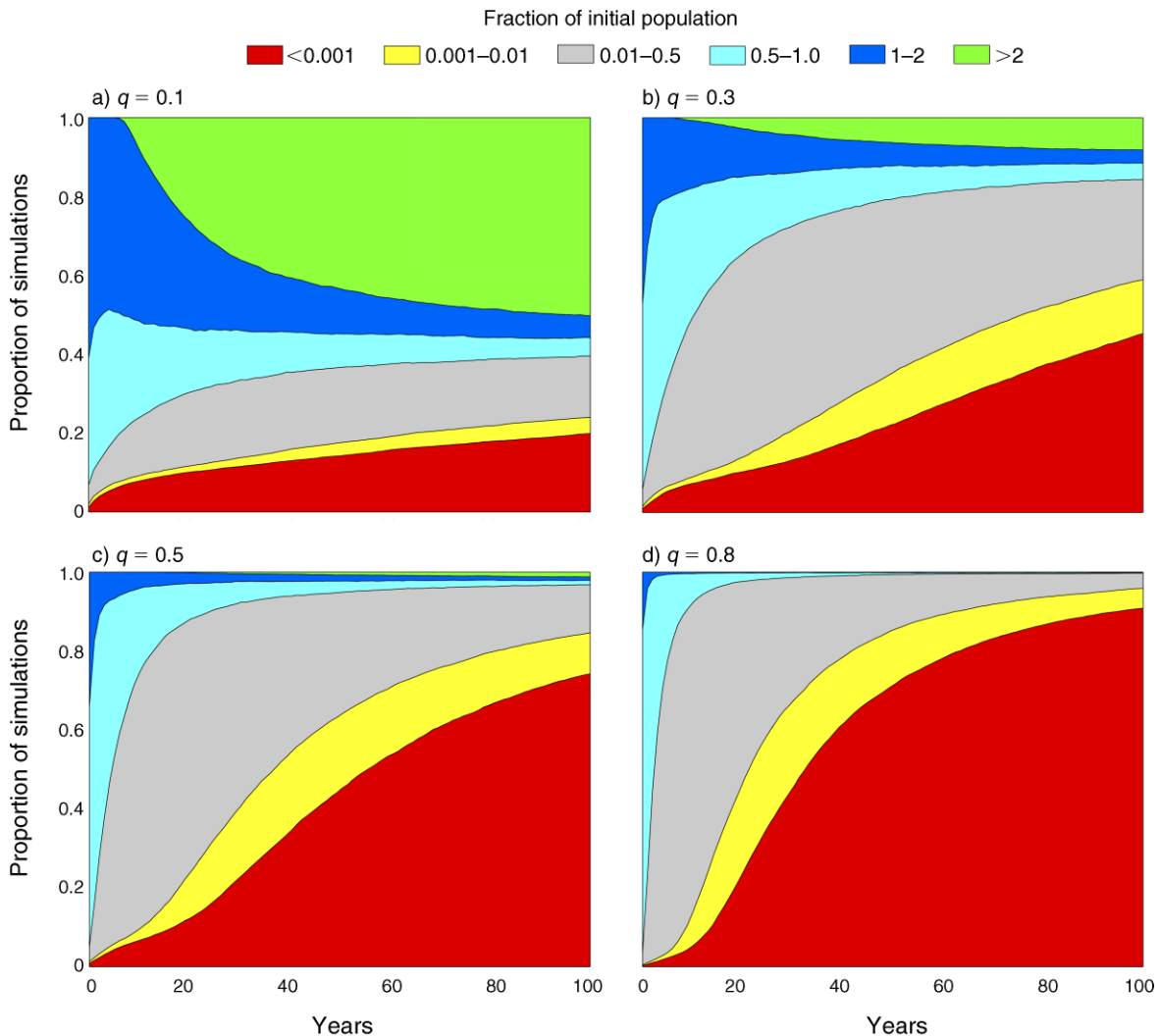


FIG. 7. Uncertainty analysis of transient stochastic projections. Area plots show the proportion of 10 000 simulations in which projected population size increased or declined to the specified fraction of the initial population, given the probability q of a poor ice year and vital rates from the parametric model set. Simulations were sampled from the bootstrap distribution of parameter values.

bootstrapped parameter estimates, for a total of 10 000 calculations. The resulting variability includes uncertainty due to statistical models, parameter estimation, and variation among the GCMs.

Climate projection results

The estimates of $q(t)$ from the output of the 10 GCMs differ in detail, but all predict an increase in the frequency of poor Ice years over the next century (Fig. 6). The frequency of such years reaches 1 by the year 2100 (indeed, this level is reached by all but one of the climate models by the year 2055). Because the environment forecast by the GCMs is not stationary (both the mean and the variance change over time), it is impossible to calculate asymptotic stochastic growth rates from this model. Transient projections, however, are shown in Fig. 8, for both model sets. The projections by the year

2100 are overwhelmingly negative; the probability of a decline of 50% or more is 0.92 (nonparametric model set) or 0.99 (parametric model set). The probability of decline of 99% or more is 0.80 (nonparametric) or 0.94 (parametric). There is some probability of short-term increase, over the next 20–40 years, generated largely by the differences among climate models in how soon the frequency of poor ice years begins to increase (Fig. 6). Since that frequency has, in fact, already been increasing since 1980 (Fig. 6), these short-term increases are unlikely to be realized.

DISCUSSION

Linking climate models and demography

The effect of climate change on population growth and viability is a pressing ecological problem. At the most basic level it proceeds by measuring the effect of

climate-related variables (e.g., temperature) on an ecological process (e.g., survival). If the process is related to population growth and the direction of environmental change can be predicted, then a qualitative prediction of the effect of climate change can be obtained.

To go beyond such a qualitative prediction requires information on the sensitivity of the entire life cycle (or as much of it as possible) to the environment, and a quantitative prediction of future environmental changes. In this paper, we obtained such a quantitative prediction by a novel approach to linking environment-dependent demographic models to the output of GCMs. This approach, which is applicable to other species, has three steps. First, a life cycle model was parameterized as a function of the environment, in this case, an index of sea ice extent. Second, a stochastic demographic model was developed to compute population growth as a function of environmental conditions and their fluctuations. Third, a forecast of environmental changes was extracted from GCM output. In our case, that forecast consists of a time series of the frequency of poor ice conditions.

This approach can be applied to other species and situations (e.g., Jenouvrier et al. 2009). The discretization of the environmental states, as we did here, avoids the need to extrapolate continuous relationships between the environment and the vital rates beyond the range of observed conditions. This makes our predictions of polar bear responses conservative, because no matter how large $I_{ce}(t)$ becomes, the vital rates in the model will be no worse than those observed during the poor ice years of the study. However, given sufficiently detailed information on both climate and the response of vital rates, the analysis could use a continuous environment model (see Jenouvrier et al. 2009 for a comparison of discrete and continuous approaches).

Uncertainties

Management decisions must often be made in the face of uncertainty, because information is limited and environments are variable. Therefore, where possible, analyses of climate effects should quantify the uncertainty of the results on which management decisions are based. This was particularly important in the listing decision for the polar bear, and our analyses purposely included several different kinds of uncertainty.

Burnham and Anderson (2002) and Anderson (2007) have emphasized the importance of including model selection uncertainty along with estimation uncertainty. Our parametric bootstrap distributions include both types of uncertainty. We also recognize the uncertainty involved in parametric specification of the ice-dependence of the vital rates, and therefore analyzed both nonparametric and parametric model sets. Although projections based on the nonparametric model set, excluding parametric ice dependence, are conservative in the sense of yielding a weaker response to sea ice conditions, it is important to remember that the

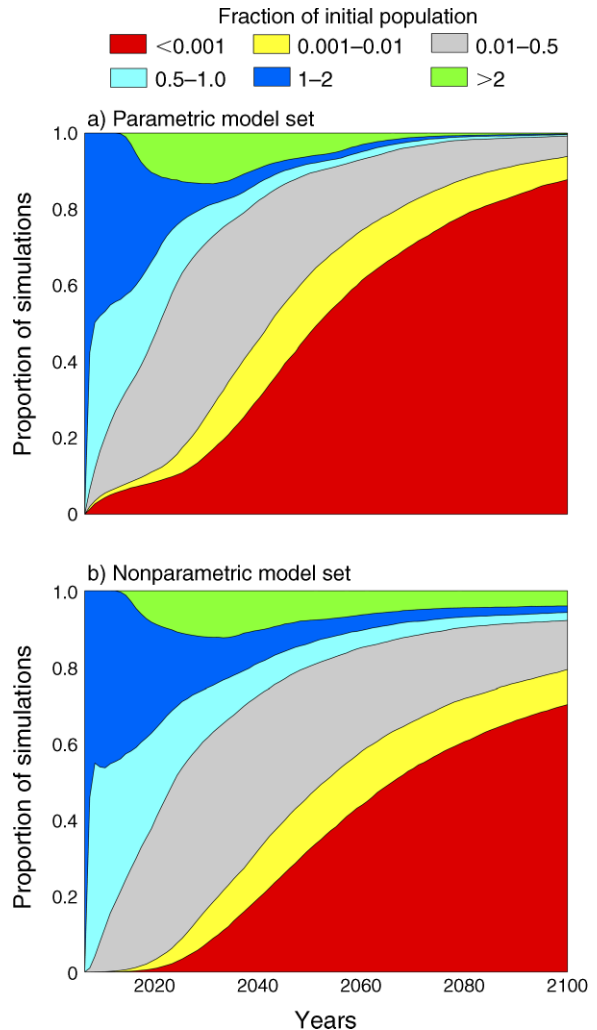


FIG. 8. Stochastic simulations of population growth under conditions predicted by 10 IPCC climate models. Area plots show the proportion of 10 000 simulations in which projected population size after t years increased or declined to a specified fraction of initial population size for (a) the parametric model set and (b) the nonparametric model set. Simulations were obtained as samples of 1000 from the bootstrap distribution of parameter values, for each climate model.

parametric model set is the one most well-supported by the data. Both analyses lead to the same conclusions (Fig. 3).

In addition, we used a series of deterministic and stochastic population models to assess potential population response to changing ice conditions. The consistency of results across this series of models strengthens our inference. Such a sequence is the only way to quantitatively assess the effects of different types of uncertainty in assessment of population status and response to environmental conditions.

Two aspects of the estimation procedures are worth discussing because they might have artificially reduced survival probabilities. One is harvest, which is not



PLATE 1. A subadult polar bear contemplates how to negotiate an area of melting sea ice. Polar bears are classified as marine mammals, but they are not aquatic. They feed upon ringed and bearded seals and other aquatic mammals that they catch from the sea-ice surface. They travel mainly by walking on the sea ice rather than swimming. Rising global temperatures mean that polar bears increasingly are exposed to marginal ice or open water where historically there were stable sea-ice habitats. The future population impacts of more prolonged periods, during which suitable sea ice is unavailable, are projected to be severe. Photo © 2009 Daniel J. Cox/NaturalExposures.com.

incorporated in our projections. Polar bears in the southern Beaufort Sea are subject to regulated hunts by native user groups in the United States and Canada (Brower et al. 2002). Hunters are discouraged from taking females with dependent cubs but subadult females and adult females without cubs are currently subject to harvest at a rate of ≈ 0.019 (Regehr et al. 2007). Although the impact of this harvest is included in the survival estimates for these stages; this level of harvest has a negligible effect on population growth rate (Hunter et al. 2007).

The second issue is emigration. Nonrandom temporary emigration can lead to survival estimates that are negatively biased at the end of a study. However, Regehr et al. (2009) investigated this, and found no evidence of non-random temporary emigration. Although the power of the analysis was limited due to the short study duration, available data indicated that temporary emigration did not create an important bias of survival rates used in this study. Permanent emigration cannot be distinguished from mortality. However, radio telemetry studies, which began in the Beaufort Sea in 1981, have confirmed that polar bears maintain a high degree of fidelity to this geographic region. Although individual animal utilization distributions are very large and variable, over multi-year periods they do constitute “home ranges” (Amstrup et al. 2000). The permanent migration of collared animals beyond the Beaufort Sea region has been so rare that the description of the

movement of the one bear that did permanently emigrate was deemed worthy of publication (Durner and Amstrup 1995).

Polar bear population status

Summer sea ice in the Arctic is expected to continue to decline (e.g., IPCC 2007, Overland and Wang 2007, Stroeve et al. 2007). Our analyses demonstrate that this decline poses a serious threat to the continued persistence of the southern Beaufort Sea population of polar bears. The current southern Beaufort Sea population numbers about 1500 individuals (Regehr et al. 2006), so a decline to 1% of current size would almost certainly imply extinction. The probability of this outcome is estimated at 0.80–0.94 by the year 2100, which is certainly a serious risk.

The ice-free period in the southern Beaufort Sea increased by approximately 50% between 2001–2003 and 2004–2005. At the same time, survival and breeding probabilities declined (Regehr et al. 2007). The vital rates estimated in years with low values of $\text{Ice}(t)$ led to positive population growth, but when $\text{Ice}(t)$ exceeds about 127 days, the population growth rate becomes negative due to reductions in adult survival and breeding probabilities. Asymptotic and short-term transient projections showed the same results.

Our stochastic analysis found that a frequency of poor ice years greater than $q \approx 0.17$ produces a negative stochastic growth rate. This critical frequency is less

than the observed frequency of poor years from 1979 to 2005, the available record from satellite imagery. The observed frequency of poor ice years, $q = 0.2$, from 1979 to 2005 (the available satellite record) exceeds this threshold, and would lead to a stochastic growth rate of $\log \lambda_s = -0.012$ (parametric model) or -0.006 (non-parametric model).

Arctic sea ice extent at the end of the summer of 2005 was the lowest ever observed. This record was broken in 2007, and approached in 2008. If thinning multiyear ice, more extensive open water and albedo effects create positive feedback loops leading to further reductions (Maslanik et al. 2007), the fate of polar bears in other locations, even where populations have been stable (e.g., the northern Beaufort Sea) will also be in doubt. Recent shipboard surveys in the southern Beaufort Sea (Barber et al. 2009) found summer sea ice there to be even thinner and more broken than shown in satellite images.

Comparisons of these growth rates estimated here with trajectories of population size are hampered by the lack of reliable population size estimates. The claim, commonly repeated in the press, that worldwide polar bear populations have increased fourfold since the 1960s has no basis in the scientific literature (Dykstra 2008). Some increases in polar bear populations occurred in the 1970s as harvesting was reduced, but there is no evidence that these increases continued, and such recoveries, where they occurred, are irrelevant to the effects of recent changes in the availability of sea ice. In the southern Beaufort Sea, Amstrup et al. (1986) reported a crude estimate of population size of $N \approx 1800$ bears in the mid-1980s. Regehr et al. (2006) estimated $N \approx 1500$ bears in 2006. Amstrup et al. (2001) suggested the population may have remained constant or even increased between the 1980s and the late 1990s. However, if the difference between 1800 bears and 1500 bears represents a real decline, and if that decline occurred over 15 years, it would represent an average annual growth rate of -0.012 . Over 20 years, such a decline would imply an average annual growth rate of -0.009 . This further suggests that our estimates of stochastic growth rate are reasonable. This comparison with our calculated growth rate is very rough, because of the different sources of historical data and the high degree of uncertainty around these population estimates. Nevertheless, the comparison supports the model results.

The mechanisms linking sea ice to survival and reproduction of polar bears are not known in detail. Reduced prey availability no doubt plays a role (Stirling and Smith 2004), because polar bears are dependent upon sea ice for capturing prey (Amstrup 2003) and their preferred foraging area is the water over the continental shelf. In addition, reduced sea ice extent may force polar bears to swim longer distances, increasing their risk of drowning or starvation (Monnett and Gleason 2006). The thinner ice that reforms after large summer ice retreats also may be less suitable for polar

bear foraging (Stirling et al. 2008). Reduced sea ice will undoubtedly also affect other ice-dependent species (see, e.g., Gaston et al. 2005) and many food web links may be involved in these effects (Huntington and Moore 2008, Moline et al. 2008).

We have shown that global warming is likely to have profoundly negative effects on future growth rates of polar bear populations. A warmer world will have less sea ice and hence less polar bear habitat. Geographical variation in the nature of sea ice and in predictions of the retreat of sea ice habitat (Durner et al. 2009) suggests that polar bears in different parts of their current range will be affected at different rates. Nonetheless, our analyses, which incorporated sea ice and other uncertainties, projected that by mid century, the effects of global warming on polar bears will be severe. If current GCM outcomes are correct, there is a high probability that the Beaufort Sea population of polar bears will disappear by the end of the century. Because all polar bears are dependent on sea ice for securing their prey, it is reasonable to expect that the effects of global warming on polar bears of the southern Beaufort Sea will ultimately extend to polar bears throughout their range. This and other related findings provided the primary motivation for listing polar bears, in May of 2008, as a threatened species under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 2008).

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APPENDIX A

Projection matrices (*Ecological Archives* E091-204-A1).

APPENDIX B

Calculation of fertility (*Ecological Archives* E091-204-A2).

APPENDIX C

IPCC models and bootstrap sampling results (*Ecological Archives* E091-204-A3).