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USGS Science Strategy to Support U.S. Fish and Wildlife Service Polar Bear Listing Decision

Polar Bears in the Southern Beaufort Sea I: Survival and Breeding in Relation to Sea Ice Conditions, 2001-2006

By Eric V. Regehr[1], Christine M. Hunter[2], Hal Caswell[3], Steven C. Amstrup[1], and Ian Stirling[4]

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Abbreviations, Acronyms, and Symbols

Abbreviations, Acronyms, and Symbols	Meaning
AIC	Akaike Information Criterion
AS	Arnason-Schwarz multistate models
COY	Cub-of-the-year
CWS	Canadian Wildlife Service
GOF	Goodness-of-fit
IUCN	International Union for the Conservation of Nature and Natural Resources
JMV	JollyMove multistate model
RSF	Resource Selection Function
SB	Southern Beaufort Sea
USFWS	U.S. Fish and Wildlife Service
USGS	U.S. Geological Survey

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Abstract

Climatic warming and associated declines in Arctic sea ice have raised concerns about the long-term conservation of polar bears (*Ursus maritimus*). We used multistate capture-recapture models that classified individuals by sex, age, and reproductive category to estimate vital rates (survival and breeding probabilities) for polar bears in the southern Beaufort Sea (SB), using data collected from 2001-2006. We quantified the availability of sea ice using remote sensing data and evaluated polar bear vital rates in relation to the duration of the ice-free period over the continental shelf in the SB region. We estimated model-averaged vital rates for three sets of models: time-invariant models, models with vital rates that depended upon sea ice, and models with vital rates that varied with time but did not depend on sea ice. Sampling and model selection uncertainty were quantified using parametric bootstrap procedures. The most supported models included dependence of yearly survival rates on the duration of the ice-free period, and included time variation in breeding probabilities. In 2001 and 2002, the ice-free period was relatively short (mean 92 days) and survival of adult female polar bears was high (approximately 0.99, 90%CI = 0.10-1.0). In 2004 and 2005, the ice-free period was long (mean 135 days) and survival of adult female polar bears was lower (approximately 0.77, 90%CI = 0.53-0.94). Breeding and cub-of-the-year litter survival also declined from high rates in early years to lower rates in latter years of the study. Although the precision of estimated vital rates was low, subsequent analyses (Hunter et al. 2007) indicated that the

declines in vital rates associated with longer ice-free periods have ramifications for the probability of persistence of the SB population. Our results are relevant to over one-third of the world's polar bears, which inhabit regions of the polar basin with sea ice dynamics similar to the SB and have experienced more severe declines in the extent and duration of sea ice than the SB. This study was short in duration relative to the life history of polar bears. Therefore, continued monitoring will be necessary to increase our confidence in the relationships between declining sea ice and polar bear vital rates, to elucidate the ecological mechanisms underlying these relationships, and to understand how polar bears will respond to the continued declines in the sea ice that are projected for many parts of the Arctic.

Introduction

The U.S. Fish and Wildlife Service (USFWS) proposed listing polar bears as a threatened species under the Endangered Species Act in January 2007 (USFWS 2007). To help inform their final decision, they requested that the U.S. Geological Survey (USGS) conduct additional analyses of existing data for polar bears and their sea ice habitat. Part of this effort involved demographic analyses to better understand the status of polar bears in the southern Beaufort Sea (SB). Between February and August 2007, USGS and collaborators developed nine reports targeting specific questions considered especially informative to the final decision. This is one of the nine reports. The SB is one of 19 local management units or subpopulations for polar

bears identified by the International Union for the Conservation of Nature and Natural Resources (IUCN) Polar Bear Specialist Group (Aars et al. 2006). In this report, we refer to polar bears that occur in the IUCN management units as populations. Demographic analyses for the SB population were conducted in two parts. The first part, presented here, estimates SB polar bear vital rates (survival and breeding probabilities) and investigates the relationship between vital rates and sea ice. The second part, presented in Hunter et al. (2007), evaluates population growth rate and projects future population trends in relation to environmental variability.

Recent declines in the extent, duration, and thickness of Arctic sea ice have raised concerns about the long-term conservation of polar bears (Stirling and Derocher 1993, Derocher et al. 2004, Stirling and Parkinson 2006). Polar bears depend on sea ice for nearly every aspect of their life history, particularly access to their primary prey, ringed seals (*Phoca hispida*) and bearded seals (*Erignathus barbatus*). Sea ice characteristics and dynamics differ among broad regions of the Arctic, resulting in regional differences in polar bear ecology. In their forecast of the future status of polar bears throughout their range, Amstrup et al. (2007) recognized four ecoregions for polar bears based upon differences in historic and projected sea ice conditions. The SB population occurs in the "divergent ice ecoregion" of the polar basin, where polar bears historically have remained on multiyear sea ice as it retreats toward the center of the polar basin during the summer (Amstrup 2003, Amstrup et al. 2007). Rates of decline in sea ice extent in this ecoregion have been among the highest in the Arctic (Meier et al. 2007). Declining ice extent and degrading ice character in the SB have been associated with a shift toward more land-based denning and less denning in regions with higher rates of ice degradation (Fischbach et al. 2007), declines in cub survival (Regehr et al. 2006), and observations of drowned, emaciated, and

cannibalized polar bears (Amstrup et al. 2006, Monnett and Gleason 2006, Stirling et al. 2008). Changes in the sea ice have not yet been associated with changes in the size of the SB polar bear population (Regehr et al. 2006).

Long-term demographic data are available for only one other polar bear population in the polar basin. The northern Beaufort Sea polar bear population, which occurs in the "ice convergent ecoregion", has not experienced sea ice changes similar to the SB and appears to have remained stable since the 1970s (Stirling et al. 2007). Declining sea ice in the southerly "seasonal ice ecoregion", where the sea ice melts completely each year and forces polar bears to spend several months on shore, has been associated with reduced body condition, reproduction, survival, and abundance for the western Hudson Bay population (Stirling et al. 1999, Stirling and Parkinson 2006, Regehr et al. 2007). The adjacent southern Hudson Bay population has experienced less severe changes in the sea ice and, although there is evidence for declines in polar bear body condition (Obbard et al. 2006), a recent study found equivocal evidence for declines in survival and no evidence for a decline in the size of the population since the 1980s (Obbard et al. 2007).

Quantifying how changes in the extent, duration, and character of sea ice may affect polar bears depends on estimating vital rates, understanding the relationships between vital rates and sea ice, and understanding how vital rates affect demography. Multistate capture-recapture models allow investigation of the relationship between vital rates and environmental conditions (e.g., Arnason 1973, Nichols et al. 1992, Fujiwara and Caswell 2002). They can be tailored to a species' life history allowing the estimation of rates associated with important states, e.g., survival of females with cubs, and transitions among states, e.g., breeding probabilities. Multistate models have been used to examine survival, recruitment, breeding, dispersal, and costs of reproduction in a variety of taxa (e.g., Blums et

al. 2003, Reed et al. 2003, Cam et al. 2004, Beauplet et al. 2005, Crespin et al. 2006, Hadley et al. 2007). An important advantage of multistate models is that use of the life history structure provides a direct link between vital rate estimation and demographic modeling (Fujiwara and Caswell 2001, Caswell and Fujiwara 2004).

We applied multistate models to data collected on polar bears in the SB between 2001 and 2006, and estimated state-specific survival, breeding, and recapture probabilities. We quantified the extent and duration of sea ice in the SB region using remote sensing data and evaluated survival and breeding probabilities in relation to sea ice. We also used radiotelemetry data to determine whether the movement of polar bears in and out of the study area had the potential to affect survival estimates.

Methods

Study area and sampling design

The study area boundaries were coincident with the boundaries of the SB management unit (Aars et al. 2006), extending from west of Wainwright, Alaska (approx. 160°W) to east of Paulatuk, Northwest Territories, Canada (approx. 125°W; Figure 1, see also Amstrup et al. 1986). In the U.S. portion of the study area, the USGS captured polar bears between Barrow, Alaska, and the Canadian border from late March through early May of 2001-2006. In the Canadian portion of the study area, the Canadian Wildlife Service (CWS) captured polar bears in April and May of 2003-2006. We focused search efforts on areas of active sea ice (e.g., leads and floe edges) which are preferred by polar bears (Stirling et al. 1993, Durner et al. 2004, 2007), and within approximately 100 km of the coastline, the flight range of our capture helicopters. Each year, we attempted to maximize sample size and the geographic distribution of capture effort.

We captured all sighted polar bears older

than 1 year by injection with Telazol® (Warner-Lambert Co.) using projectile darts fired from a helicopter (Stirling et al. 1989). Cubs-of-the-year (COYs) were injected using hand-held syringes and yearlings were injected using projectile darts fired from the ground. Each polar bear was marked with a unique identification number using plastic ear tags and permanent tattoos on both sides of the inner surface of the upper lip. The age of independent polar bears was determined by extracting a vestigial premolar and counting the cementum annuli (Calvert and Ramsay 1998). Dependent young (COYs, yearlings, and some 2-year-olds) were visually aged based on body size and dentition.

We applied satellite radio collars (Telonics Inc., Mesa, AZ) to 84 adult females between 2001 and 2006, and attempted to recapture all females with active radio collars in subsequent years using VHF and satellite telemetry. Radio collars generally remained active for 2 to 3 years. We did not apply radio collars to subadults because their necks grow too rapidly, nor to adult males because their necks are larger in circumference than their heads. All capture and marking protocols were approved by independent animal care and welfare committees.

Model structure

Multistate capture-recapture models allow individuals to be categorized into states to account for differences in recapture, survival, or transition probabilities resulting from factors such as life cycle stage, geographic location, physiological condition, or behavior (Arnason 1972, 1973, Hestbeck et al. 1991, Nichols et al. 1992, Brownie et al. 1993, Schwarz et al. 1993, Fujiwara and Caswell 2002). We used multistate models to account for differences in recapture probability and vital rates (survival and breeding probabilities) between sex, age, and reproductive states (hereafter referred to as stages). The results provide a direct connection between vital rate estimation and demographic

modeling (Caswell and Fujiwara 2004).

Polar bear life cycle

We defined the structure of the multistate model based on a life cycle graph for polar bears in the SB region (Figure 2). Female polar bears in the SB are generally first available to mate in April–June of their fifth year. Implantation of the conceptus is delayed until September-October, just before pregnant females enter maternal dens (Derocher et al. 1992, Amstrup and Gardner 1994). Females give birth in December–January and nurse their COYs until they are large enough to leave the den in March–April. Cubs remain with their mothers for approximately 2.3 years until they are weaned as 2-year-olds in the spring of their second year. To represent this life cycle we distinguished 6 female and 4 male stages. Stages 1, 2, and 3 are subadult females of age 2, 3, and 4 years, respectively. To represent the 3-year reproductive cycle of females, we classified adult females into three stages: available to breed (single or accompanied by 2-year-olds; stage 4), accompanied by COYs (stage 5), and accompanied by yearlings (stage 6). Stages 7, 8, and 9 are subadult males of age 2, 3, and 4 years, respectively. Stage 10 is males 5 years or older. By modeling mother-litter units rather than individuals, we account for the dependent fates of mothers and their offspring. Dependent young (COYs and yearlings) were captured and given individual markings and their capture data were used to inform the reproductive stage of their mother. However, individuals are not explicitly included in the life cycle graph, or the multistate model, until capable of independent survival as 2-year-olds. This life cycle graph differs from a demographic life cycle (e.g., Caswell 2001, Hunter et al. 2007) in that it does not include the production of new individuals via reproduction, i.e., the production of 2-year-olds via the transitions from stage 6 to stages 1 and 7.

Transitions among stages, represented by arcs in the life cycle graph, depend on three types of parameters: survival, litter survival, and breeding probabilities. Transitions among stages 4, 5, and 6, which represent reproductive stages for adult females, depend on COY litter survival, breeding probabilities, and adult female survival. Transitions among all other stages depend only on survival. Apparent survival (hereafter survival), $\sigma_i(t)$, is the probability that an individual in stage i ($i = 1, 2, \ldots, 10$) in the spring of year t survives to the spring of year $t+1$. Losses include both mortality and permanent emigration. We use the symbol σ for survival, instead of φ, to maintain consistency with the demographic and multistate capture-recapture literature. The probability that at least one member of a litter of COYs survives from the spring of year t to the spring of year $t+1$ is $\sigma_{L0}(t)$. Breeding probability, $\beta_i(t)$ (for $i = 4, 5$), is the probability that a female in stage i produces a litter of COYs in year t, conditional on survival. Because sampling occurred in the spring, $\beta_i(t)$ represents the cumulative probability of a female giving birth to a litter of COYs and at least one member of the litter surviving from birth through den emergence. The breeding probability $\beta_5(t)$ is conditional on both the loss of the litter of COYs and survival of the mother. Thus, $\beta_5(t)$ implicitly includes the probability that a female loses her litter early enough in the spring to end lactational anestrous and re-mate before the end of the mating season.

The transition from stage 6 to 5 was biologically possible but did not occur in the data. Thus, the transition from stage 6 to stage 4 occurs with probability 1 if the female survives, because adult females with yearlings in the spring of year t were available to breed in year $t+1$ whether their yearlings died or were successfully weaned.

Associated with each stage is a recapture probability, $p_i(t)$, which is the probability that an animal in stage i is captured at time t given that it is alive. Recapture probabilities do not appear in the life cycle graph, but are estimated by

capture-recapture methods to remove the effects on parameter estimates of failure to capture living bears.

Modeling approach

The life cycle graph defines the structure of the model, but within that structure many different statistical models, embodying different hypotheses about the relationships among the parameters, are possible. These models are defined by constraints, which set various survival, breeding, or recapture probabilities to be equal, and by hypotheses about time variation and/or covariate dependence of the vital rates. We created a candidate set of such models based on biological considerations and study design, and then used model selection and model averaging to obtain the estimates most supported by the data.

Recapture constraint models

We considered three constraint models for recapture probability, based on a previous capture-recapture analysis of the SB data (Regehr et al. 2006). The first model set recapture probabilities equal for all stages. The second model included separate recapture probabilities for females (stages 1-6) and males (stages 7-10). We added this constraint model *a posteriori*, because of patterns that we observed in the data during initial model fitting, and because in the spring male polar bears move long distances in search of mates (Ramsey and Stirling 1986), which may increase the probability of field crews encountering their tracks in the snow. The third model included separate recapture probabilities for adult females with COYs (stage 5), equal recapture probabilities for all other female stages (stages 1-4, 6), and equal recapture probability for all male stages (stages 7-10). We considered this model because females with COYs may have selected for land-fast ice along the coastline to minimize encounters with other polar bears (Stirling et al. 1993), and we may have searched

this habitat less thoroughly than active sea ice areas farther from shore.

We included an individual covariate and a group covariate in all recapture models. The individual covariate *radio* indicated whether a polar bear wore a functional radio collar at a given sampling occasion. The group covariate *agency* indicated whether a polar bear was first captured in the U.S. or Canada. We included *agency* because polar bears in the SB region exhibit geographic fidelity (Amstrup et al. 2004), and capture effort, weather, and polar bear distribution differed between the U.S. and Canadian portions of the SB. All models included a separate recapture probability for Canadian agency bears in 2006, irrespective of time dependence in other recapture probabilities, because of known lower effort (related to weather conditions) and recapture rates in the Canadian region in 2006.

Survival constraint models

We defined 3 constraint models for female survival and 3 constraint models for male survival (Table 1). The simplest female model, F1, set survival equal for all stages. Model F2 assumed equal survival among subadults (stages 1-3) and equal survival among adults (stages 4-6), because higher survival rates for adults have been observed in previous studies (Derocher and Stirling 1992, 1996, Eberhardt 2002, Regehr et al. 2007). Model F3, assumed equal survival among subadults but allowed survival of females with COYs to differ from that of other adult females. This model was based on expected effects of the physiological stress of cub production and fasting experienced by females with COYs.

For males, model M1 set subadult male survival equal to subadult female survival, and adult male survival equal to adult female survival. Model M2 assumed equal survival for all male stages, but allowed male and female survival to differ. Model M3 assumed equal survival among subadult males and a separate survival for adult males, with no equality

constraint between males and females. Models M1 and M3 permitted higher survival for adults than subadults, and models M2 and M3 allowed female and male survival to differ because of sex-selective harvest (Brower et al. 2002) and the physiological stresses of reproduction.

There were nine possible combinations of female and male survival constraint models (Table 2). Depending on the combination, models could have between 1 and 5 stage-dependent survival parameters.

Breeding constraint models

No equality constraints were imposed on the breeding probabilities β_4 and β_5.

Sea ice covariate

Each year the SB region is covered with annual sea ice from approximately October-June, and partially or completely ice free from July-September when the sea ice retreats northward into the Arctic basin (Comiso 2006, Richter-Menge et al. 2006). We developed an index of ice conditions, ice(t), for use as an environmental covariate in the capture-recapture analysis. This let us quantify the relationships between polar bear vital rates and interannual variation in the duration of annual sea ice in the SB region. We defined ice(t) as the number of ice-free days during calendar year t in the region of preferred habitat for polar bears. Preferred habitat was defined as waters within the SB management unit that were less than 300 m deep (International Bathymetric Chart of the Arctic Ocean; *http://www.ngdc.noaa.gov/mgg/bathymetry/arctic/arctic.html*), because aerial surveys of ringed seals hauled out on the sea ice confirmed they prefer depths less than 300m (Stirling et al. 1982). Durner et al. (2004, 2007) also demonstrated that polar bears in the SB region select strongly for sea ice over the shallow waters of the continental shelf. A day was considered ice free if the mean ice concentration in the region of preferred habitat

was less than 50%. Mean ice concentration was the arithmetic mean of daily ice concentration values for the 139 grid cells (25×25 km) in the region (based on passive microwave satellite imagery from the National Snow and Ice Data Center, Boulder, CO; *ftp://sidads.colorado.edu/pub/*). To understand ice conditions in the context of the historical record, we calculated the number of ice-free days for the entire available time series of remote sensing sea ice data, from 1979-2006. For use in the capture-recapture analysis, we standardized the 2001-2005 values of the ice(t) covariate by subtracting the mean and dividing by the standard deviation.

We used resource selection functions (RSFs) developed by Durner et al. (2007) to evaluate whether the covariate ice captured the interannual variation in sea ice conditions most important to polar bears. The RSFs identified the extent of optimal polar bear habitat, based on bathymetry, proximity to land, ice concentration, and distance to ice edges, within the 95% spatial utilization distribution for the SB population (as determined from radiotelemetry data, Amstrup et al. 2004). Monthly values of optimal habitat area were summed for each year to generate an annual RSF habitat index (km^2×month). We compared the RSF index to the covariate ice for the period of this study (2001-2005) and for the entire time series of data available. We did not use the RSF habitat index as a covariate because the RSF analysis (Durner et al. 2007) and the multistate analysis were developed concurrently.

Time and covariate dependence

To investigate interannual variation in vital rates, we evaluated 4 types of time dependence for survival and breeding probabilities:

1. Time-invariant (.), where the value of a parameter was equal for all sampling occasions (for p) or intervals (for σ).

2. Additive time variation (+t), which allowed the value of one parameter of a given type

(e.g., survival) to change from year to year and constrained other parameters of the same type to vary in parallel on the logit scale. For example, a model with additive time variation for survival for constraint models F2 and M1 would estimate

$$\sigma_1(t) \qquad\qquad t = 1, 2, \ldots, N\text{-}1$$

$$\text{logit}[\sigma_4(t)] = \text{logit}[\sigma_1(t)] + c,$$

where N is the number of sampling occasions and c is a constant. By definition of the constraint models F2 and M1, each of the remaining σ_i are equal to either σ_1 or σ_4.

3. Additive covariate time variation (+ice), which allowed one parameter of a given type to vary from year to year as a logistic function of the environmental covariate *ice*(t), and constrained other parameters of the same type to vary in parallel on the logit scale. For example, a model with additive covariate time variation for survival for constraint models F2 and M1 would estimate

    $$\text{logit}[\sigma_1(t)] = a_1 + b_1 \, ice(t)$$

    $$\text{logit}[\sigma_4(t)] = \text{logit}[\sigma_1(t)] + c.$$

4. Covariate time variation (ice), which allowed parameters of the same type to vary as independent logistic functions of the environmental covariate *ice*(t). For example,

    $$\text{logit}[\sigma_1(t)] = a_1 + b_1 \, ice(t)$$

    $$\text{logit}[\sigma_4(t)] = a_2 + b_2 \, ice(t).$$

We considered only models that imposed the same type of time dependence on all parameters of a given type, to limit the number of candidate models and because a previous analysis of the SB data did not support differences in time dependence among sex and age classes (Regehr et al. 2006). For example, we did not consider a model with time-invariant survival for females and time variation in survival for males.

We treated COY litter survival (σ_{L0}) in two ways. First, as an independent parameter, in which case σ_{L0} could be time-invariant (.), a function of time (t), or a function of the covariate (ice), irrespective of the type of time dependence in the stage-dependent survival parameters (σ_i). Second, as an additional survival parameter, in which case σ_{L0} assumed the same type of time dependence as the stage-dependent survival parameters. In this case, if time dependence in σ_{L0} was (+t) or (+ice), σ_{L0} was additive to the σ_i, which we indicate as (+σ).

We use notation similar to previous capture-recapture analyses (e.g., Lebreton et al. 1992) to define the combined model structure for parameter type, stage constraints, and time dependence. For each type of parameter we use subscripts to denote stages or the stage constraint model, and parentheses to denote the type of time dependence. For example, the model $\sigma_{F1,M2}(+t) \, \sigma_{L0}(+\sigma) \, \beta_{4,5}(ice)$ allowed additive time variation in σ for the two aggregate stages of the survival constraint model F1,M2; litter survival (σ_{L0}) varied additively with stage-dependent survival; and breeding probabilities (β_i) varied independently as functions of the covariate *ice*. Data limitations prevented us from fitting a fully time- and stage-dependent model. Our most general model was $\sigma_{F3,M3}(+t) \, \sigma_{L0}(t) \beta_i(+t)$.

Parameter estimation

Maximum likelihood estimates were obtained by constructing the likelihood from the capture histories and using specialized optimization software to minimize the negative log of the likelihood with respect to the parameters. We used the Tomlab Knitro optimization routine (Forth and Edvall 2006) which runs within Matlab (MathWorks Inc., Natik, MA). We wrote customized programs because available software (e.g., program MARK, E-SURGE) either cannot decompose transition probabilities into their individual component parameters or cannot fit multistate models with individual covariates.

To construct the likelihood function we

defined a 10×10 transition matrix $\Psi(t)$ corresponding to the life cycle graph. The elements $\Psi_{ij}(t)$ of $\Psi(t)$ are the probability of transition from stage j at time t to stage i at time $t+1$, for $t = 1,\dots, N\text{-}1$ (note the column-to-row orientation of these matrices; Fujiwara and Caswell 2002, Caswell and Fujiwara 2004). Let Φ be an $(s+1) \times (s+1)$ matrix with death as a stage and where $\mathbf{m}$ is a row vector of stage-specific probabilities of death such that $m_j = 1 - \Sigma_i \Psi_{ij}$.

$$\Phi = \begin{bmatrix} \Psi & 0 \\ \mathbf{m} & 1 \end{bmatrix}$$

We also define a diagonal capture matrix $\mathbf{P}(t)$, with $p_i(t)$ the probability of recapture of an individual in stage i for $i = 1$ to $(s+1)$ at time t, for $t = 2, \dots, N$. There were too few harvested animals to use a joint recapture-recovery model, so we set $p_{s+1} = 0$. Let $\mathbf{e}_i$ be a column vector with a 1 in the ith entry and zeros elsewhere, and $\mathbf{e}$ a column vector of ones. Then $\mathbf{E}_i = \mathbf{e}_i\mathbf{e}_i^{\mathrm{T}}$ is a matrix with a 1 in the (i,i) position and zeros elsewhere. The columns of a matrix can be summed by multiplying on the left by $\mathbf{e}^{\mathrm{T}}$.

A capture history is defined as $h = X_1, X_2, \dots, X_T$, where X_t indicates the stage of the individual or, for $X_t = 0$, the fact that it was not seen at time t. Suppose an individual was marked in stage X_1 at $t = 1$. Then the vector $\mathbf{e}_{x1}$ gives the probability distribution of its stage at $t = 1$. The probability distribution of its stage after the transition from $t = 1$ to $t = 2$ is the vector $\Phi_1\mathbf{e}_{x1}$ including the probability of death. The entries of the vector $\mathbf{P}_2\Phi_1\mathbf{e}_{x1}$ give the probability of capturing the individual in each of the stages at $t = 2$. Similarly, the entries of the vector $(1\text{-}\mathbf{P}_2)\Phi_1\mathbf{e}_{x1}$ give the probabilities of failing to capture the individual in each of the stages at $t = 2$. Continuing this process leads to the following formula for the probability of any capture history (Caswell 2001, Fujiwara and Caswell 2002, Caswell and Fujiwara 2004).

$$\mathbf{P}\left[X_1,\dots, X_T | \Phi, \mathbf{P} \right] = \ell\left(\Phi, \mathbf{P} | X_1,\dots, X_T \right)$$
$$= \mathbf{e}^{\mathrm{T}}\mathbf{Q}_{T-1}\dots\mathbf{Q}_1\mathbf{e}_{X_1}$$

$$\mathbf{Q}_t = \begin{cases} \mathbf{E}_{X_t}\mathbf{P}_{t+1}\Phi_t & \text{if } X_{t+1} \neq 0 \\ \left(\mathbf{I} - \mathbf{P}_{t=1}\right)\Phi_t & \text{if } X_{t+1} = 0 \end{cases}$$

This is a matrix extension of the familiar formula for the probability of a capture history in the Cormack-Jolly-Seber capture-recapture model (Lebreton et al. 1992). It is possible because Φ includes death as a stage.

Assuming that individual histories are independent and identically distributed, the log likelihood for the entire set of capture histories is obtained by summing the log likelihood of each history,

$$\log L\left(\Phi, \mathbf{P} \right) = \sum_k \log \ell_k \left(\Phi, \mathbf{P} \right),$$

where $\log \ell_k$ is the log likelihood obtained from the kth history.

Parametric bootstrap standard errors and confidence intervals

We used a parametric bootstrap procedure to estimate standard errors and confidence intervals for all estimated parameters, for a set of k models, averaged using their Akaike Information Criterion (AIC) weights (Burnham and Anderson 2002). We distinguish two levels of parameters: the vector π of life cycle parameters, and the parameter vector θ in terms of which the likelihood is maximized. The vector θ contains logit-transformed probabilities and additive effects, depending on which parts of the model are constant, time variant, etc. Thus each model has, in general, a different number of θ_i parameters in this vector and they cannot be averaged. The vector π contains the survival, COY litter survival, breeding, and recapture probabilities. Each model contains the same set of parameters in π, and hence these vectors can be averaged across models.

For a given model, define the parameter estimate $\hat{\theta}$, the Hessian matrix

$$\hat{\mathbf{H}} = \left(\frac{\partial^2 \log L}{\partial \theta_i \partial \theta_j} \right),$$

the covariance matrix $\hat{\mathbf{V}} = -\hat{\mathbf{H}}^{-1}$ (i.e., the observed Fisher information matrix), and the life cycle parameters $\hat{\boldsymbol{\pi}} = \boldsymbol{\pi}(\hat{\theta})$. For a single model, the bootstrap procedure generates a bootstrap sample of size B, $\{\theta_1^*,...,\theta_B^*\}$ from a multivariate normal (*MVN*) distribution with mean $\hat{\theta}$ and covariance matrix $\hat{\mathbf{V}}$. We used B =10,000 unless otherwise specified. This sample is transformed to a sample of the life cycle parameters $\{\boldsymbol{\pi}_1^*,...,\boldsymbol{\pi}_B^*\}$, where $\hat{\boldsymbol{\pi}}_i^* = \boldsymbol{\pi}_i^*(\theta_i^*)$.

The 90% confidence limits on each parameter were obtained as the 5th and 95th percentiles of the bootstrap sample (Efron and Tibshirani 1993). We used 90% rather than 95% confidence limits because the bootstrap sampling distributions were left-skewed and bimodal, which made the use of more extreme confidence limits unreliable as a description of uncertainty. The standard errors of each parameter were obtained as the standard deviations of the bootstrap sample for that parameter.

To calculate a bootstrap sample from a weighted model, we partition the B bootstrap samples among the models. Consider a set of k models with estimates $\hat{\theta}_i$, covariance matrices $\hat{\mathbf{V}}_i$, and AIC weights

$$w_i = \frac{\exp(-\Delta AIC_i / 2)}{\sum_j \exp(-\Delta AIC_j / 2)} \qquad i = 1,...,k.$$

The life cycle parameter estimates for the weighted model are

$$\hat{\boldsymbol{\pi}} = \sum_i w_i \hat{\boldsymbol{\pi}}_i.$$

The bootstrap sample of the life cycle estimates is obtained by sampling from all the models in the set, with probabilities given by the w_i. We generate a multinomial random variable $\mathbf{b} = (b_1,...,b_k)$ with probabilities $w_1,...,w_k$ and sample size B. Then we generate bootstrap samples,

$$\theta_1^*,...,\theta_{b_1}^* \sim MVN\left(\hat{\theta}_1, \hat{\mathbf{V}}_1\right)$$
$$\vdots$$
$$\theta_1^*,...,\theta_{b_k}^* \sim MVN\left(\hat{\theta}_k, \hat{\mathbf{V}}_k\right),$$

and from these the bootstrap samples of the life cycle parameters

$$\boldsymbol{\pi}_1^*,...,\boldsymbol{\pi}_{b_1}^* \text{ from model 1}$$
$$\vdots$$
$$\boldsymbol{\pi}_1^*,...,\boldsymbol{\pi}_{b_k}^* \text{ from model } k.$$

The complete bootstrap sample is the concatenation of all the model-specific life cycle parameter samples. It includes both parameter uncertainty (as reflected in the covariance matrix for each model) and model uncertainty (as reflected in the Akaike weights).

Model selection

We used a three-step model selection procedure to identify a well-supported set of models from which to obtain parameter estimates. First, we selected the best recapture probability model structure. Second, we selected the best type of time dependence in breeding probabilities. Third, we evaluated constraint models and time dependence in stage-dependent survival and COY litter survival.

To select the best recapture probability model we evaluated the three recapture probability constraint models with both time-invariant and additive time variation. We combined the resulting six recapture models with all nine survival constraint models. For all models we used additive time variation in survival and breeding probabilities and either independent or additive (to the σ_i) time variation in σ_{L0} [σ_z(+t)σ_{L0}(+σ) and σ_z(+t)σ_{L0}(t) for z = F1,M1;...F3,M3]. We selected the most supported constraints and time dependence for recapture rates from the resulting 108 models based on the model with the lowest ΔAIC; i.e., AIC$_i$ for model i minus the minimum AIC value

for the model set.

We then fixed the recapture model and evaluated the four types of time dependence in breeding probabilities. Again, we assessed all 9 survival constraint models and considered additive time variation for survival and either independent or additive (to the σ_i) time variation in σ_{L0}. We used AIC to select the best type of time dependence in breeding probabilities from the resulting 72 models (i.e., 4 types of time dependence for β combined with 9 constraint models for σ combined with 2 types of time dependence in σ_{L0}).

To evaluate constraint models and time dependence in σ_i and σ_{L0}, we fixed the recapture and breeding models and jointly evaluated all combinations of female and male survival constraint models and time dependence for both the σ_i and σ_{L0}, a total of 123 unique models. We derived model averaged parameter estimates for two sets of time-varying models. The first set represented the overall best model set, containing all models with ΔAIC < 4. The second set represented the best non-covariate model set, containing all models with ΔAIC < 4 that did not include the covariate *ice*. We derived parameter estimates for non-covariate models because there was large uncertainty associated with the estimated slope and the intercept of the covariate *ice*(t), and we wanted an independent evaluation of interannual variation in vital rates that did not rely on a particular form of covariate dependence. In addition, we report model-averaged results for the best time-invariant models (9 total), which provide the best single estimates of each parameter.

Goodness-of-fit

For model selection to be valid, at least one model in the candidate set must provide an adequate fit to the data. Goodness-of-fit (GOF) tests are not available for Arnason-Schwarz (AS) multistate models, such as those considered here (Arnason 1972). However, an approximate evaluation of GOF can be derived using GOF tests for the JollyMove (JMV) multistate model, which generalizes the AS model by allowing recapture probabilities at occasion $t+1$ to vary by state occupancy at occasion t (Brownie et al. 1993). The GOF test for the JMV model has 5 components. The first three components (WBWA, 3G.SR, 3G.SM) address hypotheses about heterogeneity in survival by evaluating whether the state of next encounter depends upon the state of previous encounter or previous marking status (i.e., whether the bear was a first-time capture or a recapture). The last two components (MITEC, MLTEC) address hypotheses about heterogeneity in recapture by evaluating whether the time to next encounter depends upon state of previous encounter (Choquet et al. 2005).

We used program U-CARE (Pradel et al. 2003, Choquet et al. 2005) to evaluate GOF for a model with four female stages and two male stages. We combined female stages 1, 2, and 3, and male stages 7, 8, and 9, because recapture, survival, and transition probabilities were equal for these stages in all our models.

Test components checking for heterogeneity in survival probabilities were not significant (Table 3). There were insufficient data to test the components related to heterogeneity in recapture probabilities. The overall test based on components 1-3 was not significant, suggesting that the model provided an adequate fit to the data and that it was not necessary to correct for overdispersion or un-modeled heterogeneity.

Parameter estimability

The small size of the data set (few occasions and individuals) relative to the number of stages and groups in our models led to concerns about whether it would be possible to estimate all parameters in the time-varying models. We evaluated parameter estimability for all candidate models based on the rank of the

Jacobian matrix of the likelihood. All parameters in a model were considered estimable if the Jacobian was full rank, i.e., the rank of the Jacobian was equal to the number of θ parameters in the model (Catchpole et al. 1996, Catchpole and Morgan 1997, Giminez et al 2003). We constructed the components of the likelihood from the $\boldsymbol{\Phi}$ and $\boldsymbol{P}$ matrices as described above. We used Tomlab's Matlab Automatic Differentiation package (Forth and Edvall 2006) to calculate the Jacobian (Hunter and Caswell in press). All candidate models were full rank for our data set, meaning that all parameters could be estimated.

Harvest mortality from tag returns

Polar bears in the SB management unit are harvested as part of a hunt regulated by Native user groups in the U.S. and Canada (Brower et al. 2002). We used tag return data from the harvest to estimate an annual harvest mortality component, h, for the years 2001-2005 that could be used to adjust the 2001-2005 estimates of total survival from the multistate analysis to produce estimates of natural survival (σ_i^N; survival of polar bears in stage i in the absence of harvest mortality). Although sample sizes were too small to estimate harvest mortality for individual stages, we derived separate estimates for females and males because there is a male bias in the SB harvest (Brower et al. 2002). For females, we estimated harvest mortality for stages 1-4 only because hunters in the SB rarely take females with dependent young. Harvest mortality for each sex was estimated as

$$\hat{h} = H / \sum_j \hat{M}_j ,$$

where H is the number of research-marked polar bears killed in the harvest from 2001 to 2005. We estimated $\hat{M}_j$, the number of polar bears in recapture group j (i.e., polar bears with the same *agency* and *radio* designation) from 2001 to 2005 that bore research marks as $\hat{M}_j = m_j / \hat{p}_j$, where m_j is the number of research-marked

bears in recapture group j captured from 2001 to 2005 and $\hat{p}_j$ is the recapture probability of polar bears in recapture group j captured from 2001 to 2005. Natural survival is estimated as $\hat{\sigma}_i^N(t) = \hat{\sigma}_i(t)/[1 - \hat{h}]$. This approach assumes that harvest in any given year occurred at the beginning of the inter-sampling interval, and that there is no compensation for harvest mortality by changes in other sources of mortality (Derocher and Taylor 1994). We used only harvest data that coincided spatially and temporally with the capture-recapture data. For example, we did not consider harvest data from the Canadian portion of the SB for 2001-2002 because there were no Canadian research captures in those years.

Temporary emigration

Survival estimates from capture-recapture models represent the probability of surviving from time t to $t+1$ and not permanently emigrating from the sampling area (Lebreton et al. 1992). Temporary emigration from the sampling area influences estimates of recapture probability, but does not affect survival estimates if movement in and out of the sampling area is completely random. However, if there is Markovian dependence in the probability of temporary emigration (i.e., if the probability of being an emigrant at sampling occasion $t+1$ depends on emigration status at t), survival estimates from multistate models can be biased (Kendall et al. 1997, Schaub and Pradel 2004). To evaluate the movement behavior of polar bears, we used radiotelemetry data collected from 1984-2006 to quantify the proportion of the SB population that was exposed to sampling each spring, and to determine if polar bear movement with respect to the sampling area was random or Markovian. We restricted the analysis to the U.S. portion of the SB management unit because few radio collars were deployed in Canada.

To estimate the probability of being available for capture we constructed an observation

matrix, with rows corresponding to radio-collared bears captured at least once by standard search methods during 1984-2006 and columns corresponding to yearly sampling occasions. Entries in the matrix were coded 0 for occasions when a bear was not wearing a functional radio collar, 1 if a bear with a functional radio collar had at least one observation within the sampling area during the spring capture season (approximately 25 March-10 May), and 2 if a bear with a functional radio collar was only observed outside of the sampling area during the spring capture season. Observations consisted of standard-quality locations (Argos Location Classes 1, 2 or 3). Polar bears were included in the observation matrix on occasion t only if they wore a functional radio collar for at least 6 months prior to t. We defined the sampling area as the 90% density contour of global positioning system track log locations for helicopter capture effort during U.S. spring field work from 2001-2006 (Amstrup et al. 2004). We estimated the mean proportion, from 1984-2006, of radio-collared bears that were within the sampling area during the spring capture season by dividing the number of observations in the sampling area (1's) by the total number observations (1's and 2's) in the matrix. To obtain variance estimates, we re-sampled individual bears with replacement from the observation matrix to create 1000 bootstrap datasets. We recalculated the proportion of radio-collared bears within the sampling area and used the standard deviation of the bootstrap distribution to approximate the standard error.

We evaluated whether movement patterns were random or Markovian by creating a 2×2 contingency table classifying whether sequential observations of individual polar bears were inside or outside the sampling area at time t and time $t+1$. We compared the frequency of bears who moved from inside to outside with the frequency of bears who remained outside. If the probability of temporary emigration is independent of location, these frequencies should be equal. As above, variance estimates were calculated from 1000 bootstrap samples.

Results

Recapture data

The combined 2001-2006 USGS data and 2003-2006 CWS data for independent (age ≥ 2 year) polar bears consisted of 818 captures of 627 individuals (Table 4). Approximately 6% of captures were for polar bears encountered by radiotelemetry. The mean date of capture was 14 April. The capture data consisted of individual capture histories coded for the 10-stage multistate model. For example, female BearID_20413 had the capture history {345004}, which indicated capture as a 4-year-old (stage 3) in 2001, as an adult available to breed (stage 4) in 2002, as an adult with a COY litter in 2003 (stage 5), not captured in 2004 or 2005, and recaptured as an adult available to breed (stage 4) in 2006.

Sea ice covariate

The annual number of ice-free days over the continental shelf increased during the study: $ice(t) = \{90, 94, 119, 135, 134\}$, for $t = 2001, 2002…, 2005$. Using the entire available time series, the mean duration of the ice-free period in 2006 was 16.7 days longer than in 1979, although the trend was not statistically significant (Figure 3; simple linear regression, $\hat{\beta} = 0.62$ days/year, SE($\hat{\beta}$)= 0.97 days/year, $P = 0.34$). However, changes in the number of ice free days are more complicated than a simple linear trend. Nonparametric smoothing suggests there has been a tendency for a higher frequency of years with a longer ice-free season (Hunter et al. 2007).

The covariate ice and the RSF habitat index were highly correlated for years of the current study (Pearson product-moment correlation coefficient $r^{2001\text{-}2005} = -0.87$, $t = -3.0$, df = 3, $P = 0.03$) and for the entire time series available

$(r^{1979-2006} = -0.82, t = -7.4, df = 26, P < 0.001)$.

Model selection and parameter estimates

The most well-supported model for recapture probabilities was time invariant and included separate recapture probabilities for females (stages 1-6) and males (stages 7-10). This model also included the individual covariate *radio,* the group covariate *agency,* and a separate recapture probability for Canadian agency bears in 2006. All subsequent modeling, for both time-invariant and time-varying parameter estimates, used this 5-parameter model for recapture probabilities.

Time-varying models

Additive time variation was clearly the most supported type of time dependence in breeding probabilities (Table A1, Appendix A). Models with additive time variation had a lower ΔAIC than models with time-invariant or covariate time dependence for all nine survival constraint models.

Thirty-seven of the models we evaluated for survival constraints and time dependence had a ΔAIC<4 (Table 5; Table A2, Appendix A). Eight of these models were removed from further consideration because, while formally estimable, they yielded extremely large variances ($>1.0 \times 10^5$). For the logit-normal distribution of the π parameters, this means that the distribution of estimates is almost completely concentrated at 1 or 0 (Frederick and Lad 2003). The weight of evidence in favor of a specific model *i* being the best model under consideration (i.e., the Akaike weight, w_i) was relatively evenly spread among these 29 models. The highest support for any single model was 12%, and all other models had less than 5.5% support (Table 5). However, there was clear support for modeling covariate time variation in survival [i.e., modeling $\sigma(t)$ as a function of *ice*(t)]. The summed AIC weight

was 0.62 for models with additive covariate time variation (+ice), and 0.9 for models with additive and independent covariate time variation (ice) combined (Table 5). For COY litter survival, support for a time-invariant model (summed $w_i = 0.50$) was equivalent to the combined support for time-varying models. The summed w_i was 0.23 for models with additive time variation, 0.16 for models with covariate time variation, and 0.11 for models with independent time variation (Table 5).

Nearly 80% of support for the survival constraint models was shared among 4 models: F1M3, F2M1, F1M2 and F3M1 with 26%, 21%, 19% and 13% of the total support, respectively.

Model-averaged parameter estimates from all models with ΔAIC < 4 showed high survival rates for all stages in 2001-2003 (Figures 4 and 5; Tables A3 and A4, Appendix A). Survival rates were markedly lower in 2004 and 2005 for all stages except adult males (stage 10). However, bootstrap confidence intervals for all years were very wide and showed a large amount of overlap. Model-averaged estimates for breeding probabilities and COY litter survival showed a similar pattern with high values 2001-2003 and much lower values in 2004 and 2005, again with wide confidence intervals.

Within the range of observed values, survival varied little with the covariate *ice* up to a threshold value of about 127 ice-free days (Figure 6). Beyond that threshold, the decline in survival appears to accelerate as the number of ice-free days increases. Although the relationship between *ice* and survival in covariate models was determined by use of the logit link function, a similar transition from very high to very low survival was observed in parameter estimates from non-covariate models. This pattern was evident for survival of all stages with only a slight shifting of the threshold value among stages.

Model-averaged survival estimates for models with ΔAIC < 4 that did not include the covariate *ice* (Appendix B) were slightly lower

than estimates for all models with ΔAIC<4 in 2001-2003 and slightly higher in 2004-2005. The two sets of parameter estimates exhibited similar interannual variation (Figure 7). Confidence intervals on survival estimates were narrower for the non-covariate model set in 2001-2003. Estimates and confidence intervals for all other parameters were similar between the two models sets. The mean percent relative difference in survival estimates for the two model sets was approximately 2.9% (SD = 6.9%). The largest differences occurred for subadult males (stages 7-9) in 2004 and 2005, for which the non-covariate models produced survival estimates approximately 21% higher than the all-model candidate set. Most differences in parameter estimates between the two model sets for a given stage and year were less than 6%.

Time-invariant models

To derive time-invariant estimates of survival and breeding probabilities we fitted the nine survival constraint models with time-invariant survival, COY litter survival, and breeding probabilities (Appendix C). Models with a simpler structure received the greatest amount of support as measured by the AIC weights (Table 6). As would be expected, model-averaged survival estimates for the time-invariant models fell between the high survival probabilities for 2001-2003 and the low survival probabilities for 2004-2005 from the time-varying models (Figure 8; Table C2, Appendix C). Model-averaged estimates of COY litter survival and breeding probabilities from the time-invariant models also fell between the high and low time-varying estimates (Figure 9; Table C2, Appendix C).

Harvest mortality from tag returns

Harvest in the SB management unit occurred throughout the year. From 2001 to 2005, 10 female and 17 male independent (age ≥ 2 year)

polar bears with a previous research capture were harvested in the portion of the SB that coincided with the spatial and temporal distribution of research effort. For females without dependent young (stages 1-4), average annual harvest mortality for the period 2001-2005 was 0.019. For males (stages 7-10), average annual harvest mortality for the period 2001-2005 was 0.029.

Temporary emigration

A total of 195 observations of 114 polar bears with radio collars were made from 1985-2006. The mean proportion of radio-collared polar bears that were within the U.S. sampling area during the spring capture season was 0.51 (SE = 0.04). The probability of being located outside of the sampling area on occasion $t+1$, conditional upon being located within the sampling area on occasion t, was 0.20 (SE = 0.04). The probability of being located outside of the sampling area on occasion $t+1$, conditional upon being located outside of the sampling area on occasion t, was 0.19 (SE = 0.04). This suggests that temporary emigration with respect to the U.S. sampling area was random ($P = 0.91$ vs. the null hypothesis that emigration status at t did not affect the probability of being an emigrant at $t+1$).

To determine the potential for survival in 2004 and 2005 to be negatively biased by higher emigration in those years, we calculated the proportion of radio-collared bears in the sampling area in 2005 and 2006. High proportions of radio-collared bears in the sampling area, 53% in 2005 and 64% in 2006, suggest that the low survival estimates in 2004 and 2005 did not reflect increased movement out of the study area.

Discussion

Longitudinal individual-based data allow the robust estimation of vital rates (Williams et al. 2002) but are logistically difficult and expensive to collect for polar bears because they occur in remote areas at low densities (Amstrup 2003). The data analyzed here come from a SB polar bear study originally designed to investigate the status of the population and evaluate sustainable harvest quotas. However, three years of record minimum sea ice extent in the Arctic (2002, 2004, 2005; Meier et al. 2007) led to concerns about the effects of sea ice loss for polar bears in the SB region (Regehr et al. 2006) and throughout their range (Aars et al. 2006, USFWS 2007). Our findings provide insight into how declining sea ice may affect the 6 polar bear populations which also inhabit the divergent ice ecoregion of the polar basin (SB, Chukchi Sea, Laptev Sea, Kara Sea, and Barents Sea; Amstrup et al. 2007). This is important because, although the rate of sea ice decline has been much greater in other portions of the divergent ice ecoregion than in the SB (Meier et al 2007), the data necessary to estimate vital rates are not available for other polar bear populations throughout this ecoregion. Because more than one-third of the world's polar bears reside in this ecoregion (Amstrup et al. 2007), knowledge of the SB can provide insights to the responses of a large portion of the world's polar bears to declines in the sea ice associated with climatic warming.

Our analyses found evidence that survival and breeding probabilities were high in 2001-2003 and declined markedly in 2004 and 2005. These declines were associated with increases in the duration of the ice-free period over the continental shelf, as measured by the covariate *ice*. We propose two primary mechanisms by which the duration of the ice-free period affects polar bear vital rates. First, in years with long ice-free periods, polar bears can spend less time in early summer and autumn foraging over the biologically productive waters of the continental shelf. This may cause polar bears to enter the winter in poorer nutritional condition than in years with short ice-free periods, thereby increasing their risk of nutritional stress, reproductive failure, or possible starvation. Second, the abrupt and distant retreat of sea ice from the SB region during the ice-melt period may be associated with immediate risks of mortality that are not related to polar bear nutrition. For example, recent observations of polar bears that drowned attempting to make long swims in ice-free water (Monnett and Gleason 2006) suggest that an increasingly dynamic sea ice environment may present additional physical risks to polar bears.

The two mechanisms we propose above are related to the availability of sea ice as a substrate that polar bears use for foraging and movement. However, ecological responses to climatic change are complex and regionally variable (Stenseth et al. 2002, Walther et al. 2002). As warming temperatures and sea ice loss affect the polar marine ecosystem polar bears are likely to experience a suite of effects, including changes in distribution and currently unknown responses to changes at lower trophic levels (e.g., Tynan and Demaster 1997, Derocher et al. 2004).

Progressively earlier breakup of sea ice in the early summer, which shortens the time that bears can hunt seals prior to fasting for several months onshore, has also been associated with declines in body condition and demographic parameters for polar bears in some seasonal ice regions near the southern limit of the species' range (Stirling et al. 1999, Obbard et al. 2006, Stirling and Parkinson 2006, Regehr et al. 2007). In western Hudson Bay, Canada, survival of juvenile (0-1 yr), subadult (2-4 yr), and senescent-adult (≥ 20 yr) polar bears declined by 2-5% for each week earlier than average that the sea ice broke up in the spring (Regehr et al. 2007). In our analyses, the covariate *ice* was highly correlated with an RSF index of polar bear habitat conditions,

suggesting that *ice* captured the interannual variation in sea ice conditions most important to polar bears in the SB region.

Interpretation of parameter estimates

The models most supported by the data included survival rates that declined as functions of the covariate *ice.* Model-averaged parameter estimates showed much lower survival and breeding probabilities in 2004 and 2005 than in 2001-2003. These declines coincided with anecdotal reports of emaciated, drowned, and cannibalized polar bears, and of (largely unsuccessful) attempts by polar bears to claw through solid ice to capture seals (Amstrup et al. 2006, Monnett and Gleason 2006, Regehr et al. 2006, Stirling et al. 2008). Although observations of the above incidents were few, normally these incidents are observed very rarely or not at all. Thus, to have so many rare incidents reported in the last three years, compared to few or none in previous decades, is consistent with the statistical relationships between sea ice and vital rates evidenced in our analyses.

Fitting parameters as functions of environmental covariates is difficult for complex life-cycle models and short time series of data. This difficulty was exacerbated in our study because the covariate *ice* had similar values in the first two years (90 and 94 days in 2001 and 2002 respectively) and in the last two years (135 and 134 days in 2004 and 2005 respectively). As a result, the pointwise confidence intervals on survival estimates were extremely wide.

The wide confidence intervals were partly caused by the restriction of probability estimates to the unit interval [0, 1]. The bootstrap distributions of estimates for some survival probabilities included significant probability mass near 0 (cf. Frederick and Lad 2003). This part of the distribution was biologically implausible; all of the polar bears in the SB region certainly did not die in those

years. If these implausible values are excluded, the confidence intervals become much narrower. For example, survival of adult females available to breed (σ_4) in 2001 had a 90% confidence interval of [0.085, 1.000]. Eliminating the bootstrap values less than 0.1 (5.2% of the total sample) yields a 90% confidence interval of [0.666, 1.000]. The distribution of the bootstrap values shows why confidence intervals do not give a complete picture of the uncertainty in distributions of this form (Figure 10). For this reason, we present parameter estimates using boxplots that more accurately represent the bootstrap sampling distributions.

Our analyses used a simple form of dependence between vital rates and the covariate *ice*: a linear function on the logit-transformed scale. Although simple, this function required estimating two parameters (slope and intercept) from only five data points. The results were thus potentially sensitive to the exact form of this function. Unfortunately, it was not feasible to examine alternative functions or to use nonparametric alternatives (e.g., splines) in such a short-term study. Instead we evaluated the effects of this parametric function by deriving a second set of parameter estimates from well-supported non-covariate models, i.e., models completely excluding *ice*. In the non-covariate models, vital rates varied freely with time without any *a priori* constraint to sea ice conditions. The resulting estimates had tighter confidence intervals (cf. Tables A4 and B3) but exhibited temporal patterns similar to those of the full model set (Figures 6 and 7). The conclusions of the two model sets reinforce each other.

The changes in survival and breeding probabilities documented here have important implications for the SB population. Hunter et al. (2007) use the vital rates and the relationships between sea ice and vital rates as estimated in this study to explore the current and future demographic status of polar bears in the SB region. Their analysis suggests that declines in

survival and breeding probabilities associated with longer ice-free periods in 2004 and 2005, coupled with projections of future sea ice scenarios, indicate a risk of decline for the SB polar bear population within the next century.

Sampling issues

To produce unbiased parameter estimates, multistate models must adequately represent major sources of variation in the data (Williams et al. 2002). We paid particular attention to two issues with the potential to affect parameter estimates: capture heterogeneity and temporary emigration. If not incorporated in the model, heterogeneity in capture probability can in some cases introduce a progressive negative bias into survival estimates, which has the potential to suggest a spurious declining trend or be confounded with external covariates (Pledger and Efford 1998, Pledger et al. 2003, Devineau et al. 2006). To avoid this, we allowed recapture probabilities to vary by sex, reproductive stage, tagging method (i.e., non-transmissive tags vs. radio collars), and region of capture (as coded by the covariate *agency*, with the last year of the study treated differently for Canadian bears). Multistate GOF tests found no evidence for heterogeneity, although small sample size resulted in low statistical power.

Polar bears are highly mobile and radiotelemetry studies indicate that there is considerable overlap between the SB population and adjacent populations (Amstrup et al. 2004). Therefore it is possible that polar bears with fidelity to the core of the sampling area were more likely to be exposed to capture efforts than polar bears with home ranges near the edges of the sampling area. Similarly, the home ranges of individual polar bears in the SB region can vary in size from approximately 7,000-600,000 km^2 (Amstrup et al. 2000). Therefore, polar bears with small home ranges centered in the sampling area may have been consistently more likely to be exposed to sampling efforts than polar bears with large home ranges that were

also centered in the sampling area. Thus, it is possible that individual variation in the geographic fidelity and mobility of polar bears introduced some heterogeneity into recapture probabilities.

The long history of radiotelemetry studies on polar bears in the SB region allowed us to investigate temporary emigration more thoroughly than is usually possible in capture-recapture studies. We found that radio-collared bears had a high probability (0.49) of being outside the sampling area during the spring capture season, indicating that temporary emigration was common. However, temporary emigration does not bias survival estimates if it is random rather than Markovian (Kendall et al. 1997, Kendall and Nichols 2002, Schaub and Pradel 2004), and our longitudinal analysis of radiotelemetry data found no evidence of Markovian emigration. We found no evidence of a decrease in the proportion of radio-collared bears in the sampling area in 2004 and 2005. Thus, the low survival rates in these years do not appear to be caused by high emigration.

Comparison with previous SB survival estimates

The time-invariant vital rates reported here are broadly consistent with other published estimates for polar bears. Survival estimates for 2001-2002 were similar to survival rates for adult females in the SB region estimated by following radio-collared individuals from 1981-1992 (0.97, 95%CI = 0.952-0.983; Amstrup and Durner 1995). Regehr et al. (2006) found that reproduction and COY survival had declined since the 1980s and that survival of all polar bears may have declined from 2001 to 2005. Comparison of survival estimates from Regehr et al. (2006) with the current analysis is complicated by the different sex, age, and reproductive stages considered. Nonetheless, time-invariant survival estimates generally agree between the two analyses, considering the large confidence intervals.

We found that survival varied as a function

of the covariate *ice*, and that survival rates declined markedly in the latter two years of the study. By contrast, Regehr et al. (2006) found equivocal support for survival varying as a function of the covariate *ice* and estimated a less severe decline in survival. There are two potential explanations for the difference. First, Regehr et al. (2006) modeled data that explicitly included captures of COYs and yearlings, which were not used in the present study. Second, the multistate analysis was more general because it included reproductive stages for adult females and allowed different recapture probabilities for females and males.

Conclusions

Polar bears depend on sea ice (Amstrup 2003) and our analyses show evidence for an association between declining sea ice and reduced survival. Recent changes in temperature and atmospheric circulation have led to marked declines in the thickness, extent, and duration of sea ice in many parts of the Arctic (Rigor and Wallace 2004, Belchansky et al. 2005, Stroeve et al. 2005, Holland et al. 2006a). From 1979-2006 the duration of the ice-free period over the continental shelf in the SB region exhibited an increasing trend, which although not statistically significant ($P = 0.34$), was consistent with the Arctic-wide trend toward diminished sea ice (Lindsay and Zhang 2005, Stroeve et al. 2005). The duration of the ice-free period in 2003 was above average and in 2004 and 2005 was in the upper quartile of the observational record. This suggests that during the current study SB polar bears may have experienced the cumulative negative effects of several difficult years. Forecasts of sea ice declines, for the SB region and most parts of the Arctic, are long-term and severe (Arctic Climate Impact Assessment 2004, Holland et al. 2006b, Stroeve et al. 2007). A month prior to the end of the sea ice melt season, declines in Arctic sea ice extent in 2007 have set a new record for the available time series from 1979-2006 (National Snow and Ice Data Center, http://nsidc.org/news/press/2007_seaiceminimum/20070810_index.html).

Polar bear studies in the SB region began in 1967 and constitute the longest and most consistent dataset on polar bears in the polar basin. However, past research objectives did not always permit the robust estimation of vital rates (Regehr et al. 2006). Long-term, individual-based data collected under a consistent sampling protocol are required to detect, model, and interpret the impacts of ecological change on polar bears, and to delineate demographic trends from short-term fluctuations. It is very difficult to quantify demographic trends on the basis of only 5 data points (i.e., vital rates for the 5 yearly intervals from 2001-2006), especially for a species with a multiyear reproductive cycle that lives in a complex and dynamic ecosystem. Nonetheless, the intensive capture-recapture study in the SB region from 2001-2006 established a relationship between declining sea ice and decreased survival.

Summary

We summarize our main findings here.

1. Survival and breeding of polar bears in the SB region were high from 2001-2003 and markedly lower for 2004 and 2005.

2. The declines in survival and breeding were associated with increases in the duration of the ice-free period over the continental shelf. The most supported models included a logistic decline in survival as a function of the duration of the ice-free period.

3. Because of the short duration of the study (5 years), there was considerable uncertainty associated with the logistic relationship between the sea ice covariate and survival, and we were not able to explore other forms of this relationship. However, the most supported non-covariate models also estimated declines in survival and breeding

from 2001 to 2005 that were in close agreement to the declines estimated by the full model set.

4. The ability to detect and quantify the response of polar bears to declining sea ice was limited by the short duration of the study and the low precision of parameter estimates. Long-term data on marked individuals are necessary to understand the response of polar bears in the SB region to future changes in the Arctic environment.

5. More than one-third of the world's polar bears occur in the divergent ice ecoregion of the polar basin, where ice dynamics are similar to the SB. Because data are lacking for other populations in this ecoregion, continued monitoring in the SB will provide insight to the response of a large portion of the world's polar bears to declining sea ice.

Acknowledgements

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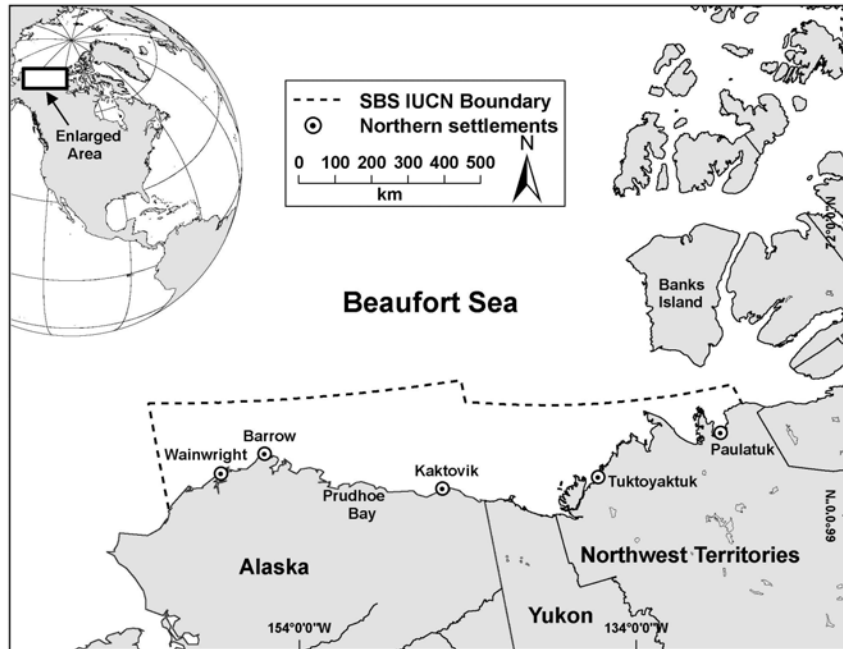
Figure 1. The southern Beaufort Sea (SB) management unit for polar bears, established by the International Union for the Conservation of Nature and Natural Resources (IUCN) Polar Bear Specialist Group.

Polar bears were captured from 2001-2006 in the U.S. portion of the SB between Barrow, AK and the U.S.-Canada border; and from 2003-2006 in the Canadian portion of the SB.
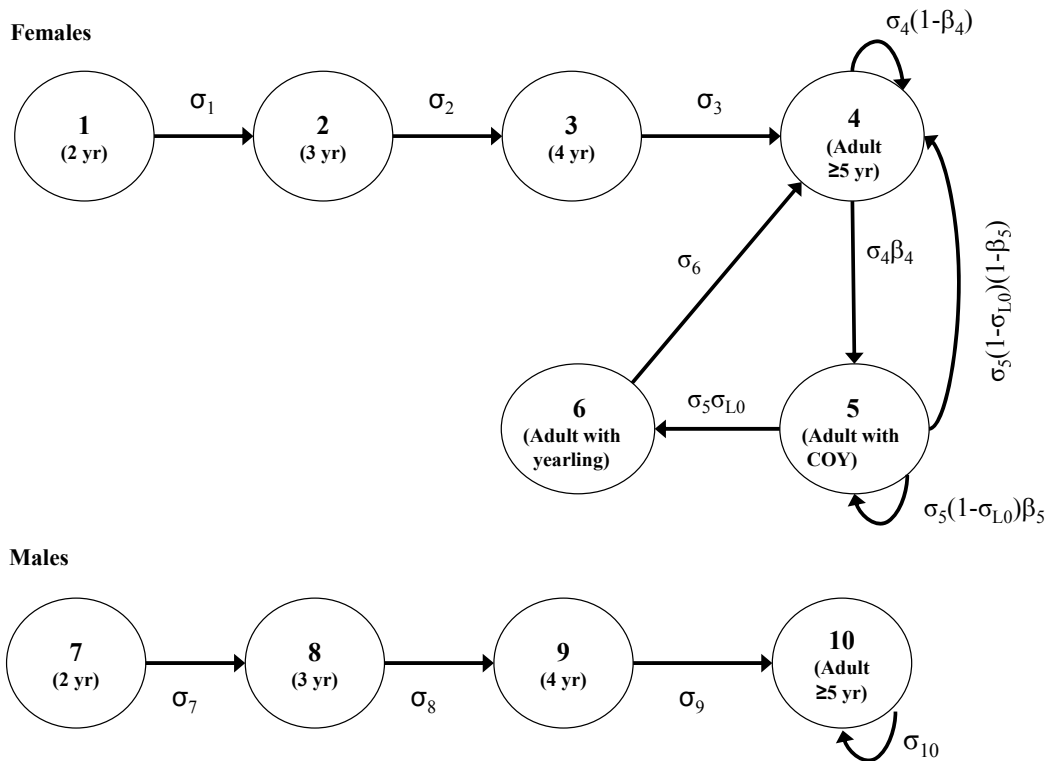
Figure 2. Ten-stage life cycle graph for polar bears in the southern Beaufort Sea.

Stages 1-6 are females and stages 7-10 are males. $\sigma_i(t)$ is the probability of an individual in stage i surviving from the spring of year t to the spring of year $t+1$; $\sigma_{L0}(t)$ is the probability of at least one member of a cub-of-the-year (COY) litter surviving to the following spring; $\beta_i(t)$ is the probability of an individual in stage i breeding, thus producing a litter of COYs, conditional on survival.
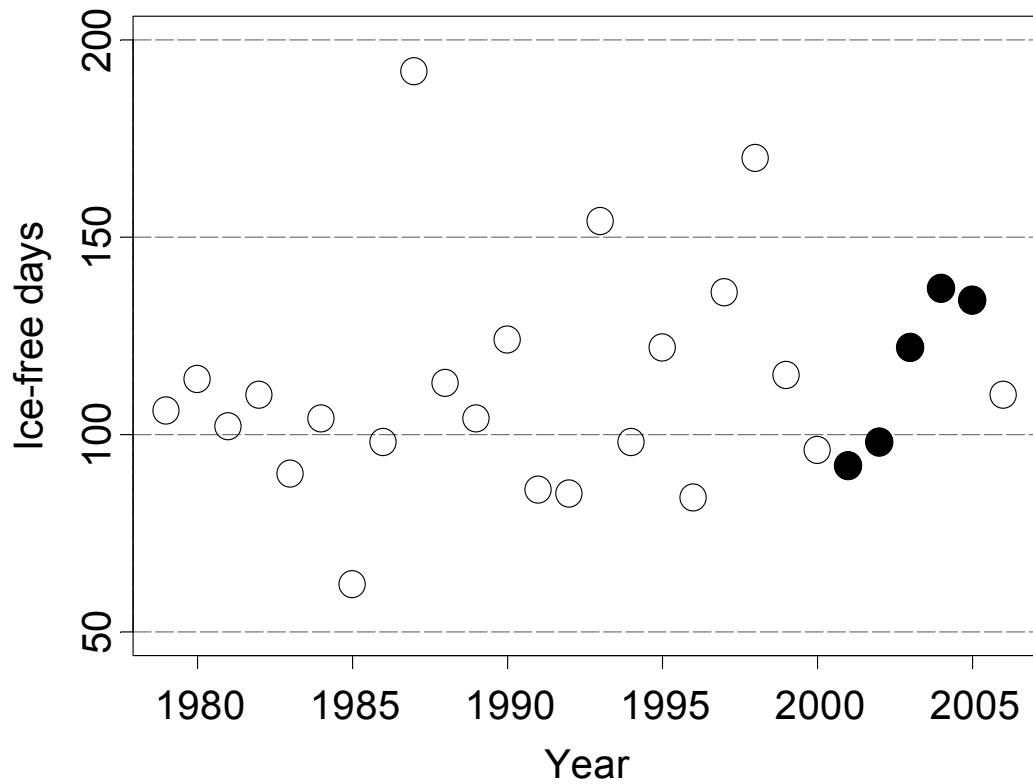
Figure 3. Number of ice-free days per year (i.e., the covariate *ice*) over the waters of the continental shelf within the southern Beaufort Sea polar bear management unit, 1979-2006.

Solid circles are the 2001-2005 values used as a covariate for survival and breeding probabilities in multistate capture-recapture models.
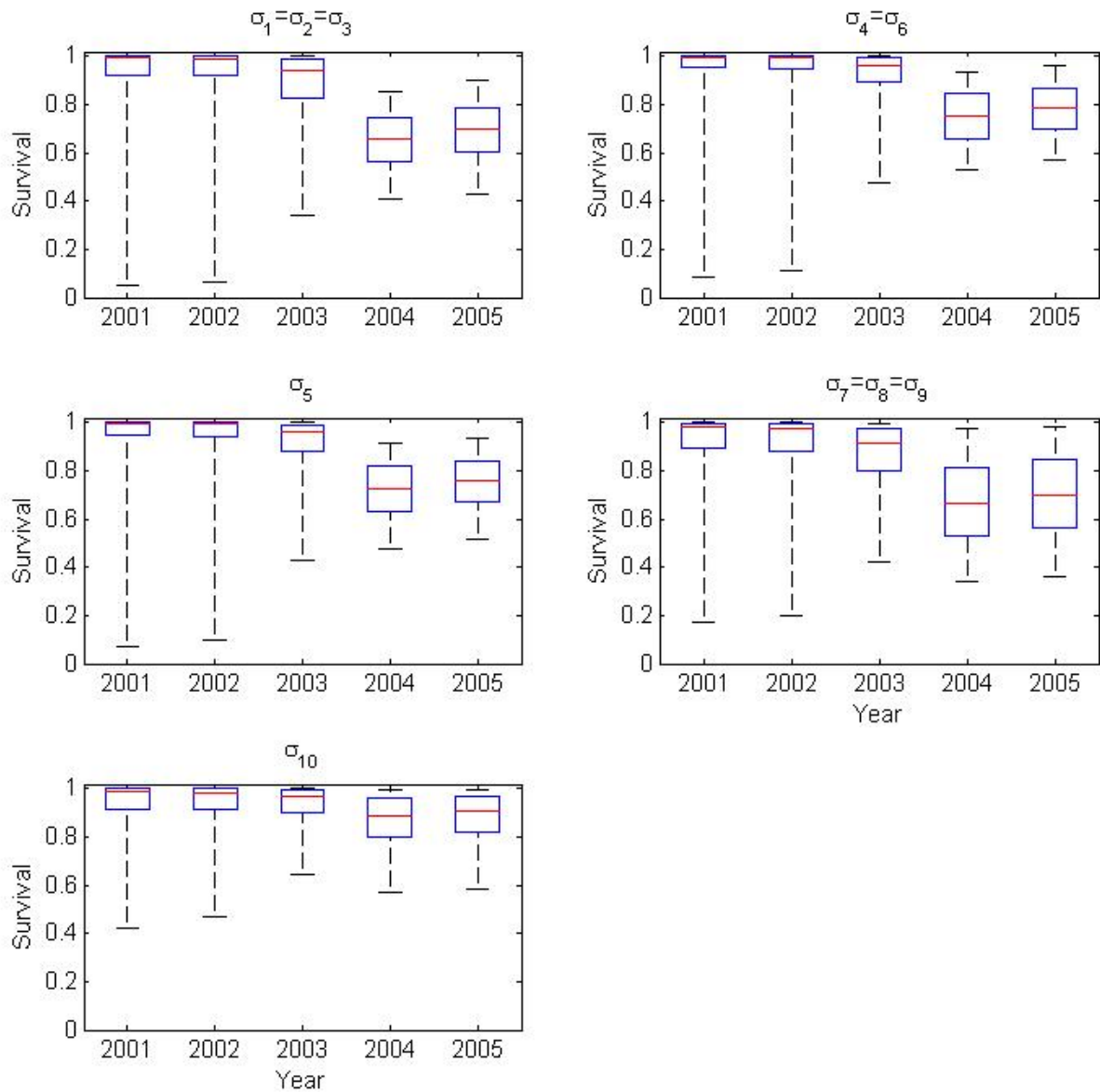
Figure 4. Boxplots showing the median, lower, and upper quartiles of 10,000 bootstrap survival probabilities (σ_i) for all models with ΔAIC < 4 for polar bears in the southern Beaufort Sea, 2001-2005.

Whiskers are 5th and 95th percentiles. Survival probabilities are plotted for the five stages or combinations of stages with unique estimates: subadult females (stages 1-3), adult females available to breed or with a yearling litter (stages 4 and 6), adult females with a COY litter (stage 5), subadult males (stages 7-9) and adult males (stage 10).

Figure 5. Boxplots showing the median, lower, and upper quartiles of 10,000 bootstrap cub-of-the-year (COY) litter survival (σ_{L0}) and breeding probabilities (β_i) for adult females available to breed (stage 4) and adult females with a COY litter (stage 5) for all models with $\Delta AIC < 4$ for polar bears in the southern Beaufort Sea, 2001-2005.

Whiskers are 5th and 95th percentiles.
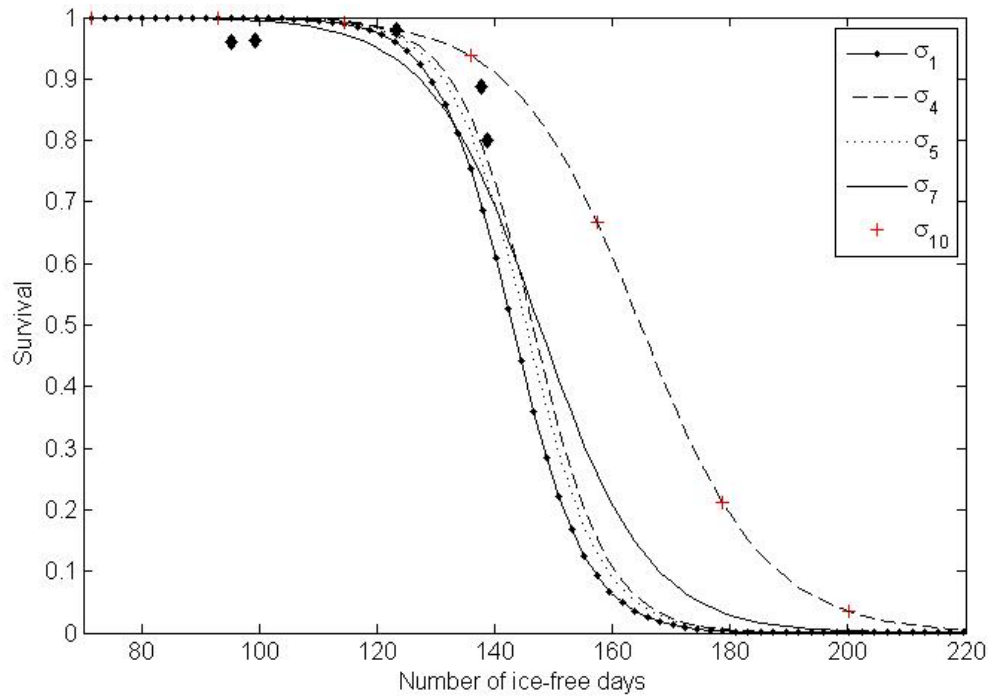
Figure 6. Survival probability (σ_i) as a logistic function of the number of ice-free days per year (i.e., the covariate *ice*) over the waters of the continental shelf within the southern Beaufort Sea management unit averaged over all covariate models with ΔAIC < 4.

Survival curves are plotted for the five stages or combinations of stages with unique estimates: subadult females (stages 1-3), adult females available to breed or with a yearling litter (stages 4 and 6), adult females with a cub-of-the-year litter (stage 5), subadult males (stages 7-9), and adult males (stage 10). Solid diamonds are model-averaged survival estimates for adult females available to breed, σ_4, for non-covariate models for 2001-2005 plotted against the covariate value for that year.
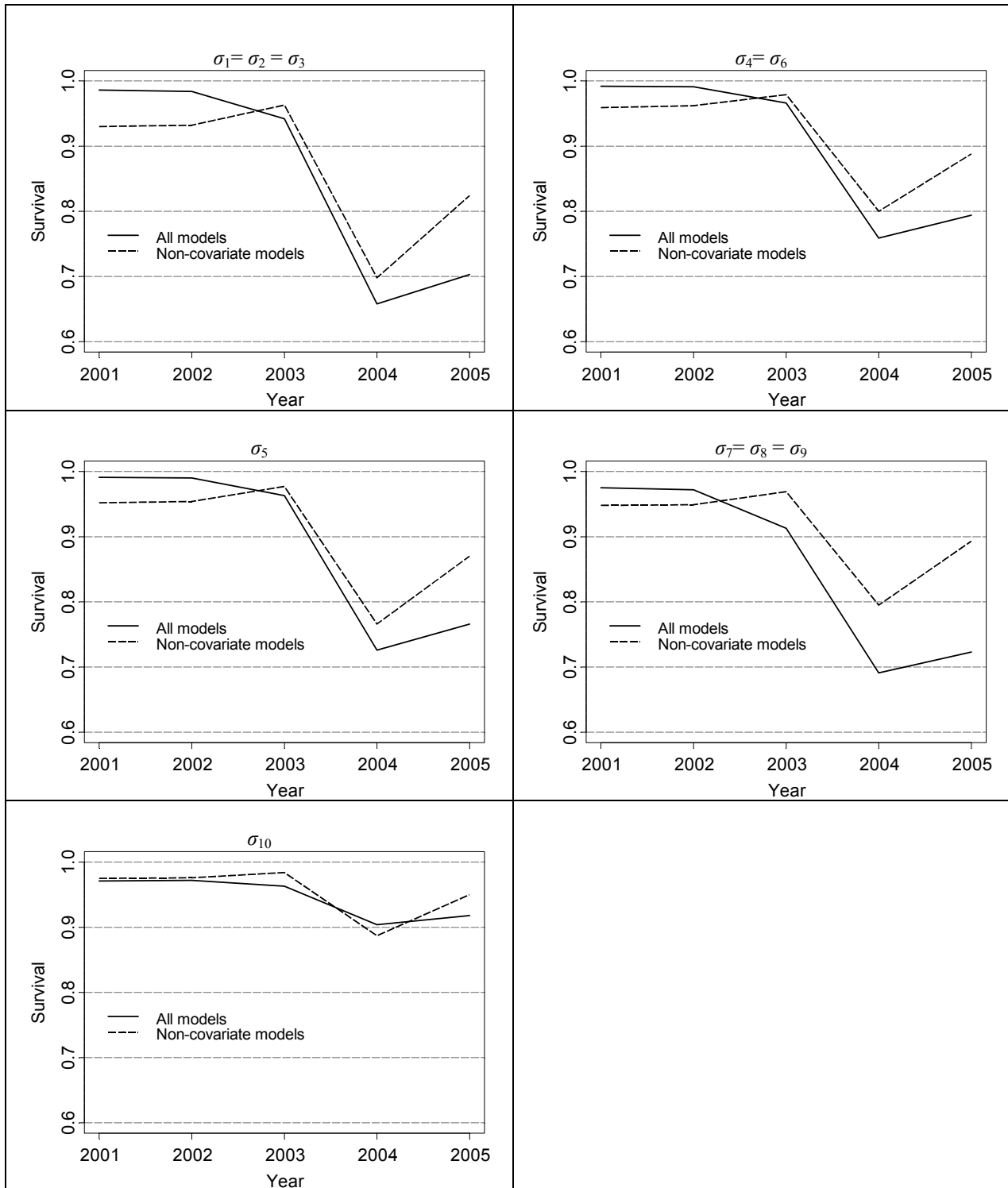
Figure 7. Model-averaged estimates of survival probability (σ_i) for all models with ΔAIC < 4 (solid line) and for non-covariate models (i.e., excluding the covariate *ice*; dashed line) with ΔAIC < 4 for polar bears in the southern Beaufort Sea, 2001-2005.

Survival rates are plotted for the five stages or combinations of stages with unique estimates: subadult females (stages 1-3), adult females available to breed or with a yearling litter (stages 4 and 6), adult females with a cub-of-the-year litter (stage 5), subadult males (stages 7-9), and adult males (stage 10).
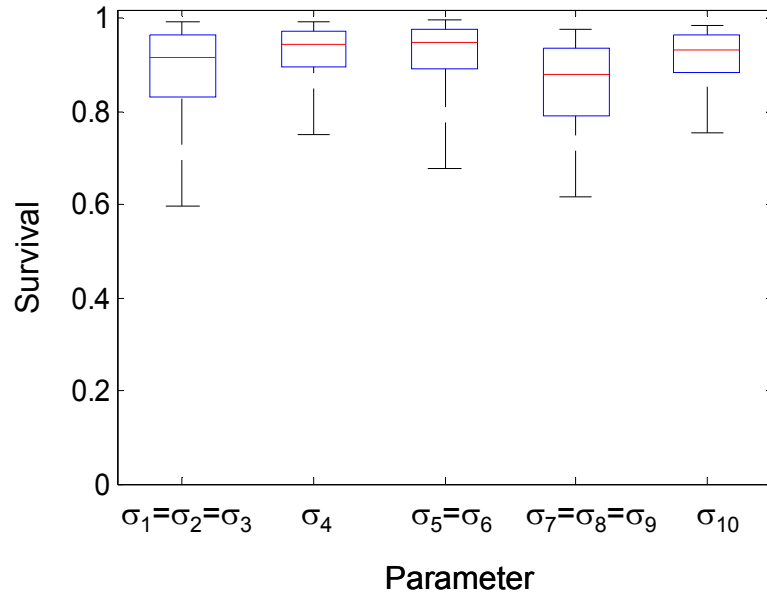
Figure 8. Boxplots showing the median, lower, and upper quartiles of 10,000 bootstrap survival probabilities (σ_i) for all time-invariant models for polar bears in the southern Beaufort Sea, 2001-2005.

Whiskers are 5th and 95th percentiles. Survival probabilities are plotted for the five stages or combinations of stages with unique estimates: subadult females (stages 1-3), adult females available to breed or with a yearling litter (stages 4 and 6), adult females with a COY litter (stage 5), subadult males (stages 7-9), and adult males (stage 10).
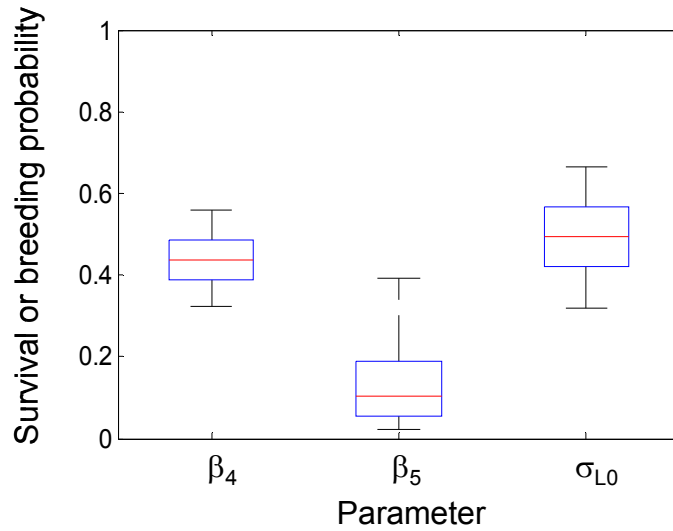
Figure 9. Boxplots showing the median, lower, and upper quartiles of 10,000 bootstrap cub-of-the-year (COY) litter survival (σ_{L0}) and breeding probabilities (β_i) for adult females available to breed (stage 4) and adult females with a COY litter (stage 5) for all time-invariant for polar bears in the southern Beaufort Sea, 2001-2005.

Whiskers are 5th and 95th percentiles
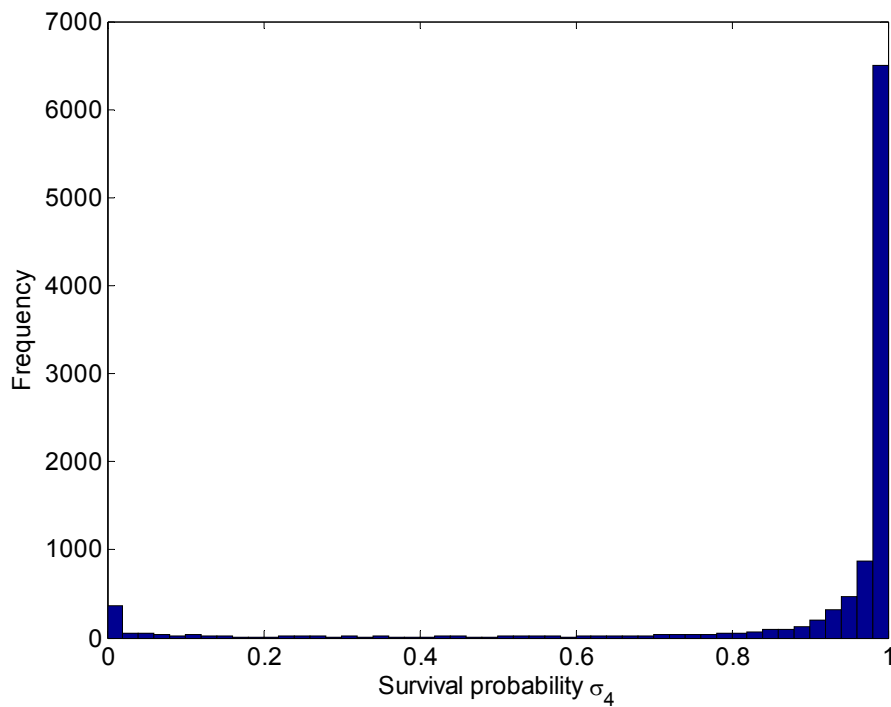
Figure 10. The distribution of 10,000 bootstrap samples of model-averaged estimates of survival probability for adult females available to breed (σ_4), in 2001, for models with ΔAIC < 4.

Note the bimodal nature of the distribution, which makes confidence intervals unreliable as a description of uncertainty.

Table 1. Constraint models for female (F1, F2, F3) and male (M1, M2, M3) survival probabilities implemented in multistate modeling of capture-recapture data for polar bears in the southern Beaufort Sea, 2001-2006.

Constraint model	Survival equalities
F1	$\sigma_1 = \sigma_2 = \sigma_3 = \sigma_4 = \sigma_5 = \sigma_6$
F2	$\sigma_1 = \sigma_2 = \sigma_3, \sigma_4 = \sigma_5 = \sigma_6$
F3	$\sigma_1 = \sigma_2 = \sigma_3, \sigma_4 = \sigma_6, \sigma_5$
M1	$\sigma_1 = \sigma_2 = \sigma_3 = \sigma_7 = \sigma_8 = \sigma_9, \sigma_4 = \sigma_{10}$
M2	$\sigma_7 = \sigma_8 = \sigma_9 = \sigma_{10}$
M3	$\sigma_7 = \sigma_8 = \sigma_9, \sigma_{10}$

Table 2. Equality among state-dependent survival rates for combinations of female and male constraint models implemented in multistate modeling of capture-recapture data for polar bears in the southern Beaufort Sea, 2001-2006.

k is the number of state-dependent survival parameters.

Constraint model	Survival equalities	k
F1, M1	$\sigma_1 = \sigma_2 = \sigma_3 = \sigma_4 = \sigma_5 = \sigma_6 = \sigma_7 = \sigma_8 = \sigma_9 = \sigma_{10}$	1
F1, M2	$\sigma_1 = \sigma_2 = \sigma_3 = \sigma_4 = \sigma_5 = \sigma_6, \sigma_7 = \sigma_8 = \sigma_9 = \sigma_{10}$	2
F1, M3	$\sigma_1 = \sigma_2 = \sigma_3 = \sigma_4 = \sigma_5 = \sigma_6, \sigma_7 = \sigma_8 = \sigma_9, \sigma_{10}$	3
F2, M1	$\sigma_1 = \sigma_2 = \sigma_3 = \sigma_7 = \sigma_8 = \sigma_9, \sigma_4 = \sigma_5 = \sigma_6 = \sigma_{10}$	2
F2, M2	$\sigma_1 = \sigma_2 = \sigma_3, \sigma_4 = \sigma_5 = \sigma_6, \sigma_7 = \sigma_8 = \sigma_9 = \sigma_{10}$	3
F2, M3	$\sigma_1 = \sigma_2 = \sigma_3, \sigma_4 = \sigma_5 = \sigma_6, \sigma_7 = \sigma_8 = \sigma_9, \sigma_{10}$	4
F3, M1	$\sigma_1 = \sigma_2 = \sigma_3 = \sigma_7 = \sigma_8 = \sigma_9, \sigma_5, \sigma_4 = \sigma_6 = \sigma_{10}$	3
F3, M2	$\sigma_1 = \sigma_2 = \sigma_3, \sigma_4 = \sigma_6, \sigma_5, \sigma_7 = \sigma_8 = \sigma_9 = \sigma_{10}$	4
F3, M3	$\sigma_1 = \sigma_2 = \sigma_3, \sigma_4 = \sigma_6, \sigma_5, \sigma_7 = \sigma_8 = \sigma_9, \sigma_{10}$	5

Table 3. Goodness-of-fit tests for a multistate model with four female states (states 1-3, 4, 5, and 6) and two male states (states 7-9 and 10) fitted to capture-recapture data for polar bears in the southern Beaufort Sea, 2001-2006.

The symbol "--" indicates test components with insufficient data.

Test component	χ^2	P	df
WBWA	1.49	0.48	2
3G.SR	30.33	0.11	22
3G.SM	9.43	1.00	30
MITEC	--	--	--
MLTEC	--	--	--
GLOBAL	41.23	0.90	54

Table 4. Number of independent polar bears (age $\geq$ 2 years) captured in the southern Beaufort Sea, 2001-2006.

State	Description	2001	2002	2003	2004	2005	2006
1 to 3	Subadult female (2-4 yr)	5	9	16	39	29	13
4	Adult female ($\geq$ 5 yr) available to breed	17	24	26	52	54	34
5	Adult female with cub-of-the-year litter	10	12	13	21	18	9
6	Adult female with yearling litter	7	6	8	14	13	7
7 to 9	Subadult male (2-4 yr)	3	10	19	27	19	6
10	Adult male ($\geq$ 5 yr)	15	19	55	72	68	49

Table 5. All models with ΔAIC < 4 for multistate modeling of capture-recapture data for polar bears in the southern Beaufort Sea, 2001-2006.

All models included the most supported model for recapture probabilities and additive time variation for breeding probabilities. np = total number of estimated parameters in the model; AIC = Akaike's Information Criterion, ΔAIC = difference in AIC from the minimum AIC value, w = AIC weight.

Survival model	Litter survival model	np	AIC	ΔAIC	w
$\sigma_{F1,M3}$(+ice)	σ_{L0}(.)	16	1187.8	0.0	0.12
$\sigma_{F1,M2}$(+ice)	σ_{L0}(.)	15	1189.4	1.6	0.05
$\sigma_{F2,M1}$(+ice)	σ_{L0}(.)	15	1189.4	1.6	0.05
$\sigma_{F2,M3}$(+ice)	σ_{L0}(.)	17	1189.5	1.6	0.05
$\sigma_{F1,M3}$(ice)	σ_{L0}(.)	18	1189.6	1.8	0.05
$\sigma_{F2,M1}$(+ice)	σ_{L0}(+σ)	15	1189.7	1.9	0.05
$\sigma_{F1,M2}$(ice)	σ_{L0}(.)	16	1189.7	1.9	0.05
$\sigma_{F3,M1}$(+ice)	σ_{L0}(.)	16	1189.8	2.0	0.04
$\sigma_{F2,M1}$(+ice)	σ_{L0}(ice)	16	1190.2	2.4	0.04
$\sigma_{F1,M3}$(ice)	σ_{L0}(ice)	19	1190.4	2.5	0.03
$\sigma_{F1,M1}$(+ice)	σ_{L0}(+σ)	14	1190.4	2.6	0.03
$\sigma_{F1,M3}$(+ice)	σ_{L0}(+σ)	16	1190.5	2.7	0.03
$\sigma_{F1,M2}$(ice)	σ_{L0}(ice)	17	1190.5	2.7	0.03
$\sigma_{F2,M1}$(+ice)	σ_{L0}(+t)	19	1190.6	2.8	0.03
$\sigma_{F1,M2}$(+t)	σ_{L0}(+σ)	18	1190.7	2.8	0.03
$\sigma_{F1,M3}$(ice)	σ_{L0}(+t)	22	1190.8	2.9	0.03
$\sigma_{F1,M1}$(ice)	σ_{L0}(.)	14	1190.8	2.9	0.03
$\sigma_{F2,M1}$(+t)	σ_{L0}(+σ)	18	1190.8	2.9	0.03
$\sigma_{F1,M2}$(ice)	σ_{L0}(+t)	20	1190.9	3.1	0.03
$\sigma_{F3,M1}$(+ice)	σ_{L0}(ice)	17	1191.0	3.1	0.02
$\sigma_{F1,M1}$(+t)	σ_{L0}(+σ)	17	1191.0	3.1	0.02
$\sigma_{F2,M2}$(+ice)	σ_{L0}(.)	16	1191.0	3.2	0.02
$\sigma_{F2,M1}$(ice)	σ_{L0}(.)	16	1191.1	3.3	0.02
$\sigma_{F3,M3}$(+ice)	σ_{L0}(.)	18	1191.4	3.5	0.02
$\sigma_{F3,M1}$(+ice)	σ_{L0}(+t)	20	1191.5	3.7	0.02
$\sigma_{F3,M1}$(+ice)	σ_{L0}(+σ)	16	1191.5	3.7	0.02
$\sigma_{F1,M1}$(ice)	σ_{L0}(ice)	15	1191.6	3.7	0.02
$\sigma_{F3,M1}$(+t)	σ_{L0}(+σ)	19	1191.6	3.7	0.02
$\sigma_{F2,M2}$(+ice)	σ_{L0}(ice)	17	1191.8	4.0	0.02

Table 6. Models with time-invariant survival, cub-of-the-year litter survival, and breeding probabilities for multistate modeling of capture-recapture data for polar bears in the southern Beaufort Sea, 2001-2006.

All models included the most supported model for recapture probabilities. np = total number of estimated parameters in the model; AIC = Akaike's Information Criterion, ΔAIC = difference in AIC from the minimum AIC value, w = AIC weight.

Survival model	np	AIC	ΔAIC	w
$\sigma_{F1,M1}$	9	1196.3	0.0	0.318
$\sigma_{F2,M1}$	10	1197.0	0.7	0.208
$\sigma_{F1,M2}$	10	1198.1	1.7	0.131
$\sigma_{F1,M3}$	11	1198.1	1.8	0.128
$\sigma_{F3,M1}$	11	1199.0	2.7	0.084
$\sigma_{F2,M2}$	11	1200.1	3.7	0.049
$\sigma_{F2,M3}$	12	1200.1	3.8	0.048
$\sigma_{F3,M2}$	12	1202.1	5.7	0.018
$\sigma_{F3,M3}$	13	1202.1	5.8	0.017

APPENDIX A: Model selection and parameter estimates for all models with ΔAIC < 4 for multistate modeling of capture-recapture data for polar bears in the southern Beaufort Sea, 2001-2006.

Table A1. ΔAIC values for models with four types of time dependence in breeding probabilities (β_i) for adult females available to breed (stage 4) and adult females with a cub-of-the-year litter (stage 5).

This represents step 2 of the model selection procedure. For all models, survival (σ) was additive time varying [$\sigma(+t)$]. Cub-of-the-year litter survival (σ_{L0}) was either additive to stage-dependent survival rates [$\sigma_{L0}(+\sigma)$], or time varying and independent from stage-dependent survival rates [$\sigma_{L0}(+t)$]. Values represent ΔAIC with respect to the minimum AIC value in the table. All models have the most supported recapture model structure.

Survival constraint model	$\beta(.)$	$\beta(+ice)$	$\beta(ice)$	$\beta(+t)$	$\beta(.)$	$\beta(+ice)$	$\beta(ice)$	$\beta(+t)$
	Additive time dependence for litter survival [$\sigma_{L0}(+\sigma)$]				Independent time dependence for litter survival [$\sigma_{L0}(+t)$]			
F1,M1	6.3	6.1	7.4	1.8	13.4	13.0	14.4	8.7
F1,M2	5.4	5.5	6.8	1.5	11.2	10.8	12.2	6.5
F1,M3	3.7	3.9	5.1	0.0	8.9	8.5	9.8	4.1
F2,M1	5.7	5.6	6.9	1.6	11.9	11.5	12.9	7.2
F2,M2	7.1	7.2	8.5	3.2	12.8	12.4	13.8	8.1
F2,M3	5.4	5.5	6.8	1.7	10.4	10.0	11.4	5.7
F3,M1	7.3	7.1	8.4	2.4	13.7	13.1	14.5	7.9
F3,M2	8.9	9.2	10.4	5.2	14.4	14.3	15.6	10.1
F3,M3	6.9	7.4	8.6	3.7	11.6	11.8	13.1	7.7

Table A2. ΔAIC values for models representing combinations of survival constraints and time dependence in survival (σ) and cub-of-the-year (COY) litter survival probabilities (σ$_{L0}$).

This represents step 3 of the model selection procedure. For all models, breeding probabilities (β$_i$) for adult females available to breed (stage 4) and adult females with a COY litter (stage 5) were additive time-varying [β$_i$(+t)] and the most supported recapture model was used. Values represent ΔAIC with respect to the minimum AIC value in the table.

Survival constraint model	Equivalent time dependence in survival and COY litter survival				Different time dependence in survival and COY litter survival									
	σ(.) σ$_{L0}$(.)	σ(+ice) σ$_{L0}$(+σ)	σ(ice) σ$_{L0}$(ice)	σ(+t) σ$_{L0}$(+σ)	σ(.) σ$_{L0}$(ice)	σ(.) σ$_{L0}$(+t)	σ(+ice) σ$_{L0}$(.)	σ(+ice) σ$_{L0}$(ice)	σ(+ice) σ$_{L0}$(+t)	σ(ice) σ$_{L0}$(.)	σ(ice) σ$_{L0}$(+t)	σ(+t) σ$_{L0}$(.)	σ(+t) σ$_{L0}$(ice)	σ(+t) σ$_{L0}$(+t)
F1,M1	4.3	2.6	3.7	3.1	5.1	5.5	NA	NA	NA	2.9	4.1	8.9	9.7	10.1
F1,M2	6.1	4.0	2.7	2.8	6.9	7.3	1.6	2.3	2.7	1.9	3.1	6.7	7.5	7.9
F1,M3	6.1	2.7	2.5	1.4	6.9	7.3	0.0	0.8	1.2	1.8	2.9	4.3	5.1	5.5
F2,M1	5.1	1.9	4.1	2.9	5.8	6.2	1.6	2.4	2.8	3.3	4.5	7.4	8.1	8.5
F2,M2	8.1	5.7	6.3	4.6	8.9	9.3	3.2	4.0	4.4	5.6	6.7	8.3	9.1	9.5
F2,M3	8.1	4.4	6.2	3.1	8.9	9.3	1.6	2.4	2.8	5.4	6.6	5.9	6.7	7.1
F3,M1	7.0	3.7	6.1	3.7	7.8	8.2	2.0	3.1	3.7	4.9	6.7	7.5	8.7	9.2
F3,M2	10.1	7.7	10.2	6.6	10.9	11.2	5.1	5.9	6.3	9.3	10.7	10.1	11.0	11.4
F3,M3	10.1	6.3	10.1	5.1	10.9	11.3	3.5	4.4	4.8	9.2	10.5	7.8	8.7	9.1

Table A3. Model-averaged estimates and 90% confidence intervals for recapture probability (p_i, for i = 1, 2…, 10) for all models with ΔAIC < 4.

We report recapture probabilities for females (stages 1-6) and males (stages 7-10), *agency* is a group covariate indicating whether a polar bear was first captured in the U.S. or Canada, *radio* is an individual covariate for polar bears wearing functional radio collars. No male polar bears were instrumented with radio collars. Recapture probabilities for Canada *agency* polar bears were not estimated in 2002 and 2003 (denoted NA), because 2003 was the first year of sampling in the Canadian portion of the southern Beaufort Sea.

State	agency	radio	Estimate					Lower 90% CI					Upper 90% CI				
			2002	2003	2004	2005	2006	2002	2003	2004	2005	2006	2002	2003	2004	2005	2006
1-6	US	No	0.138	0.138	0.138	0.138	0.138	0.104	0.104	0.104	0.104	0.104	0.181	0.181	0.181	0.181	0.181
7-10	US	No	0.170	0.170	0.170	0.170	0.170	0.127	0.127	0.127	0.127	0.127	0.224	0.224	0.224	0.224	0.224
1-6	US	Yes	0.395	0.395	0.395	0.395	0.395	0.308	0.308	0.308	0.308	0.308	0.487	0.487	0.487	0.487	0.487
1-6	Canada	No	NA	NA	0.195	0.195	0.058	NA	NA	0.136	0.136	0.031	NA	NA	0.271	0.271	0.102
7-10	Canada	No	NA	NA	0.236	0.236	0.072	NA	NA	0.168	0.168	0.040	NA	NA	0.322	0.322	0.126
1-6	Canada	Yes	NA	NA	0.496	0.496	0.058	NA	NA	0.370	0.370	0.031	NA	NA	0.625	0.625	0.102

Table A4. Model averaged estimates and 90% bootstrap confidence intervals of survival (σ_i, for i = 1, 2…, 10), cub-of-the-year (COY) litter survival (σ_{L0}), and breeding probabilities (β_i, for i = 4, 5) for all models with ΔAIC < 4.

Parameter estimates are reported for stages or combinations of stages with unique estimates: subadult females (stages 1-3), adult females available to breed or with a yearling litter (stages 4 and 6), adult females with a COY litter (stage 5), subadult males (stages 7-9), and adult males (stage 10).

Parameter	State	Estimate					Lower 90% CI					Upper 90% CI				
		2001	2002	2003	2004	2005	2001	2002	2003	2004	2005	2001	2002	2003	2004	2005
σ	1-3	0.986	0.984	0.942	0.658	0.703	0.048	0.067	0.343	0.406	0.429	1.000	1.000	1.000	0.858	0.904
σ	4, 6	0.992	0.991	0.966	0.759	0.794	0.085	0.115	0.479	0.530	0.569	1.000	1.000	1.000	0.936	0.961
σ	5	0.991	0.990	0.963	0.726	0.766	0.073	0.096	0.427	0.475	0.519	1.000	1.000	1.000	0.913	0.938
σ	7-9	0.975	0.972	0.913	0.691	0.723	0.173	0.202	0.424	0.340	0.362	1.000	1.000	1.000	0.979	0.984
σ	10	0.971	0.972	0.963	0.904	0.918	0.423	0.469	0.647	0.570	0.581	1.000	1.000	1.000	0.997	0.997
σ_{L0}	NA	0.549	0.549	0.536	0.370	0.425	0.284	0.306	0.307	0.074	0.167	0.833	0.811	0.880	0.628	0.681
β	4	0.490	0.540	0.706	0.293	0.090	0.237	0.334	0.471	0.138	0.017	0.745	0.735	0.867	0.512	0.364
β	5	0.152	0.181	0.310	0.072	0.018	0.024	0.030	0.065	0.013	0.002	0.563	0.599	0.739	0.325	0.182

APPENDIX B: Model selection and parameter estimates for non-covariate models with ΔAIC < 4 for multistate modeling of capture-recapture data for polar bears in the southern Beaufort Sea, 2001-2006.

Table B1. Non-covariate models with ΔAIC < 4.

All models included the most supported model for recapture probabilities and additive time variation for breeding probabilities. np = total number of estimated parameters in the model; AIC = Akaike's Information Criterion, ΔAIC = difference in AIC from the minimum AIC value, w = AIC weight.

Survival model	Litter survival model	np	AIC	ΔAIC	w
$\sigma_{F1,M2}(+t)$	$\sigma_{L0}(+\sigma)$	18	1190.70	1.50	0.21
$\sigma_{F2,M1}(+t)$	$\sigma_{L0}(+\sigma)$	18	1190.80	1.60	0.20
$\sigma_{F1,M1}(+t)$	$\sigma_{L0}(+\sigma)$	17	1191.00	1.80	0.19
$\sigma_{F3,M1}(+t)$	$\sigma_{L0}(+\sigma)$	19	1191.60	2.40	0.14
$\sigma_{F1,M1}(.)$	$\sigma_{L0}(.)$	13	1192.20	3.00	0.10
$\sigma_{F2,M2}(+t)$	$\sigma_{L0}(+\sigma)$	19	1192.40	3.20	0.09
$\sigma_{F2,M1}(.)$	$\sigma_{L0}(.)$	14	1192.90	3.70	0.07

Table B2. Model-averaged estimates and 90% confidence intervals for recapture probability (p_i, for i = 1, 2…, 10) for non-covariate models with ΔAIC < 4.

We report recapture probabilities for females (stages 1-6) and males (stages 7-10), *agency* is a group covariate indicating whether a polar bear was first captured in the U.S. or Canada, *radio* is an individual covariate for polar bears wearing functional radio collars. No male polar bears were instrumented with radio collars. Recapture probabilities for Canada *agency* polar bears were not estimated in 2002 and 2003 (denoted NA), because 2003 was the first year of sampling in the Canadian portion of the southern Beaufort Sea.

State	agency	radio	Estimate					Lower 90% CI					Upper 90% CI				
			2002	2003	2004	2005	2006	2002	2003	2004	2005	2006	2002	2003	2004	2005	2006
1-6	US	No	0.133	0.133	0.133	0.133	0.133	0.097	0.097	0.097	0.097	0.097	0.180	0.180	0.180	0.180	0.180
7-10	US	No	0.164	0.164	0.164	0.164	0.164	0.121	0.121	0.121	0.121	0.121	0.214	0.214	0.214	0.214	0.214
1-6	US	Yes	0.392	0.392	0.392	0.392	0.392	0.302	0.302	0.302	0.302	0.302	0.493	0.493	0.493	0.493	0.493
1-6	Canada	No	NA	NA	0.187	0.187	0.051	NA	NA	0.129	0.129	0.028	NA	NA	0.262	0.262	0.094
7-10	Canada	No	NA	NA	0.228	0.228	0.065	NA	NA	0.160	0.160	0.037	NA	NA	0.313	0.313	0.113
1-6	Canada	Yes	NA	NA	0.492	0.492	0.051	NA	NA	0.366	0.366	0.028	NA	NA	0.623	0.623	0.094

Table B3. Model averaged estimates and 90% bootstrap confidence intervals of survival (σ_i, for i = 1, 2…, 10), cub-of-the-year (COY) litter survival (σ_{L0}), and breeding probabilities (β_i, for i = 4, 5) for non-covariate models with ΔAIC < 4.

Parameter estimates are reported for stages or combinations of stages with unique estimates: subadult females (stages 1-3), adult females available to breed or with a yearling litter (stages 4 and 6), adult females with a COY litter (stage 5), subadult males (stages 7-9), and adult males (state 10).

Parameter	State	Estimate					Lower 90% CI					Upper 90% CI				
		2001	2002	2003	2004	2005	2001	2002	2003	2004	2005	2001	2002	2003	2004	2005
σ	1-3	0.930	0.932	0.963	0.698	0.824	0.689	0.692	0.763	0.404	0.299	0.990	0.992	0.998	0.946	0.986
σ	4, 6	0.959	0.962	0.979	0.800	0.888	0.789	0.809	0.858	0.544	0.446	0.996	0.996	0.999	0.969	0.993
σ	5	0.952	0.954	0.977	0.766	0.870	0.760	0.775	0.844	0.488	0.398	0.993	0.994	0.998	0.964	0.990
σ	7-9	0.948	0.949	0.969	0.795	0.893	0.526	0.536	0.668	0.219	0.187	1.000	1.000	1.000	1.000	1.000
σ	10	0.975	0.976	0.984	0.887	0.950	0.619	0.646	0.757	0.224	0.277	1.000	1.000	1.000	1.000	1.000
σ_{L0}	NA	0.559	0.575	0.742	0.204	0.332	0.234	0.271	0.363	0.042	0.065	0.852	0.847	0.950	0.560	0.725
β	4	0.498	0.513	0.721	0.319	0.089	0.246	0.317	0.490	0.150	0.017	0.749	0.710	0.873	0.550	0.357
β	5	0.134	0.142	0.286	0.068	0.015	0.020	0.022	0.054	0.011	0.001	0.545	0.546	0.742	0.325	0.159

APPENDIX C: Model selection and parameter estimates for time-invariant models for multistate modeling of capture-recapture data for polar bears in the southern Beaufort Sea, 2001-2006.

Table C1. Model-averaged estimates and 90% confidence intervals of recapture probability (p_i for i = 1, 2…, 10) for time-invariant multistate models.

We report recapture probabilities for females (stages 1-6) and males (stages 7-10), *agency* is a group covariate indicating whether a polar bear was first captured in the U.S. or Canada, and *radio* is an individual covariate for polar bears wearing functional radio collars. No male polar bears were instrumented with radio collars.

State	*agency*	*radio*	Estimate	Lower 90% CI	Upper 90% CI
1-6	US	No	0.118	0.087	0.157
7-10	US	No	0.172	0.128	0.227
1-6	US	Yes	0.372	0.284	0.470
1-6	Canada	No	0.161	0.114	0.223
7-10	Canada	No	0.229	0.165	0.312
1-6	Canada	Yes	0.459	0.336	0.591

Table C2. Model-averaged estimates and 90% confidence intervals of survival (σ_i, for i = 1, 2…, 10), cub-of-the-year (COY) litter survival (σ_{L0}), and breeding probabilities (β_i, for i = 4, 5) for time-invariant multistate models.

Parameter estimates are reported for stages or combinations of stages with unique estimates: subadult females (stages 1-3), adult females available to breed or with a yearling litter (stages 4 and 6), adult females with a COY litter (stage 5), subadult males (stages 7-9), and adult males (stage 10).

Parameter	State	Estimate	Lower 90% CI	Upper 90% CI
σ	1-3	0.916	0.605	0.995
σ	4, 6	0.947	0.750	0.992
σ	5	0.950	0.679	0.995
σ	7-9	0.870	0.622	0.976
σ	10	0.933	0.753	0.985
σ^{L0}	NA	0.496	0.326	0.668
β	4	0.437	0.325	0.558
β	5	0.104	0.021	0.384