Survival and breeding of polar bears in the southern Beaufort Sea in relation to sea ice

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Summary

1. Observed and predicted declines in Arctic sea ice have raised concerns about marine mammals. In May 2008, the US Fish and Wildlife Service listed polar bears (*Ursus maritimus*) – one of the most ice-dependent marine mammals – as threatened under the US Endangered Species Act.

2. We evaluated the effects of sea ice conditions on vital rates (survival and breeding probabilities) for polar bears in the southern Beaufort Sea. Although sea ice declines in this and other regions of the polar basin have been among the greatest in the Arctic, to date population-level effects of sea ice loss on polar bears have only been identified in western Hudson Bay, near the southern limit of the species' range.

3. We estimated vital rates using multistate capture–recapture models that classified individuals by sex, age and reproductive category. We used multimodel inference to evaluate a range of statistical models, all of which were structurally based on the polar bear life cycle. We estimated parameters by model averaging, and developed a parametric bootstrap procedure to quantify parameter uncertainty.

4. In the most supported models, polar bear survival declined with an increasing number of days per year that waters over the continental shelf were ice free. In 2001–2003, the ice-free period was relatively short (mean 101 days) and adult female survival was high (0·96–0·99, depending on reproductive state). In 2004 and 2005, the ice-free period was longer (mean 135 days) and adult female survival was low (0·73–0·79, depending on reproductive state). Breeding rates and cub litter survival also declined with increasing duration of the ice-free period. Confidence intervals on vital rate estimates were wide.

5. The effects of sea ice loss on polar bears in the southern Beaufort Sea may apply to polar bear populations in other portions of the polar basin that have similar sea ice dynamics and have experienced similar, or more severe, sea ice declines. Our findings therefore are relevant to the extinction risk facing approximately one-third of the world's polar bears.

Key-words: climate change, habitat loss, life-cycle graph, stage-specific vital rates

Introduction

Changes in habitat due to climatic warming have been associated with changes in distribution, phenology and demography for a wide range of species (Walther *et al.* 2002; Parmesan & Yohe 2003). Some of the most pronounced habitat changes are expected to occur at high latitudes (Arctic Climate Impact Assessment 2005), where both observed and forecasted warming are the greatest (Serreze & Francis 2006). In Arctic marine regions, a major effect of warming has been

a decline of 8–9·5% per decade in minimum (i.e. summer) sea ice extent since 1979. Loss of sea ice has been associated with a major ecosystem shift (Grebmeier *et al.* 2006) and has raised concerns about species with obligate relationships to sea ice (Tynan & Demaster 1997; Hunt *et al.* 2002; Gaston, Woo & Hipfner 2003; Moore & Huntington 2008).

Polar bears (*Ursus maritimus*; Kurtén 1964) are among the most ice-dependent Arctic marine mammals (Amstrup 2003; Laidre *et al.* 2008). They require sea ice as a substrate for long-distance movements, mating, some maternal denning, and for access to their primary prey, ringed seals (*Phoca hispida*) and bearded seals (*Erignathus barbatus*). In western

Hudson Bay, Canada, where the sea ice melts completely each year and forces polar bears to spend several months on shore, earlier sea ice breakup has been associated with declines in body condition, reproduction, survival of all age classes except prime-adults and population size (Stirling, Lunn & Iacozza 1999; Regehr *et al.* 2007b). In the southern Beaufort Sea, declines in sea ice extent have been associated with changes in habitat use (Fischbach, Amstrup & Douglas 2007; Durner *et al.* 2009) and indicators of nutritional stress (Regehr, Amstrup & Stirling 2006; Cherry *et al.* 2008; Rode, Amstrup & Regehr 2009). Until now, sea ice loss in the southern Beaufort Sea and other regions of the polar basin has not been linked directly to polar bear population dynamics.

Polar bears in the southern Beaufort Sea strongly prefer sea ice situated over shallow waters of the continental shelf (Durner *et al.* 2009), where biological productivity (Pomeroy 1997; Wang, Cota & Comiso 2005) and seal densities are high (Stirling, Kingsley & Calvert 1982). As sea ice melts each summer, most polar bears in this region remain on the pack ice as it retreats from the coast towards the centre of the polar basin, although at least 4–8% of the population has remained on land in recent years (Schliebe *et al.* 2008). Polar bears on land are largely food deprived, although some may take advantage of beach-cast marine mammals or the carcasses of subsistence-harvested bowhead whales (Bentzen *et al.* 2007). Whether polar bears are on sea ice beyond the continental shelf or on land, they cannot hunt in their preferred habitat. Longer ice-free periods over the continental shelf could thus lead to reduced foraging success, nutritional stress, reproductive failure and starvation.

We used multistate models (e.g. Nichols *et al.* 1992; Fujiwara & Caswell 2002) to estimate stage-specific vital rates, and the relationships between vital rates and sea ice, from capture–recapture data collected on polar bears in the southern Beaufort Sea from 2001 to 2006. The parameters and relationships from this study were used in analyses published elsewhere to evaluate the demography of southern Beaufort

Sea polar bears, and to project future population growth in relation to forecasted sea ice conditions (Hunter *et al.* 2007).

Materials and methods

STUDY AREA AND CAPTURE DATA

The data consisted of 818 captures of 627 individual polar bears in the southern Beaufort Sea population (Fig. 1; Aars, Lunn & Derocher 2006). Details of the study area, field methods and capture sample are provided in Appendix S1.

SEA ICE

The dependence of polar bears on sea ice, particularly for access to seals, suggests their survival and breeding probabilities are linked to sea ice conditions. The southern Beaufort Sea is typically ice covered from October to June and partially or completely ice free from July to September. In recent years, the distance of sea ice retreat from the coast in summer has increased (Comiso 2006a, b; Richter-Menge *et al.* 2006). We developed an environmental covariate, which we denote as $ice(t)$, for use in multistate analyses to evaluate the relationships between polar bear vital rates and sea ice.

We defined $ice(t)$ as the number of days during the calendar year t on which the ice cover in waters over the continental shelf was less than a threshold value. Continental shelf waters were defined as waters within the study area < 300 m deep. We quantified sea ice cover in only this relatively near-shore area because of the strong preference of polar bears (Durner *et al.* 2004, 2009) and ringed seals (Stirling *et al.* 1982) for shallow waters. Ice concentration was derived from passive microwave satellite imagery from the National Snow and Ice Data Center, Boulder, CO, USA (ftp://sidads.colorado.edu/pub/). A day was considered to be below the threshold (we call such days 'ice free') if the mean ice concentration of the 139 imagery grid cells (25×25 km) over the continental shelf was $< 50\%$, based on previous studies suggesting that polar bears abandon the sea ice below this concentration (Stirling *et al.* 1999; Durner *et al.* 2006).

The number of ice-free days per year in waters over the continental shelf increased during the study: $ice(t) = \{90, 94, 119, 135, 134\}$, for $t = 2001,\ldots, 2005$. For analyses, we standardized the values of $ice(t)$
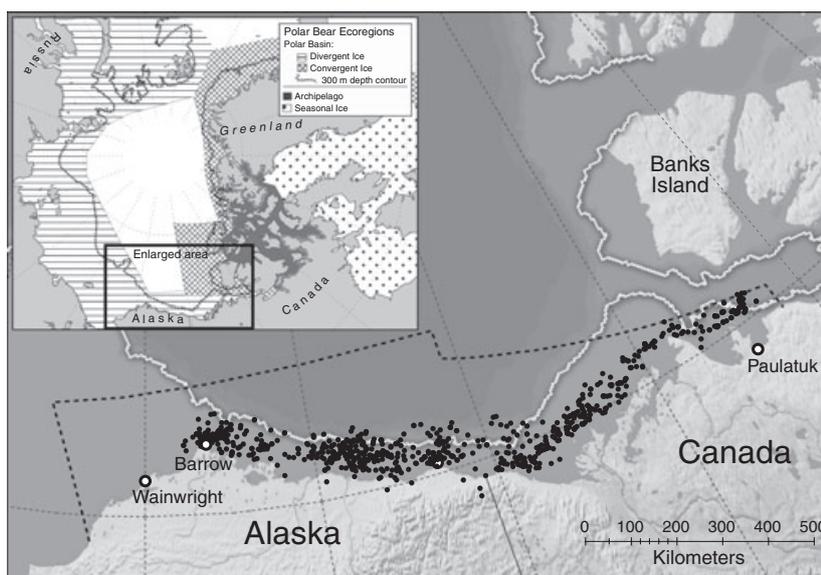

Fig. 1. Locations of polar bears captured in the southern Beaufort Sea, from 2001–2006 (black dots). The dashed line is the population boundary, established by the International Union for the Conservation of Nature and Natural Resources (IUCN) Polar Bear Specialist Group. The white line is the 300 m bathymetry contour. Inset shows the four circumpolar 'ecoregions' for polar bears per Amstrup *et al.* (2008).

by subtracting the mean and dividing by the standard deviation. Longer-term trends in $ice(t)$ and a comparison of this covariate with a more detailed habitat metric are provided in Appendix S2.

MODEL STRUCTURE

Polar bear life-cycle graph

We used multistate capture–recapture models to account for differences in survival, breeding and recapture probabilities between sex, age and reproductive states. These states, hereafter referred to as stages, are defined by the life-cycle graph for polar bears in the southern Beaufort Sea (Fig. 2). Female polar bears in this region are generally first available to mate in April–June of their fifth year (Stirling, Pearson & Bunnell 1976; Lentfer & Hensel 1980). Pregnant females enter dens in autumn, give birth in December–January, and nurse their cubs until they are large enough to leave the den in March–April. Young remain with their mothers for *c*. 2·3 years and are weaned in the spring of their third year (Amstrup 2003).

We modelled the polar bear life cycle with six female and four male stages (Fig. 2). Stages 1, 2 and 3 are subadult females age 2, 3 and 4 years respectively. We included three adult female stages: females available to breed (solitary or accompanied by 2-year-olds; stage 4), females accompanied by cubs (stage 5) and females accompanied by yearlings (stage 6). This structure considered mothers and dependent young (cubs or yearlings) as units rather than individuals, to account for the dependent fates of family groups. Young polar bears were not explicitly included in the life-cycle graph, or the multistate model, until capable of independent survival as 2-year-olds. Stages 7, 8 and 9 were subadult males age 2, 3 and 4 years respectively. Stage 10 included males ≥5 years of age.

Transitions among stages, represented by arcs in the life-cycle graph, depend on three types of parameters: survival, cub litter survival and breeding probabilities. Apparent survival (hereafter referred to as survival), $\sigma_i(t)$, is the probability that an individual in stage i ($i = 1, 2, …, 10$) in the spring of year t survives to the spring of year $t + 1$ and remains in the study area. Losses include natural mortality, harvest and permanent emigration. The probability that at least one member of a litter of cubs 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 cubs in year t, conditional on survival. Because sampling occurred in the spring, $\beta_i(t)$ represents the probability that a female gives birth and that at least one member of the litter survives until den emergence. The breeding probability for a female that already has cubs, $\beta_5(t)$, is conditional on both loss of the litter and survival of the mother. Thus, $\beta_5(t)$ implicitly accounts for the probability that a female with cubs loses her litter early enough in the spring to end lactational anestrous and breed before the end of the mating season. The transition from stages 6 to 5 is biologically possible but did not occur in the data, most likely because yearling survival was high (Amstrup & Durner 1995) and this transition is conditional on the loss of a yearling litter. Thus, the transition from stages 6 to 4 occurs with probability 1 if the female survives, because females with yearlings were available to breed the following year whether their yearlings died or were successfully weaned.

The life-cycle graph defines the structure of the multistate model. Within that structure, many statistical models can be specified by constraining various survival, breeding and recapture probabilities to be equal, or by allowing parameters to vary as functions of time or external covariates. We created a candidate set of multistate models based on biology and study design, and used model selection and model averaging to obtain parameter estimates.

Recapture models

Each stage has a recapture probability, $p_i(t)$, the probability that an animal in stage i is recaptured at time t given that it is alive. We considered three constraint models for recapture probability, based on study design and a previous analysis of the southern Beaufort Sea data (Regehr *et al.* 2006). The first model constrained recapture probabilities to be equal for all stages. The second model included separate recapture probabilities for females (stages 1–6) and males (stages 7–10). This allowed for the possibility that long movements of male polar bears in search of mates (Ramsay & Stirling 1986) might increase our probability of encountering their tracks in the snow. The third model included separate recapture probabilities for adult females with cubs (stage 5), all other females (stages 1–4 and 6) and all males (stages 7–10). This allowed for a different encounter rate for females with cubs, which could occur if family groups avoided areas of active sea ice preferred by other polar bears (Stirling, Andriashek & Calvert 1993).

We considered both time-invariant models and models with additive time variation in recapture probability. Additionally, all recapture models included an individual covariate and a group covariate. The time-varying, individual covariate *radio* indicated whether a polar bear wore a functional radiocollar at each sampling occasion. Because most radiocollared polar bears were located by telemetry, we expected recapture probabilities for these individuals to be high. The group covariate *agency* indicated whether a polar bear was first captured in the USA or Canada. Polar bears in the southern Beaufort Sea exhibit geographic fidelity (Amstrup, McDonald & Durner 2004). Thus, regional differences in weather, polar bear distribution and other variables could lead to different recapture probabilities for bears with fidelity to the USA and Canadian portions of the study area. Finally, all models included a separate recapture probability for Canadian agency bears in 2006, irrespective of time dependence in other recapture probabilities, because of apparently lower densities of polar bears in the Canadian region in 2006.
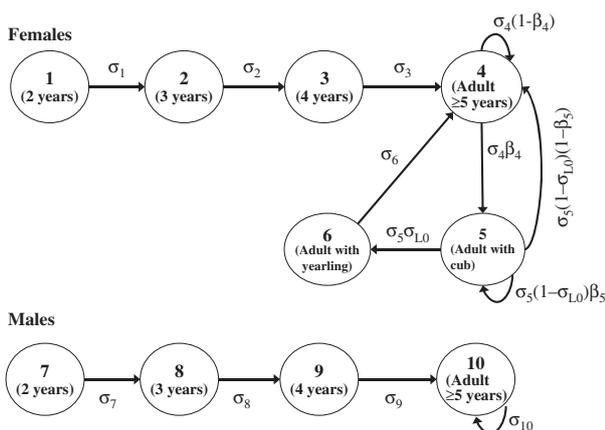

Fig. 2. Ten-stage life-cycle graph for polar bears in the southern Beaufort Sea. Stages 1–6 are females and stages 7–10 are males. $\sigma_i(t)$ is the probability of an individual in stage i surviving from the spring of year t to the spring of year $t + 1$; $\sigma_{L0}(t)$ is the probability of at least one member of a cub litter surviving to the following spring; $\beta_i(t)$ is the probability of an individual in stage i breeding, thus producing a litter of cubs, conditional on survival.

Survival and breeding models

We defined three constraint models for female survival and three constraint models for male survival, for a total of nine combinations of survival constraint models (Table 1). The simplest female model, F1, constrained survival to be equal for all females (stages 1–6). Model F2 assumed equal survival among subadult females (stages 1–3) and equal survival among adult females (stages 4–6). Model F3 assumed equal survival among subadult females and allowed survival of females with cubs (stage 5) to differ from other adult females (stages 4 and 6). This allowed for potential effects of the physiological stress of cub production and fasting experienced by reproducing females (Ramsay & Stirling 1986).

Model M1 constrained subadult male (stages 7–9) survival to be equal to subadult female survival, and adult male (stage 10) survival to be equal to adult female survival. Model M2 assumed equal survival for all males (stages 7–10), 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 constraints between males and females. Models M1 and M3 permitted different survival for adults than subadults. Models M2 and M3 allowed female and male survival to differ due to potential effects of sex-selective harvest (Brower *et al.* 2002), stresses associated with the competition for mates among males (Ramsay & Stirling 1986; Cherry *et al.* 2008) and the physiological stress of reproduction for females.

No equality constraints were imposed on the breeding probabilities β_4 and β_5. We evaluated four types of time dependence in survival and breeding probabilities:

1. Time-invariant models, denoted by (.), where each parameter of a given type was equal for all sampling occasions (for p) or intervals (for σ and β).
2. Additive time variation ($+t$), which allowed the value of one parameter of a given type (e.g. survival of adult

males) to vary freely from year to year and constrained other parameters of the same type (e.g. survival of subadult males) to vary in parallel on the logit scale.

3. Additive covariate time variation ($+ice$), which allowed one parameter of a given type to vary 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.
4. Covariate time variation (ice), which allowed each parameter of a given type to vary as independent logistic functions of the environmental covariate $ice(t)$.

To limit the size of the candidate model set (Burnham & Anderson 2002), we considered only models that imposed the same type of time dependence on all parameters of a given type (p, σ or β). For example, we did not consider a model with time-invariant female survival and time-varying male survival. This acknowledged that previous analyses did not support differences in time dependence among sex and age classes (Regehr *et al.* 2006).

We treated cub litter survival (σ_{L0}) in two ways: (i) as an independent parameter, in which case σ_{L0} could be time-invariant (.), a function of time (t), or a function of the environmental covariate (ice), irrespective of the type of time dependence in the stage-dependent survival parameters (σ_i); and (ii) as a survival parameter, in which case σ_{L0} assumed the same type of time dependence as stage-dependent survival. Thus, if time dependence in σ_i was ($+t$) or ($+ice$), σ_{L0} was additive to the σ_i and was denoted ($+\sigma$).

We used model notation similar to previous capture–recapture analyses (e.g. Lebreton *et al.* 1992). For each parameter type, subscripts denote stages or stage constraint models, and parentheses denote time dependence. For example, the model $\sigma_{F1,M2}(+t)$ $\sigma_{L0}(+\sigma)$ $\beta_{4,5}(ice)$ has additive time variation in σ for the two aggregate stages of the survival constraint models F1,M2; cub litter

Table 1. (a) Constraint models for female (F1, F2, F3) and male (M1, M2, M3) stage-dependent survival probabilities (σ_i, for $i = 1,…, 10$) implemented in multistate modelling. (b) Equalities among survival probabilities for combinations of female and male constraint models

Constraint model	Survival equalities	
(a)		
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	$\sigma_7 = \sigma_8 = \sigma_9, \sigma_{10}$	

Constraint model	Survival equalities	k
(b)		
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

k is the number of parameters. Stages are subadult females (1–3), solitary adult females or adult females with 2-year-olds (4), adult females with a cub litter (5), adult females with a yearling litter (6), subadult males (7–9) and adult males (10).

survival (σ_{L0}) varies additively with stage-dependent survival; and breeding probabilities (β_i) vary independently as functions of the covariate $ice(t)$. Data limitations precluded a fully time- and stage-dependent model. Thus, our most general model was $\sigma_{F3,M3}(+t)$ $\sigma_{L0}(t) \beta_{4,5}(+t)$.

MODEL SELECTION AND MODEL AVERAGING

Before model selection, we analysed the goodness-of-fit of the data to multistate models (Appendix S3). We then used Akaike's information criterion (AIC) to evaluate support for the various statistical models and to calculate model-averaged parameter estimates (Burnham & Anderson 2002). To explore the large potential model space created by multiple equality constraints and types of time dependence, we used a three-step model-selection procedure (Appendix S3). First, we selected the most supported constraint model and type of time dependence for p. Second, we fixed the model for p and selected the most supported type of time dependence for β. Finally, we fixed models for p and β, and jointly evaluated all combinations of constraints and time dependence for σ_i and σ_{L0}.

We derived model-averaged parameter estimates based on AIC weights (Burnham & Anderson 2002, Section 4.2) from two sets of time-varying models. First, the overall best model set containing all models with ΔAIC < 4 (i.e. AIC$_i$ for model i minus the minimum AIC value for the model set). Second, the best non-covariate model set containing models with ΔAIC < 4 that did not include the covariate $ice(t)$. The non-covariate model set provided an evaluation of temporal variation in vital rates that was not influenced by the use of the logistic function to link $ice(t)$ to the life-cycle parameters. We also derived model-averaged results for the best time-invariant models (nine total), which provide the best single estimates of each parameter.

PARAMETER ESTIMATION

We estimated parameters by constructing the likelihood function from individual capture histories (Caswell & Fujiwara 2004) and maximizing the log of the likelihood with respect to the parameters (Appendix S4). We fit models using customized programmes in MATLAB (MathWorks Inc., Natik, MA, USA) with the Tomlab Knitro optimization routine (Forth & Edvall 2006). Before fitting models, we checked parameter estimability by computing the rank of the Jacobian matrix for each candidate model (Hunter & Caswell 2009). All models were full rank, implying that all parameters could be estimated (Appendix S4).

Bootstrap confidence intervals

We developed a parametric bootstrap procedure to evaluate uncertainty in model-averaged parameter estimates (Appendix S5). The procedure generated bootstrap sampling distributions for each parameter, which included sampling uncertainty (as reflected in the covariance matrix for each model), model uncertainty (as reflected in differences in parameter estimates among models) and the relative support for different models (as reflected in the AIC weights). The 90% confidence limits on each parameter were obtained as the 5th and 95th percentiles of the bootstrap sample (Efron & Tibshirani 1993). We used 90% rather than 95% confidence limits because some bootstrap sampling distributions were left-skewed and bimodal, which made more extreme confidence limits unreliable as a description of uncertainty. Standard errors were obtained as the standard deviations of the bootstrap sample for each parameter.

Temporary emigration

Each year, some members of the southern Beaufort Sea population were outside of the relatively near-shore area accessible by helicopter, and therefore temporarily unavailable for capture (Amstrup *et al.* 2004). If such temporary emigration is not random it can bias survival estimates (Kendall, Nichols & Hines 1997; Schaub *et al.* 2004). We used radiotelemetry data collected from 1985 to 2006 in the US portion of the study area to investigate whether, in general, movements with respect to the sampling area were random, or Markovian, in which case the probability of being outside the sampling area depended on an individual's location on the previous occasion. Radiotelemetry data collected during the period of this study alone were too few for a similar investigation. Whether Markovian or random, disproportionate movement outside the sampling area in the last years of a short study could affect parameter estimates. We tested for such a change in movements by comparing the proportion of radio-collared bears that were within the sampling area during capture efforts each year from 2001 to 2006.

Results

VITAL RATES IN RELATION TO SEA ICE

The overall best model set included models in which survival and, in some cases, cub litter survival varied as functions of the sea ice covariate $ice(t)$. This model set contained 29 models with ΔAIC < 4 (Table 2). The weight of evidence in support of a specific model, based on AIC weights, was relatively evenly spread among these models, emphasizing the importance of model averaging to estimate parameters.

Survival

Model-averaged survival estimates from the overall best model set were high for all stages in 2001–2003 and markedly lower in 2004 and 2005 (Fig. 3; Appendix S6). For example, estimated survival of adult females available to breed (stage 4) declined from 0·99 to 0·79 between 2001 and 2005. The decline was less pronounced for adult males than for other stages. Bootstrap confidence intervals showed a large amount of overlap among years. However, the wide confidence intervals in 2001–2003 were the result of left-skewed probability distributions, and most of the probability was centred on the maximum likelihood estimate (note the narrow boxes and long tails in Fig. 3).

There was clear support for the hypothesis that survival is a function of sea ice conditions. Twenty-five of the top 29 models included the covariate $ice(t)$, supporting a link between geophysical aspects of climatic variation and polar bear biology. The sum of the AIC weights was 0·62 for models with additive covariate time variation ($+ice$), and 0·90 for models with additive or independent covariate time variation ($+ice$ or ice; Table 2). Within the observed range in the number of ice-free days over the continental shelf, survival varied little up to about 127 ice-free days (Fig. 4). Beyond that threshold, survival declined as the number of ice-free days increased. This pattern was evident for all stages, with only a slight shifting of the threshold value among stages.

Table 2. Overall best model set (i.e. all models with ΔAIC < 4) for multistate modelling

Survival model	Litter survival model	np	AIC	ΔAIC	w
$\sigma_{F1,M3}(+ice)$	$\sigma_{L0}(.)$	16	1187·8	0·0	0·12
$\sigma_{F1,M2}(+ice)$	$\sigma_{L0}(.)$	15	1189·4	1·6	0·05
$\sigma_{F2,M1}(+ice)$	$\sigma_{L0}(.)$	15	1189·4	1·6	0·05
$\sigma_{F2,M3}(+ice)$	$\sigma_{L0}(.)$	17	1189·5	1·6	0·05
$\sigma_{F1,M3}(ice)$	$\sigma_{L0}(.)$	18	1189·6	1·8	0·05
$\sigma_{F2,M1}(+ice)$	$\sigma_{L0}(+\sigma)$	15	1189·7	1·9	0·05
$\sigma_{F1,M2}(ice)$	$\sigma_{L0}(.)$	16	1189·7	1·9	0·05
$\sigma_{F3,M1}(+ice)$	$\sigma_{L0}(.)$	16	1189·8	2·0	0·04
$\sigma_{F2,M1}(+ice)$	$\sigma_{L0}(ice)$	16	1190·2	2·4	0·04
$\sigma_{F1,M3}(ice)$	$\sigma_{L0}(ice)$	19	1190·4	2·5	0·03
$\sigma_{F1,M1}(+ice)$	$\sigma_{L0}(+\sigma)$	14	1190·4	2·6	0·03
$\sigma_{F1,M3}(+ice)$	$\sigma_{L0}(+\sigma)$	16	1190·5	2·7	0·03
$\sigma_{F1,M2}(ice)$	$\sigma_{L0}(ice)$	17	1190·5	2·7	0·03
$\sigma_{F2,M1}(+ice)$	$\sigma_{L0}(+t)$	19	1190·6	2·8	0·03
$\sigma_{F1,M2}(+t)$	$\sigma_{L0}(+\sigma)$	18	1190·7	2·8	0·03
$\sigma_{F1,M3}(ice)$	$\sigma_{L0}(+t)$	22	1190·8	2·9	0·03
$\sigma_{F1,M1}(ice)$	$\sigma_{L0}(.)$	14	1190·8	2·9	0·03
$\sigma_{F2,M1}(+t)$	$\sigma_{L0}(+\sigma)$	18	1190·8	2·9	0·03
$\sigma_{F1,M2}(ice)$	$\sigma_{L0}(+t)$	20	1190·9	3·1	0·03
$\sigma_{F3,M1}(+ice)$	$\sigma_{L0}(ice)$	17	1191·0	3·1	0·02
$\sigma_{F1,M1}(+t)$	$\sigma_{L0}(+\sigma)$	17	1191·0	3·1	0·02
$\sigma_{F2,M2}(+ice)$	$\sigma_{L0}(.)$	16	1191·0	3·2	0·02
$\sigma_{F2,M1}(ice)$	$\sigma_{L0}(.)$	16	1191·1	3·3	0·02
$\sigma_{F3,M3}(+ice)$	$\sigma_{L0}(.)$	18	1191·4	3·5	0·02
$\sigma_{F3,M1}(+ice)$	$\sigma_{L0}(+t)$	20	1191·5	3·7	0·02
$\sigma_{F3,M1}(+ice)$	$\sigma_{L0}(+\sigma)$	16	1191·5	3·7	0·02
$\sigma_{F1,M1}(ice)$	$\sigma_{L0}(ice)$	15	1191·6	3·7	0·02
$\sigma_{F3,M1}(+t)$	$\sigma_{L0}(+\sigma)$	19	1191·6	3·7	0·02
$\sigma_{F2,M2}(+ice)$	$\sigma_{L0}(ice)$	17	1191·8	4·0	0·02

All models included the most supported model for capture probabilities and additive time variation for breeding probabilities. Survival (σ) constraint models are defined in Table 2. The covariate *ice* is the number of ice-free days per year in waters over the continental shelf. 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 estimates varied slightly among stages, generally with lower values for subadults than adults. Survival estimates were similar for the three adult female reproductive stages (stages 4–6). Nearly 80% of support for the survival constraint models was shared among 4 models: F1,M3; F2,M1; F1,M2 and F3,M1 with 26%, 21%, 19% and 13% of the total support respectively.

Breeding probabilities and cub litter survival

Model-averaged estimates for breeding and cub litter survival probabilities showed a similar pattern to survival, with high values in 2001–2003 and lower values in 2004 and 2005 (Fig. 5). For example, estimated breeding probability of adult females in stage 4 (β_4) declined from 0·49 to 0·09 between 2001 and 2005.

Additive time variation was the most supported type of time dependence in breeding probabilities (Appendix S6). In step 2 of the model-selection procedure, the sum of the AIC weights for models with $\beta_t(+t)$ was 0·68. Although breeding probabilities declined in 2004 and 2005, when annual ice-free periods were long, the relationship between β_i and *ice(t)* was not logistic, probably because of the high values of β_i in 2003.

For cub litter survival, support for a time-invariant model (summed AIC weights = 0·50) was equivalent to the combined support for time-varying models. The sum of the AIC weights 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 2).

Recapture probabilities

Recapture probabilities for polar bears without radiocollars ranged from 0·06 to 0·24 (Appendix S6). The most supported model for *p* was time invariant and allowed *p* to differ for females (stages 1–6) and males (stages 7–10). This model included the individual covariate *radio*, the group covariate *agency* and a separate parameter for Canadian agency bears in 2006.

Temporary emigration

We did not find evidence for Markovian dependence in temporary emigration. From 1985 to 2006, the mean proportion of radiocollared polar bears outside the sampling area during the spring capture period was 0·40 (SE = 0·05). The probability of being located outside the sampling area at $t + 1$ was 0·11 (SE = 0·04) for polar bears inside the sampling area at t, and 0·18 (SE = 0·05) for polar bears outside the sampling area at t. The null hypothesis that being in or out of the sampled area at t did not affect the probability of being in or out at $t + 1$ could not be rejected ($P = 0.30$).

Ten of 19 (53%) and 9 of 14 (64%) radiocollared polar bears were within the sampling area during spring capture operations in 2005 and 2006 respectively. The mean proportion of radiocollared polar bears within the sampling area in 2005 and 2006 (0·59, $n = 33$) was lower than in 2002–2004 (0·76, $n = 32$), although this difference was not statistically significant ($P = 0.14$).

NON-COVARIATE AND TIME-INVARIANT MODELS

Model-averaged parameter estimates from the non-covariate model set were similar to estimates from the overall best model set. Importantly, they exhibited a similar transition from high to low survival and breeding probabilities in years with longer ice-free periods. Survival estimates from the non-covariate model set were slightly lower than estimates from the overall best model set in 2001–2003, and slightly higher in 2004 and 2005 (Regehr *et al.* 2007a). The mean per cent difference for all stages and years was 2·9 (SD = 6·9%). In general, confidence intervals on survival estimates were narrower for the non-covariate model set in 2001–2003. Estimates and confidence intervals for breeding and cub litter survival probabilities were similar between the two models sets.

Fig. 3. Survival probabilities (σ_i, for $i = 1,\ldots, 10$) from the overall best model set for polar bears in the southern Beaufort Sea, 2001–2005. Boxplots show the median, lower and upper quartiles of the bootstrap sampling distribution. Whiskers are 5th and 95th percentiles. Survival probabilities are plotted for the five stages or combinations of stages with unique estimates: subadult females (1–3), adult females available to breed or with a yearling litter (4 and 6), adult females with a cub litter (5), subadult males (7–9) and adult males (10).
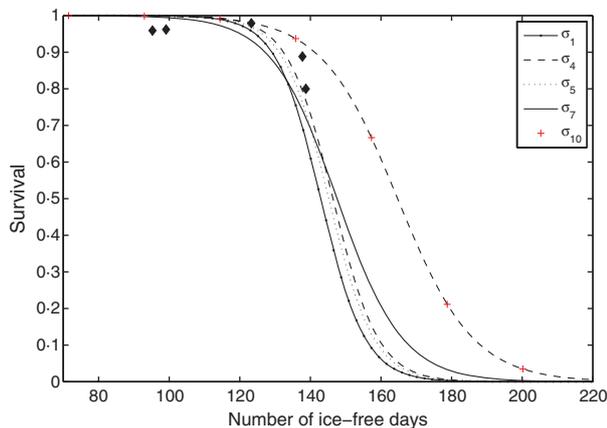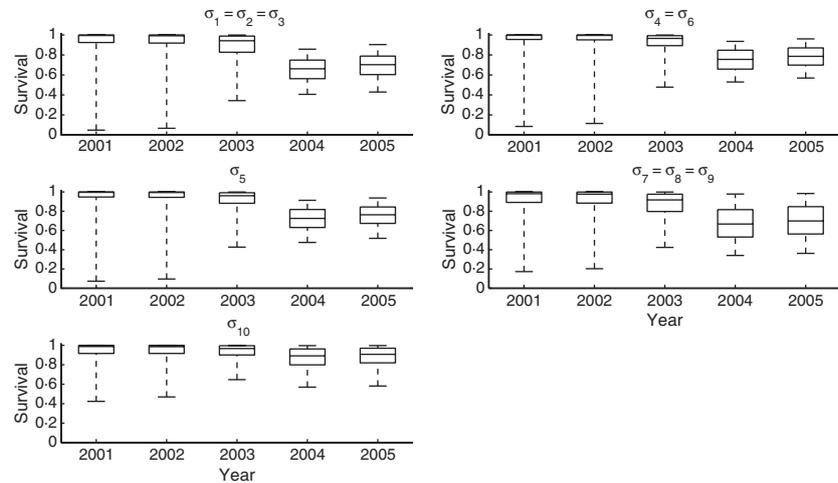
Fig. 4. Survival probability (σ_i, for $i = 1,\ldots, 10$) as a logistic function of the number of ice-free days per year in waters over the continental shelf from 2001 to 2005 [i.e. the covariate $ice(t)$], averaged over the overall best model set. Survival curves are plotted for the five stages or combinations of stages with unique estimates: subadult females (1–3), adult females available to breed or with a yearling litter (4 and 6), adult females with a cub litter (5), subadult males (7–9), and adult males (10). Solid diamonds are model-averaged survival estimates for adult females available to breed (σ_4) for non-covariate models, plotted for comparison with the covariate-based values from the overall best model set.

The time-invariant survival, breeding and cub litter survival probabilities were between the high values for 2001–2003 and the low values for 2004 and 2005 from the time-varying models (Table 3).

Discussion

POLAR BEARS AND SEA ICE

Declines in polar bear survival during the period 2001–2005 were associated with longer annual ice-free periods over the continental shelf. Breeding probabilities also declined, but did not exhibit the same relationship to sea ice conditions as survival. We hypothesize that declining sea ice affects polar bear vital rates primarily via increased nutritional stress. In years with longer ice-free periods, polar bears have less time in summer and autumn to hunt over the continental shelf. Instead, they spend more time on multiyear ice over less-productive Arctic basin waters (Pomeroy 1997), or on land (Schliebe *et al.* 2008). Reduced foraging opportunities associated with longer ice-free periods, whether spent on land or over deep waters, likely cause polar bears to enter the winter in poorer nutritional condition.

Additional evidence suggests that polar bears in the southern Beaufort Sea are under increasing nutritional stress. From 1982 to 2006, body size and body condition for most sex and age classes were positively correlated with the availability of sea ice habitat, and exhibited a statistically significant decline during this period. Cub litter mass and the number of yearlings per female also declined following years with lower availability of sea ice habitat (Rode *et al.* 2009). Using serum biomarkers, Cherry *et al.* (2008) found that a higher proportion of polar bears were fasting in the springs of 2005–2006 (21·4% and 29·3%), compared to 1985–1986 (9·6% and 10·5%). The year 1985 had one of the lowest numbers of ice-free days on record, and 1986 was similar to 2001–2002, so this comparison is particularly relevant to our findings. Finally, the longer ice-free periods in 2004 and 2005 were associated with an unusual number of reports of inefficient foraging behaviours by polar bears (Stirling *et al.* 2008), observations of cannibalism (Amstrup *et al.* 2006) and observations of polar bears that had apparently starved to death (Regehr *et al.* 2006). Historically, such observations were rare or non-existent.

Polar bears depend on sea ice for movement and reproduction, as well as for hunting. In 2004, abrupt retreat of sea ice from the coast, combined with stormy weather, resulted in drownings in the southern Beaufort Sea (Monnett & Gleason 2006). Extensive open water and increased ice roughness, caused by the action of winter storms on thinner ice, may reduce foraging success (Stirling *et al.* 2008), increase the energetic costs of locomotion (Derocher, Lunn & Stirling 2004) and increase the risk of injury or death for cubs. Less stable sea ice also has apparently led to more females denning on land (Fischbach *et al.* 2007). Finally, the increasing seasonal retreat
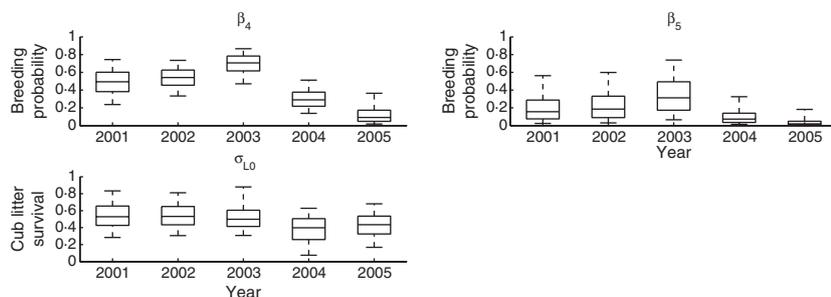
Fig. 5. Cub litter survival (σ_{L0}), breeding probability for adult females available to breed (β_4), and breeding probability for adult females with a cub litter (β_4) from the overall best model set for polar bears in the southern Beaufort Sea, 2001–2005. Boxplots show the median, lower and upper quartiles of the bootstrap sampling distribution. Whiskers are 5th and 95th percentiles.

Table 3. Time-invariant estimates and 90% confidence intervals for survival (σ_i, for $i = 1,\ldots, 10$), cub litter survival(σ_{L0}), and breeding probabilities (β_i, for $i = 4, 5$) for multistate capture–recapture modelling for polar bears in the southern Beaufort Sea, 2001–2006

Parameter	Stage	Estimate	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

Stages are subadult females (1–3), solitary adult females or adult females with two-year-olds (4), adult females with a cub litter (5), adult females with a yearling litter (6), subadult males (7–9) and adult males (10).

of sea ice may require polar bears to travel farther between multiyear pack ice, where most animals spend the summer, and the onshore denning areas or coastal hunting areas that they use at other times of the year (Bergen *et al.* 2007).

Climatic warming is likely also to have indirect ecological effects on Arctic marine mammals (Tynan & Demaster 1997; Derocher *et al.* 2004; Laidre *et al.* 2008). Polar bears are susceptible to changes in the abundance and age structure of seal populations (Stirling 2002). In particular, mortality rates of ringed seal pups, the most important component of the polar bear's diet, may increase in years when the sea ice breaks up early. Pup mortality also may increase when warmer temperatures lead to rains early in the breeding season, which can melt the under-snow lairs that pups need for shelter (Smith & Harwood 2001; Stirling & Smith 2004). In some regions, climatic warming may temporarily increase the availability of alternate prey species for polar bears, such as recent increases in harp seals on the sea ice in Davis Strait (Iverson, Stirling & Lang 2006) and walruses in coastal haul-outs in the Chukchi Sea (N. Ovsyanikov, unpublished data). As top predators, polar bears can be expected to integrate ecological changes at lower trophic levels, which have been documented in northern Hudson Bay (Gaston *et al.* 2003) and may be occurring in other parts of the Arctic. Simultaneous with ecological changes, polar bears face increasing potential for conflicts with humans in a warming Arctic, as industrial activity expands (Arctic Climate Impact Assessment 2005), longer ice-free periods force polar bears to spend more time on land

(Schliebe *et al.* 2008) and nutritional stress encourages polar bears to seek anthropogenic food sources (Regehr *et al.* 2007b).

Our time-varying survival estimates for 2001–2003 were similar to estimates for adult females in the southern Beaufort Sea from 1981 to 1992 (0·969; Amstrup & Durner 1995) and similar to, or higher than, estimates for adult females in other populations (0·940–0·997; Table 2 in Aars *et al.* 2006). Our survival estimates for 2004 and 2005 were lower than have been previously reported for polar bears. In an earlier, single-state analysis of capture–recapture data from the southern Beaufort Sea, Regehr *et al.* (2006) also found that survival may have declined from 2001 to 2005. Although Regehr *et al.* (2006) found weak support for a relationship between survival and the covariate *ice*(*t*), comparison of the two analyses is complicated by different model structures and data sets. We may have been more successful in detecting sea ice effects because the multistate models included different reproductive stages for adult females and because, unlike Regehr *et al.* (2006), we evaluated models with different recapture probabilities for females and males.

Our conclusions are strengthened by the use of multimodel inference and model averaging, and by agreement between models with parametric dependence on the environmental covariate *ice*(*t*) and models that allowed parameters to vary freely over time. Multimodel inference is particularly important for estimating statistical relationships from short time series of data in a variable environment. By permitting recapture probabilities to vary by sex, reproductive stage, tagging method and region of capture, we accounted for sources of heterogeneity often present in capture–recapture studies. Nonetheless, some individual heterogeneity may have resulted from the movement of polar bears with respect to the sampling area. For example, polar bears with small home ranges centred in the core of the sampling area may have been more likely to be captured than those with home ranges that were either large or centred near the edge of the sampling area. Our analysis of radiotelemetry data collected from 1985 to 2006 suggests emigration patterns in the southern Beaufort Sea are random, making it unlikely that survival estimates in the current study were biased due to Markovian dependence in temporary emigration (Kendall *et al.* 1997; Kendall & Nichols 2002; Schaub *et al.* 2004). Nonetheless, sea ice loss and increased variability in annual sea ice extent have the potential to affect polar bear distribution and movements, including the possible breakdown of historic population

boundaries (Derocher *et al*. 2004). Although statistical tests for within-study changes in emigration were not significant, our ability to evaluate the type of emigration that occurred 2001–2006, and its potential effects on parameter estimates, was limited by the small sample size of radiotelemetry data. The lower-point estimate of the proportion of radiocollared polar bears inside the sampling area in 2005 and 2006, compared to 2002–2004, suggests caution in interpreting the magnitude of estimated declines in apparent survival.

IMPLICATIONS FOR CONSERVATION

The apparent dependence of polar bear vital rates on sea ice is relevant to evaluations of conservation status for this and other species. Moore & Huntington (2008) classify Arctic marine mammals into ice-obligate species (polar bear, walrus, bearded and ringed seals) and ice-associated species (beluga and bowhead whales; narwhal; harp, hooded, ribbon and spotted seals). Our results generalize most readily to ice-obligate marine mammals and to subarctic ice seals (see the analysis of sensitivity to climate change in Laidre *et al*. 2008). However, even species that depend directly on sea ice as a platform for foraging and other aspects of their life history may exhibit different responses to sea ice loss. Walrus, for example, are generally limited to foraging in waters < 100 m deep. Their demography will be most affected by the distribution of sea ice over these shallow waters, although some walrus may be buffered from the effects of sea ice loss by their ability to use terrestrial haul-outs between feeding excursions (Sheffield & Grebmeier 2009). Additional demographic studies are needed to understand the impacts of climate change on Arctic marine mammals.

We believe that the analyses reported here and in a companion manuscript (Hunter *et al*. 2007) provide a template for assessments of extinction risk for other species with similar types of data. The first step is to estimate vital rates, which determine the potential for population growth, and to evaluate the relationships between vital rates and environmental conditions. If environmental conditions are expected to change, both the environment-dependent vital rates and the forecasted range of environmental conditions can be incorporated into a demographic model to project future population status. For polar bears in the southern Beaufort Sea, Hunter *et al*. (2007) used matrix-based projection models (e.g. Caswell 2001) to combine the vital rates estimated here with sea ice forecasts. That analysis indicated that the southern Beaufort Sea population faces a high risk of extirpation within the 21st century if sea ice loss continues as projected.

Sea ice declines and the associated impacts on marine mammals are expected to vary across the Arctic (Laidre *et al*. 2008; Moore & Huntington 2008; Thiemann, Derocher & Stirling 2008). Units based on taxonomy, genetic distinction, ecology and distribution are common in evaluations of conservation status (Green 2005), and can be used to extrapolate from well-studied populations to larger portions of a species' range. Amstrup, Marcot & Douglas (2008) used regional differences in sea ice dynamics and ecology to identify four 'eco-regions' for polar bears. The Divergent Ice Ecoregion, characterized by the formation and subsequent melting or advection of annual sea ice, includes the southern Beaufort, Chukchi, Laptev, Kara and Barents seas (Fig. 1). It is reasonable to expect that the relationships between sea ice loss and polar bears in the southern Beaufort Sea also apply to other portions of the Divergent Ice Ecoregion, where sea ice loss has been greater (Meier, Stroeve & Fetterer 2007) but data on polar bears are not available. Sea ice declines throughout the Divergent Ice Ecoregion are projected to be long term and severe (Amstrup *et al*. 2008). Because this region includes *c*. 7500 polar bears, one-third of the current world population (Aars *et al*. 2006), our findings in the southern Beaufort Sea were considered relevant to the extinction risk facing a large portion of the world's polar bears. This contributed to the listing, in May 2008, of polar bears as a threatened species under the US Endangered Species Act.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1. Study area, field methods and capture data.
Appendix S2. Sea ice covariate details.
Appendix S3. Goodness-of-fit and model-selection details.
Appendix S4. Multistate modelling and parameter estimation details.
Appendix S5. Bootstrap confidence interval details.
Appendix S6. Model-selection results and parameter estimates for the overall best model set.

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