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Polar Bear Population Status in the Southern Beaufort Sea

Open-File Report 2006–1337

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U.S. Geological Survey, Reston, Virginia: 2006

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Conversion Factors

Multiply	By	To obtain
kilometer (km)	0.6214	mile (mi)
meter (m)	3.281	foot (ft)
meter (m)	1.094	yard (yd)

Abbreviations, Acronyms, and Symbols

Abbreviations, Acronyms, and Symbols	Meaning
AIC	Akaike's information criterion
CI	confidence interval
CJS	Cormack-Jolly-Seber
COYs	cubs of the year
CWS	Canadian Wildlife Service
GOF	goodness-of-fit
PRB	percent relative bias
QAIC	quasi-likelihood adjustment of AIC
SE	standard error
SBS	southern Beaufort Sea
USGS	U.S. Geological Survey

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Polar Bear Population Status in the Southern Beaufort Sea

By Eric V. Regehr[1], Steven C. Amstrup[1], and Ian Stirling[2]

Abstract

Polar bears depend entirely on sea ice for survival. In recent years, a warming climate has caused major changes in the Arctic sea ice environment, leading to concerns regarding the status of polar bear populations. Here we present findings from long-term studies of polar bears in the southern Beaufort Sea (SBS) region of the U.S. and Canada, which are relevant to these concerns. We applied open population capture-recapture models to data collected from 2001 to 2006, and estimated there were 1,526 (95% CI = 1,211; 1,841) polar bears in the SBS region in 2006. The number of polar bears in this region was previously estimated to be approximately 1,800. Because precision of earlier estimates was low, our current estimate of population size and the earlier ones cannot be statistically differentiated. For the 2001–06 period, the best fitting capture-recapture model provided estimates of total apparent survival of 0.43 for cubs of the year (COYs), and 0.92 for all polar bears older than COYs. Because the survival rates for older polar bears included multiple sex and age strata, they could not be compared to previous estimates. Survival rates for COYs, however, were significantly lower than estimates derived in earlier studies (P = 0.03). The lower survival of COYs was corroborated by a comparison of the number of COYs per adult female for periods before (1967–89) and after (1990–2006) the winter of 1989–90, when warming temperatures and altered atmospheric circulation caused an abrupt change in sea ice conditions in the Arctic basin. In the latter period, there were significantly more COYs per adult female in the spring (P = 0.02), and significantly fewer COYs per adult female in the autumn (P < 0.001). Apparently, cub production was higher in the latter period, but fewer cubs survived beyond the first 6 months of life. Parallel with declining survival, skull measurements suggested that COYs captured from 1990 to 2006 were smaller than those captured before 1990. Similarly, both skull measurements and body weights suggested that adult males captured from 1990 to 2006 were smaller than those captured before 1990. The smaller stature of males was especially notable because it corresponded with a higher mean age of adult males. Male polar bears continue to grow into their teens, and if adequately nourished, the older males captured in the latter period should have been larger than those captured earlier. In western Hudson Bay, Canada, a significant decline in population size was preceded by observed declines in cub survival and physical stature. The evidence of declining recruitment and body size reported here, therefore, suggests vigilance regarding the future of polar bears in the SBS region.

Introduction

Polar bears are entirely dependent on sea ice as a platform to access the marine mammals that provide their nutritional needs (Amstrup, 2003). In recent years, a warming climate and changing atmospheric circulation patterns have resulted in major changes in the Arctic sea ice environment (Comiso, 2002; Rigor and others, 2002; Comiso and Parkinson, 2004; Rigor and Wallace, 2004; Stroeve and others, 2005). Polar bears residing in the southern Beaufort Sea (SBS) region of the U.S. and Canada have been studied since 1967. Results of these studies provide insights into how changes in the environment may affect the status of polar bears in this region.

Radiotelemetry data collected from female polar bears during the mid-1980s suggested that the SBS region contained a single population of polar bears, extending from west of Barrow, Alaska, to east of Paulatuk, Northwest Territories, Canada (Amstrup and others, 1986; Amstrup and DeMaster, 1988). In response to that finding, an agreement was established between U.S. and Canadian user groups to cooperatively manage the hunting of polar bears throughout the entire SBS region (Brower and others, 2002).

To determine sustainable harvest levels, early polar bear research in the SBS region was focused on estimating population size and developing indices of recruitment and survival which could be used to evaluate trends in population status. The size of the SBS polar bear population was first estimated to be approximately 1,800 animals in 1986 (Amstrup and others, 1986). Survival rates of adult females and dependent young were estimated from radiotelemetry data collected from the early 1980s to the mid-1990s (Amstrup

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and Durner, 1995). Throughout the 1980s and early 1990s, empirical observations such as the frequency of encounters of polar bears during research flights over the sea ice, increased sightings of polar bears near onshore human settlements, and increasing numbers of maternal dens observed on land, suggested that the population of the SBS region was increasing. Because of interest among user groups in a larger harvest, population size and trend were re-assessed in the late 1990s (Amstrup and others, 2001a; McDonald and Amstrup, 2001). That analysis was limited to female polar bears because research objectives resulted in the under-sampling of males in some years. The estimate of 1,180 females (95% CI = 635; 1,725) for the late 1980s was consistent with the previous estimate of at least 1,800 total polar bears (i.e., females and males) in the SBS region at that time (Amstrup and others, 1986). For the late 1990s, the estimated number of females developed by Amstrup and others (2001a) suggested that the total population may have increased to as many as 2,500 polar bears. However, because of interannual variation in sample size and other sources of heterogeneity within the data for the late 1990s, the estimate of 2,500 polar bears was not considered reliable. Therefore, managers took a conservative approach and harvest decisions continued to be based on a total population size of 1,800 polar bears in the SBS region.

We initiated a new study in 2001, to re-assess the status of the SBS polar bear population and to address the potential effects, on polar bear status, of changing sea ice conditions in the Arctic basin. Here we present estimates of survival and population size derived from capture-recapture data collected from 2001 to 2006, and compare these estimates to those developed earlier. We also document changes in the productivity and physical stature of polar bears using data collected from the late 1960s through the present.

Methods

Polar bear research began in the SBS region in 1967, and has continued through 2006. We captured polar bears by injecting the drugs tiletamine hydrochloride plus zolazepam hydrochloride (Telazol®, Warner-Lambert Co.), using projectile syringes fired from helicopters (Stirling and others, 1989). All captured polar bears were ear-tagged with a unique identification number, and tattooed on both sides of the inner surface of the upper lip. We determined body weight of captured bears with a spring or dynamometer scale and recorded various body measurements, including the condylobasal length and zygomatic width of the skull. Age was determined for all captured bears. Cubs-of-the-year (COYs; approximately 3 months old in spring) were always with their mothers and could be visually aged without error (Ramsay and Stirling, 1988). A vestigial premolar was extracted from other captured polar bears and age was

estimated by counting cementum annuli (Calvert and Ramsay, 1998). Beginning in 1981, selected adult females were fitted with radio-tracking collars that allowed us to relocate them from aircraft. All capture and marking protocols were approved by independent animal care and welfare committees.

Capture-Recapture Analysis

For the purpose of estimating population size and survival rates in this study, we captured polar bears in coastal areas of the SBS region, from Point Barrow, Alaska (about 157°W) to Cape Parry, Northwest Territories, Canada (about 125°W). Capture-recapture data were collected by the U.S. Geological Survey (USGS) in the U.S. portion of the SBS region, from late March through early May of 2001–06, and in October and November of 2001. Additional capture-recapture data were collected by the Canadian Wildlife Service (CWS) in the Canadian portion of the SBS region in April and May of 2003–06 (fig. 1). In each year from 2001 to 2006, our objectives were to maximize sample size, maximize the geographic distribution of capture effort throughout the SBS region, and ensure that all polar bears in the study area were equally exposed to capture efforts. Sample sizes in many years before 2001 were approximately equivalent to those of 2001–06, but sampling strategies and time-frames of capture varied among many early years of study. Therefore, all animals were not subjected to equal capture effort in many of those early years. Previous studies have shown the difficulties of estimating demographic parameters from data collected under a non-random sampling protocol that varied among years, and did not include the entire study area (Amstrup, 1995; Amstrup and others, 2001a; McDonald and Amstrup, 2001). Therefore, we limited the current capture-recapture analyses to data collected from 2001 to 2006.

In our analysis of survival and population size for the 2001–06 period, we included data for polar bears encountered by standard search methods (polar bears encountered randomly, while flying in polar bear habitat), and data for polar bears encountered by radiotelemetry. We use the term "capture" to refer to the physical capture of a polar bear, or the visual sighting of a polar bear for which the individual identity was known via radiotelemetry. Although some polar bears were captured multiple times per year, we used a maximum of one capture per bear per year in our analyses.

The data for each polar bear were summarized as an individual capture history and covariates. For example, bear 20579 had the capture history {101100}, where 0 indicates not captured at sampling occasion j, and 1 indicates captured and released alive at sampling occasion j ($j = 1, 2… k$). Individual covariates for this polar bear included *sex* = female, *age* (at-first-capture) = 0 yr, and *agency* = U.S., based on which agency originally captured bear 20579. The time-dependent covariate *radio* indicated when adult female polar bears were
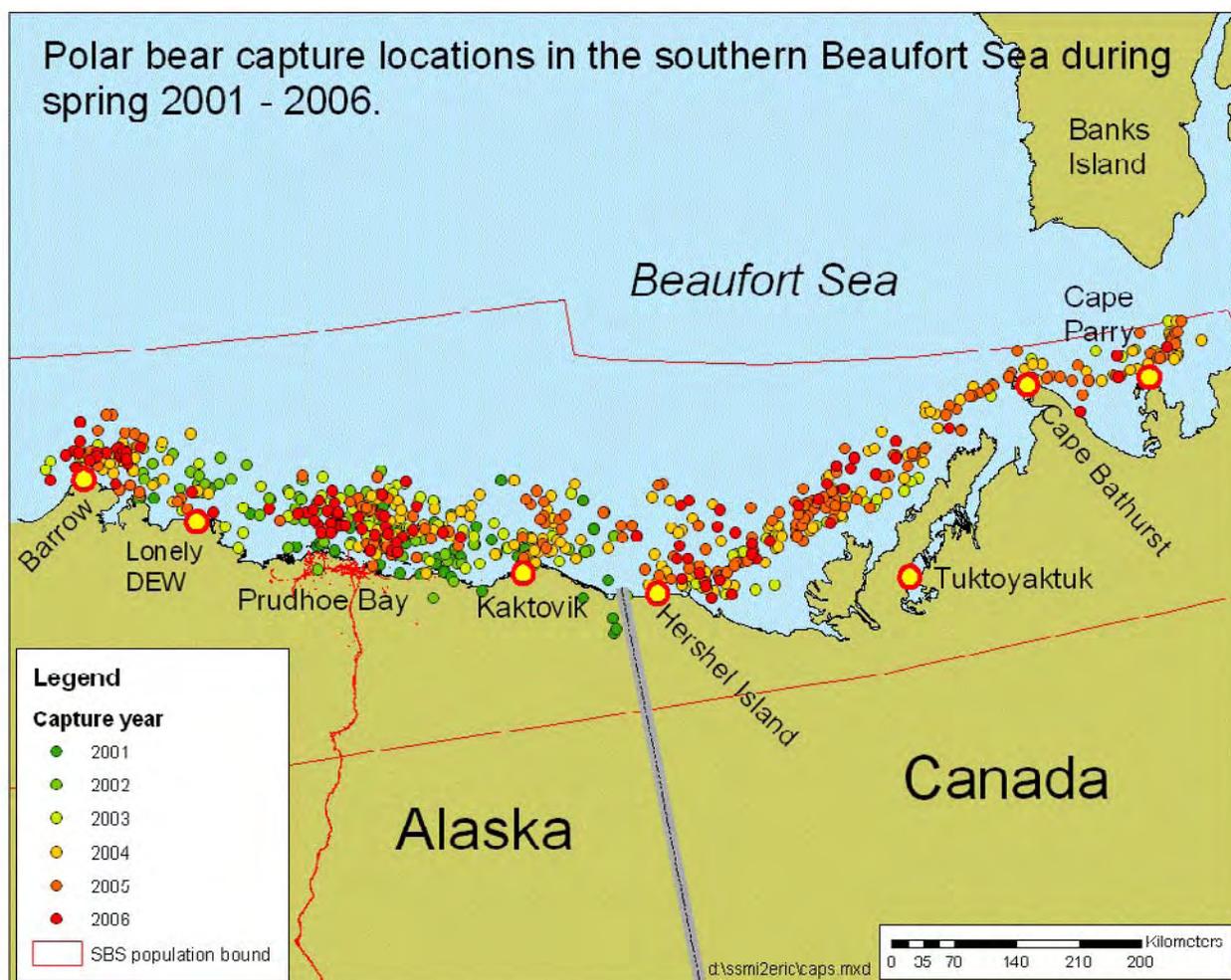
Figure 1.   Distribution of polar bear captures from 2001 to 2006 that were included in capture-recapture estimates of survival and population size.

available for recapture by radiotelemetry, based on radiocollar deployment information and real-time satellite telemetry data (Harris and others, 1990). Dependent young that accompanied radiocollared females also were considered to be available for recapture by radiotelemetry.

To investigate the potential relationship between sea ice and polar bear survival, we quantified spatiotemporal trends in sea ice coverage from 2001 to 2006 using sea ice concentration data for 25 × 25 km grid cells, derived from passive microwave imagery using the NASA Team algorithm (National Snow and Ice Data Center, Boulder, Co., ftp://sidads.colorado.edu/pub/). First, we defined an area of preferred polar bear habitat as all grid cells in the SBS population boundary with an ocean depth of less than 300 m (International Bathymetric Chart of the Arctic Ocean, http://www.ngdc.noaa.gov/mgg/bathymetry/arctic/arctic.html). We then averaged daily ice concentrations in the area of preferred habitat, and calculated the number of days during each calendar year j that the mean ice concentration was

less than 50% (x_j). We derived the covariate ice_j for use in capture-recapture models, by standardizing x_j via the formula: $ice_j = (x_j - \bar{x}) / SD(x)$, where $\bar{x}$ is the mean and $SD(x)$ is the standard deviation of x_j for j = 2000–05 (Franklin, 2001).

Goodness-of-Fit

The valid estimation of demographic parameters from capture-recapture data requires an analysis of goodness-of-fit (GOF), to determine how well the data meet the assumptions of the model being used (Lebreton and others, 1992; Cooch and White, 2005, Chapter 5; McDonald and others, 2005). Because no single method is sufficient in practice, we used multiple methods to obtain a thorough consideration of GOF. First, we partitioned the data into sex- and age-based strata and used program RELEASE (Burnham and others, 1987) to investigate patterns in the data. Second, we used the parametric bootstrap procedure in program MARK (White and Burnham, 1999) to evaluate the fit of a general model,

and to estimate a bootstrapped value of the variance inflation factor $\hat{c}$ (White and others, 2001). We also used MARK to estimate a value of median $\hat{c}$ (Cooch and White, 2005: Chapter 5). Third, we estimated a "biological" $\hat{c}$ based on the lack of independence among the fates of adult female polar bears and their dependent young, via the formula: $\hat{c} = n/(n - n_c)$, where n is the total number of captures, and n_c is the number of captures of dependent young (Taylor and others, 2002). Finally, we note that radiotelemetry captures present methodological difficulties for program RELEASE and the parametric bootstrap, and were excluded from the GOF analysis. However, it is unlikely that this lead to an underestimation of $\hat{c}$, because all reasonable capture-recapture models explicitly allowed for telemetry-based variation in recapture probabilities by incorporating the individual covariate *radio*.

Estimating Survival Rate and Population Size

We estimated survival using Cormack-Jolly-Seber (CJS) models (Lebreton and others, 1992) fitted to the data with R-language software for the "general regression" approach to capture-recapture (McDonald and others, 2005, http://www.west-inc.com). The CJS model conditions on first capture, and estimates the probabilities of survival (φ) and recapture (*p*) most likely to produce the observed capture histories. Estimates of φ_j represent total apparent survival, which is the cumulative probability of remaining alive and in the study area between sampling occasions *j* and *j*+1.

We considered models that allowed φ to vary by time, sex, and four age classes: COYs, yearlings, subadults (2–4 yr), and adults (5+ yr). We modeled φ_j as a function of ice_j and ice_{j-1}, to investigate the hypothesis that reduced sea ice coverage would affect polar bear survival by limiting access to the biologically productive waters over the continental shelf. We also fitted models with a generic linear trend that allowed for a monotonic change in survival. Finally, we considered an additive effect in φ following the occasion of first capture for male subadults and adults, based on the indication of "transient" males within the population from program RELEASE (Pradel and others, 1997). Transients are defined as individuals that entered the study population, were captured once, and subsequently emigrated. In theory, the influence of these individuals on estimates of apparent survival can be mitigated using a parameterization for φ that allows the transients to "die" (i.e., leave the study area) following first capture.

For recapture probability (*p*), we considered models that included the individual covariate *agency*, and the covariate *effort*, which was based on the annual number of helicopter hours flown in capture operations. For example, an interaction between *agency* and *effort* produced estimates of p_j for "U.S." bears as a function of USGS capture effort, and separate estimates of p_j for "Canadian" bears as a function of CWS capture effort. This approach was based on evidence that individual polar bears exhibit geographic fidelity in the SBS region (Amstrup and others, 2004, 2005), which we hypothesized would lead to a correlation between where an individual was originally captured, and where it was available for recapture. We considered models with time-dependence in *p*, and with interactions between time-dependence and *agency*. This reflected the hypothesis that p_j varied as a cumulative function of sampling effort, general fidelity patterns, and unknown ecological phenomena (e.g., interannual variation in the spatial distribution of polar bears, as influenced by sea ice conditions). We also considered models with an intermediate form of time-dependence in *p*, based on observations by the CWS that polar bear densities in the eastern portion of the SBS region were dramatically lower in 2006 than in other years. Finally, in nearly all models the covariate *radio* allowed for an additive effect in *p* for polar bears that were available for recapture by radiotelemetry.

Model selection was based on Akaike's information criterion (AIC) (Burnham and Anderson, 2002), as well as considerations of biological plausibility and other statistical issues (e.g., the number of parameters in the model that could be estimated). We adjusted AIC for overdispersion (i.e., QAIC) based on the GOF analysis, and evaluated 152 CJS models representing all combinations of the hypothesized parameterizations for φ and *p*. We derived final parameter estimates by averaging across models in the candidate set with ΔQAIC ≤ 7.0. We used this cutoff because ΔQAIC = 7.0 corresponds to a normalized Akaike weight (w_i) of approximately 0.01, below which the impact on model-averaged estimates is negligible. This approach ensured that model selection uncertainty was reflected in all real parameter estimates, and their associated variances (Burnham and Anderson, 2002).

We estimated population size (*N*) from the model-averaged estimates of recapture probability (*p*) derived from the CJS models, via a Horvitz-Thompson estimator (McDonald and Amstrup, 2001). This approach has several advantages over traditional Jolly-Seber methods (McDonald and others, 2005). First, it retains the flexibility of the CJS modeling framework. Second, it is straightforward to estimate *N* from models in which *p* is a function of individual covariates. Third, it is straightforward to estimate *N* from model-averaged estimates of *p*. We estimated the variance of *N* by bootstrapping (Manly, 1997), because conventional variance estimators for the HT approach (e.g., the Laake estimator in Taylor and others, 2002) require estimates of the covariance among *p* for all strata, which were not available for the model-averaged estimates. The bootstrap procedure involved re-sampling the individual capture histories (and covariates) to generate 1,000 new datasets, fitting each dataset with all models in the original candidate set with ΔQAIC ≤ 7.0, and deriving model-averaged parameter estimates for each iteration. We then estimated the variance of *N* by assuming that the distribution of bootstrapped, model-averaged $\hat{N}_j$ represented the sampling distribution of true population size.

Cub Production and Physical Stature

We analyzed numbers of young accompanying adult female polar bears captured each spring in 1967–79, 1982–92 (except 1990) and 1998–2006, and each autumn in 1981–86, 1988, 1989, 1994, 1997, and 1998–2001. We analyzed physical stature using skull size and body weight data for polar bears captured in the spring only. For both analyses, we compared data from two periods: 1967–89 and 1990–2006. This comparison was motivated by dramatic changes in the polar basin sea ice beginning in 1989–90 (Rigor and others, 2002). We hypothesized that these changes would affect the nutritional condition of polar bears, resulting in altered production and survival of cubs, and altered physical stature for all polar bears (Stirling and others, 1999).

We compared data between the two periods using logistic regression, the Kruskal-Wallis rank sum test, and contingency tables. Cub production and survival were assessed using the proportion of adult females accompanied by litters, and the number of dependent young (COYs, yearlings, and 2-year-olds) per female. Because the comparison of indices requires the assumption of equal detectability among years, we limited our analysis of spring cub production rates to data collected in April and May. In early years of the study, COYs were under-sampled because much of the field work occurred in March before new family groups emerged from their dens (Amstrup and DeMaster, 1988; Amstrup, 1995). Almost all females with COYs, however, had emerged from dens by the first week in April (Amstrup and Gardner, 1994).

Results

The combined 2001–06 USGS data, and 2003–06 CWS data, consisted of 1,099 captures of 843 individual polar bears (table 1, fig. 1). Approximately 90 percent of captures were for polar bears encountered by standard search, and 10 percent of captures were for polar bears encountered by radiotelemetry. Approximately 87 percent of captures occurred during the annual spring capture seasons (mean date of capture April 14), and 7 percent of captures occurred during the autumn capture season by the USGS in 2001 (mean date of capture October 30). The remaining 6 percent of captures occurred as visual sightings during winter aerial radiotelemetry surveys. Appendix A includes a statistical description of the sex and age composition of the capture sample, information regarding marked polar bears that were harvested, and other summary statistics.

A total of 45 individual polar bears occurred in both the USGS and CWS samples: 38 "U.S." bears (i.e., bears originally captured by the USGS) appeared in the Canadian sample, while 7 "Canadian" bears appeared in the U.S. sample. Although the larger number of U.S. bears in the

Canadian sample may reflect the deployment of more marks into the U.S. portion of the SBS region, it also may reflect a distributional phenomenon. Annual encounter rates with polar bears were higher in Canada than in the U.S., except in 2006.

The covariate ice_j was based on sea ice concentration data for 2000–05, because we hypothesized that ice conditions in year j could predict polar bear survival in year j+1, and because CJS models cannot estimate survival following the final sampling occasion (i.e., 2006). For j = 2000, 2001… 2005: ice_j = {-1.03, -0.89, -0.71, 0.41, 1.13, 1.09}, where larger values indicate a longer ice-free period. A simple linear regression on the covariate (prior to standardization) indicated that the mean number of days with less than 50 percent ice concentration in the SBS region of preferred habitat increased from approximately 82 days in 2000, to 138 days in 2005 ($\hat{\beta}$ = 11.29 d/yr, $\widehat{SE}(\hat{\beta})$ = 1.84, P = 0.004).

Goodness of Fit

Program RELEASE investigates whether capture-recapture data meet the assumptions of the standard CJS model $\varphi(t)\,p(t)$, which allows φ and p to vary independently with time for a single stratum (see appendix B for a detailed description of model notation). We found no evidence for lack of fit in the female data (overall χ^2 = 14.23, df = 12, P = 0.29). In contrast, the male data did not fit model $\varphi(t)\,p(t)$ due entirely to a lack of fit in the program RELEASE component TEST3.SR (χ^2 = 25.45, df = 4, P < 0.001). The directionality of TEST3.SR indicated a lower future recovery rate of newly marked male animals, which is often caused by age-specificity in φ (Choquet and others, 2002). However, the lack of fit in the male data persisted despite progressive subsetting on age (i.e., from polar bears of all ages, to adults only), and despite the complete removal of harvested polar bears, which could exacerbate lack of fit due to a male bias in the harvest. Therefore, it is possible that the lack of fit in the male data represented a biological phenomenon, such as the presence of "transient" individuals (Cooch and White, 2005, Chapter 8).

In theory, program RELEASE can be used to estimate $\hat{c}$ for a global model that is equivalent to independently fitting model $\varphi(t)\,p(t)$ to multiple strata in the data (Sendor and Simon, 2003). In this study, small sample size resulted in estimation problems for highly parameterized models that incorporated sex × time and age × time interactions in both φ and p. Therefore, we estimated $\hat{c}$ using an 11-parameter model that was sufficiently general to allow for major hypothesized sources of variation, but did not suffer from estimation problems, and thus was a reasonable starting point for model selection. The 11-parameter general model estimated time-constant φ for three strata: COYs of both sexes, female polar bears older than COYs, and male polar bears older than COYs. Recapture probabilities were time-dependent

Table 1.   Total number and proportion each sex and age class of polar bears captured by standard search and radiotelemetry in the Southern Beaufort Sea by the U.S. Geological Survey, 2001–06, and by the Canadian Wildlife Service, 2003–06.

		Females captured		Males captured	
		Number	Proportion	Number	Proportion
2001	Adult[1] without dependent young	21	0.15	21	0.15
	Adult with dependent young	36	0.26	NA	0.00
	Subadult[1]	5	0.04	2	0.01
	Two-year-old	4	0.03	1	0.01
	Yearling	16	0.12	11	0.08
	Cub-of-the-year	11	0.08	9	0.07
2002	Adult without dependent young	21	0.19	20	0.18
	Adult with dependent young	24	0.21	NA	0.00
	Subadult	5	0.04	3	0.03
	Two-year-old	4	0.04	7	0.06
	Yearling	2	0.02	6	0.05
	Cub-of-the-year	11	0.10	10	0.09
2003	Adult without dependent young	14	0.08	55	0.32
	Adult with dependent young	33	0.19	NA	0.00
	Subadult	9	0.05	11	0.06
	Two-year-old	7	0.04	8	0.05
	Yearling	3	0.02	7	0.04
	Cub-of-the-year	10	0.06	13	0.08
2004	Adult without dependent young	39	0.14	70	0.25
	Adult with dependent young	48	0.17	NA	0.00
	Subadult	27	0.09	20	0.07
	Two-year-old	15	0.05	10	0.04
	Yearling	9	0.03	9	0.03
	Cub-of-the-year	17	0.06	21	0.07
2005	Adult without dependent young	47	0.19	67	0.27
	Adult with dependent young	39	0.16	NA	0.00
	Subadult	17	0.07	13	0.05
	Two-year-old	12	0.05	7	0.03
	Yearling	9	0.04	7	0.03
	Cub-of-the-year	14	0.06	17	0.07
2006	Adult without dependent young	28	0.19	49	0.34
	Adult with dependent young	22	0.15	NA	0.00
	Subadult	6	0.04	6	0.04
	Two-year-old	7	0.05	0	0.00
	Yearling	10	0.07	1	0.01
	Cub-of-the-year	8	0.06	8	0.06

[1]Adult (≥5 yr); Subadult (3-4 yr).

with an interactive *agency* effect, which allowed independent estimates of p_j for U.S. versus Canadian polar bears. Program MARK gave a bootstrap $\hat{c} = 1.45$ and a median $\hat{c} = 1.21$ (SE = 0.01) for this model, which indicated a moderate amount of overdispersion. The "biological" $\hat{c}$ based on the number of dependent young in the capture sample was 1.34, which was similar to the statistically based estimates. Because there was no clear theoretical basis for deciding which value of $\hat{c}$ to select, we used the arithmetic mean of the three values, which gave $\hat{c} = 1.33$.

As noted above, the simulation-based estimates of $\hat{c}$ were derived for a model that was a compromise between an ideal (i.e., very general) global model, and limitations in the data. The parameterization for φ in that model also was influenced by the practical difficulty of bootstrapping in MARK with complex group structure. In the actual CJS analysis, we considered several models with more general parameterizations for φ. It is therefore possible that the simulation-based estimate of $\hat{c}$ was larger than necessary.

Estimating Survival Rate and Population Size

The low-QAIC model included a simple parameterization for φ that estimated time-constant survival for two groups: COYs versus all polar bears older than COYs (model No. 1, table B1, appendix B). This model provided estimates of "average" φ for 2001–05, which could be compared to time-constant estimates of φ published for other polar bear populations. Estimates of total apparent survival probability (φ) from the low-QAIC model were 0.43 (SE = 0.11) for COYs, and 0.92 (SE = 0.04) for all polar bears older than COYs.

Although the low-QAIC model estimated time-constant φ for two groups, there also was support in the data for models that included other sex- and age-based groups, and allowed for temporal variation in φ (table B1, appendix B). Because all these models represented valid biological hypotheses, we derived estimates of φ by averaging across models in the candidate set with ΔQAIC ≤ 7.0, with two exceptions. First, we excluded model No. 13 (ΔQAIC = 4.0) because of difficulty in interpreting the transient effect for male subadults and adults (see appendix C). Second, we excluded model No. 14 (ΔQAIC = 6.0), which was the only model with a time-dependent parameterization for φ, because it resulted in confounded estimates of p_{2006} for some individuals.

We report model-averaged estimates of survival probability for three groups: COYs, female polar bears older than COYs, and male polar bears older than COYs (table 2). Although some models considered for model-averaging included additional groupings (e.g., subadult females separated

from adult females), the resulting differences in parameter estimates were limited to the third or fourth significant digit, and therefore are not reported. The unconditional standard errors in table 2 reflect both the sampling variance of each model, and the additional variance associated with model selection uncertainty (Buckland and others, 1997). The percent variation due to model selection uncertainty was approximately 14 percent for COYs, 20 percent for females older than COYs, and 32 percent for males older than COYs.

All CJS models with ΔQAIC ≤ 7.0 included a single parameterization for *p*, with the exception of model No. 15 (table B1, appendix B). Recapture probabilities differed between U.S. and Canadian polar bears, and were time-constant with the exception of p_{2006} for Canadian bears. Also, an additive effect was allowed for polar bears that were available for recapture by radiotelemetry. We derived final estimates of *p* by model-averaging over the same candidate model set as considered for survival. We used this approach because the point estimates of *p* varied slightly among models, due to interdependence with φ. The model-averaged estimates of *p* were 0.14 (SE = 0.02) for U.S. bears, 0.20 (SE = 0.04) for Canadian bears in 2004 and 2005, 0.06 (SE = 0.02) for Canadian bears in 2006, and 0.49 (SE = 0.07) for all polar bears available for recapture by radiotelemetry. Overall, approximately 4 percent of the variation in recapture probability was due to model selection uncertainty.

We estimated *N* by applying the HT estimator to model-averaged estimates of *p* (fig. 2). Valid estimates of population size were available for 2004–06 only, because of interactions between sampling design, the parameterization for *p*, and properties of the CJS model. The explanation is as follows. First, the CJS model cannot produce estimates of *N* in the first year of the study (i.e., 2001). Second, $\hat{N}_{2002}$ was biased low because it only represented polar bears in the portion of the SBS region that was sampled by the USGS. Third, $\hat{N}_{2003}$ also was biased, because 2003 was the first year of sampling by the CWS, and therefore the estimate of p_{2003} for Canadian bears

Table 2. Model-averaged estimates of total apparent survival probability for polar bears in the southern Beaufort Sea.

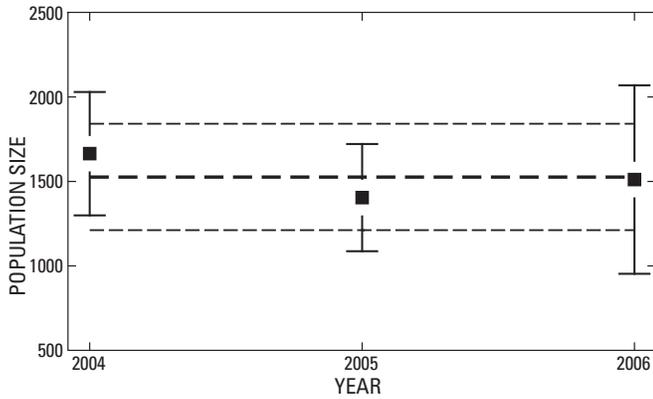| Year	COYs of both sexes		Females older than COYs		Males older than COYs	
	φ	SE(φ)	φ	SE(φ)	φ	SE(φ)
2001	0.47	0.14	0.92	0.05	0.94	0.05
2002	0.45	0.13	0.92	0.05	0.94	0.05
2003	0.43	0.12	0.92	0.05	0.93	0.05
2004	0.39	0.14	0.90	0.05	0.92	0.06
2005	0.37	0.16	0.90	0.07	0.91	0.07

Figure 2.   Total size of the southern Beaufort Sea polar bear population. Squares are annual, model-averaged estimates of population size with bootstrapped 95% confidence intervals. Heavy dashed line is the mean population size from 2004 to 2006 with bootstrapped 95% confidence intervals.

was not valid. Finally, we note that N_{2006} represents a valid estimate, because all models considered for model-averaging had time-constant parameterizations for φ, which allowed for the estimation of non-confounded p_{2006}.

The best estimate of the total size of the SBS polar bear population in 2006 (denoted $\hat{N}^{*}_{2006}$) was 1,526 (95% CI = 1,211; 1,841). We estimated $\hat{N}^{*}_{2006}$ by taking the arithmetic mean of the model-averaged point estimates of N from 2004 to 2006. This approach was based on the observation that interannual variability in $\hat{N}$ from 2004 to 2006 was within the limits of sampling variation, and most likely not a reflection of real changes in population size (fig. 2). We estimated SE($\hat{N}^{*}_{2006}$) using the standard deviation of the mean, model-averaged population size estimates from 2004 to 2006, for the 1,000 bootstrap iterations. Appendix D provides additional results from the bootstrap procedure regarding the statistical properties of the parameter estimates and model selection process.

Cub Production and Physical Stature

We compared numbers of young accompanying adult female polar bears captured between 1967 and 1989, to those accompanying females captured between 1990 and 2006. The spring data consisted of 788 captures of adult females (age $\geq$ 5 yr) located by standard search during April and May (table 3). The proportion of adult females accompanied by COYs increased from 0.15 for the earlier period, to 0.22

for the later period (logistic regression; period model versus intercept-only model, $G = 5.8$, df = 1, $P = 0.016$). The number of COYs per adult female also increased, from 0.25 to 0.39 (Kruskal-Wallis test; $\chi^{2} = 6.35$, df = 1, $P = 0.012$). In contrast to the pattern observed for COYs, indices of yearling production declined between the two periods, although the changes were not statistically significant. The proportion of adult females accompanied by yearlings decreased from 0.22 to 0.19 ($G = 1.28$, df = 1, $P = 0.258$), while the number of yearlings per adult female decreased from 0.34 to 0.26 ($\chi^{2} = 1.90$, df = 1, $P = 0.168$).

The autumn data, which consisted of 190 captures of adult females during October and November, showed a different pattern than the spring data (table 4). The proportion of adult females accompanied by COYs in autumn decreased from 0.40 to 0.16 ($G = 14.53$, df = 1, $P < 0.001$), while the number of COYs per adult female decreased from 0.61 to 0.25 ($\chi^{2} = 12.70$, df = 1, $P < 0.001$). Similarly, although the differences were not significant, the proportion of adult females accompanied by yearlings decreased from 0.33 to 0.23 ($G = 2.39$, df = 1, $P = 0.122$) and the number of yearlings per adult female decreased from 0.47 to 0.34 ($\chi^{2} = 2.13$, df = 1, $P = 0.144$).

Litter sizes in the two periods were not statistically different (table 5). For the spring data, COY litters were slightly larger in the later period (2 × 3 contingency table of litter sizes versus period; $\chi^{2} = 2.49$, df = 2, $P = 0.288$), while yearling litters were somewhat smaller ($\chi^{2} = 5.60$, df = 2, $P = 0.061$). For the autumn data, litter size was similar between periods for both COYs ($\chi^{2} = 0.43$, df = 1, $P = 0.511$) and yearlings ($\chi^{2} = 0.10$, df = 1, $P = 0.750$).

We compared the physical stature of polar bears between the two periods using data for COYs, yearlings of both sexes, and adults (age $\geq$ 5 yr) of both sexes that were captured by standard search and radiotelemetry, from March-May. Statistically significant decreases in skull measurements were observed for COYs and adult males (table 6). Body weight decreased significantly for adult males (table 7). Because male polar bears continue to grow into their teen years (Derocher and others, 2005), it was possible that changes in skull measurements and body weight were related to changes in age structure. However, the mean age of adult male polar bears in the 1990–2006 capture sample—10.9 (SE = 0.30) years—was greater than the mean age—9.4 (SE = 0.23) years—in the 1967–89 capture sample (Kruskal-Wallis test; $\chi^{2} = 15.62$, df = 1, $P < 0.001$). Given equal nutrition, the older male bears captured in more recent years should have been larger. Therefore, it is likely that the observed changes in physical stature reflected a real shift towards smaller adult male polar bears in the SBS region.

Table 3 Cub production rates for polar bears in the southern Beaufort Sea, 1967–89 and 1990–2006.

[Data are included for polar bears captured by standard search in the spring (April-May)]

Adult female age (yr)	1967–89							1990–2006						
	Number of adult females	Prop. with COYs	COYs per adult female	Prop. with yearlings	Yearlings per adult female	Prop. with 2-year-olds	2-year-olds per adult female	Number of adult females	Prop. with COYs	COYs per adult female	Prop. with yearlings	Yearlings per adult female	Prop. with 2-year-olds	2-year-olds per adult female
5	68	0.09	0.15	0.02	0.03	0.00	0.00	38	0.18	0.26	0.00	0.00	0.03	0.03
6	58	0.16	0.21	0.16	0.21	0.02	0.03	28	0.29	0.43	0.04	0.04	0.04	0.04
7	50	0.12	0.14	0.30	0.46	0.12	0.14	34	0.15	0.27	0.27	0.29	0.03	0.03
8	48	0.19	0.27	0.33	0.44	0.13	0.23	18	0.11	0.22	0.33	0.44	0.00	0.00
9	38	0.16	0.29	0.24	0.42	0.26	0.32	25	0.16	0.32	0.24	0.32	0.04	0.04
10	33	0.09	0.18	0.33	0.52	0.18	0.27	16	0.25	0.50	0.44	0.50	0.00	0.00
11	26	0.27	0.54	0.15	0.23	0.12	0.12	17	0.41	0.77	0.18	0.18	0.12	0.18
12	17	0.35	0.59	0.24	0.35	0.12	0.12	23	0.30	0.35	0.17	0.22	0.04	0.04
13	19	0.05	0.11	0.42	0.68	0.21	0.32	20	0.20	0.35	0.20	0.25	0.10	0.15
14	13	0.23	0.39	0.23	0.39	0.08	0.15	14	0.14	0.36	0.29	0.43	0.14	0.21
15	15	0.33	0.60	0.33	0.67	0.13	0.20	11	0.18	0.36	0.18	0.27	0.18	0.36
16	20	0.20	0.40	0.20	0.25	0.25	0.35	18	0.39	0.72	0.28	0.50	0.06	0.11
17	9	0.11	0.22	0.22	0.33	0.22	0.33	9	0.11	0.22	0.33	0.44	0.11	0.22
18	5	0.00	0.00	0.40	0.80	0.20	0.40	10	0.40	0.80	0.20	0.30	0.10	0.10
19	3	0.00	0.00	0.33	0.33	0.00	0.00	5	0.40	0.80	0.00	0.00	0.20	0.40
20+	13	0.08	0.15	0.15	0.31	0.08	0.15	32	0.13	0.25	0.19	0.28	0.19	0.31
Overall[1]	**437**	**0.15**	**0.25**	**0.22**	**0.34**	**0.11**	**0.16**	**351**	**0.22**	**0.39**	**0.19**	**0.26**	**0.07**	**0.11**

[1]Overall counts include data for 2 (1967–89) and 33 (1990–2006) females that were field-aged as adults, but did not have cementum-derived ages.

Table 4. Cub production rates for polar bears in the southern Beaufort Sea, 1967–89 and 1990–2006.

[Data are included for polar bears captured by standard search in the autumn (October-November)]

Adult female age (yr)	1967–89					1990–2006				
	Number of adult females	Proportion with COYs	COYs per adult female	Proportion with yearlings	Yearlings per adult female	Number of adult females	Proportion with COYs	COYs per adult female	Proportion with yearlings	Yearlings per adult female
5-9	54	0.35	0.48	0.30	0.37	36	0.06	0.08	0.19	0.31
10-14	30	0.40	0.60	0.33	0.53	26	0.35	0.58	0.19	0.27
15-19	17	0.47	0.88	0.47	0.71	8	0.00	0.00	0.38	0.63
20+	6	0.67	1.00	0.17	0.33	10	0.20	0.30	0.40	0.50
Overall[1]	**107**	**0.40**	**0.61**	**0.33**	**0.47**	**83**	**0.16**	**0.25**	**0.23**	**0.34**

[1]Overall counts include data for 3 (1990–2006) females that were field-aged as adults, but did not have cementum-derived ages.

Table 5.   Litter sizes of dependent young polar bears in the southern Beaufort Sea, 1967–89 and 1990–2006.

[Data are included for polar bears captured by standard search in the spring (April-May) and autumn (October-November)]

	Season	COY litter size			Yearling litter size			Two-year-old litter size		
		1	2	3	1	2	3	1	2	3
1967–89	Spring	23	44	0	47	48	2	29	21	0
	Autumn	22	22	0	19	15	2	1	0	0
	Both	45	66	0	66	63	4	30	21	0
1990–2006	Spring	21	55	2	44	23	0	11	14	0
	Autumn	5	8	0	10	8	3	1	1	0
	Both	26	63	2	54	31	3	12	15	0
	Overall	71	129	2	120	94	7	42	36	0

Table 6.   Sum of skull length and skull width measurements (cm) for polar bears in the southern Beaufort Sea, 1967–89 and 1990–2006.

[Data are included for all polar bears captured in the spring (March-May)]

	1967–89			1990–2006			ANOVA		
	n	Mean	SD	n	Mean	SD	F	df	P versus equal means
COY males and females	70	27.8	1.8	191	26.8	1.8	16.2	1	0.000
Yearling males	34	44.6	2.4	43	44.5	2.2	0.1	1	0.771
Yearling females	26	42.2	1.9	57	41.5	2.1	2.5	1	0.121
Adult males	137	65.3	4.2	315	64.3	4.7	4.9	1	0.028
Adult females	234	55.4	1.9	425	55.3	2.6	0.6	1	0.431

Table 7.   Scale weights (kg) for polar bears in the southern Beaufort Sea, 1967–89 and 1990–2006.

[Data are included for all polar bears captured in the spring (March-May)]

	1967–89			1990–2006			ANOVA		
	n	Mean	SD	n	Mean	SD	F	df	P versus equal means
COY males and females	66	14.1	4.0	164	13.2	3.9	2.4	1	0.124
Yearling males	13	85.8	16.2	16	94.5	25.2	1.2	1	0.286
Yearling females	11	74.9	17.6	29	74.8	15.1	0.0	1	0.988
Adult males	38	367.6	80.6	83	329.0	89.0	5.2	1	0.024
Adult females	92	185.3	28.3	180	184.1	27.6	0.1	1	0.731

Discussion

Capture-Recapture Analyses

The survival estimates derived from the 2001 to 2006 capture-recapture data appear lower than previously published estimates for this population. Amstrup and Durner (1995) derived precise estimates of survival for COYs (0.65, 95% CI = 0.610–0.675), yearlings (0.86, 95% CI = 0.751–0.903), and adult females (0.97, 95% CI = 0.952–0.983) in the SBS region by following radiocollared females. Comparison of the earlier estimates with those from the current study, however, is complicated by strata-related issues. The comparison also is complicated by the fact that estimates of apparent survival from capture-recapture studies reflect both biological survival and the probability of remaining in the study area, whereas estimates of survival from radiotelemetry data reflect biological survival only. In the current study, estimates of apparent survival from the best fitting model were 0.43 (95% CI = 0.21–0.65) for COYs and 0.92 (95% CI = 0.84–1.00) for all polar bears older than COYs. Identifying a stratum that includes all bears older than COYs represented a compromise between actual sex- and age-based variation in survival, and the ability to detect this variation in the data using capture-recapture models. For example, we know from the life history of polar bears that recently weaned subadults generally have lower survival than prime age adults. Hence, a single estimate of survival for all polar bears older than COYs represents an average over biologically distinct strata. This issue, and the distinction between apparent survival and biological survival, precluded a meaningful comparison of current survival estimates for adult females with those derived previously.

Differences in COY survival between the two studies, however, can be meaningfully compared. Adult females with COYs are less mobile than other polar bears (Amstrup and others, 2000), and therefore more likely to remain in the study area. Estimates of apparent survival for COYs, therefore, should be similar to biological survival. Also, assuming that survival rates for adult females have not changed dramatically since the early 1990s, the difference between the radiotelemetry-based survival estimate for adult females (0.97, Amstrup and Durner, 1995) and the current estimate of apparent survival for all polar bears older than COYs (0.92) sets an upper limit on the emigration component of apparent survival for COYs. Because COYs are completely dependent on their mothers and cannot leave the study area on their own, the maximum emigration component of apparent survival for COYs cannot exceed 0.05. Finally, the actual emigration component has to be less than 0.05, because the current estimate of 0.92 was an average survival rate, derived for both adult females and other polar bears with lower biological survival (e.g., subadults, senescent adults).

In contrast to the maximum possible emigration component of <0.05, the difference between the radiotelemetry-based survival estimate for COYs (Amstrup and Durner, 1995) and the current estimate of apparent survival for COYs was 0.22 (i.e., 0.65–0.43). This difference was statistically significant (P versus the null hypothesis of equal or increasing survival = 0.03), and clearly represents a decline in biological survival since the early 1990s. The decline in COY survival is consistent with the statistically significant changes in COY and yearling production that we report here.

In our capture-recapture analysis, we used a weight of evidence approach (Burnham and Anderson, 2002) that allowed us to derive estimates of survival by averaging over multiple, well supported models. Model-averaged estimates of apparent survival were different for three sex and age groups. All three exhibited declining survival for the years 2001–05 (table 2). Because the best fitting (i.e., low-QAIC) model estimated time-constant survival, these declines in model-averaged survival are not "statistically significant" in the classical sense of testing versus the null hypothesis of no trend. However, the declines do reflect the existence of a similar degree of support in the data for several models, some of which estimated survival probabilities that changed over the course of the study. The evidence ratio between two models can be calculated as the ratio of normalized Akaike weights (w_i) (Burnham and Anderson, 2002). For example, the evidence ratio for the low-QAIC model versus model No. 3, which estimated survival as a function of sea ice conditions, was 0.18/0.12 = 1.5 (table B1, appendix B). In other words, the low-QAIC model was approximately 1.5 times as well supported as model No. 3. This low evidence ratio indicates considerable ambiguity as to which model was actually a better representation of the data (Burnham and Anderson, 2002). Therefore, we cannot simply overlook the suggestion of a declining trend in survival.

Estimates of survival are generally robust to model assumption violations (Williams and others, 2002, Chapter 17). Because estimates of survival derived from CJS models represent "total apparent survival," however, changes in survival can arise from interactions between study design and animal movement patterns, as well as from changes in biological survival. In the SBS region, radiotelemetry data confirm that polar bears do not restrict their movements to the areas that we can access during helicopter supported capture efforts (Amstrup and others, 2000, 2004) . Over periods of multiple years, every bear in the population spends considerable time in the sampling region. However, the shorter the time-frame considered for sampling, the greater the probability that previously marked polar bears will be located outside of the effective study area, and not available for recapture prior to the end of the study. Thus, the declines we observed in model-averaged survival rates may reflect an increase in the number of "emigrants" toward the end of the study, and not an actual decrease in biological survival.

Our model selection process did not support a transient effect in survival for male subadults and adults. We were, however, curious whether there might be sex or age specific differences in recapture probability. Therefore, we performed a limited amount of secondary modeling to investigate this and other *a posteriori* hypotheses (appendix C). Although inference regarding transience remained equivocal, the secondary modeling provided some evidence for differential movement patterns between males and females, and emphasized that this is a topic worthy of further investigation.

In our analysis of the 2001–06 data, we did not find clear evidence for a relationship between sea ice coverage in the SBS region (i.e., the covariate *ice*) and survival. However, this should be interpreted in light of the short duration of the study and the limitations of the data. Polar bears are long-lived mammals that are well adapted to periods of resource shortage. Our study may not have been long enough, and may not have included enough interannual variation in sea ice, to detect a significant relationship between changing sea ice and survival. This also may be due to our inability to resolve survival patterns for subadult and senescent polar bears, which may be most affected by annual changes in sea ice conditions (Regehr and others, unpub. data, 2006). Because polar bears are entirely dependent on sea ice for foraging, reduced access to sea ice translates directly into reduced feeding opportunity. In other parts of the polar bear range, reductions in the spatiotemporal availability of sea ice have been shown to negatively impact polar bear stature, productivity, and survival of juvenile, subadult and senescent animals (Stirling and others, 1999; Stirling, 2002).

Our best estimate of the population size for the SBS region was 1,526 polar bears (95% CI = 1,211; 1,841). We believe that this estimate—the mean for the period 2004–06—is relatively unbiased for several reasons. First, it was derived from capture-recapture data that were, for the first time, collected throughout the entire SBS region under a well-defined and consistent sampling protocol. Second, a thorough GOF analysis suggested that the data met the most important capture-recapture assumptions. The CJS models fitted to the data included covariates for all major sources of variation of which we were aware, and the resulting coefficient estimates were biologically plausible. Third, estimates of population size were insensitive to model selection, as evidenced by the low percent variation in recapture probability associated with model selection uncertainty (appendixes C and D). Finally, the point estimates of population size were relatively stable for 2004–06 (i.e., the years for which valid estimates could be derived).

Stability in point estimates for 2004–06 is further evidence that they reflect the total number of polar bears in the SBS region. In each year of the study, some individuals probably were located outside of the effective sampling area. However, the estimates of population size derived from CJS models represent the total number of individuals that had a finite probability of being exposed to sampling (i.e.,

the "superpopulation"), whether or not they were actually accessible to the USGS or CWS in every year (Kendall and others, 1997). The stability of estimated population sizes for the latter years of the study, when both agencies were performing field work, indicates that new individuals were not continuing to be "recruited" into the superpopulation as they cycled through the area exposed to sampling efforts.

Amstrup and others (2001a) estimated that there were 1,180 (95% CI = 635; 1,725) female polar bears in the SBS region in the late 1980s. Sample sizes during this period were similar to those in the 2001–06 study, which allows for a reasonable comparison of estimated population sizes. If the sex ratio of the population in the late 1980s was similar to what (54 percent female) we estimated for the 2001–06 period, the Amstrup and others (2001a) female-only estimate corresponded to a total population size in the late 1980s of approximately 2,185 polar bears. Because the estimate and confidence interval were calculated for females only, however, we do not know the statistical variance associated with this estimate of the total population size. We do know, however, that the variance associated with the estimate of the total population was necessarily greater than the variance for the female-only estimate (SE = 278). Therefore, the confidence interval around the total population size estimate of 2,185 must have exhibited considerable overlap with the confidence interval around the current estimate of 1,526 (95% CI = 1,211; 1,841). This overlap, in conjunction with the similarity between the current estimate and the original Amstrup and others (1986) estimate of 1,800 (95% CI not available), precludes a statistical determination that the total number of polar bears in the SBS region has changed in recent years.

Estimating the size of wildlife populations is inherently difficult (e.g., Pollock and others, 1990; Pledger and Efford, 1998). This is especially true for animals that occur at low densities in remote regions, because of the potential for bias introduced by heterogeneity in recapture probability (e.g., due to differences in distribution, behavior, sightability). We believe that the estimated population sizes for 2004–06 are accurate. However, evaluation of long-term trends in population size via *post hoc* comparison with previous analyses is clearly a challenge. To address this issue more thoroughly, we are preparing an integrated analysis of historic and current data for polar bears in the SBS region, including both capture-recapture and radiotelemetry data.

Cub Production and Physical Stature

The changes we observed in cub production between the early (1967–89) and latter (1990–2006) time periods appear to reflect a decrease in the survival of polar bear cubs during their first 6 months of life. Polar bears have a multi-year reproductive cycle (Amstrup, 2003). Females give birth in January and emerge from the maternal den with new cubs in March or early April. Young typically accompany their mother for 2.3 years while they learn the methods of survival

in the Arctic (Amstrup, 2003). For polar bears captured during the autumn, the number of COYs per adult female declined significantly ($P < 0.001$) from a mean of 0.61 in the early period to a mean of 0.25 in the latter period. This decline can only be explained by lower survival of cubs after den emergence. In contrast to the autumn data, the numbers of COYs per adult female captured in the spring increased between the two periods. This reflects a shortened inter-birth interval for the recent period. Apparently, more females are losing their cubs shortly after den emergence, breeding again shortly after losing their cubs, denning again the following autumn, and emerging with another litter the following spring. In short, numerous cubs are currently being born in the SBS region, but many of them are not being recruited into the population.

The evaluation of changes in cub production requires the recognition of possible sampling differences between the early and latter study periods. Amstrup and DeMaster (1988) and Amstrup (1995) suggested that COYs were often under-sampled in spring captures. In the early period, this under-sampling was reflected by a higher proportion of yearlings than COYs in spring captures, and by a higher proportion of COYs captured in the autumn than in the spring. Because it is not possible for actual cub production to increase between the spring and autumn of a single year, a higher proportion of females with cubs in the autumn must represent a bias in the index. Two sampling issues may contribute to the bias against the spring capture of COYs. First, polar bear families often do not emerge from the maternal den until early April (Amstrup and Gardner, 1994). Because family groups located in dens are not available for capture, capture efforts conducted in March are likely to under-sample females with COYs. Second, Amstrup and Gardner (1994) showed that many female polar bears in the Beaufort Sea denned on the far offshore pack ice. Females emerging from dens far offshore may be less available to capture by research crews operating from logistical bases onshore.

In our analysis of cub production data, we controlled for the first source of bias by excluding capture data from March. For the 1967–89 period, however, spring samples still included a higher proportion of yearlings than of COYs. This suggests that the under-representation of COYs in the spring sample for the early period was due to bears that denned far offshore. Indeed, new analyses of the distribution of denning in the U.S. portion of the SBS region confirm that more bears denned in far offshore regions in early years of polar bears studies than in the recent decade (Fischbach and others, unpub. data, 2006). We attribute this shift in denning distribution to sea ice conditions that have become less suitable as a substrate for denning.

The suspected shift over time towards more onshore denning cannot account for the profound decline in the number of COYs per adult female captured in the autumn (0.61 versus 0.25). During the freeze-up period of our autumn

sampling, polar bears in the SBS region are concentrated in the nearshore areas (Durner and others, 2004) where they are highly vulnerable to capture by shore-based research crews. Therefore, the observed decline in the number of COYs per adult female captured in the autumn must reflect an actual decline in the survival of cubs between den emergence and the autumn sampling period, and not a sampling artifact. This decline in turn appears to be the principal cause of the increase in COYs and decrease in yearlings that we observed in the spring capture data after 1989.

Observed changes in the physical stature of polar bears in the SBS region appear to parallel declines in recruitment. Declines in skull size for both COYs and adult males were significant. The decline in body weight for adult males was significant. Such changes in physical stature may suggest different impacts of reduced summer sea ice on adult male and female polar bears. In the spring, adult males often forgo foraging opportunities and focus their efforts on locating females for mating. Therefore, adult males enter the summer period in relatively poorer nutritional condition. They may then be more vulnerable to summer sea ice retreats, which can separate polar bears from foraging habitats thought to be the most productive (Amstrup and others, 2006). Conversely, reduced foraging opportunity for adult females usually is first reflected in poorer survival of young. Although the average body weight of COYs did not decline significantly between the two periods, their weights were slightly lower in the latter period. Evidence from other portions of the polar bear's range suggest lower weights, combined with significantly smaller skull sizes, may be related to the poorer survival we observed for COYs in recent years. In western Hudson Bay, Canada, which is near the southern extreme of the species range, declines in cub survival and physical stature were recorded for years (Stirling and others, 1999; Derocher and others, 2004) before a statistically significant decline in population size was confirmed. In western Hudson Bay, we associated the decline in population size with reduced survival of juvenile polar bears and adults that were beyond prime ages. Poorer survival of animals in those age classes was directly related to the reduced availability of sea ice (Regehr and others, unpub. data, 2006). The situation in western Hudson Bay offers insight into the future status of polar bears in more northern regions such as the SBS, because recently observed declines in the area and extent of sea ice are predicted to continue throughout the polar basin (Overpeck and others, 2005; Stroeve and others, 2005)

Evidence of declining physical stature and poorer survival of COYs in the SBS region is consistent with other observations, which suggest that changes in the sea ice may be adversely affecting polar bears. Previously, human harvest accounted for most documented polar bear mortalities in the SBS region (Amstrup and Durner, 1995). In contrast, several recently observed mortalities were directly related to sea ice retreat, or appeared related to changes in food availability that may be associated with sea ice retreat. In autumn of

2004, four polar bears were observed to have drowned while attempting to swim between shore and the distant pack ice. Despite offshore surveys extending back to 1987, similar observations had not previously been recorded (Monnett and Gleason, 2006). During winter and early spring of 2004, three observations were recorded of polar bears hunting, killing, and consuming other polar bears in the Beaufort Sea (Amstrup and others, 2006). Similar observations had not been recorded in that region despite studies extending back for decades. In spring of 2006, three adult female polar bears and one yearling were found dead. Two of these females and the yearling had depleted their lipid stores and apparently starved to death. Although the third adult female was too heavily scavenged to determine a cause of death, her death appeared unusual because prime age females have had very high survival rates in the past (Amstrup and Durner, 1995). Similarly, the yearling that was found starved was the offspring of another radiocollared prime age female that had recently disappeared from the airwaves. Annual survival of yearlings, given survival of their mother, was previously estimated to be 0.86 (Amstrup and Durner, 1995). Therefore, the probability that this yearling died while its mother was still alive was only approximately 14 percent. These anecdotal observations, in combination with both the changes in survival of young and in physical stature reported here, suggest mechanisms by which a changing sea ice environment can affect polar bear demographics and the status of populations.

Conclusions

Information on changes in survival and physical stature, reported here, indicate that the status of polar bears in the SBS region is changing. Annual survival rates of COYs estimated from the 2001 to 2006 capture-recapture study were lower than survival rates estimated in previous studies. The increased loss of cubs during the first 6 months of life may be associated with the smaller physical stature of COYs observed in recent years. The smaller physical stature of COYs was paralleled by a smaller physical stature of adult males, even though the average age of adult males has increased. Despite these indicators of a declining status for the SBS polar bear population, our best estimate of the current size of the population does not show a statistically significant decline. This may mean there has been no change in numbers in recent years, or it could reflect insufficient precision in current and past estimates to resolve such a change.

Although our 2001–06 capture-recapture study did not provide evidence for a change in the size of the SBS polar bear population, significant changes in cub survival and physical stature must ultimately have population level effects. Lowered body weight has been implicated in declining survival of polar bear cubs in western Hudson Bay, Canada. There, reduced cub survival, associated with declines in physical stature caused by reduced foraging opportunity, was recorded long

before a statistically significant decline in population size was confirmed. The relationship between decreased availability of sea ice and declining population size in western Hudson Bay, which is near the southern extreme of polar bear range, is cause for concern regarding the future status of polar bears in more northern regions such as the SBS. Because more profound declines in sea ice area and extent are predicted for these northern regions, continued monitoring and conservative management of the SBS polar bear population is warranted.

Acknowledgments

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Appendix A. Description of Sex Composition, Age Composition, and Other Summary Statistics for Polar Bears Captured in the Southern Beaufort Sea, 2001–06.

We summarized the sex composition, age composition, and proportion of marked versus unmarked bears using captures of polar bears encountered by standard search only, because polar bears encountered by radiotelemetry consisted mostly of adult females and dependent young. Trends were described using standard regression techniques (e.g., Boyce, 1984; Comiso, 1986). For example, we assessed temporal variation in the sex ratio by computing a likelihood ratio test for a logistic model with an intercept only (H_0), versus a logistic model with an intercept and five design variables, which allowed the proportion of females to differ among years (H_A).

Table A1 summarizes the proportion of adult polar bears in the capture sample that were previously marked. The proportion of females in the capture sample was variable among years (logistic regression; time-dependent model versus time-constant model, $G = 19.22$, df = 5, $P = 0.002$), due to the difference between a high proportion of females in 2001 and a low proportion of females in 2003 (Tukey-type multiple comparison test for proportions; $q_{2001-2003} = 1.07$, SE ($q_{2001-2003}$) = 0.25). The high in 2001 reflects the fact that autumn sampling occurred in that year of the study. Historically, autumn samples have included high proportions of females and young. The overall proportion of females in the capture sample was 0.54 (SE = 0.02).

Table A1.   Proportion of adult (age $\geq$ 5 yr) polar bears with a previous capture in the current study.

[Data are for polar bears captured by standard search in the southern Beaufort Sea by the U.S. Geological Survey, 2001–06, and the Canadian Wildlife Service, 2003–06]

Year	Total captures	Recaptures	Proportion recaptures
2001	73	0	0.00
2002	50	10	0.20
2003	93	12	0.13
2004	157	29	0.18
2005	146	45	0.31
2006	100	39	0.39

The overall age class composition of the capture sample was 0.12 (SE = 0.03) COYs, 0.09 (SE = 0.03) yearlings, 0.07 (SE = 0.03) 2-year-olds, 0.12 (SE = 0.03) subadults, and 0.60 (SE = 0.02) adults. The proportion of females in each age class was 0.47 for COYs, 0.55 for yearlings, 0.62 for 2-year-olds, 0.56 for subadults, and 0.55 for adults. The proportion of adult polar bears in the capture sample was stable among years (logistic regression; time-dependent model versus time-constant model, $G = 6.62$, df = 5, $P = 0.251$), with an overall value of 0.60 (SE = 0.02). The age of adult (i.e., age $\geq$ 5 yr) females was stable among years (Kruskal-Wallis test; $\chi^2 = 4.16$, df = 5, $P = 0.527$), with a mean value of 11.8 yr (SE = 0.33). The age of adult males was stable among years (Kruskal-Wallis test; $\chi^2 = 6.18$, df = 5, $P = 0.289$), with a mean value of 10.8 yr (SE = 0.33).

From 2001 to 2006, 37 previously marked polar bears were killed as part of a legal, regulated harvest by Inuit hunters in the SBS region (table A2). Because CJS models are appropriate for live-recapture data only, we excluded these deaths and 15 natural deaths (i.e., polar bears that we found dead on the sea ice, or cubs that were presumed dead because their mothers were later observed alone) from the data. We included death records for two research-related mortalities that occurred from 2001 to 2006, which the CJS model effectively handles by right-censoring the individual capture histories of animals not released back into the population following capture.

Table A2.   Previously marked polar bears harvested in the southern Beaufort Sea, 2001–06.

	Female	Male
Adult[1]	7	13
Subadult	1	10
Two-year-old	5	1
Yearling	0	0
Cub-of-the-year	0	0

[1]Adult ($\geq$5 yr); Subadult (3-4 yr)

Appendix B. Description of Model Notation, and the Model Selection Table for Cormack-Jolly-Seber (CJS) Models Fitted to Capture-Recapture Data for Polar Bears in the Southern Beaufort Sea, 2001–06.

The model notation used in table B1 is an extension of the standard CJS notation developed by Lebreton and others (1992). We fitted models that allowed survival (φ) and recapture (p) probability to vary as functions of individual, group, and environmental covariates. Time-constant and time-dependent parameterizations were denoted (.) and (t), respectively. In the parameterization for φ, we considered four age classes: cubs-of-the-year (i.e., COYs, 0 yr; denoted a1), yearlings (1 yr; a2), subadults (2-4 yr, a3), and adults (5+ yr; a4). We denoted combinations of age classes using the letter "a" followed by several integers. For example, an aggregate age class comprising COYs (a1) and yearlings (a2) was written a12. Age structure was written in square brackets. For example, the model φ([a12, a3, a4]) estimated time-constant survival probabilities for three age classes: a12, a3, and a4. We denoted models that included both additive ("+") and interactive ("×") effects using nested brackets. For example, model φ(al + {[a2, a3, a4] × sex}) estimated a single survival

probability for COYs, but included age × sex interactions for yearlings, subadults, and adults. The environmental covariates ice^{j, φ_j} and $ice^{j, \varphi_{j+1}}$ were used to relate the sea ice conditions in the year j to survival probabilities in the year j and j+1, respectively. The covariate *linear* represented a generic linear trend in φ. The covariate *trans* represented transience, which was parameterized as an additive effect in φ following the occasion of first capture for subadult and adult male polar bears.

In the parameterization for p, the covariate *effort* represented the number of helicopter hours flown in capture operations each year. The individual covariate *agency* indicated whether each polar bear was first captured by the USGS or CWS. We used the notation *agency** to indicate a parameterization for p that estimated time-constant p for U.S. and Canadian bears, but allowed p_{2006} to differ for Canadian bears. The time-dependent individual covariate *radio* indicated whether each polar bear was available for recapture by radiotelemetry.

Table B1.   Model selection table for CJS models fitted to capture-recapture data for polar bears in the southern Beaufort Sea, 2001–06.

[QAIC = Akaike's information criterion adjusted for on a variance inflation factor ($\hat{c}$) of 1.33; dev = model deviance, np = number of estimated parameters, and w_i = normalized Akaike weight. Of the 152 total CJS models fitted in the analysis, only models with ΔQAIC ≤ 7.0 (which corresponds to approximately $w_i ≥ 0.01$) were considered for model averaging, and are shown here]

No.	Survival	Recapture	np	dev	QAIC	w_i
1	φ([a1,a234])	p(agency*+radio)	6	1416.10	1076.73	0.18
2	φ([a1+{[a234]×sex}]	p(agency*+radio)	7	1414.06	1077.20	0.14
3	φ([a1,a234]+$ice^{j, \varphi_{j+1}}$)	p(agency*+radio)	7	1414.51	1077.54	0.12
4	φ([a1,a234]+linear)	p(agency*+radio)	7	1414.75	1077.73	0.11
5	φ([a1,a234]+$ice^{j, \varphi_{j+1}}$)	p(agency*+radio)	7	1414.94	1077.86	0.10
6	φ({a1× $ice^{j, \varphi_{j+1}}$}+[a234])	p(agency*+radio)	7	1415.82	1078.53	0.08
7	φ({a1× linear}+[a234])	p(agency*+radio)	7	1415.96	1078.64	0.07
8	φ({a1× ice^{j, φ_j}}+ [a234])	p(agency*+radio)	7	1415.98	1078.65	0.07
9	φ([a1,a234])	p(agency*+radio)	7	1416.03	1078.68	0.07
10	φ([a1+{[a2a3a4]×sex}]	p(agency*+radio)	9	1413.20	1080.56	0.03
11	φ [a1a2a3a4]	p(agency*+radio)	8	1415.99	1080.65	0.03
12	φ([a12,a34])	p(agency*+radio)	6	1423.30	1082.15	0.01
13	φ([a1,a2,a34]+trans)	p(agency*+radio)	8	1416.02	1080.68	NA[1]
14	φ([a1,a2,a3,a4]+t)	p(agency*+radio)	10	1413.45	1082.74	NA[1]
15	φ([a1,a234]+$ice^{j, \varphi_{j+1}}$)	p(radio)	5	1428.00	1083.68	0.01

[1]Models No. 13 and 14 were excluded from model averaging; see Results: Estimating survival rate and population size.

Appendix C. Secondary Capture-Recapture Analysis to Investigate *a posteriori* Hypotheses.

After completing the main analysis, we performed a secondary analysis to investigate sex-specificity in recapture probability. This was motivated by the *a posteriori* hypothesis that females with dependent young may avoid male polar bears by limiting their use of preferred habitats (Stirling and others, 1981), which also were the habitats that we searched most intensively in our capture efforts. We began by modifying the most general model from the main analysis, to include an additive sex effect in *p* for subadult and adult males. After including this more general parameterization for *p*, we found that the data supported a "transient" effect in φ for subadult and adult males. Transience had been considered in the main analysis, but was poorly supported at that time (table B1, appendix B). Because differential capture probabilities between males and females and transience among males were both reasonable biological hypotheses, we evaluated their impact by continuing with a complete secondary model selection process.

The low-QAIC model from the secondary analysis was identical to the low-QAIC model from the main analysis, except that for subadult and adult males it included both the additive effect in *p* ($\hat{\beta}$ = 0.78, $\widehat{SE}(\hat{\beta})$ = 0.23; likelihood ratio test versus null model without $\hat{\beta}$: χ^2 = 13.37, df = 1, $P < 0.001$), and the additive transient effect in φ ($\hat{\beta}$ = -2.23, $\widehat{SE}(\hat{\beta})$ = 0.83; likelihood ratio test versus null model without $\hat{\beta}$: χ^2 = 7.06, df = 1, $P = 0.008$). The magnitude of the sex effect in *p* was such that subadult and adult males had nearly twice the recapture probability of other polar bears (e.g., 0.21 versus 0.11 for "U.S." polar bears). Although a higher *p* for males was consistent with our hypothesis of sex-based habitat segregation, the magnitude of this effect was not realistic. Apparently, the estimated *p* for males was exaggerated by interaction with the transient effect (see below).

Evidence for transience was consistent with the GOF analysis, which indicated that the data contained an unusually large number of subadult and adult males that were captured once, and never recaptured. These polar bears were considered "transients" based on the assumption that they were present in the study area for a relatively short period (during which they were exposed to sampling efforts), after which they emigrated permanently. The transient parameterization of the CJS model handles this by estimating a different survival probability following first capture. From a modeling perspective, this allows transient individuals to "die" (i.e., to leave the study population), and therefore minimizes their impact on the estimates of apparent survival for non-transient individuals. We considered that this approach might be reasonable,

because the annual use areas of highly mobile polar bears were potentially large with respect to the study area (Amstrup and others, 2000).

Both the GOF analysis and the secondary modeling indicated that transience was limited to male polar bears, which suggests differential movement patterns between males and females. This finding may be significant, because although there are few movement data for male polar bears, the limited information that is available suggests that movements of male and female polar bears are similar (Amstrup and others, 2001b). The low-QAIC model from the secondary analysis estimated that φ was 0.63 (SE = 0.10) for newly marked subadult and adult males. The estimated value of φ for all other polar bears older than COYs (i.e., females, and males subsequent to their first capture) was 0.94 (SE = 0.04). This "transient-corrected" value of φ was higher than the estimate of 0.92 (SE = 0.04) from the main analysis, and likely represents an intermediate value between apparent survival and biological survival. We used the ratio of the two survival probabilities from the low-QAIC model to derive a rough estimate of the proportion of transients among newly-captured subadult and adult males: 1 – 0.63 / 0.94 = 0.33 (Cooch and White, 2005, Chapter 8).

Aside from the inclusion of the two effects discussed above, model selection was similar for the main and secondary analyses. Also, the mean of the 2004–06 model-averaged estimates of population size from the secondary analysis was 1,523, which is nearly identical to the estimate of 1,526 from the main analysis. However, the inclusion of a sex effect in *p* in the secondary analysis resulted in a strongly skewed sex ratio in the subadult and adult components of the population (approximately 0.70 female). This was unrealistic, and largely an artifact of model structure. The CJS model that allowed for both sex-specificity in *p* and transience in φ for males, effectively estimated values of *p* (and consequently *N*) that applied only to the males in the population that were considered "residents." However, the delineation of "transients" versus "residents" was somewhat arbitrary, because it was a cumulative function of study duration, movement patterns, and other unknown phenomena. Furthermore, valid estimation of population size requires the assumption that estimated recapture probabilities apply to all animals in the population, which is clearly not the case here. In conclusion, the 2001–06 capture-recapture data suggested the potential for differences in movement patterns for males and females. Ultimately, these differences were beyond the ability of the data to resolve.

Appendix D. Statistical Properties of Parameter Estimates and the Model Selection Process

The bootstrap procedure that we used to estimate the variance in $\hat{N}_j$ also allowed us to investigate some statistical properties of the real parameter estimates, and of the model selection procedure. For survival, mean percent relative bias (PRB) was less than 1% between the model-averaged point estimates, and the mean values of the bootstrapped estimates. For population size, mean PRB was -1% between the model-averaged point estimates, and the mean values of the bootstrapped estimates. Mean PRB was 17% between SE($\hat{N}_j$) derived from the Laake estimator (Taylor and others, 2002) for the low-QAIC model, and SE($\hat{N}_j$) estimated from the distribution of the model-averaged bootstrapped estimates. This suggests reasonable agreement between theoretical and simulation-based variance estimators. Finally, we found that model selection frequencies from the bootstrap procedure were similar to the QAIC weights for models with ΔQAIC ≤ 7.0 (Burnham and Anderson, 2002) (table D1).

Table D1. Comparison between QAIC weights and bootstrapped model selection frequencies for the CJS models as defined in table B1.

No.	QAIC weight	Frequency
1	0.18	0.25
2	0.14	0.29
3	0.12	0.14
4	0.11	0.06
5	0.10	0.07
6	0.08	0.04
7	0.07	0.02
8	0.07	0.02
9	0.07	0.00
10	0.03	0.05
11	0.03	0.01
12	0.01	0.03
13	NA	NA
14	NA	NA
15	0.01	0.04