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

Polar Bear Population Status in the Northern Beaufort Sea

By Ian Stirling[1], Trent L. McDonald[2], Evan S. Richardson[1], and Eric V. Regehr[3]

Administrative Report

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Abbreviations, Acronyms, and Symbols

Abbreviations, Acronyms, and Symbols	Meaning
AIC	Akaike's Information Criterion
CJS	Cormack-Jolly-Seber models
COY	Cub-of-the-year
HT	Horvitz-Thompson estimator
IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for Conservation of Nature and Natural Resources
MSY	Maximum sustainable yield
NASA	National Aeronautics and Space Administration (U.S.)
NB	Northern Beaufort Sea
NSIDC	National Sea Ice Data Center (U.S.)
RSF	Resource selection function
SB	Southern Beaufort Sea
SH	Southern Hudson Bay
USFWS	U.S. Fish and Wildlife Service
USGS	U.S. Geological Survey
WH	Western Hudson Bay

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Abstract

The Northern Beaufort (NB) Sea polar bear (*Ursus maritimus*) population is situated on the perimeter of the polar basin in a region where sea ice converges on shorelines throughout most of the year. In this study, we present data on the status of this population, based on our research between 1971 and 2006. We applied open population capture-recapture models to data collected from 1971-2006 to assess the relationship between polar bear survival and sex, age, time period, and a number of environmental covariates. Model-averaged estimates of survival (which include harvest mortality) for senescent adults ranged from 0.33 (1980s, males) to 0.92 (1990s, females). Estimates of cub-of-the-year (COY) and yearling survival ranged between 0.10 (1980s, male yearlings) and 0.97 (1990s, female COY). Survival of 2–4 year olds and adults were nearly identical and ranged from 0.61 (1980s, males) to 0.97 (1990s, females). Relatively wide confidence intervals for survival of young age classes were largely due to small sample sizes. In addition, we modeled recapture probability as a function of three covariates (*effort, radio.vhf, radio.satellite*) and used a Horvtiz-Thompson (HT) estimator to estimate long term trends in the size of the NB population. Models that allowed associations between annual variation in survival, habitat, or relative seal abundance variables were not, in general, supported by the data. The model-averaged estimate of population size from 2004 to 2006 = 980 ($\pm$ 155, 95% CI) and was not significantly different from estimates for the periods of 1972 to 1975 and 1985 to 1987 of 745 ($\pm$ 246, 95% CI) and 867 ($\pm$ 141, 95% CI), respectively.

These abundance estimates apply primarily to that segment of the NB population residing west and south of Banks Island to the mainland coast, plus a relatively small but unknown fraction of the population residing further north around Prince Patrick Island. In 1992 to 1994, a capture effort focused in the area around Prince Patrick Island confirmed significant mixing between northern and southern segments of the population, that some bears residing in the extreme northern portions of the population may not have been equally available for capture during other sampling periods, and that the number of polar bears around Prince Patrick Island was not large relative to the rest of the population. Thus, we consider our estimates of total abundance during the other three sampling periods to be slightly low. Currently the NB polar bear population appears to be stable, probably because ice conditions remain suitable for feeding through much of the summer and fall in most years and the Inuvialuit harvest has not exceeded sustainable levels.

Introduction

The U.S. Fish and Wildlife Service (USFWS) proposed listing the polar bear as a threatened species under the Endangered Species Act in January 2007. To help inform their final decision, they requested that the U.S. Geological Survey (USGS) conduct additional analyses about polar bear populations and their sea ice habitats. Between February and August 2007, USGS and collaborators developed nine reports targeting specific questions considered especially informative to the final decision. This is one of the nine reports. This report presents new information on the status of the population

of polar bears residing in the NB region of Canada.

Polar bears are distributed throughout the ice-covered waters of the circumpolar Arctic in 19 relatively discrete populations (Aars et al. 2006). Their preferred habitat is the annual ice over the relatively shallower waters of the continental shelf and inter-island channels of various archipelagos, which are more biologically productive and where seals are more abundant than in the deep polar basin (Stirling et al. 1982; Kingsley et al. 1985; Stirling and Øritsland 1995). Although polar bears may occasionally capture a seal in open water (e.g., Furnell and Oolooyuk 1980), they are fundamentally dependent upon sea ice as a platform from which to hunt seals in both winter and summer (Stirling 1974; Stirling and Latour 1978; Smith 1980). Thus, changes in the distribution, total amount, and types of sea ice, and the patterns of freeze-up and breakup, have the potential to influence significantly the survival and reproductive success of polar bears. For example, progressively earlier breakup of the sea ice in Western (WH) and Southern (SH) Hudson Bay (Figure 1), because of climate warming, has shortened the critical polar bear feeding period in late spring and early summer. The shortened feeding period causes bears to be in poorer condition when they come ashore to fast through the open-water season until freeze-up later in the fall (Stirling et al. 1999; Obbard et al. 2006). In WH, the deterioration of physical condition has further resulted in lowered reproductive and survival rates, and a decline in the total population size (Regehr et al. 2007b). Stirling and Parkinson (2006) also predict that if climate warming in the Arctic continues as projected by the Intergovernmental Panel on Climate Change (IPCC; Solomon et al. 2007), then the trend toward progressively earlier breakup and a longer ice-free period in Hudson Bay would continue, and the SH polar bear population would decline, as well as would adjacent populations, where bears also fast on their

stored fat reserves through an extended open-water period in summer and fall.

In polar bear populations such as the Southern Beaufort Sea (SB) and NB (Figure 1) that are distributed around the southern edge of the polar basin, where the annual ice along the coast melts in early summer, the bears move north to remain on ice along the southern edges of the polar pack, where they can continue to hunt seals until the ice re-freezes again in fall (e.g., Amstrup et al. 2000; Mauritzen et al. 2003; Wiig et al. 2003).

Since 1979, when it first became possible to monitor patterns of break- and freeze-up of sea ice over the entire Arctic Ocean using satellite images, the total amount of ice remaining at the annual minimum in late summer has declined at a rate of 9.8% per decade (Comiso 2006). In recent years, there have been several record sea ice minima in the Arctic (Comiso 2006; Serreze et al. 2007; Stroeve et al. 2007). One consequence has been a shift of the southern edge of the pack ice over much of the Beaufort and Chukchi seas, from remaining over the continental shelf in summer and fall, to being positioned further north, away from the shelf and over the deep polar basin where biological productivity is much lower (Pomeroy 1997). Correlated with the trend toward a longer open-water season and sea ice being further offshore, there have been several indications that the polar bear population in the SB is being nutritionally stressed (e.g., Amstrup et al. 2006; Stirling et al. 2008), and it now appears to be in decline due to decreased recruitment (Regehr et al. 2006, 2007a).

In contrast, through most of the open-water period in the NB, at least some sea ice remains over the continental shelf along the west coast of Banks and Prince Patrick islands, M'Clure Strait, and often into western Amundsen Gulf, south of Sachs Harbor. Thus, in most years, the bears still have access to ice over the continental shelf, where seals are more available than they are over the deep polar basin. Possibly because of that difference, polar bears in the NB have

been in better overall condition than those in the SB, through 2003-2006 at least (Amstrup et al. 2006; Stirling et al. 2008).

Since 1968, the NB polar bear population has also been harvested by Inuvialuit hunters under a quota system. Between 1968 and the present, the annual quota has increased from 36 to 65, partly because scientific studies have suggested that a higher annual harvest level could be sustained and partly as a result of arbitrary (non-biological) re-assignment of portions of adjacent quotas by management agencies (unpublished data). Using estimates from the previous study of population abundance (Stirling et al. 1988) as a basis, a population size of 1200 was agreed upon for management purposes and a sustainable annual harvest of 54 was recommended, based on calculations in Taylor et al. (1987). More recent modeling suggests the sustainable annual harvest may be closer to 50 (Lunn et al. 2006). Regardless, the annual harvest has been less than 40 for over 15 years (Lunn et al. 1998, 2002, 2006), mainly because of difficult travel conditions for hunters and a reduced hunting effort in parts of the area. Because the annual harvest has remained well below the allowable limit, subsequent evaluations of change in the maximum sustainable yield have been postponed.

In this study, we set out to estimate demographic parameters (survival) and size of the NB population, as well as the factors that influence these parameters. We were specifically interested in whether apparent changes in sea ice habitat were correlated with NB polar bear demographic parameters. This is an important question because of its implications for management, but also because the NB population is adjacent to another polar basin population (SB) that appears to be declining, possibly because of reduced access to suitable sea-ice habitat (Regehr et al. 2007a). Moreover, these population parameters are needed to re-assess harvest quotas to ensure they remain sustainable. We utilized all available live capture-recapture and radio telemetry data collected over the last 35 years, including those from the most recent field study in 2003-2006, to estimate trends in population size and to assess factors that might be influencing survival, particularly those related to habitat (i.e., sea ice) loss.

Study Area

The NB polar bear population is distributed over the sea ice of eastern and northeastern Amundsen Gulf, the south and west coast of Banks Island, the western end of M'Clure Strait, and the west coast of Prince Patrick Island (Figures 1, 2).

A defining feature of the marine ecosystem in the NB is that it borders the Arctic Ocean, from which it receives a steady inflow of cold and relatively unproductive polar water (Pomeroy 1997) via a continuous clockwise current (the Beaufort Gyre; Wilson 1974). This current flows south from the polar basin along the west coast of Banks Island through the Cape Bathurst Polynya, where it mixes with westerly currents from Amundsen Gulf, passes westward along the Alaska coast, and then flows back north toward the pole. In almost all months, there is at least some open water in the shore lead and polynya system that parallel the coast from Prince Patrick Island south through the Cape Bathurst Polynya and west along the mainland coast (Smith and Rigby 1981). The distributions of ringed (*Phoca hispida*) and bearded (*Erignathus barbatus*) seals, and consequently also that of the polar bears that hunt them, are influenced strongly by the distribution of shore leads and polynyas, areas of annual and multi-year ice, and by both short- and long-term variations in the pattern of freeze- and break-up (Stirling et al. 1982; Stirling et al. 1993; Durner et al. 2004).

Freeze-up of the open water between land and the offshore multi-year ice usually occurs between mid-October and mid-November, and breakup follows between late May and late June

(Smith and Rigby 1981). In most years, significant amounts of ice remain over the continental shelf near Banks and Prince Patrick islands as well as further offshore. For a review of the oceanography of the eastern Beaufort Sea, see Carmack and MacDonald (2002).

Methods

Field Methods

Polar bears were captured in the central portion of the NB around the southern and western coastlines of Banks Island during the springs (March through May) of 1971-1979, 1985-1987, 1989, 1991, 1992-1994, 2000, and 2003-2006 (Figure 3). During the main large-scale population assessments in the mid-1970s, mid-1980s, and mid-2000s, search and capture of polar bears was conducted throughout most of the NB to a maximum of about 160 km offshore. During these periods of intensive sampling, we attempted to catch all bears encountered, provided weather and ice conditions were suitable for safe immobilizations. In 1992-1994, a principal objective was to determine if a substantial number of bears existed in the area between northwestern Banks Island and the west coast of Prince Patrick Island (Lunn et al.1995). Sampling this area was important because it had not been possible to adequately survey there in previous studies. Thus, the polar bear capture effort was focused only in the more northerly part of the NB during those years.

During physical capture events, polar bears were anaesthetized with immobilizing drugs delivered remotely in projectile syringes fired from a helicopter. From 1971 through 1985, polar bears were drugged with either Sernylan or a combination of Ketamine and Rompun (Schweinsburg et al. 1982). Beginning in 1986, all bears were immobilized with Telazol® (Stirling et al. 1989). All captured polar bears were given ear tags and tattooed on both sides of the inner surface of the upper lip with the same unique identification number. If ear tags were missing on a subsequent capture, bears were given a new set of numbered ear tags that were referenced to the original tattoo number in our database. The straight-line body length (tip of nose to tip of tail), axillary girth, number and age of accompanying bears, and fat condition were recorded, and a vestigial pre-molar tooth was collected for age determination (Calvert and Ramsay 1998). Ages of cubs and yearlings were determined visually by size. After formation of an independent Animal Care Committee by the Canadian Wildlife Service in 1992, all capture and marking protocols were reviewed and approved annually.

During capture events, radio collars were deployed on some adult female polar bears. No other age-class of bears carried radio collars. Between 1986 and 1987, 14 adult female polar bears were wearing VHF radio collars with potential use in relocating the bears. These relocations, when successful, were included as a 1 ("captured") in the capture history. When unsuccessful, a standard 0 ("not captured") was included in the capture history. A total of 48 bears were wearing satellite collars at various times between 1989 and 2006. These collars also had VHF transmitters to facilitate relocation of bears for removal or replacement of collars, as well as to relocate bears carrying satellite collars that had ceased to signal. Satellite collars were not used to locate polar bears for capture in the field, but provided locations approximately every 5-6 days during their lifetime of 2-4 years (e.g., Amstrup et al. 2000). When ≥ 1 satellite relocation in a given year was within population boundaries, a 1 ("captured") was included in the bear's capture history that year. Otherwise, a standard 0 ("not captured") was included. Without specific information on when a collar was dropped or became non-operational, we assumed collars operated for 2 years post-deployment.

Capture-Recapture Analysis

Survival, recapture probabilities, and ultimately the size of segments of the NB polar bear population were estimated using capture-recapture data collected from 1971 through 2006 (Figure 3). Our analysis included capture-recapture data from bears located using standard search methods as well as polar bears encountered by means of radiotelemetry. Data for each polar bear were summarized as individual capture histories and covariates. For example, bear number X02548 had a capture history of (0001101000000000000000), where 1 indicates capture and live release during sampling occasion j ($j = 1,2……22$) and a 0 indicates not captured during sampling occasion j. Multiple captures or relocations of an individual within a season were amalgamated and treated as a single capture (single 1) that year. No bears died during capture and all were released alive back into the population. Known harvests of bears previously marked during our study were ignored (i.e., harvested animals were not censored). As a consequence, mortality estimates (1 – survival) include both natural and harvest mortality. Survival estimates included emigration in the sense that they estimated the annual probability of an individual bear naturally surviving, avoiding the harvest, and remaining on the study area. Our analysis included 1031 marked bears from 22 capture occasions over the 35 year study period.

We estimated apparent survival and recapture probabilities using open population Cormack-Jolly-Seber (CJS) models (Lebreton et al. 1992; McDonald and Amstrup 2001; Williams et al. 2002; McDonald et al. 2005) that contained covariates quantifying physical and environmental factors that potentially influenced demographic parameters. We estimated survival directly from the CJS models, and then model-averaged these estimates across all supported models. Multi-year gaps in capture histories were raised to the size of the gap, as done in program MARK. We estimated population size during year j (Nj) using estimates of recapture probabilities derived from a particular CJS model and the HT estimator (McDonald and Amstrup 2001; Taylor et al. 2002; Amstrup et al. 2005, Chapter 9). We estimated the variance of Nj using the estimator derived by Huggins (1989; see also, Taylor et al. 2002). We then model-averaged these estimates of Nj across all supported models to derive our final estimates.

Technically, the HT estimator assumes that an un-equal probability sample of bears was obtained each year, and that the recapture probability model is correct for all bears ever captured one or more times. This size estimator technically makes inference to the population of bears that have non-zero capture probability in the particular year for which it was constructed. While the geographic extent of the bears with non-zero capture probability is difficult to assess, we describe (in Results and Discussion) those areas and periods for which we met this assumption. Low sample size is known to adversely affect HT size estimates. During some primary sampling years, we captured very few bears (primarily during the 1990s) and consequently we were uncomfortable relying on these years' estimates when assessing trend. Although we report estimates for all years of intensive capture effort, including those with low sample size, we required an adequate sample (arbitrarily defined as >50 captures) in a particular year in order for that year to be included in average size and trend assessments.

All models were fitted to the data using R-language software that implemented the "general regression" approach to capture-recapture (McDonald et al. 2005, *http://www.west-inc.com*). This approach implemented the CJS model, which assumed captures came from a multinomial distribution. We assumed a logit link function related linear combinations of covariates to probability of survival and probability of recapture.

Survival Covariates

Our survival parameters (φ_{ij}) represented apparent survival, which was the probability of animal i remaining alive and within the study area between sampling occasions j and $j+1$. We fitted models that allowed φ_{ij} to vary by sex, age class (age classes = COYs, yearlings, subadults [2-4 yrs old], adults [5-19 yrs old], and senescents [20+ yrs old]), and time or study period. We also modeled φ as a function of several environmental covariates to test ecological hypotheses regarding the effects of sea ice and seal productivity on polar bear survival.

To investigate the potential effects of variation in sea-ice dynamics on survival, we included two sea-ice habitat covariates. The first sea-ice covariate was the number of square kilometers over the continental shelf (defined as waters < 300 m deep) with > 50% ice concentration (*PMIce*, Table 1). Ice concentration values were measured on 25 km pixels, from which we calculated square kilometers with > 50% ice. Data were obtained from the National Sea Ice Data Center (NSIDC). NSIDC data in turn were derived from passive microwave data collected by the National Aeronautics and Space Administration (NASA) team algorithm at the Goddard Space Flight Center (*ftp://sidads.colorado.edu/pub/*). From 1979 to late 1987, sea-ice concentrations were available every other day. Daily sea-ice concentrations were available from late 1987 through 2006. We excluded pixels that overlapped land, which excluded a buffer of sea along all coastlines that was approximately 25 km wide. To derive a single number to associate with survival between capture occasions, we averaged the every-other-day or daily square kilometers of ice values for the year in question. These average values were then standardized to a mean of 0 and standard deviation of 1 to increase stability of the CJS model estimates. Standardized ice values associated with survival intervals >1 year were set to 0, which

effectively used the intercept of the model, or the mean of all other covariates in the model, to estimate survival during those intervals.

The second sea-ice covariate was mean seasonal volume under the resource selection function (RSF) estimated by Durner et al. (2007; *RSF*, Table 1). *RSF* volume measurements were obtained by integrating (summing) the height of the estimated *RSF* surface over the International Union for the Conservation of Nature and Natural Resources (IUCN) population boundary for the NB (Figures 1, 2). Again, mean *RSF* values were standardized to a mean of 0 and standard deviation of 1, and those centered values associated with survival intervals >1 year were set to 0 to effectively use the mean of all other covariates in the model for estimation of survival.

We also included a categorical seal productivity covariate to investigate its influence on polar bear survival (*Seal*, Table 1). Stirling (2002) documented a decadal scale oscillation in seal productivity from which we created a categorical covariate to quantify good and poor seal productivity years. Years of low seal productivity were known to have occurred in 1966, 1974-1976, and 1984-1986 (Stirling 2002), and some of the years between 2004-2006 (unpublished data). Thus, we introduced a covariate that allowed for a three-year low, starting in 1974, and repeating this pattern every ten years to examine whether seal productivity follows some sort of decadal oscillation that in turn affects survival of polar bears in the NB.

Recapture Covariates

Recapture probability (p_{ij}) represented the probability that the ith marked polar bear alive and in the study population was recaptured or relocated during the spring of year j. We fitted capture probability models that included effects of sex (*sex*), age class (*age01*, *age2*, *age34*), study period (*effort.2*), capture effort (*flight.km*), and whether or not a bear was wearing a VHF

or satellite radio collar (*radio.vhf, radio.sat*; Table 1). Study period was related to capture effort because *effort.2* quantified years of more rigorous capture effort as a binary variable. However, we also reasoned that recapture probability might be a function of a continuous measure of effort and included *flight.km* as well. Because adult males were searching for females in estrus during the spring season, we hypothesized that their increased movement rates would result in a higher probability of encountering their tracks, and therefore increase our chances of recapturing males relative to females. Thus, we also modeled the effect of sex on recapture probability. We also expected annual environmental conditions (e.g., weather, sea ice, distribution of bears and their prey) to affect recapture probability, and thus allowed p_{ij} to vary by year.

Goodness-of-fit

We used both program RELEASE (Burnham et al. 1987) as well as a parametric bootstrap procedure in program MARK (White and Burnham 1999) to estimate the variance inflation factor ($\hat{c}$) for our dataset. The variance inflation factor is a measure of extra variation in the data not predicted by the underlying multinomial distribution. When applied to the entire NB data set, the standard RELEASE CJS goodness-of-fit test that used Fisher's exact test to back calculate chi-square statistics when expected cell counts were less than 2 estimated $\hat{c} = 1.16$. However, when we exclude the 26 captures of bears that were available for capture by VHF or satellite telemetry, RELEASE estimated $\hat{c} = 0.95$. Also, when we exclude the 299 captures of COYs and yearlings, $\hat{c} = 0.95$. We obtained similar results using the parametric bootstrap technique in program MARK. When radio-telemetry recaptures were excluded, and a CJS model with age classes was modeled, we obtained a parametric bootstrap estimate of $\hat{c} = 0.98$. Thus, we concluded that minor heterogeneity existed in the data due to the presence of radiotelemetry captures and age classes. Because our models allowed for both of these sources or variation, we set $\hat{c} = 1.0$, the level indicative of no overdispersion.

Model Selection

We based model selection on Akaike's Information Criterion (AIC; Akaike 1981), biological realism, and model interpretability. We corrected AIC for small sample size (AIC$_c$) and used $\hat{c} = 1.0$ from the goodness-of-fit analysis (Burnham and Anderson 2002). When appropriate, we based inference regarding important hypotheses on the strength of evidence across multiple models. For pairwise comparisons, we quantified relative support for a model using ΔAIC$_c$, where ΔAICc < 2 indicated similar support for both models and ΔAIC$_c$ > 10 indicated strong support for the lower-AIC$_c$ model (Burnham and Anderson 2002). For each fitted model, we also considered the magnitude and variance of the estimated parameters. This was necessary because while AIC attempts to optimize the overall trade-off between model fit and precision, it does not indicate which model parameters explain appreciable variation in the data.

We ultimately estimated survival and population size as the AIC$_c$-weighted model averages across supported models, which we developed in several steps. Covariates were combined additively and interactively to build biologically relevant model structures for recapture and survival parameters (Tables 2, 3). These basic structures were then combined in a stepwise approach because estimation of all possible combinations of models was not feasible. These steps are summarized in Table 4.

We combined estimation of the model structures in a stepwise fashion as follows:

1. We selected and fixed a recapture (p_{ij}) parameterization that was general and expected to be well supported. We expected that capture probability might be dependent on whether a bear was wearing a VHF or satellite radio collar, the study period, whether a bear was an independent 2 – 4 year old, and whether a bear was an adult or senescent male. Because they are with their mothers, we reasoned that COYs and yearlings might have recapture probabilities approximating those of adult females. Thus, our general model for recapture probability was *p*(*radio.vhf + radio.sat + effort.2 + age2 + age34.sex*). Using this recapture parameterization we fit survival (φ_{ij}) parameterizations representing all individual constraints (sex and age classes) and two types of temporal variation: time-constant and time-dependent;

2. We selected the most supported individual constraint parameterization with and without temporal variation. Using these 2 φ_{ij} parameterizations we fit p_{ij} parameterizations representing all individual constraints, with no time variation (i.e., time-constant models);

3. We selected the two most supported p parameterization for each of the 2 φ_{ij} parameterizations and added several different types of temporal variation in *p*;

4. Using all previous fitted models, we selected the most supported parameterizations for p_{ij}. Then, using the most supported individual constraint parameterization in φ_{ij} from Step 1 and the final pij parameterization(s) from Step 3, we fit models with all types of temporal variation in phi including appropriate interactions between temporal variation and individual constraints.

Results

Captures

Capture-recapture information was available on 1031 individual polar bears. A total of 376 bears were captured or recaptured from 1971 to 1979, 279 from 1985 to 1989, 87 from 1991 to 1994, and 330 were captured from 2000 to 2006. A total of 14 bears were "captured" by VHF radio telemetry during 1986 – 1987. Forty-eight bears were "captured" by satellite telemetry during 1989 – 2004. Captures were distributed similarly among years except for the period 1990 – 1999 during which search effort was more northerly, to the exclusion of southern areas, than in other decades (Figure 3). During all capture periods, bears were captured non-selectively in order to have samples that were as representative as possible of the population, wherever sampling was conducted. During the 35 year study period the proportion of recaptures in the capture samples varied from 0.00 to 0.53 (Table 5).

Model Selection

1. A total of 46 survival models were fitted with the recapture model *p*(*radio.vhf + radio.sat + effort.2 + age2 + age34.sex*). After Step 1, the top AICc-ranked models included individual-level effects of sex and age class as well as time variability in φ, i.e., φ (*Int + yr70s + yr80s + yr90s + sex + age0 + age1 + age4*; AIC_c weight = 0.322). The top AIC_c-ranked model that did not include time variation in survival included the same individual heterogeneity covariates, i.e., φ (*Int + sex + age0 + age1 + age4*). Although this model was not well supported (AIC_c weight < 0.0001), we used it in Step 2 according to our model selection protocol.

2. A total of 24 recapture models were fitted during Step 2, 12 with the top time constant survival model (φ (*Int* + *sex* + *age0* + *age1* + *age4*)) and 12 with the top time varying survival model (φ (*Int* + *yr70s* + *yr80s* + *yr90s* + *sex* + *age0* + *age1* + *age4*)). After Step 2, the top 2 recapture probability models (combined AIC$_c$ weight = 0.555) included individual covariates for whether a bear was wearing a VHF or satellite radio collar and whether a bear was an adult male. The top model for recapture probability at the end of Step 2 was p(*Int* + *radio.vhf* + *radio.sat*), while the second most supported model was p(*Int* + *radio.vhf* + *radio.sat* + *age34.sex*; Table 4).

3. We fitted an additional 12 recapture models by combining the best 2 recapture models from Step 2 with time varying effects of year, study period, and flight kilometers on recapture probability. Survival was modeled according to the best time varying and time constant survival models from Step 1. The supported form of temporal variation in p included effects for whether a bear was wearing a radio collar (*radio.vhf* and *radio.sat*), whether a bear was an adult male (*age34.sex*), and study period (*effort.2*; AIC$_c$ weight = 0.377).

4. Using the top-ranked recapture probability model, Step 4 fitted 40 survival models that included interactions between age class and standardized RSF values (*RSF*), standardized ice extent (*PMIce*), low or high seal abundance (*Seal*), and decadal time effects (*yr70's*, *yr80's*, *yr90's*, and *yr00's*). Following Step 4, all 187 models from Steps 1, 2, 3, and 4 were ranked to determine our final list of models. The top 20 models in the final ranking appear in Table 6. AIC$_c$ weight of the top model was 0.377, and the combined AIC$_c$ weight of the top 20 models was >0.9999. Because the top 3 models had an AIC$_c$ weight of 0.716, and because these models had the same structure for survival, model-averaged estimates of survival essentially followed this structure. Similarly, estimates of population size were primarily derived from the top 3 models for recapture probability.

Survival Estimates

Model-averaged estimates of survival appear in Figure 4 and Tables 7-8. Since we did not estimate mortality due to harvest separately, these rates include both natural mortality and harvest mortality. Estimates of survival of senescent adults ranged from 0.33 (1980s, males) to 0.92 (1990s, females). Estimates of COY and yearling survival ranged from 0.10 (1980s, male yearlings) to 0.87 (1990s, female COY). Survival of 2–4 year olds and adults were nearly identical and ranged from 0.61 (1980s, males) to 0.97 (1990s, females). The wider confidence intervals on the younger age classes were largely due to small sample sizes (Figure 4). Survival of COYs and senescent adults were not statistically different (in the top model, Wald t-ratio = -0.52, p = 0.6011). Survival of COY and senescent adults combined was statistically higher than that of yearlings (in the top model, Wald t-ratio = 2.16, p = 0.0305). Survival of 2 – 4 year olds and adults combined was statistically higher than survival of COY and senescent adults combined (in the top model, Wald t-ratio = 3.91, p = 0.0001).

Survival of males was estimated to be lower than that of females (in the top model, Wald t-ratio = -2.86; p = 0.0043). In the 1970s, female survival was on average 16% higher than males. In the 1980s, female survival was on average 34% higher. In the 1990s, female survival was on average 7% higher than males, and in the 2000s, female survival averaged 21% higher than males. Although these results technically apply to all age classes, the majority of bears were either 2–4 year olds or adult, and the preponderance of evidence for this effect came from those classes.

Models that allowed associations between annual variation in survival and habitat or relative seal abundance variables were not, in general, supported by the data. The top model containing relative seal abundance (*seal*) was ranked 56th and had a delta AIC$_c$ value of 44.9. The top model containing habitat resource selection values (*RSF*) was ranked 49th and had a delta AIC$_c$ value of 42.4. The top model containing *PMIce* was ranked 53rd and had a delta AIC$_c$ value of 43.6.

The top survival models all allowed survival probability to differ in each decade of the study. Survival in the 1970s was comparable to that in the 2000s (in the top model, p = 0.6393), significantly lower in the 1980s than in the 2000s (in the top model, p = 0.0140), and nearly statistically higher in the 1990s than in the 2000s (in the top model, p = 0.0952).

Recapture Probabilities

All recapture probability models with high support indicated that wearing a radio collar had a large effect on recapture probability (as evidenced by the coefficient estimates for *radio.vhf* and *radio.sat*) and generally led to a high chance of recapturing an individual (*p*(recapture) ~ 80% for VHF radios, *p*(recapture) ~ 94% for satellite radios). Adult and senescent males had marginally higher probability of recapture than other bears throughout the study (p = 0.0692). Probability of recapture averaged 9.3% for females without radios and non-adult male bears during intensive capture periods, while probability of recapture averaged 13.8% for non-radioed adult males during intensive capture periods. During non-intensive capture periods, recapture probability averaged 2.3% for non-radioed females and non-adult males (p < 0.0001 when comparing to equivalent recapture probability during intensive capture periods).

Estimates of Population Size

During the 1990s a significant number of bears were captured off the western and southern coasts of Prince Patrick Island and in M'Clure Strait (Figure 3C), particularly during 1992-1994 when the capture effort focused on that area. A significant fraction of the captures in the 1990s were of bears that had been previously marked further south, indicating significant mixing between the northern and southern regions of the study area. At the same time, the relatively large fraction of unmarked bears captured in the northern region indicated that some bears might not have been susceptible to capture during other sampling periods. If true, our estimates of population size during the 1970s, 1980s, and 2000s would estimate a consistent segment of the NB population residing off the western and southern coasts of Banks Island plus an unknown fraction residing north of M'Clure Strait. For reasons stated in the Discussion, we believe our population size estimates for the 1970s, 1980s, and 2000s include the vast majority of bears in the NB population, but should also be considered slightly low.

Model-averaged estimates of abundance during the 1980s, including model selection uncertainty, were remarkably similar to independent analyses and estimates of population size derived from the same data by different authors (Figure 5). Both the DeMaster et al. (1980) and Stirling et al. (1988) estimates of abundance were well within the confidence intervals of abundance estimates produced here.

Overall, estimates of abundance were remarkably similar through the 1970s, 1980s, and 2000s (Figure 6; Table 9). The average numbers of bears estimated to be in this segment of the population during each decade were as follows: 1972 to 1975 = 745 ($\pm$ 246, 95% CI), 1985 to 1987 = 867 ($\pm$ 141, 95% CI), 1992 to 1994 = 289 ($\pm$ 62, 95% CI), and during 2004 to 2006 = 980 ($\pm$ 155, 95% CI). Estimates during the 1990s were lower but, as previously stated, capture effort was also focused on the

area between the north-western corner of Banks Island to the west coast of Prince Patrick Island during that period. These results are not included when considering long term trends in NB. Note that the confidence interval on the size estimate in 2006 (i.e., 617 bears $\pm$ 220 95% CI) did not overlap the confidence interval for the size estimate in 2005, indicating a significant decline in 2006 relative to 2005, in statistical terms at least (but see Discussion).

Discussion

Survival

There was considerable variability between the survival rates of bears in different age and sex classes within the same time periods (i.e., mid-1970s, mid-1980s, early 1990s, and 2000s). However, there was less variability among bears of the same age and sex classes among the different sampling periods of the study. Yet, in general, survival rates of all groups were lower in the mid-1980s than during other periods (Figure 4; Tables 7-8). Although there was enough overlap in the confidence limits of the estimated survival rates of bears of each age and sex class between sampling periods to make them not significantly different (statistically), the point estimates within each period were remarkably consistent. As reported in other analyses of demographic data on polar bears, e.g., Regehr et al. (2007b), the annual survival rates of prime adult females and males were higher than all other groups and were less affected by apparent fluctuations in ecological conditions, although they too varied among sampling time periods.

The survival rates of bears in all age and sex classes were lower in the 1980s than during the other sampling periods. Although we cannot be definitive about the explanation, we note that three of the lowest known years for production of ringed seal pups (the most important component of the diet of polar bears in the eastern Beaufort Sea; Stirling and Øritsland 1995; Iverson et al. 2006), were 1985-1987. As

in the mid-1970s, these declines were associated with periods of very heavy ice in the first year of reduced productivity. In the mid-1970s, the drop in survival of COYs coincided with the large drop in ringed seal productivity, apparently resulting in those cohorts being under-represented in subsequent years (Stirling 2002). Thus, it is possible that the marked reduction in seal productivity had a negative effect on the survival of all age and sex classes of polar bears during that period and not just on their natality as reported by Stirling (2002). The ringed seal reproductive rates in years prior to the first of the three low natality years in 1985 are unknown. We do know that they were high in the early and late 1970s, both of which were periods of high survival rates for bears of all ages and sex classes.

It is possible that the covariate for seals we applied to our analyses did not improve our overall estimates of survival because it was too insensitive. As applied, it simply incorporated three year downturns in seal productivity at ten year intervals, beginning with the documented downturn in the mid-1970s and overlapping with the similarly documented downturn of the 1980s. However, neither ringed seal nor polar bear productivity and survival were quantified during much of the rest of the total period of the study which may have simply reduced the robustness of the data we were able to test for a statistically significant association.

An unexpected and unexplained apparent anomaly in the survival calculations was that in all years and in all samples, the survival of COYs was higher than the survival of yearlings, rather than the other way around. Although the confidence intervals for both age groups were wide, and had some overlap, the absolute consistency of this result suggests either something was real in biological terms or there was a consistent bias in the way COYs and yearlings were sampled. We also confirmed that a coding error that reversed COYs and yearling records in the analysis did not occur. However, at this point, we do not have an explanation for

this result, which differs from the results of most other polar bear population analyses (e.g., Obbard et al. 2007; Regehr 2007b).

In general adult male survival was lower than that of females, as has been similarly reported for bears in SB (Regehr et al. 2007a) and has also been documented in other studies (e.g., Regehr et al. 2007b). In the adjacent Viscount Melville polar bear population, Taylor et al. (2002) estimated total annual apparent survival of adult males and adult female polar bears to be 0.774 and 0.905, respectively. Although our results are similar, they are not directly comparable to Taylor et al.'s (2002) results because they estimated a pooled survival rate for all bears greater than 1 year of age and did not allow survival to vary over time.

The low estimates of model-averaged survival for adult males relative to adult females in NB could be a product of incorporation of harvest in the model data. The higher mortality of adult males may also have been affected by the sex-selective harvest of polar bears in NB (2 males:1 female) and the focus of the guided sport hunt on the largest adult males. The sex ratio of all adult bears ($\geq$ 5 years old) captured in NB and the Canadian portion SB from 2003-2006 was 42.1:57.9 (189 males, 260 females), which was skewed strongly in favor of females and significantly different from a 1:1 sex ratio (χ^2= 11.27, p = 0.001; Stirling et al. 2006). The proportion of male bears over 10 years of age was also reduced in NB, especially in 2006, an aspect that should probably be monitored further. Sex-selective harvesting also occurs in SB (Brower et al. 2002) and a comparison of the adult sex ratio of bears from NB during 2003-2006 of 38:62 (73 males, 118 females) to that in the Canadian portion of SB of 45:55 (116 males, 142 females), including recaptures was not statistically significant (χ^2 = 2.05, p = 0.152; Stirling et al. 2006). Derocher et al.(1997) noted that the sex ratio of the polar bear population in WH has become skewed in favor of females, in part at least because of the long-term effect of sex-selective harvesting. Thus, at least in some

polar bear populations, it seems that a sex-selective harvest can affect adult sex ratios.

The age and sex-specific survival rates in NB were not directly comparable to those of SB (Regehr et al. 2007a) because the former included harvest mortality while the latter removed harvest mortality in an effort to estimate natural mortality. However, the marked reduction in survivorship for COYs noted in SB in 2005 and 2006 (Regehr et al. 2006) was not observed in NB. It is possible the drop in survivorship in SB was related to ecological changes resulting from several years of successively more extensive and extended open water (Regehr et al. 2007a) while, in comparison, ice conditions have remained relatively stable in NB. Because of the relative stability of the distribution and abundance of ice in NB, the ice covariate in our analysis was not significant.

Population Size and Trend

Previous to this study only one other study directly estimated the size of the NB polar bear population. Stirling et al. (1988) used a capture-recapture analysis following DeMaster et al. (1980) and the Fisher-Ford method (see Begon 1979) to estimate population size from 1985-1987. The point estimates from the latter method were very similar to those of our estimates while the confidence intervals from our analysis indicated the estimates were not significantly different from the estimates derived by DeMaster et al.(1980; Figure 5).

We produced population size estimates for all years of intensive capture effort (Figure 6). However, for estimation of average population size during the major capture-recapture periods, we considered only estimates made in years when the annual capture sample exceeded 50. The only intensive capture years with fewer than 50 captures were 1972, 1989, and 1992 – 1994. Excluding these years, the three averaged decadal estimates for the mid-1970s, mid-1980s, and 2000s were 745 ± 246 (95% CI), 867 ± 141 (95% CI), and 980 ± 155 (95% CI;

Figure 6). For reasons stated below, we believe these estimates include nearly all bears in NB, but should be considered slightly low. Unfortunately, we cannot objectively estimate how much too low these estimates might be.

Although there is a trend in the point estimates toward a slow increase in population size over these time periods, the averaged estimates are not significantly different from each other statistically. However, Stirling (2002) reported that in the 1970s, polar bears in the Canadian sector of the Beaufort Sea were recovering from a period of overharvest that ceased only when quotas were established in 1968. In the decade or more that followed, the average age of both males and females increased from about 4 to about 8, after which they fluctuated over a narrower range, apparently in relation to fluctuations in ice conditions and ringed seal productivity (Stirling 2002). Similarly, in the early 1970s when the population was still in the early stages of recovery from being overharvested, there were few bears older than 10 years of age. For example, in harvest samples collected between 1970 – 1971 and 1972 – 1973, the oldest animal recorded was only 11 years old, and the next oldest bears were both 8 years old. By the late 1970s, the proportion of bears 10 years of age or older had increased to 20 – 30% for males and slightly more for females, after which there were decadal-scale fluctuations similar to those of the average age (Stirling 2002). Taken together, these data suggest that, even though the estimates for the three periods were not statistically different, it is likely the population increased in size from the early 1970s into the 1980s, after which it remained relatively stable.

The reduced estimate of population size in 2006 should be viewed with caution because the last capture probability and the last survival parameter are confounded in standard CJS models, and it is unclear what extent of confounding may exist between these parameters in our model because we included individual covariates. In any event, this estimate was made using known covariate values and coefficients that were estimated from parts of the model where survival and capture parameters are not confounded. In other words, we used the relationship between covariates and capture probability to estimate size in 2006, even though capture probability that year was not separately estimable. Also, partly because of poor weather during the 2006 capture season, we obtained a smaller capture sample than in previous years despite flying a similar number of kilometers in search of polar bears. However the recapture rate (19%) was double that of the previous two years (8% and 9%) which would also have the effect of reducing the estimate of population size. Thus, although we have estimated the average population size in the 2000s to be 980 ± 155 (95% CI), at this point, we suggest that may be conservative because of the strong possibility of an underestimate in 2006. The estimates of 1100-1200 in 2004 and 2005 may more accurately reflect the current number of polar bears in NB.

The averaged population estimate for the 1990s was 289 ± 62 (95% CI), which is significantly lower than for the other three sampling periods. Despite our efforts to model reduced capture probability of southern bears in the 1990s using period and other effects, we may not have succeeded fully, and it is difficult to determine mathematically whether the decline in the 1990s is real or an artifact of sampling. However, estimates for the 1990s are not directly comparable to those of the other three study periods because much of the area sampled during the three main years (1992-1994) was north of the northern limit of most of the areas surveyed in the other main periods and very little was done near Sachs Harbor (Figure 3C). Subjectively, during field sampling in the northern areas in the 1990s, bears were not determined to be abundant and in each year sample size was < 50, despite substantial search effort (Lunn et al. 1995). However, even in the first year of surveying in areas that had largely not been searched before 1992, recapture

probability was 0.21 and by 1994 reached 0.53 which appears to confirm that the bears to the north of the main study area (i.e., south of the northwest end of Banks Island) mix with other parts of the overall NB population. Additionally, the averaged population estimate of only 289 ± 62 (95% CI) appears to confirm that polar bears are not as abundant in the most northerly areas in spring as they were further south along the western and southern coasts of Banks Island and in Amundsen Gulf.

All this leads us to believe that the segment of the NB population in the north that was uncatchable (probability of capture = 0) during the primary study periods, if it existed at all, was small and inconsequential. Unfortunately, we cannot objectively estimate the fraction of the overall population that was sampled during the primary periods. We conclude that our abundance estimates during primary sampling periods are for a large but unknown fraction of the overall NB population, and should be considered slightly low.

Inuvialuit Harvest of Polar Bears From the Northern Beaufort

Between 1968 and the present, the annual quota for Inuvialuit hunters in NB has increased from 36 to 65, although for at least the last 15 years or more, the annual harvest has been less than 40 animals per year (Lunn et al. 1998, 2002, 2006), which has been well below the sustainable harvest of 50-55 bears, depending on the way it is estimated. The low harvest, relative to maximum sustainable yield (MSY), was likely driven by difficult travel conditions for hunters and a reduced hunting effort in parts of the area. Thus, it appears the level of annual harvesting has not yet reached MSY for over 15 years. Nevertheless, a more thorough population viability analysis would inform consideration of new quotas.

Future Trend

One of the most important factors influencing both polar bear survival and population dynamics is the availability of sea ice. At the southern limit of polar bear range, a progressive change toward earlier breakup of sea ice has been shown to negatively influence body condition, reproductive rates and survival of bears (Stirling et al. 1999; Obbard 2006; Regehr 2007b). Most recently, Regehr et al. (2007a) and Hunter et al. (2007) have shown that both survival rates and total population size of the SB polar bear population appear to be in decline and are also significantly correlated with changes in ice distribution and the duration of the open water season. To date, one of the most obvious ecological differences between NB and SB is that the sea ice adjacent to the coast and over the continental shelf within the NB population boundary does not melt completely each year. Thus bears in NB probably have greater access to seals in late summer and fall than do bears from SB and that difference, along with a sustainable annual harvest, may explain why the NB population has remained fairly stable over the last 20 years. However, we predict that if there is either a decline in the amount and duration of the sea ice as predicted by Comiso (2002) and Stroeve et al. (2007), or the harvest becomes unsustainable, the population will likely decline. Thus, continued monitoring and reassessment of the status of the NB population, along with that of SB, should be undertaken at regular intervals in the future. Such a quantitative comparison would also provide a basis for quantifying the importance of loss of sea ice on the population dynamics of polar bear populations adjacent to the polar basin.

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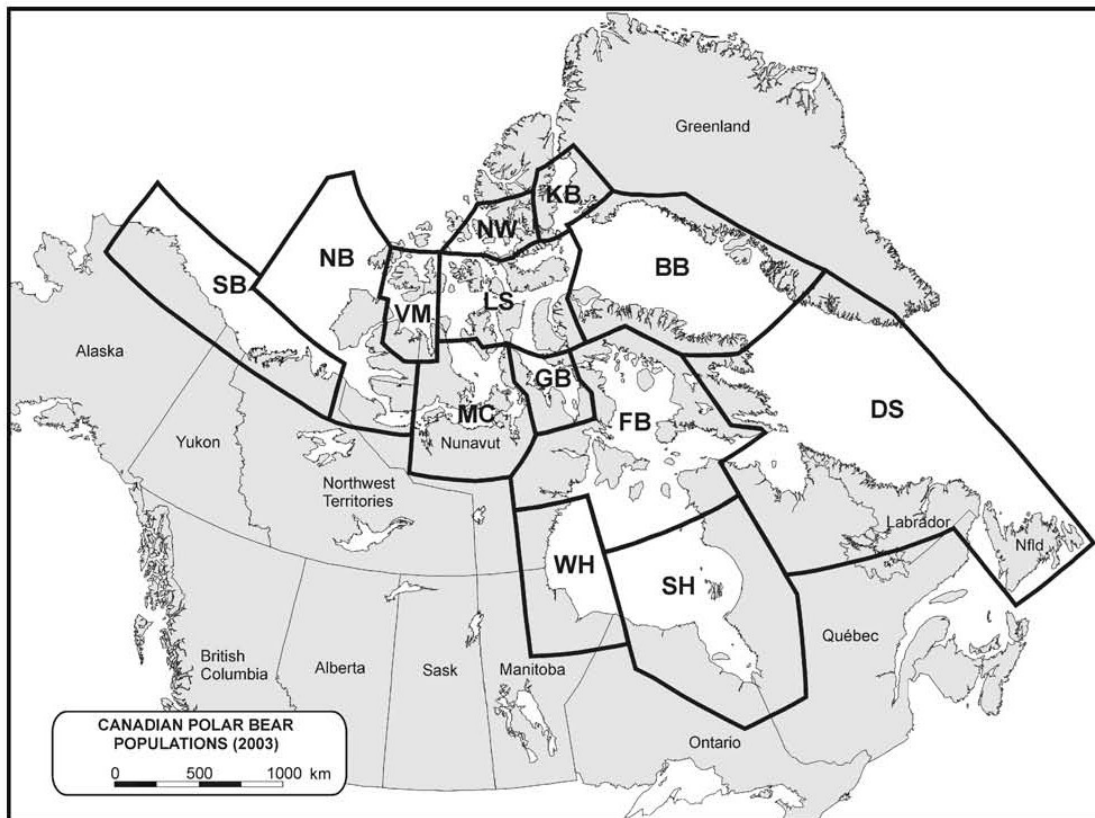
Figure 1. Polar bear subpopulations of Canada, and neighboring Alaska and Greenland, as of 31 December 2003.

BB: Baffin Bay; DS: Davis Strait; FB: Foxe Basin; GB: Gulf of Boothia; KB: Kane Basin; LS: Lancaster Sound; MC: M'Clintock Channel; **NB**: Northern Beaufort Sea ; NW: Norwegian Bay; SB: Southern Beaufort Sea; SH: Southern Hudson Bay; VM: Viscount Melville Sound; WH: Western Hudson Bay.
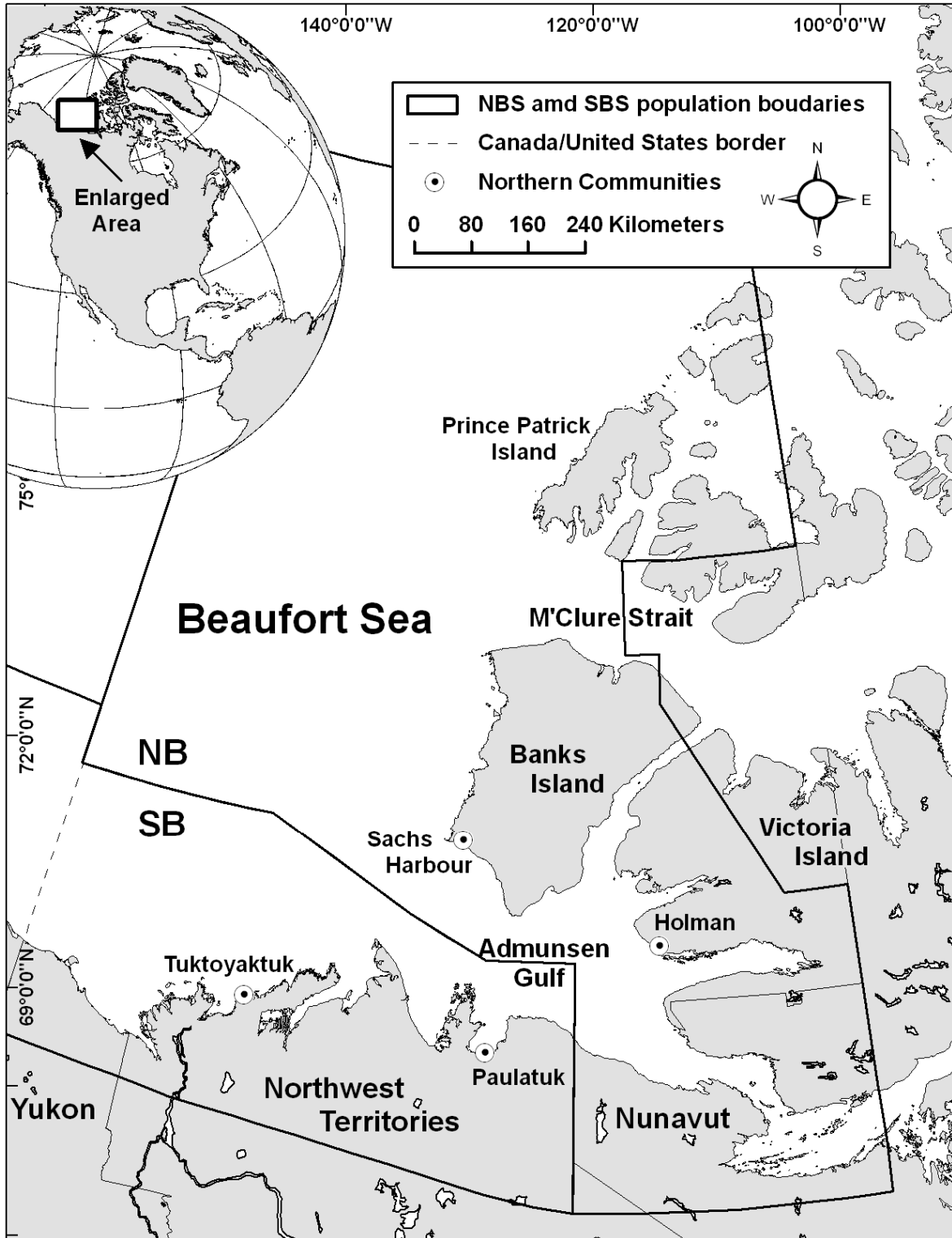
Figure 2. Northern Beaufort Sea (NB) population boundary and study area in relation to the Southern Beaufort Sea (SB) population boundary.
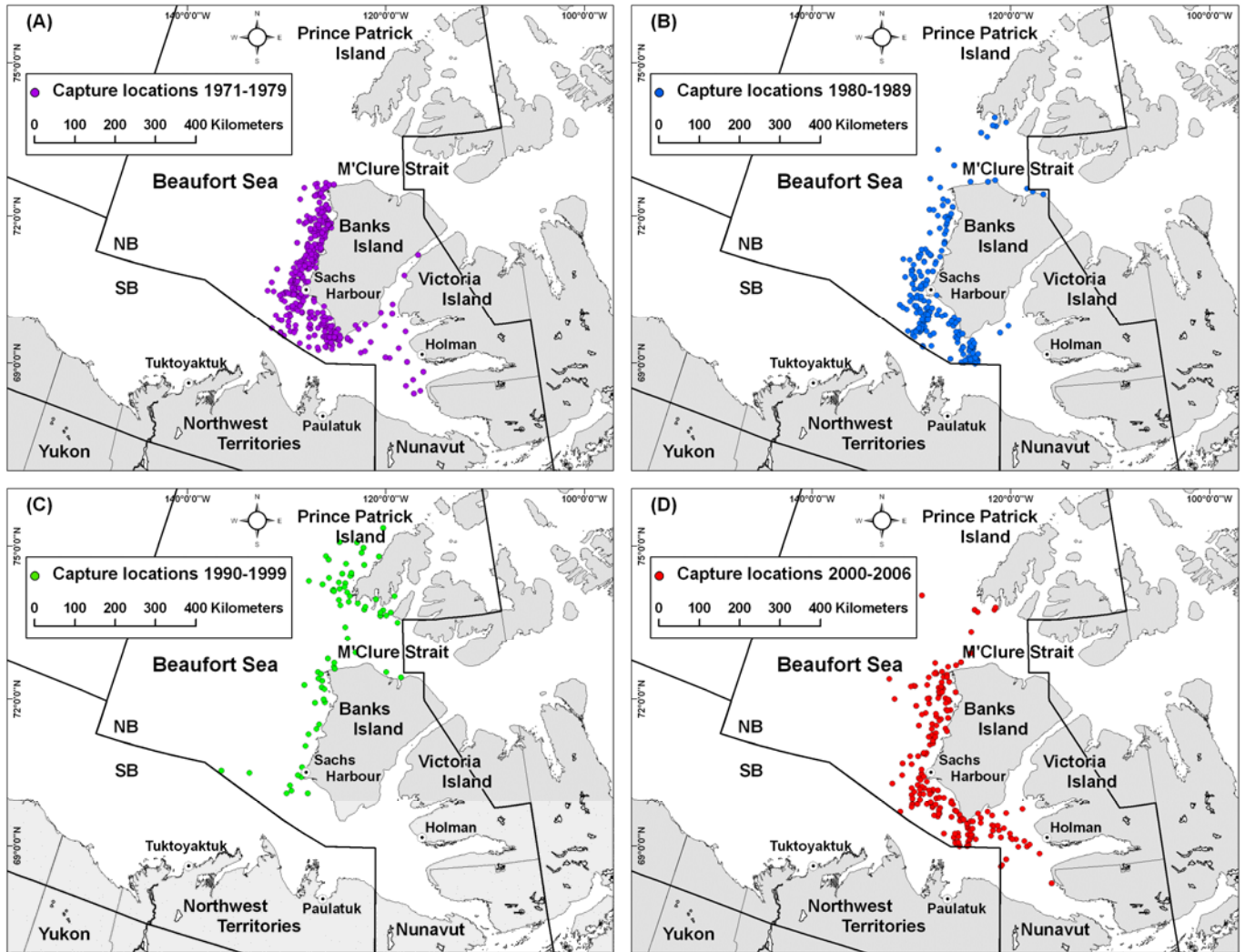
Figure 3. Distribution of polar bear captures during the (A) 1970s, (B) 1980s, (C) 1990s, and (D) 2000s included in the capture-recapture estimates of survival and population size in the Northern Beaufort Sea (NB).
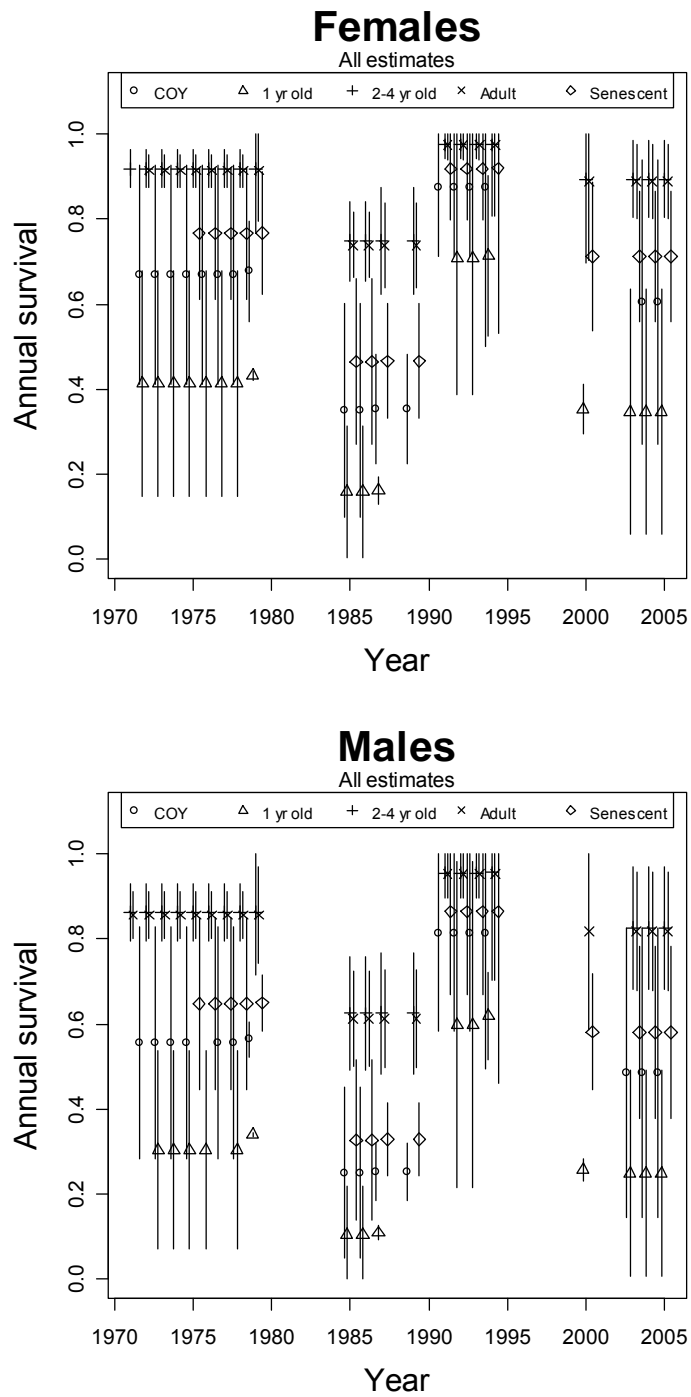
Figure 4.   Model-averaged estimates of polar bear survival derived from 35 years of capture-recapture information in the Northern Beaufort Sea.

Bars indicate 95% confidence intervals.
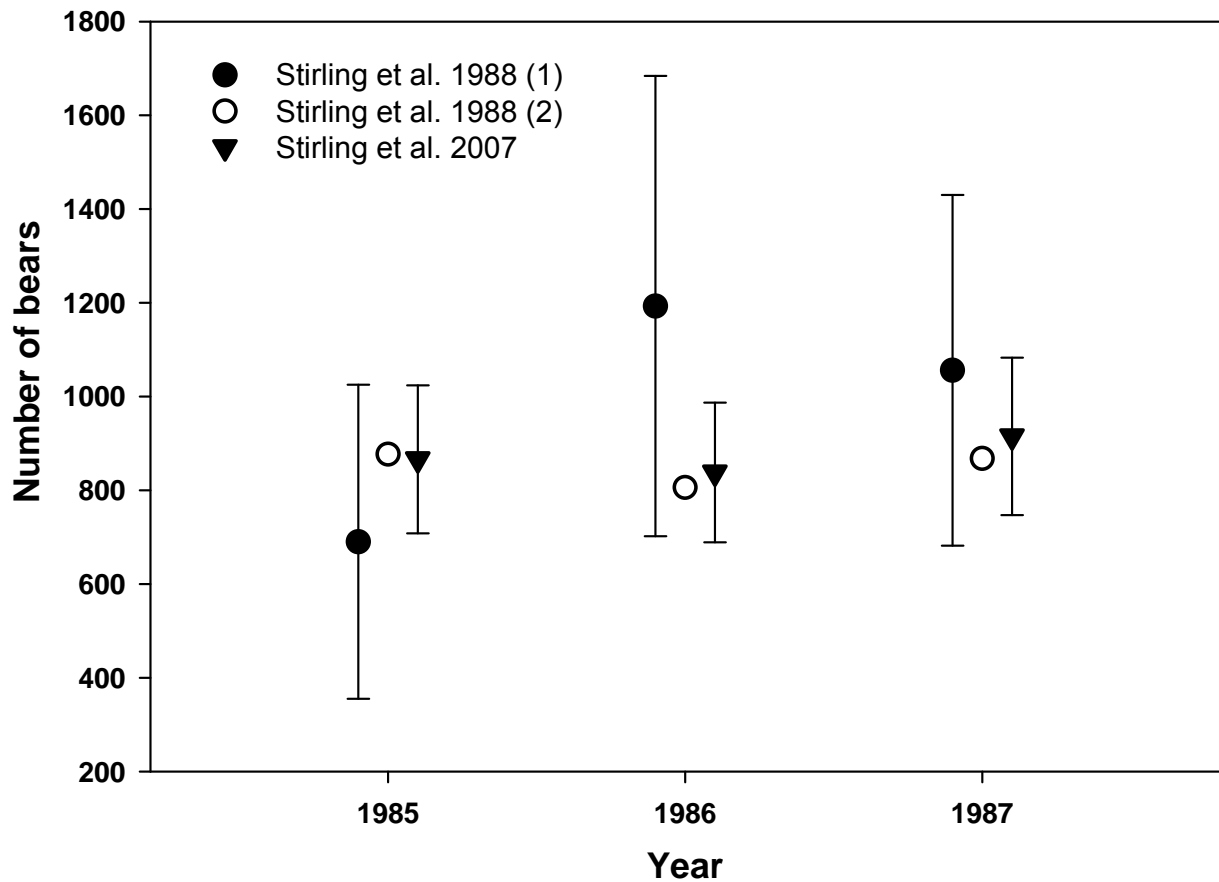
Figure 5. Population estimates from 1985-1987 from Stirling et al. (1988) and this report.

Stirling et al. (1988) used two methods to estimate population size. The first method followed that of DeMaster et al. (1980) and shows the population estimate ± SD. The second method was the Fisher-Ford method (see Begon 1979) which does not provide a variance estimate. The most recent analysis reports population size ± SE.

Northern Beaufort Sea

Estimates during intensive capture years
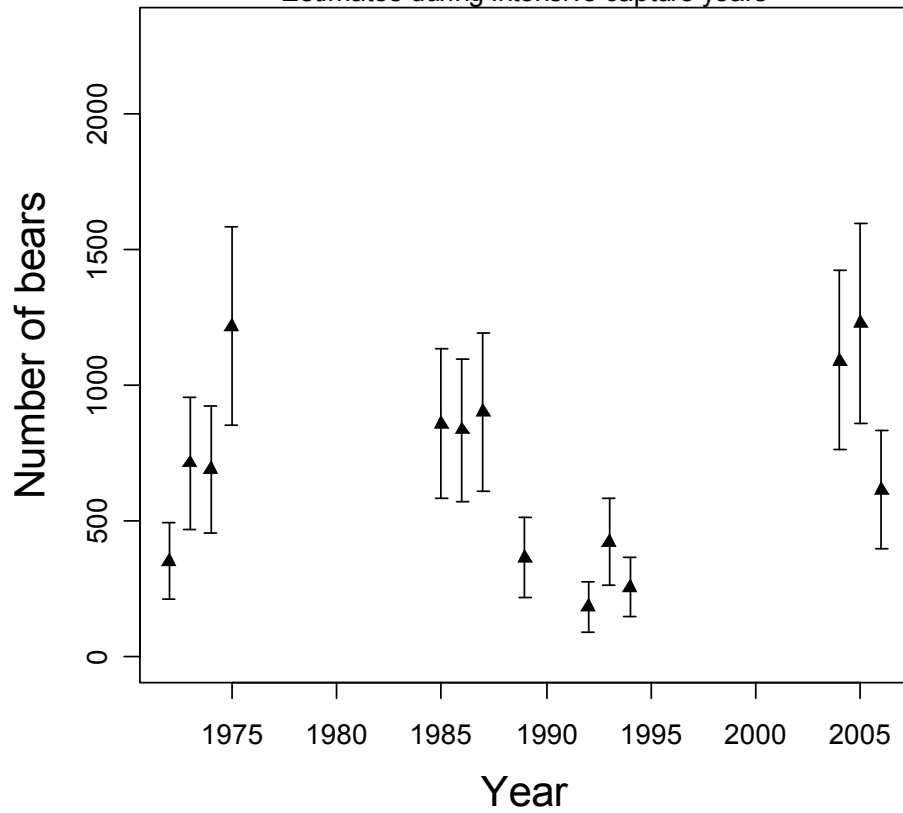
Figure 6. Model-averaged estimates of abundance for the Northern Beaufort Sea polar bear population during intensive capture years.

Years with fewer than 50 captures were 1972, 1989, and 1992 – 1994. Bars indicate 95% confidence intervals that include model selection uncertainty.

Table 1. Individual and temporal covariates included in models of apparent survival (Phi) and recapture probability (p).

In the Effect Allowed column, M = male, F = female, coy = cub of the year, yrlg = yearling, subad = subadult, and ad = adult.

Covariate	Affects	Effect Allowed
Individual covariates		
age0	Phi	coy (aged 0-1) $\neq$ older bears
age1	Phi	yrlgs (aged 1-2) $\neq$ other age classes
age2	p, Phi	subads (aged 2-4 years) $\neq$ other age classes
age3	Phi	adults (aged 5 – 20 years) $\neq$ other age classes
age4	Phi	senescent animals (aged 21+) $\neq$ other age classes
age01	p, Phi	coy = yrlgs $\neq$ other age classes
age23	Phi	subads = ads $\neq$ other age classes
age234	Phi	subads = ads = senescent $\neq$ other age classes
age0124		coy = yrlgs = subads = senescent $\neq$ adults
age1234	Phi	yrlgs = subads = ads = senescent $\neq$ coys
age34	p, Phi	ads = senescent $\neq$ other age classes
age012	Phi	coy = yrlgs = subads $\neq$ other age classes
SBage	Phi	relative differences in survival rates among age classes = those from Southern Beaufort Sea
Sex	p, Phi	M $\neq$ F
age234.sex	Phi	subad M = ad M = senescent M $\neq$ subad F = ad F = senescent F
age1234.sex	Phi	yrlg M = subad M = ad M = senescent M $\neq$ yrlg F = subad F = ad F = senescent F
age34.sex	p	ad M = senescent M $\neq$ ad F = senescent F
radio.vhf	p	bear available for capture using radio telemetry
radio.sat	p	bear available for location using a satellite radio
Temporal Covariates		
RSF	Phi	See text
PMIce	Phi	See text
Seal	Phi	See text
yr1971-yr2006	Phi	all years $\neq$ other years (Phi varies for all years)
yr70's	Phi	1970's $\neq$ other intervals
yr80's	Phi	1980's $\neq$ other intervals
yr90's	Phi	1990's $\neq$ other intervals
yr00's	Phi	1985 $\neq$ other years
Flight km	p	Number of kilometers flown searching for bears in a capture year
effort.2	p	Study effort (intensive study years, high effort = 1971 – 1975, 1985 – 1989, 1992 – 1994, and 2004 – 2006)

Table 2: Parameterizations considered for models of recapture probability

Model #	Regression Equation (all structures included intercepts)
1	(null)
2	age2 + age34.sex
3	age2
4	age34.sex
5	age01 + age2 + age34.sex
6	age01 + age34.sex
7 – 12	radio.vhf + radio.sat + equations 1 – 6
13 – 24	effort.2 + equations 1 – 12
19 – 24	Flight km + radio.vhf + radio.sat +equations 1 – 12
25 – 36	Year + equations 1-12

Table 3: Parameterizations considered for models of apparent survival.

Model #	Regression Equation (all structures included intercepts)
1	(null)
2	SBage
3	age0 + age1 + age2 + age4
4	age01 + age2 + age4
5	age01 + age4
6	age01
7	age0 + age1 + age4
8	age0 + age1
9	age0 + age1 + age2
10	age01 + age2
11	age0
12 - 22	sex + equations 1 – 11
23	age0 + age1 + age2 + age4 + age1234.sex
24	age0 + age1 + age4 + age1234.sex
25	age0 + age1 + age1234.sex
26	age0 + age1 + age2 + age1234.sex
27	age0 + age1234.sex
28	age01 + age2 + age4 + age234.sex
29	age01 + age4 + age234.sex
30	age01 + age234.sex
31	age01 + age2 + age234.sex
32 – 62	yr70's + yr80's + yr90's + equations 1-31
63 – 93	RSF + equations 1 – 31
94 – 124	PMIce + equations 1 – 31
125 – 155	Year + equations 1 – 31
156-186	Seals + equations 1 – 31

Table 4. Stepwise model selection.

(Int = intercept)

Step	Objective	Outcome
1	Identify appropriate models of individual heterogeneity in Phi (p structure fixed at (radio.vhf + radio.sat + effort.2 + age2 +age34.sex).	Phi structures carried forward to steps 2 & 3: 1. *Int + sex + age0 + age1 + age4* 2. *Int + yr70's + yr80's + yr90's + sex + age0 + age1 + age4*
2	Identify appropriate models of individual heterogeneity in p using the best time-constant and time-varying Phi structures from step 1.	p structures carried forward to step 3: 1. *Int + radio.vhf + radio.sat* 2. *Int + radio.vhf + radio.sat + age34.sex*
3	Identify appropriate models of temporal variation in p using the structures of individual heterogeneity in p from step 2 and the Phi structures from step 1.	p structure carried forward to step 4: *Int + radio.vhf + radio.sat + age34.sex + effort.2*
4	Identify appropriate models of temporal and individual variation in Phi by considering interactions, and using the top p structure from steps 1, 2 and 3. Compare AICc across all fitted models.	See Table 6 for top 20 models.

Table 5. Proportion of recaptures in sample from 1971-2006.

Year	Total Captures	Recaptures	Proportion recaptures
1971	4	0	NA
1972	36	0	0.00
1973	72	3	0.04
1974	70	4	0.06
1975	127	24	0.19
1976	31	6	0.19
1977	23	5	0.22
1978	24	3	0.13
1979	36	4	0.11
1985	88	13	0.15
1986	90	13	0.14
1987	92	20	0.22
1989	37	3	0.08
1991	7	1	0.14
1992	19	4	0.21
1993	47	5	0.11
1994	34	18	0.53
2000	21	2	0.10
2003	37	6	0.16
2004	113	9	0.08
2005	125	11	0.09
2006	62	12	0.19

Table 6. Model selection table for Cormack-Jolly-Seber models fitted to capture-recapture data for polar bears in the Northern Beaufort Sea from 1971-2006.

No. indicates the model rank; np = the number of estimated parameters; ΔAICc = difference in AICc value from the top model; and AICc weights = Akaike weights for each of the models.

No.	Survival	Recapture	np	AICc	AICc weight
1	φ (yr70's + yr80's + yr90's sexmales + age0 + age1 +age4)	p(radio.vhf + radio.sat + age34.sex + effort.2)	13	0.000	0.37711
2	φ (yr70's + yr80's + yr90's sexmales + age0 + age1 +age4)	p(radio.vhf + radio.sat + effort.2)	12	1.234	0.20347
3	φ (yr70's + yr80's + yr90's sexmales + age0 + age1 +age4)	p(radio.vhf + radio.sat + effort.2 + age2 + age34.sex)	14	2.053	0.13514
4	φ (yr70's + yr80's + yr90's + age0 + age1 + age4 + age234.sex)	p(radio.vhf + radio.sat + effort.2 + age2 + age34.sex)	14	3.094	0.08027
5	φ (yr70's + yr80's + yr90's sexmales + age0 + age1 + age2 + age4)	p(radio.vhf + radio.sat + effort.2 + age2 + age34.sex)	15	3.664	0.06038
6	φ (yr70's + yr80's + yr90's + sexmales + age01 + age2 + age4)	p(radio.vhf + radio.sat + effort.2 + age2 + age34.sex)	14	3.910	0.05338
7	φ (yr70's + yr80's + yr90's + sexmales + age0 + age1 + age2 + age4 + age234.sex)	p(radio.vhf + radio.sat + effort.2 + age2 + age34.sex)	15	4.718	0.03564
8	φ (yr70's + yr80's + yr90's + age01 + age2 + age4 + age234.sex)	p(radio.vhf + radio.sat + effort.2 + age2 + age34.sex)	14	4.876	0.03294
9	φ (yr70's + yr80's + yr90's + age0 + age1 + age4)	p(radio.vhf + radio.sat + effort.2 + age2 + age34.sex)	13	8.053	0.00673
10	φ (yr70's + yr80's + yr90's + age01 + age2 + age4)	p(radio.vhf + radio.sat + effort.2 + age2 + age34.sex)	13	9.248	0.00370
11	φ (yr70's + yr80's + yr90's + age0 + age1 + age2 + age4)	p(radio.vhf + radio.sat + effort.2 + age2 + age34.sex)	14	9.347	0.00352
12	φ (yr70's + yr80's + yr90's + sexmales + age0 + age1)	p(radio.vhf + radio.sat + effort.2 + age2 + age34.sex)	13	9.548	0.00318
13	φ (yr70's + yr80's + yr90's + age0 + age1 + age234.sex)	p(radio.vhf + radio.sat + effort.2 + age2 + age34.sex)	13	10.378	0.00210
14	φ (yr70's + yr80's + yr90's + age01 + age2 + age234.sex)	p(radio.vhf + radio.sat + effort.2 + age2 + age34.sex)	14	10.825	0.00168
15	φ (yr70's + yr80's + yr90's + age0 + age1 + age2)	p(radio.vhf + radio.sat + effort.2 + age2 + age34.sex)	13	15.441	0.00017
16	φ (yr70's + yr80's + yr90's + age0 + age1)	p(radio.vhf + radio.sat + effort.2 + age2 + age34.sex)	12	15.663	0.00015
17	φ (yr70's + yr80's + yr90's + sexmales + SBage)	p(radio.vhf + radio.sat + effort.2 + age2 + age34.sex)	12	15.696	0.00015
18	φ (age04 + yr70s + yr80s + yr90's + age04.yr70s + age04.yr80s + age04yr90s)	p(radio.vhf + radio.sat + age34.sex + effort.2)	12	16.311	0.00010
19	φ (age01 + yr70s + yr80s + yr90's + age01.yr70s + age01.yr80s + age01yr90s)	p(radio.vhf + radio.sat + age34.sex + effort.2)	13	16.703	0.00009
20	φ (yr70s + yr 80s + yr90s + sexmales + age0)	p(radio.vhf + radio.sat + effort.2 + age2 + age34.sex)	12	18.679	0.00003

Table 7. Annual apparent survival of male cub-of-the-year, yearling, subadult, adult, and senescent adult polar bears in the Northern Beaufort Sea from 1971-2005.

	Cubs-of-the-year			Yearlings			Subadults			Adults			Senescent adults		
Year	Survival	$95\%CI_U$	$95\%CI_L$	Survival	$95\%CI_U$	$95\%CI_L$	Survival	$95\%CI_U$	$95\%CI_L$	Survival	$95\%CI_U$	$95\%CI_L$	Survival	$95\%CI_U$	$95\%CI_L$
1971	NA	NA	NA	NA	NA	NA	0.863	0.930	0.796	0.857	0.913	0.800	NA	NA	NA
1972	0.557	0.829	0.284	NA	NA	NA	0.863	0.930	0.796	0.857	0.913	0.800	NA	NA	NA
1973	0.557	0.829	0.284	0.304	0.538	0.071	0.863	0.930	0.796	0.857	0.913	0.800	NA	NA	NA
1974	0.557	0.829	0.284	0.304	0.538	0.071	0.863	0.930	0.796	0.857	0.913	0.800	NA	NA	NA
1975	0.557	0.829	0.284	0.304	0.538	0.071	0.863	0.930	0.796	0.857	0.913	0.800	0.647	0.849	0.445
1976	NA	NA	NA	0.304	0.538	0.071	0.863	0.930	0.796	0.857	0.913	0.800	0.647	0.849	0.445
1977	0.557	0.829	0.284	NA	NA	NA	0.863	0.930	0.796	0.857	0.913	0.800	0.647	0.849	0.445
1978	0.557	0.829	0.284	0.304	0.538	0.071	0.863	0.930	0.796	0.857	0.913	0.800	0.647	0.849	0.445
1979	0.564	0.605	0.524	0.340	0.344	0.336	0.863	1.000	0.715	0.857	0.971	0.743	0.650	0.715	0.584
1985	0.251	0.453	0.049	0.105	0.218	0.000	0.625	0.759	0.491	0.613	0.725	0.500	0.328	0.517	0.138
1986	0.251	0.453	0.049	0.105	0.218	0.000	0.625	0.759	0.491	0.613	0.725	0.500	0.328	0.517	0.138
1987	0.253	0.321	0.185	0.109	0.126	0.093	0.626	0.769	0.483	0.613	0.727	0.499	0.329	0.414	0.243
1989	0.253	0.321	0.185	NA	NA	NA	0.626	0.769	0.483	0.613	0.727	0.499	0.329	0.414	0.243
1991	0.813	1.000	0.585	NA	NA	NA	0.956	1.000	0.897	0.954	1.000	0.895	0.864	1.000	0.670
1992	0.813	1.000	0.585	0.599	0.982	0.216	0.956	1.000	0.897	0.954	1.000	0.895	0.864	1.000	0.670
1993	0.813	1.000	0.585	0.599	0.982	0.216	0.956	1.000	0.897	0.954	1.000	0.895	0.864	1.000	0.670
1994	0.815	1.000	0.495	0.619	0.723	0.516	0.956	1.000	0.703	0.954	1.000	0.704	0.865	1.000	0.461
2000	NA	NA	NA	0.257	0.282	0.231	NA	NA	NA	0.818	1.000	0.586	0.582	0.718	0.446
2003	0.487	0.827	0.147	0.248	0.491	0.006	0.826	0.969	0.682	0.818	0.956	0.680	0.581	0.784	0.378
2004	0.487	0.827	0.147	0.248	0.491	0.006	0.826	0.969	0.682	0.818	0.956	0.680	0.581	0.784	0.378
2005	0.487	0.827	0.147	0.248	0.491	0.006	0.826	0.969	0.682	0.818	0.956	0.680	0.581	0.784	0.378

Table 8. Annual apparent survival of female cub-of-the-year, yearling, subadult, adult, and senescent adult polar bears in the Northern Beaufort Sea from 1971-2005.

	Cubs-of-the-year			Yearlings			Subadults			Adults			Senescent adults		
Year	Survival	95%CI$_L$	95%CI$_U$	Survival	95%CI$_L$	95%CI$_U$	Survival	95%CI$_L$	95%CI$_U$	Survival	95%CI$_L$	95%CI$_U$	Survival	95%CI$_L$	95%CI$_U$
1971	NA	NA	NA	NA	NA	NA	0.918	0.963	0.874	NA	NA	NA	NA	NA	NA
1972	0.669	0.926	0.412	0.413	0.678	0.149	0.918	0.963	0.874	0.915	0.953	0.876	NA	NA	NA
1973	0.669	0.926	0.412	0.413	0.678	0.149	0.918	0.963	0.874	0.915	0.953	0.876	NA	NA	NA
1974	0.669	0.926	0.412	0.413	0.678	0.149	0.918	0.963	0.874	0.915	0.953	0.876	NA	NA	NA
1975	0.669	0.926	0.412	0.413	0.678	0.149	0.918	0.963	0.874	0.915	0.953	0.876	0.766	0.922	0.611
1976	0.669	0.926	0.412	0.413	0.678	0.149	0.918	0.963	0.874	0.915	0.953	0.876	0.766	0.922	0.611
1977	0.669	0.926	0.412	0.413	0.678	0.149	0.918	0.963	0.874	0.915	0.953	0.876	0.766	0.922	0.611
1978	0.669	0.926	0.412	0.413	0.678	0.149	0.918	0.963	0.874	0.915	0.953	0.876	0.766	0.922	0.611
1979	0.677	0.795	0.560	0.432	0.442	0.421	0.919	1.000	0.772	0.915	1.000	0.795	0.767	0.912	0.623
1985	0.352	0.603	0.100	0.159	0.313	0.004	0.749	0.843	0.655	0.739	0.816	0.662	0.465	0.661	0.270
1986	0.352	0.603	0.100	0.159	0.313	0.004	0.749	0.843	0.655	0.739	0.816	0.662	0.465	0.661	0.270
1987	0.355	0.483	0.226	0.162	0.194	0.129	0.749	0.875	0.623	0.739	0.838	0.640	0.466	0.601	0.331
1989	0.355	0.483	0.226	NA	NA	NA	0.749	0.875	0.623	0.739	0.838	0.640	0.466	0.601	0.331
1991	0.875	1.000	0.713	NA	NA	NA	0.975	1.000	0.942	0.974	1.000	0.940	0.919	1.000	0.800
1992	0.875	1.000	0.713	0.708	1.000	0.389	0.975	1.000	0.942	0.974	1.000	0.940	0.919	1.000	0.800
1993	0.875	1.000	0.713	0.708	1.000	0.389	0.975	1.000	0.942	0.974	1.000	0.940	0.919	1.000	0.800
1994	0.877	1.000	0.500	0.714	0.902	0.527	0.975	1.000	0.809	0.974	1.000	0.808	0.920	1.000	0.533
2000	NA	NA	NA	0.353	0.413	0.294	0.895	1.000	0.699	0.890	1.000	0.704	0.713	0.887	0.539
2003	NA	NA	NA	0.348	0.637	0.058	0.895	0.985	0.804	0.890	0.977	0.802	0.713	0.867	0.559
2004	0.605	0.938	0.272	0.348	0.637	0.058	0.895	0.985	0.804	0.890	0.977	0.802	0.713	0.867	0.559
2005	0.605	0.938	0.272	0.348	0.637	0.058	0.895	0.985	0.804	0.890	0.977	0.802	0.713	0.867	0.559

Table 9. Model averaged population estimates and standard errors for the Northern Beaufort Sea polar bear population from 1971-2006 using the top 20 models from Table 6.

Year	Population estimate (Nj)	Standard error (SE)
1971	-	-
1972	354.81	72.83
1973	714.96	123.41
1974	691.45	119.71
1975	1220.17	185.71
1976	1220.08	347.34
1977	1001.07	300.79
1978	901.17	265.75
1979	1391.03	381.66
1985	860.77	140.96
1986	836.88	133.49
1987	902.98	147.51
1989	366.82	75.48
1991	255.55	118.17
1992	184.03	47.99
1993	425.11	81.82
1994	257.50	54.98
2000	786.76	239.76
2003	1302.53	368.07
2004	1093.06	168.19
2005	1229.84	187.98