

Polar bear population status in the northern Beaufort Sea, Canada, 1971–2006

IAN STIRLING,^{1,2,5} TRENT L. McDONALD,³ E. S. RICHARDSON,^{1,2} ERIC V. REGEHR,^{4,6} AND STEVEN C. AMSTRUP^{4,7}

¹Wildlife Research Division, Science and Technology Branch, Environment Canada, 5320-122nd Street, Edmonton, Alberta T6H 3S5 Canada

²Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6H 3S5 Canada

³Western EcoSystems Technology, Inc., 2003 Central Ave., Cheyenne, Wyoming 82070 USA

⁴USGS Alaska Science Center, Biological Science Office, 4210 University Drive, Anchorage, Alaska 99508 USA

Abstract. Polar bears (*Ursus maritimus*) of the northern Beaufort Sea (NB) population occur on the perimeter of the polar basin adjacent to the northwestern islands of the Canadian Arctic Archipelago. Sea ice converges on the islands through most of the year. We used open-population capture–recapture models to estimate population size and vital rates of polar bears between 1971 and 2006 to: (1) assess relationships between survival, sex and age, and time period; (2) evaluate the long-term importance of sea ice quality and availability in relation to climate warming; and (3) note future management and conservation concerns. The highest-ranking models suggested that survival of polar bears varied by age class and with changes in the sea ice habitat. Model-averaged estimates of survival (which include harvest mortality) for senescent adults ranged from 0.37 to 0.62, from 0.22 to 0.68 for cubs of the year (COY) and yearlings, and from 0.77 to 0.92 for 2–4 year-olds and adults. Horvitz-Thompson (HT) estimates of population size were not significantly different among the decades of our study. The population size estimated for the 2000s was 980 ± 155 (mean and 95% CI). These estimates apply primarily to that segment of the NB population residing west and south of Banks Island. The NB polar bear population appears to have been stable or possibly increasing slightly during the period of our study. This suggests that ice conditions have remained suitable and similar for feeding in summer and fall during most years and that the traditional and legal Inuvialuit harvest has not exceeded sustainable levels. However, the amount of ice remaining in the study area at the end of summer, and the proportion that continues to lie over the biologically productive continental shelf (<300 m water depth) has declined over the 35-year period of this study. If the climate continues to warm as predicted, we predict that the polar bear population in the northern Beaufort Sea will eventually decline. Management and conservation practices for polar bears in relation to both aboriginal harvesting and offshore industrial activity will need to adapt.

Key words: aboriginal hunting; Arctic; Beaufort Sea; climate warming; open-population capture–recapture models; polar bears; population estimation; sea ice; survival rates; *Ursus maritimus*.

INTRODUCTION

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 shallow waters (<300 m) of the continental shelf and interisland channels of various archipelagos. These areas are more biologically productive and seals are more abundant than in the deep polar basin (Stirling et al. 1982, 1993, Kingsley et al. 1985, Stirling and Øritsland 1995, Durner et al. 2009).

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 significantly influence the survival and reproductive success of polar bears (e.g., Regehr et al. 2006, 2010, Stirling and Parkinson 2006). In this study, we used capture–recapture data to estimate age class-specific annual survival rates and population trend for the northern Beaufort Sea (NB) population (Fig. 1) from the mid-1970s to 2006, to assess factors that might influence survival, particularly those related to habitat (i.e., sea ice) loss. We were particularly interested in how sea ice habitat might be correlated with NB demographic parameters because NB is adjacent to the southern Beaufort Sea (SB) population,

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⁵ E-mail: ian.stirling@ec.gc.ca

⁶ Present address: U.S. Fish and Wildlife Service, 1011 E. Tudor Rd., MS341, Anchorage, Alaska 99503 USA.

⁷ Present address: Polar Bears International, 810 N. Wallace, Suite E, P.O. Box 3008, Bozeman, Montana 59772 USA.

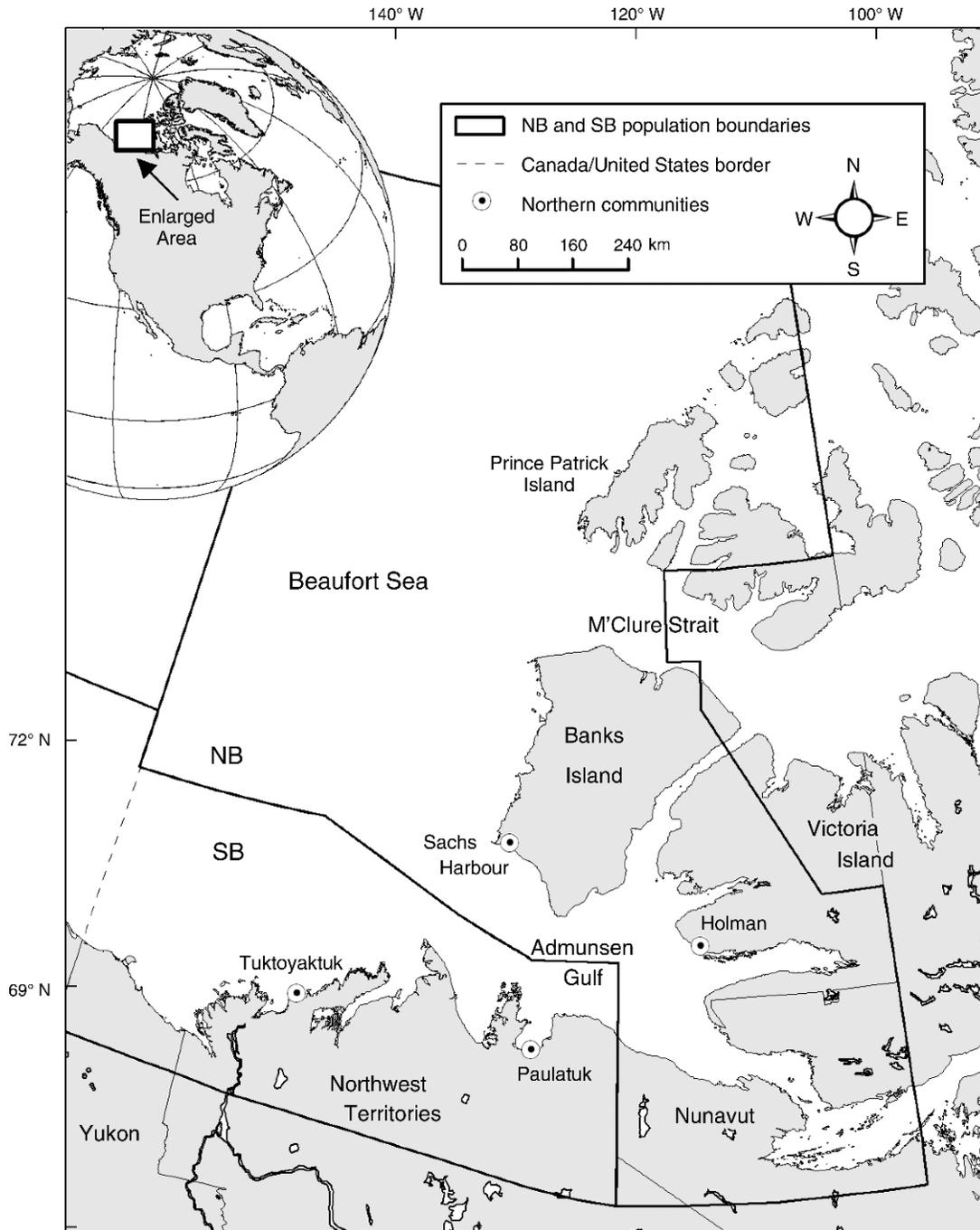


FIG. 1. Northern Beaufort Sea (NB) population boundary and study area in relation to the southern Beaufort Sea (SB) population boundary.

which appears to be declining as a result of reduced access to suitable sea ice habitat, especially that over the continental shelf, during the open-water season in summer and fall (Hunter et al. 2010, Regehr et al. 2010).

Around the edge of the polar basin, in areas such as that occupied by NB, much of the annual ice along the coast melts in early summer. The bears then move north

and northwest to remain on largely multiyear ice along the southern edge of the polar pack, where they can continue to hunt seals until the ice refreezes again in the fall (e.g., Amstrup et al. 2000).

Since 1979, when it first became possible to monitor patterns of breakup 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 in the position of the southern edge of the perennial (or multiyear pack) ice over the Chukchi and southern Beaufort seas. The southern edge of the pack ice, which used to persist over the continental shelf through the summer, now retreats far to the north over the deep polar basin, where biological productivity is much lower (Pomeroy 1997). In SB, correlated with the trend toward a longer open-water season and sea ice being farther offshore (in particular beyond the edge of the continental shelf), there have been several indications that the polar bear population is being nutritionally stressed (e.g., Amstrup et al. 2006, Stirling et al. 2008, Rode et al. 2010). The southern Beaufort Sea (SB) population now appears to be in decline due to decreased recruitment and survival (Regehr et al. 2006, 2010, Hunter et al. 2010).

In contrast to SB, during the open-water period in NB, at least some sea ice remains in most years over the continental shelf along the west coast of Banks Island and Prince Patrick Island and M'Clure Strait. Occasionally, some ice remains in the western Amundsen Gulf, south of Banks Island. Thus, in recent years, the polar bears in NB have still had access to ice over the continental shelf during winter and, most importantly, through the critical feeding period in spring and early summer when seals are more abundant there than they are over the deep polar basin (Stirling et al. 1982). Later in summer, as the ice breaks up, most bears move back north and northwest toward whatever ice remains over the continental shelf to the west of Banks Island and farther offshore until freeze-up later in the autumn. Possibly because the ice remains longer over the continental shelf areas in NB, the bears were in better overall condition than those in SB through 2003–2006 (Amstrup et al. 2006, Stirling et al. 2008).

Since 1968, the NB population has also been harvested by Inuvialuit hunters under a quota system. Over the past 15 years, harvests have consistently been below the maximum yield estimated to be sustainable (Taylor et al. 1987), in part at least, because in some years rough ice conditions have made travel difficult for hunters.

Between 1968 and the present, the annual quota has increased from 36 to 65 bears, partly because scientifically based population assessments suggested that a higher annual harvest level could be sustained and partly as a result of arbitrary (nonbiological) reassignment of portions of adjacent quotas by management agencies (I. Stirling, *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 bears was recommended, based on 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 bears for over 15 years (Lunn et al. 1998, 2002, 2006), largely because of difficult travel conditions for hunters and, to some degree, a reduced hunting effort in parts of the area. Even though the annual harvest has remained well below the allowable limit, subsequent evaluations of change in the maximum sustainable yield, along with recognition that the polar bears' sea ice habitat is changing, emphasize the importance of a new estimate of population size and demographic values for the NB population.

STUDY AREA

The NB population is distributed over the sea ice of eastern and northern Amundsen Gulf, the south and west coast of Banks Island, and the western end of M'Clure Strait up to the southwestern coast of Prince Patrick Island (Fig. 1). A defining feature of the marine ecosystem in 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 parallels the coast from Prince Patrick Island south through the Cape Bathurst Polynya and west along the mainland coast (Smith and Rigby 1981, Stirling 1997). The distributions of ringed (*Phoca hispida*) and bearded (*Erignathus barbatus*) seals, and consequently also those of the polar bears that hunt them, are influenced strongly by the distribution of shore leads and polynyas, areas of annual and multiyear ice, and by both short- and long-term variations in the pattern of freeze-up and breakup (Stirling et al. 1982, 1993, Durner et al. 2004).

Freeze-up of the open water between land and the offshore multiyear ice usually occurs between mid-October and mid-November, and breakup follows between late May and late June (Smith and Rigby 1981). Throughout most of our study, significant amounts of ice remained over the continental shelf near Banks Island and Prince Patrick Island as well as farther offshore. For a review of the oceanography of the eastern Beaufort Sea, see Carmack and MacDonald (2002).

METHODS

Field methods

Polar bears were captured nonselectively on the sea ice throughout most of NB to a maximum of ~160 km offshore from the southern and western coastlines of Banks Island, and into Amundsen Gulf (Fig. 1), during the spring (March through May) of 1971–1979, 1985–

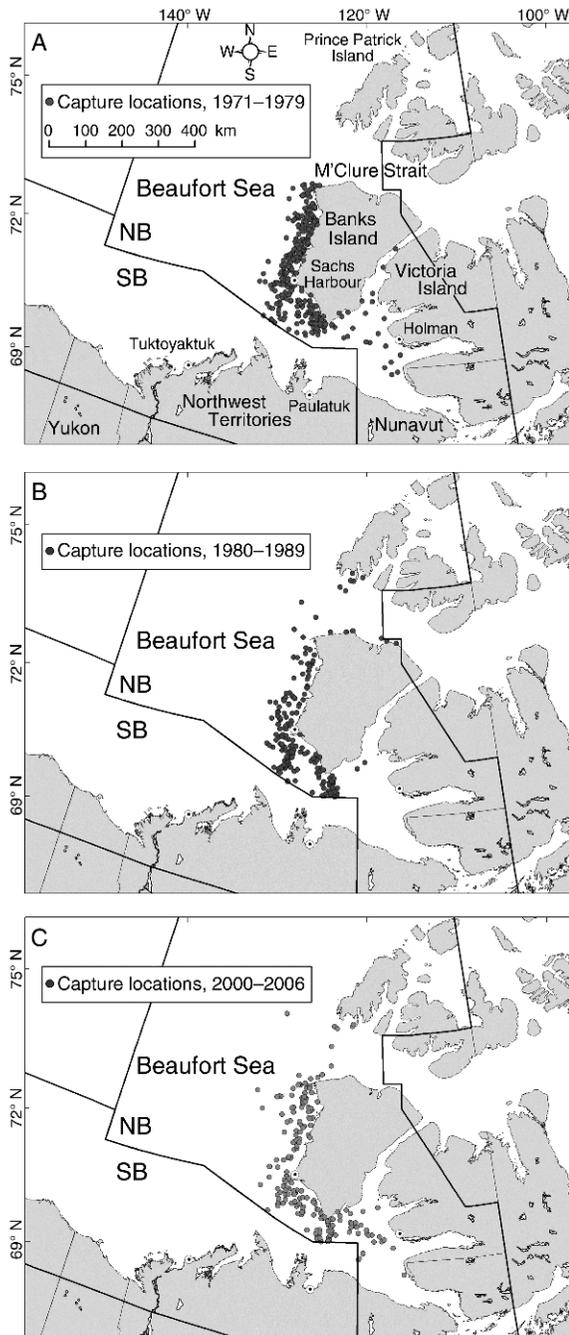


FIG. 2. Distribution of polar bear captures during the (A) 1970s, (B) 1980s, and (C) 2000s included in the capture–recapture estimates of survival and population size in the northern Beaufort Sea (NB).

1987, and 2003–2006 (Fig. 2). We attempted to catch all bears encountered, provided weather and ice conditions were suitable for safe immobilizations.

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 were 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 premolar tooth was collected for age determination (Calvert and Ramsay 1998). Ages of cubs and yearlings were determined visually by size. Capture and marking protocols were reviewed and approved by an independent Animal Care Committee for the Canadian Wildlife Service.

Capture–recapture analysis

Survival (ϕ), recapture probabilities (p), and ultimately the size of segments of the NB polar bear population were estimated using capture–recapture data collected from 1971 through 2006 (Fig. 2). 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 ($j = 1, 2, \dots, 22$) and a 0 indicates not captured during sampling occasion j .

Beginning in the 1980s, selected adult females were fitted with radio-transmitting collars (Amstrup et al. 2000). Occasionally, bears that were not recaptured by conventional methods were relocated by telemetry. When a bear was successfully relocated by VHF telemetry, or when at least one satellite relocation in a given year was within the population boundaries, a 1 (“captured”) was included in the bear’s capture history that year. Otherwise, a 0 (“not captured”) was included. Without field observations of when a collar was dropped or became nonoperational, we assumed that collars operated for two years post-deployment.

Multiple captures or relocations of an individual within a season were amalgamated and treated as a single capture (single 1) that year. Known harvests of bears previously marked during our study were ignored (i.e., harvested animals were not censored). As a consequence, mortality estimates ($1 - \text{survival}$) 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.

TABLE 1. Individual and temporal covariates considered in models of apparent survival (ϕ_{ij}) and recapture probability (p_{ij}) for the polar bear *Ursus maritimus* in the Beaufort Sea.

Covariate	Affects	Effect allowed
Individual covariates		
age0	ϕ_{ij}	COY (ages 0–1) \neq older bears
age1	ϕ_{ij}	yrlds (ages 1–2) \neq other age classes
age2	p_{ij}, ϕ_{ij}	subads (ages 2–4 years) \neq other age classes
age3	ϕ_{ij}	adults (ages 5–20 years) \neq other age classes
age4	ϕ_{ij}	senescent animals (ages 21+) \neq other age classes
age01	p_{ij}, ϕ_{ij}	COY = yrlds \neq other age classes
age23	ϕ_{ij}	subads = ads \neq other age classes
age234	ϕ_{ij}	subads = ads = senescent \neq other age classes
age0124	ϕ_{ij}	COY = yrlds = subads = senescent \neq adults
age1234	ϕ_{ij}	yrlds = subads = ads = senescent \neq COYs
age34	p_{ij}, ϕ_{ij}	ads = senescent \neq other age classes
age012	ϕ_{ij}	COY = yrlds = subads \neq other age classes
SBage	ϕ_{ij}	per southern Beaufort estimates, covariate values were -0.2139 for COY, 3.0234 for yrlds, 2.2210 for subads, 2.6477 for ads, 1.7774 for senescent adults
sex	p_{ij}, ϕ_{ij}	M \neq F (females used as reference level; females = 0, males = 1)
age234.sex	ϕ_{ij}	subad M = ad M = senescent M \neq subad F = ad F = senescent F
age1234.sex	ϕ_{ij}	yrld M = subad M = ad M = senescent M \neq yrld F = subad F = ad F = senescent F
age34.sex	p_{ij}	ad M = senescent M \neq ad F = senescent F
radio.vhf	p_{ij}	bear available for capture using radiotelemetry
radio.sat	p_{ij}	bear available for location using a satellite radio
Temporal covariates		
rsf	ϕ_{ij}	resource selection function; see <i>Methods: Survival covariates</i>
PMIce	ϕ_{ij}	annual mean daily proportion of 25×25 km cells with $>50\%$ ice concentration over the continental shelf (<300 m deep); see <i>Methods: Survival covariates</i>
seal	ϕ_{ij}	low or high seal abundance; see <i>Methods: Survival covariates</i>
yr70's, yr80's	ϕ_{ij}	1970s \neq 1980s \neq 2000s (2000s used as reference level); years included in the analysis: 1971–1979, 1985–1987, 1989, 2000, and 2003–2006
flight km	p_{ij}	number of kilometers flown searching for bears in a capture year
effort.2	p_{ij}	study effort (intensive study years, high effort in 1971–1975, 1985–1989, and 2004–2006)

Notes: The “Affects” column indicates whether the covariate in column 1 affects survival or recapture probabilities. Allowed-effects abbreviations are M, male; F, female; COY, cub of the year; yrld, yearling; subad, subadult; ad, adult. Ages are given in years.

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). Our models contained covariates quantifying physical and environmental factors that potentially influenced parameters of interest. We estimated survival between capture occasions directly from the CJS models, and then model-averaged these estimates across all supported models. Survival during gaps of j years in capture histories was estimated by raising annual survival estimates to the j th power. We estimated population size during year j (N_j) 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 N_j using the estimator derived by Huggins (1989); see also Taylor et al. (2002). We then model-averaged these estimates of N_j across all supported models to derive our final estimates.

The Horvitz-Thompson estimator implicitly assumes that each bear has a probability of being captured at each occasion, but that probabilities can differ among classes of bears. Each class is defined by its covariates as specified in the model, and we assume that captured members of each class represent all members of their class. This size estimator makes inference to the

population of bears that have nonzero capture probability in the particular year for which it was constructed. Although we report estimates for all years with positive capture effort, including those with very low sample size, low sample size is known to adversely affect HT size estimates. Therefore, more inferential weight should be placed on those years with large sample sizes (e.g., >50 captures) when assessing population size and trend.

All CJS models were fitted to the data using R-language software that implemented the “general regression” approach to capture–recapture (McDonald et al. 2005; software *available online*).⁸ We used a logit link function to relate linear combinations of covariates to survival and recapture probabilities.

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 and age class (Tables 1 and 2), where age classes considered were based on polar bear life history parameters (Ramsay and Stirling 1988, Amstrup 2003) and patterns in previous estimates of

⁸ (<http://cran.r-project.org/web/packages/mra/index.html>)

TABLE 2. Parameterizations considered for models of apparent survival.

Model no.	Regression equation (all structures included intercepts)
1	(null)
2	SBase
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 + eqs. 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 + eqs. 1–31
63–93	rsf + eqs. 1–31
94–124	PMIce + eqs. 1–31
125–155	year + eqs. 1–31
156–186	seals + eqs. 1–31

age-specific survival (Obbard et al. 2007, Regehr et al. 2007, 2010). We hypothesized that survival rates may have varied over the course of our study, and modeled temporal variation in survival with decadal time dependence (i.e., survival was equal within decades, but differed among decades). Further, because we hypothesized that variation in survival rates might have occurred as a result of interannual variation in environmental conditions, we modeled ϕ as a function of sea ice and several other environmental covariates (Table 1).

To investigate the potential effects of variation in sea ice dynamics on survival, we considered two sea ice habitat covariates. First, we defined PMIce as the annual mean daily proportion of 25×25 km cells that had greater than 50% ice concentration and that occurred over the continental shelf, defined as waters <300 m deep (Table 1). Ice concentration values were measured on 25-km pixels, from which we calculated the number of square kilometers with >50% ice. Data were obtained from the National Snow and 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 (*available online*).⁹ 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 ~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 (rsf) was derived from the resource selection functions (RSFs) developed by Durner et al. (2009). RSF values are the relative probabilities of selection of the habitats within any defined resource unit-mapped pixels in this case. All mapped pixels of the study area can be thought of as being overlain by RSF surfaces of varying heights, where heights represent relative preferences of the habitats that occur in that pixel at any time. RSF was calculated as the annual volume under the RSF surface within the NB population boundary. RSF volume measurements were obtained by integrating (summing) the heights of the estimated RSF surfaces for each grid cell throughout the region. Here the region was defined as the International Union for the Conservation of Nature and Natural Resources (IUCN) population boundary for the NB (Figs. 1 and 2). RSF values were standardized to a mean of 0 and standard deviation of 1, and those centered values that were 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. See Table 1 for age class descriptions as well as definitions and values of other covariates allowed to enter our survival models.

Goodness of fit

We used program RELEASE (Burnham et al. 1987) to assess and estimate the variance inflation factor (\hat{c}) for our data set. The variance inflation factor is a measure of unexplained variation in the data over and above that predicted by the underlying multinomial distribution. The RELEASE CJS goodness-of-fit test summed TEST2 and TEST3 (Burnham et al. 1987) chi-square test statistics computed on 2×2 tables of expected and observed counts obtained, assuming that data followed a full CJS model. When expected cell counts were less than 2, RELEASE used Fisher's exact test to back-calculate chi-square statistics. The RELEASE \hat{c} was then calculated as the chi-square test divided by its degrees of freedom. When applied to the entire NB data set, the RELEASE goodness-of-fit tests estimated $\hat{c} = 1.16$. However, when we excluded the 26 recaptures of bears that were available for capture by VHF or satellite telemetry, RELEASE estimated $\hat{c} = 0.95$. The fact that this latter estimate was below 1.0 implied that a large portion of apparent overdispersion

⁹ <ftp://sidacs.colorado.edu/pub/DATASETS/sealice/>

TABLE 3. Parameterizations considered for models of recapture probability.

Model no.	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 + eqs. 1–6
13–24	effort.2 + eqs. 1–12
19–24	flight km + radio.vhf + radio.sat + eqs. 1–12
25–36	year + eqs. 1–12

in the original data could be explained by the presence of radiotelemetry captures. When we further excluded the 259 captures of cubs of the year (COYs) and yearlings from the data without radiotelemetry captures, RELEASE again estimated $\hat{c} = 0.95$. This fact implied that a large portion of apparent overdispersion was explainable by the presence of radiotelemetry captures and age classes. We concluded that any apparent overdispersion in the original unaltered data set could be explained by known factors. Because our models allowed for both factors, 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 $\Delta\text{AIC}_c < 2$ indicated similar support for both models and $\Delta\text{AIC}_c > 10$ 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 neces-

sary 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. The basic building blocks of these steps were additive and employed interaction effect structures that were a priori deemed potentially important (Tables 2 and 3). These basic structures were then combined in a stepwise approach because estimation of all possible combinations of models was not feasible.

We combined estimation of the model structures in a stepwise fashion as follows (see also Table 4):

Step 1.—We selected and fixed a recapture (p_{ij}) parameterization that was general and expected to be well supported. A priori, 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 $p(\text{radio.vhf} + \text{radio.sat} + \text{effort.2} + \text{age2} + \text{age34.sex})$. Using this recapture parameterization we fit survival (ϕ_{ij}) parameterizations that constrained individual animal's survival according to sex and age class and two types of temporal variation (time-constant and time-dependent).

Step 2.—We selected the most supported survival models containing individual constraints with and without temporal variation. Using these two ϕ_{ij} parameterizations we fit p_{ij} parameterizations containing individual constraints, with no time variation (i.e., time-constant models).

Step 3.—We selected the two most supported p_{ij} parameterizations for each of the two ϕ_{ij} parameterizations and added several different types of temporal variation in p_{ij} .

TABLE 4. Stepwise model selection.

Step	Objective	Outcome
1	Identify appropriate models of individual heterogeneity in ϕ (p structure fixed at (radio.vhf + radio.sat + effort.2 + age2 + age34.sex).	ϕ structures carried forward to steps 2 and 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 ϕ using the best time-constant and time-varying ϕ 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 ϕ 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 ϕ by considering interactions, and using the top p structure from steps 1, 2 and 3. Compare AIC _c across all fitted models.	See Table 6 for top 20 models.

Note: Int is the y -intercept, ϕ is apparent survival, and p is recapture probability.

Step 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 p_{ij} parameterization(s) from Step 3, we fit models with all types of temporal variation in ϕ_{ij} , including appropriate interactions between temporal variation and individual constraints.

Analysis of annual sea ice minimum cover of the study area

We used multichannel passive-microwave data from NASA's Nimbus-7 Scanning Multichannel Microwave Radiometer (SMMR, 1979–1987) and Defense Meteorological Satellite Program Special Sensor Microwave/Imager (SMMI, 1987–2009) to analyze sea ice concentrations and extent within the boundaries of the northern Beaufort Sea polar bear population (Fig. 1) (Cavaliere et al. 1996, Maslanik and Stroeve 1999–2009, Meier et al. 2006). Sea ice data were obtained from the National Snow and Ice Data Center (NSIDC) in Boulder, Colorado, USA, and were converted from binary format into raster grids using a geographical information system (ArcGIS 9.2; ESRI 2008). Daily sea ice concentrations (at 1% resolution) were mapped using a polar stereographic projection at a 25-km² resolution for the entire study area. To investigate possible temporal trends in the availability of summer/fall sea ice, we calculated the mean ice concentration for the entire study area annually on 1 or 2 September, depending on the availability of data. Mean sea ice concentration was calculated by sampling the center of all 1063 raster cells that fell within the study area and calculating the average of the extracted sea ice concentration values. Although the sea ice data for our study area in 2009 are considered preliminary by the NSIDC, we chose to include them in our analyses to show the extent of interannual variation in the context of the significant long-term declines in sea ice observed in NB.

To determine the availability of suitable polar bear habitat over the continental shelf, we reclassified all raster cells in the northern Beaufort Sea study area with >50% sea ice concentration. Although each cell in the grid has a resolution of 1%, the cells do not contain information on sea ice configuration; thus we considered the entire area of all cells with sea ice concentration $\geq 50\%$ to be suitable polar bear habitat (Stirling et al. 1999, Regehr et al. 2010). After the ice images were reclassified, we calculated the number of cells of suitable habitat that overlapped the continental shelf (i.e., waters <300 m deep) and multiplied the number of cells by the area of each cell (625 km²) to get an estimate of the availability of suitable habitat.

We used the nonparametric Mann-Kendall (MK) test for statistically significant trends in fall sea ice concentration and the area of polar bear habitat over the continental shelf in the northern Beaufort Sea study area. The Mann-Kendall test is useful in examining

environmental time series: there are no assumptions regarding the underlying distribution of the data, it can handle missing values, and it tests for a trend without the need to specify whether the trend is linear or nonlinear (Libiseller and Grimval 2002, Wang et al. 2008). The MK test, however, is only valid in the absence of serial correlation. Therefore, we tested for a lag-1 autocorrelation in both of our time series using the rank von Neumann ratio test to ensure that both of our data sets were composed of independent observations (Bartels 1982). The MK test tests for monotonic (increasing or decreasing) trends in time series data, but does not estimate the slope or the magnitude of the trend. Therefore, we calculated slopes for our two time series using the standardized approach developed by Sen (1968):

$$\beta_i = \text{median} \left(\frac{Y_j - Y_i}{t_j - t_i} \right) \quad \text{for all } i > j$$

where Y is the variable tested for trend (e.g., ice concentration), and t is time. β represents the median of the slope obtained from all possible combinations of two points in the time series.

RESULTS

Captures

Capture–recapture information was available for 958 individual polar bears from 18 capture occasions over the 35-year study period, 1971–2006. From 1971 to 1979, 376 bears were captured or recaptured. Between 1985 and 1989 and between 2000 and 2006, we captured 279 and 330 bears, respectively. We “captured” 14 bears by VHF radiotelemetry in 1986–1987 and 21 by satellite telemetry during 1989–2004. Geographically, captures were similarly distributed among years (Fig. 2). During all capture periods, we nonselectively captured all bears encountered to assure that samples were as representative as possible of the composition of the population. The annual proportion of recaptures in the capture samples varied from 0.00 to 0.22 (Table 5).

Model selection

Step 1.—A total of 45 survival models were fitted with the recapture model $p(\text{radio.vhf} + \text{radio.sat} + \text{effort.2} + \text{age2} + \text{age34.sex})$. After Step 1, the top AIC_c-ranked time-constant model included individual-level effects of age class and different (lower) survival for males in age classes 2, 3, and 4 [$\phi(\text{Int} + \text{age0} + \text{age1} + \text{age4} + \text{age234.sex})$; AIC_c weight = 0.201], where “Int” is the y-intercept. The top AIC_c-ranked time-varying survival model included the same individual heterogeneity covariates plus decadal variation [$\phi(\text{Int} + \text{yr70's} + \text{yr80's} + \text{age0} + \text{age1} + \text{age4} + \text{age234.sex})$; AIC_c weight = 0.050]. Despite low support for the latter, we carried both of these models forward to Step 2, in accordance with our model selection protocol.

Step 2.—In total, 24 recapture models were fitted during Step 2; 12 with the top time-constant survival model [$\phi(\text{Int} + \text{age0} + \text{age1} + \text{age4} + \text{age234}.\text{sex})$] and 12 with the top time-varying survival model [$\phi(\text{Int} + \text{yr70}'\text{s} + \text{yr80}'\text{s} + \text{age0} + \text{age1} + \text{age4} + \text{age234}.\text{sex})$]. After Step 2, the top two recapture probability models (combined AIC_c weight = 0.427) 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 $p(\text{Int} + \text{radio.vhf} + \text{radio.sat})$, whereas the second most supported model was $p(\text{Int} + \text{radio.vhf} + \text{radio.sat} + \text{age34}.\text{sex})$; Table 4).

Step 3.—We fitted an additional 12 recapture models by adding time-varying effects of decade ($\text{yr70}'\text{s}$, $\text{yr80}'\text{s}$), study period (effort.2), and flight effort (Flight km) to the best two recapture models from Step 2. 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_{ij} included effects for whether a bear was wearing a radio collar (radio.vhf and radio.sat), whether a bear was an adult male ($\text{age34}.\text{sex}$), and study period (effort.2 ; AIC_c weight = 0.160).

Step 4.—Using the top-ranked recapture probability model, Step 4 fitted 28 survival models that included interactions between age class and standardized resource selection function values (RSF), standardized ice extent (PMIce), low or high seal abundance (Seal), and decadal time effects ($\text{yr70}'\text{s}$ and $\text{yr80}'\text{s}$). Following Step 4, all 109 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 0.130, and the combined AIC_c weight of the top 20 models was 0.832.

Survival estimates

The model-averaged estimates of survival include both natural and harvest mortality (Tables 7 and 8). Estimates of survival of senescent adults ranged from 0.37 (males in 2005) to 0.62 (females in 2004). Estimates of COY and yearling survival ranged from 0.22 (male and female COY in 2005) to 0.68 (female COY in 1986). Survival rates of 2–4 year-olds and adults were nearly identical and very consistent through time, ranging from 0.77 (males in 2005) to 0.92 (females in 2004). The wider confidence intervals on the younger age classes were largely due to small sample sizes that did not, proportionally, represent their relative frequency of occurrence in the population.

In the top model, survival of COYs and yearlings of both sexes were modeled as equal, based upon our hypothesis that survival was similar for both sexes in these age classes. The top model also constrained survival of subadult, adult, and senescent males to be equal; thus no age class comparisons of survival for males were possible. However, the top model did allow comparisons of survival for females of various age

TABLE 5. Proportion of recaptures in sample from 1971 to 2006.

Year	Total captures	Recaptures	Proportion recaptures
1971	4		
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
2000	21	2	0.10
2003	37	6	0.16
2004	113	5	0.04
2005	125	10	0.08
2006	62	11	0.18

classes to survival rates estimated for COYs and yearlings. These comparisons revealed that survival of COYs, yearlings, and senescent adult females were not statistically different (in the top model, Wald t ratio = 0.37, $P = 0.7114$ for COY vs. senescent females; Wald t ratio = -0.79 , $P = 0.4321$ for COY vs. yearlings; Wald t ratio = -1.51 , $P = 0.1309$ for senescent females vs. yearlings). Also, survival of 2–4 year-old and adult females combined was statistically higher than survival of COYs, yearlings, and senescent adult females (in the top model, Wald t ratio = 3.73, $P = 0.0002$, adults vs. senescent females; Wald t ratio = 3.18, $P = 0.0015$, adults vs. COY; Wald t ratio = 5.18, $P < 0.0001$, adults vs. yearlings).

Survival of 2–4 year-old, adult, and senescent males was estimated to be lower than that of females (in the top model, Wald t ratio = -2.29 , $P = 0.0220$). On average, female survival was 16%, 24%, and 36% higher than that of males in the 1970s, 1980s, and in the 2000s, respectively. Although these differences were calculated from all age classes, the majority of bears were either 2–4 year-olds or adults, and the preponderance of evidence for this effect came from those classes.

The top 20 models shown in Table 6 illustrate the fact that none of our top-ranked models, despite inclusion of different covariates, had overriding AIC_c weight. This similarity provided compelling support for model averaging. Nonetheless, models that allowed associations between annual variation in survival and habitat variables appeared to gain some support from the data. Models containing habitat resource selection values and the amount of ice were ranked very high in the list of fitted models. The top model containing habitat resource selection values (RSF) was ranked first, with an AIC_c weight of 12.9%. In this model, increases in the RSF value for a year were associated with increased COY

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

Rank	Survival
1	$\phi(\text{age0} + \text{age1} + \text{age4} + \text{age234.sex} + \text{age0.rsrf})$
2	$\phi(\text{age0} + \text{age1} + \text{age4} + \text{age234.sex} + \text{PMIce})$
3	$\phi(\text{age0} + \text{age1} + \text{age4} + \text{age234.sex} + \text{age0.PMIce})$
4	$\phi(\text{age0} + \text{age1} + \text{age4} + \text{age234.sex} + \text{age0.rsrf} + \text{age1.rsrf})$
5	$\phi(\text{age0} + \text{age1} + \text{age4} + \text{age234.sex} + \text{rsf} + \text{age0.rsrf})$
6	$\phi(\text{age0} + \text{age1} + \text{age4} + \text{age234.sex} + \text{PMIce} + \text{age0.PMIce})$
7	$\phi(\text{age0} + \text{age1} + \text{age4} + \text{age234.sex})$
8	$\phi(\text{age0} + \text{age1} + \text{age4} + \text{age234.sex})$
9	$\phi(\text{age0} + \text{age1} + \text{age4} + \text{age234.sex})$
10	$\phi(\text{age0} + \text{age1} + \text{age4} + \text{age234.sex})$
11	$\phi(\text{age0} + \text{age1} + \text{age4} + \text{age234.sex} + \text{rsf})$
12	$\phi(\text{age0} + \text{age1} + \text{age4} + \text{age234.sex} + \text{age0.PMIce} + \text{age1.PMIce})$
13	$\phi(\text{age0} + \text{age1} + \text{age4} + \text{age234.sex} + \text{rsf} + \text{age0.rsrf} + \text{age1.rsrf})$
14	$\phi(\text{age0} + \text{age1} + \text{age4} + \text{age234.sex} + \text{rsf} + \text{age0.rsrf} + \text{age1.rsrf} + \text{age4.rsrf})$
15	$\phi(\text{age0} + \text{age1} + \text{age4} + \text{age234.sex} + \text{PMIce} + \text{age0.PMIce} + \text{age1.PMIce})$
16	$\phi(\text{age0} + \text{age1} + \text{age4} + \text{age234.sex})$
17	$\phi(\text{age0} + \text{age1} + \text{age4} + \text{age234.sex} + \text{age0.seal})$
18	$\phi(\text{age0} + \text{age1} + \text{age4} + \text{age234.sex} + \text{seal})$
19	$\phi(\text{age0} + \text{age1} + \text{age4} + \text{age234.sex} + \text{age0.PMIce} + \text{age1.PMIce} + \text{age4.PMIce})$
20	$\phi(\text{sex} + \text{age0} + \text{age1} + \text{age4})$

Note: Models are ranked, 1 being the best fit ($\Delta\text{AIC}_c = 0$); np is the number of estimated parameters; ΔAIC_c is the difference in AIC_c value from the top model; and AIC_c weights are Akaike weights for each of the models.

survival, but not survival of other age classes. The top model containing PMIce was ranked second and had an AIC_c weight of 9.6%. This model estimated that increases in PMIce during a particular year increased survival of all age classes. Although the influence of sea ice was evident in some of our top models, the fit of those models to the data was not significantly greater than that of other models that did not include explicit habitat-related covariates. Hence, when models were averaged, the influences of variation in habitat among years were not evident in our final survival estimates (Tables 7 and 8). Models containing relative seal abundance (Seal) were not strongly supported by the

data. The top model containing Seal was ranked 17th, with an AIC_c weight of 1.6%.

Recapture probabilities

All recapture probability models with high support indicated that wearing a radio collar had a large effect on recapture probability. The estimated coefficient for radio.vhf was ~ 0.80 , whereas the coefficient for radio.sat was ~ 0.94 . These estimates are far higher than recapture probabilities unaided by telemetry. The probability of recapture averaged 6.8% for adult females without radios, while probability of recapture averaged 8.7% for non-radioed adult males. Although estimated recapture probabilities for adult and senes-

TABLE 7. Annual apparent survival of male polar bears, by age class, in the northern Beaufort Sea from 1971 to 2005.

Year	Cubs-of-the-year			Yearlings			Subadults			Adults		
	Mean	95% CI _L	95% CI _U	Mean	95% CI _L	95% CI _U	Mean	95% CI _L	95% CI _U	Mean	95% CI _L	95% CI _U
1971	NA	NA	NA	NA	NA	NA	0.832	0.763	0.900	0.833	0.770	0.897
1972	0.506	0.162	0.850	NA	NA	NA	0.832	0.763	0.900	0.833	0.770	0.897
1973	0.506	0.162	0.850	0.319	0.065	0.573	0.832	0.763	0.900	0.833	0.770	0.897
1974	0.508	0.156	0.859	0.322	0.068	0.576	0.830	0.757	0.902	0.832	0.764	0.900
1975	0.508	0.156	0.859	0.322	0.068	0.576	0.830	0.757	0.902	0.832	0.764	0.900
1976	NA	NA	NA	0.322	0.068	0.576	0.830	0.757	0.902	0.832	0.764	0.900
1977	0.506	0.162	0.850	NA	NA	NA	0.832	0.763	0.900	0.833	0.770	0.897
1978	0.506	0.162	0.850	0.319	0.065	0.573	0.832	0.763	0.900	0.833	0.770	0.897
1979	0.514	0.486	0.542	0.337	0.334	0.339	0.832	0.721	0.943	0.834	0.727	0.940
1985	0.573	0.085	1.000	0.364	0.029	0.698	0.842	0.745	0.940	0.844	0.752	0.937
1986	0.669	0.176	1.000	0.277	0.000	0.589	0.821	0.698	0.945	0.823	0.704	0.942
1987	0.517	0.242	0.793	0.317	0.206	0.427	0.830	0.716	0.943	0.832	0.725	0.938
1989	0.546	0.543	0.549	NA	NA	NA	0.831	0.765	0.898	0.833	0.768	0.898
2000	NA	NA	NA	0.318	0.278	0.358	NA	NA	NA	0.831	0.705	0.958
2003	0.495	0.107	0.884	0.295	0.041	0.550	0.823	0.738	0.908	0.825	0.745	0.905
2004	0.651	0.168	1.000	0.349	0.007	0.691	0.844	0.738	0.951	0.846	0.745	0.948
2005	0.219	0.000	0.709	0.348	0.000	0.838	0.769	0.500	1.000	0.771	0.505	1.000

Notes: CI_L and CI_U refer to the lower and upper 95% confidence limits. NA indicates that data were not available.

TABLE 6. Extended.

Recapture	np	ΔAIC_c	AIC _c weight
$p(\text{radio.vhf} + \text{radio.sat} + \text{age34.sex} + \text{effort.2})$	11	0.000	0.12957
$p(\text{radio.vhf} + \text{radio.sat} + \text{age34.sex} + \text{effort.2})$	11	0.591	0.09643
$p(\text{radio.vhf} + \text{radio.sat} + \text{age34.sex} + \text{effort.2})$	11	1.408	0.06410
$p(\text{radio.vhf} + \text{radio.sat} + \text{age34.sex} + \text{effort.2})$	12	1.563	0.05931
$p(\text{radio.vhf} + \text{radio.sat} + \text{age34.sex} + \text{effort.2})$	12	1.636	0.05717
$p(\text{radio.vhf} + \text{radio.sat} + \text{age34.sex} + \text{effort.2})$	12	1.686	0.05578
$p(\text{radio.vhf} + \text{radio.sat} + \text{age34.sex} + \text{effort.2})$	10	2.105	0.04523
$p(\text{radio.vhf} + \text{radio.sat} + \text{effort.2})$	9	2.281	0.04142
$p(\text{radio.vhf} + \text{radio.sat} + \text{age34.sex} + \text{flight.1000km})$	10	2.357	0.03988
$p(\text{radio.vhf} + \text{radio.sat} + \text{flight.1000km})$	9	2.495	0.03722
$p(\text{radio.vhf} + \text{radio.sat} + \text{age34.sex} + \text{effort.2})$	11	2.704	0.03353
$p(\text{radio.vhf} + \text{radio.sat} + \text{age34.sex} + \text{effort.2})$	12	3.006	0.02883
$p(\text{radio.vhf} + \text{radio.sat} + \text{age34.sex} + \text{effort.2})$	13	3.450	0.02309
$p(\text{radio.vhf} + \text{radio.sat} + \text{age34.sex} + \text{effort.2})$	13	3.542	0.02205
$p(\text{radio.vhf} + \text{radio.sat} + \text{age34.sex} + \text{effort.2})$	13	3.741	0.01996
$p(\text{radio.vhf} + \text{radio.sat} + \text{effort.2} + \text{age2} + \text{age34.sex})$	11	4.011	0.01744
$p(\text{radio.vhf} + \text{radio.sat} + \text{age34.sex} + \text{effort.2})$	11	4.125	0.01647
$p(\text{radio.vhf} + \text{radio.sat} + \text{age34.sex} + \text{effort.2})$	11	4.149	0.01628
$p(\text{radio.vhf} + \text{radio.sat} + \text{age34.sex} + \text{effort.2})$	13	4.336	0.01482
$p(\text{radio.vhf} + \text{radio.sat} + \text{effort.2} + \text{age2} + \text{age34.sex})$	11	4.495	0.01369

cent males were marginally higher than for other bears throughout the study, the difference was not significant (Wald t ratio = 1.39, $P = 0.1636$).

Estimates of population size

Model-averaged estimates of abundance during the 1970s, 1980s, and 2000s are summarized in Table 9. The estimates for 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 using different methods (Fig. 3). 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.

TABLE 7. Extended.

Senescent adults		
Mean	95% CI _L	95% CI _U
NA	NA	NA
0.403	0.122	0.684
0.403	0.122	0.684
0.397	0.119	0.675
0.397	0.119	0.675
0.408	0.401	0.415
0.435	0.123	0.746
0.393	0.067	0.718
0.397	0.237	0.556
0.432	0.432	0.432
0.398	0.325	0.470
0.384	0.102	0.665
0.442	0.115	0.769
0.368	0.000	0.784

Overall, estimates of abundance were remarkably similar through the 1970s, 1980s, and 2000s (Fig. 4, Table 9). The numbers of bears estimated to be in the NB population, calculated as the mean (\pm 95% CI) of annual estimates during each decade, were: 876 \pm 494 for 1972–1979; 857 \pm 482 for 1985–1989; and 1004 \pm 540 for 2000–2006. The standard error used to construct the confidence interval for each average was the square root of the variance of population size point estimates in the decade divided by the number of point estimates in the decade, plus the average point estimate variance. Note that the size estimate in 2006 appears low relative to the estimates for 2003–2005. However, the confidence interval on the size estimate in 2006 (i.e., 767 bears \pm 416 95% CI) overlapped the confidence interval for the size estimate in 2005, indicating that the estimate of size in 2006 was not statistically different from that in 2005. Empirical observations from the 2006 field season also suggest that the 2006 estimate may be too low (see *Discussion* for comments).

Annual estimation of minimum sea ice cover in the study area

Using the rank von Neumann ratio test, we found no evidence of serial correlation in either our annual sea ice concentration or area of polar bear habitat over the continental shelf ($r_1 = 0.286$, $P = 0.086$ and $r_1 = 0.376$, $P = 0.078$, respectively) between 1979 and 2009. This confirmed the assumption of independence in our data set. The MK tests for trend indicated that there were statistically significant decreases in both the total amount of ice, measured as mean ice concentration of all pixels ($z = -2.006$, $P = 0.0448$) and the total amount of polar bear habitat over the continental shelf ($z = -2.652$, $P = 0.008$) over the last 31 years. Median slopes calculated using Sen’s (1968) approach indicate that ice concentration has been declining at $\sim 0.19\%$ per year

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 to 2005.

Year	Cubs-of-the-year			Yearlings			Subadults			Adults		
	Mean	95% CI _L	95% CI _U	Mean	95% CI _L	95% CI _U	Mean	95% CI _L	95% CI _U	Mean	95% CI _L	95% CI _U
1971	NA	NA	NA	NA	NA	NA	0.910	0.865	0.956	NA	NA	NA
1972	0.512	0.169	0.855	0.324	0.067	0.582	0.910	0.865	0.956	0.912	0.870	0.954
1973	0.512	0.169	0.855	0.324	0.067	0.582	0.910	0.865	0.956	0.912	0.870	0.954
1974	0.513	0.162	0.864	0.327	0.070	0.584	0.909	0.861	0.958	0.910	0.865	0.956
1975	0.513	0.162	0.864	0.327	0.070	0.584	0.909	0.861	0.958	0.910	0.865	0.956
1976	0.513	0.162	0.864	0.327	0.070	0.584	0.909	0.861	0.958	0.910	0.865	0.956
1977	0.512	0.169	0.855	0.324	0.067	0.582	0.910	0.865	0.956	0.912	0.870	0.954
1978	0.512	0.169	0.855	0.324	0.067	0.582	0.910	0.865	0.956	0.912	0.870	0.954
1979	0.520	0.490	0.550	0.346	0.342	0.349	0.911	0.773	1.000	0.912	0.782	1.000
1985	0.579	0.094	1.000	0.369	0.034	0.704	0.916	0.857	0.975	0.917	0.862	0.973
1986	0.675	0.189	1.000	0.282	0.000	0.598	0.904	0.826	0.982	0.905	0.831	0.979
1987	0.523	0.246	0.799	0.322	0.208	0.436	0.910	0.830	0.989	0.911	0.837	0.984
1989	0.549	0.546	0.553	NA	NA	NA	0.910	0.780	1.000	0.911	0.788	1.000
2000	NA	NA	NA	0.324	0.281	0.367	0.909	0.801	1.000	0.910	0.810	1.000
2003	NA	NA	NA	0.300	0.042	0.559	0.906	0.854	0.958	0.907	0.858	0.955
2004	0.657	0.181	1.000	0.354	0.011	0.697	0.917	0.853	0.982	0.918	0.857	0.979
2005	0.224	0.000	0.727	0.353	0.000	0.847	0.867	0.678	1.000	0.868	0.682	1.000

and that the amount of polar bear habitat over the continental shelf has been declining at a rate of 250 km² per year. Overall, there was more variability in the minimum amounts of ice cover in the second half of the data set than in the first half, and a clear trend toward smaller minima at decadal intervals in 1988, 1998, and 2008. However, even in the years of lowest ice cover, at least some of the sea ice still lay over the biologically productive continental shelf.

DISCUSSION

Survival

Survival rates that we estimated for the NB appear lower than those reported in other geographic regions (Lunn et al. 2006; Table 14). Differences between

survival in the NB and some other areas may be explained by pooling of age groups or failure to explicitly include harvest in survival estimates (Taylor et al. 2002, Regehr et al. 2006). In other cases, wide confidence intervals on survival estimates (Regehr et al. 2010) may mean that apparent differences are not as great as they at first appear.

Despite analytical differences that could prevent precise comparisons of estimated survival across geographic regions, our estimates appear to be consistently lower than those estimated in several other polar bear subpopulations. We have insufficient data to explain this, but we hypothesize that part of the difference may lie in the inability of researchers to consistently sample the entire NB region. Radiotelemetry data do not indicate a pattern of permanent emigration from the

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

Year	Population estimate, <i>N_j</i>	SE
1971		
1972	408.7158	91.72382
1973	811.9275	149.7072
1974	776.5736	140.0759
1975	1340.625	222.1589
1976	989.6552	303.2986
1977	812.343	265.4078
1978	723.8707	238.5173
1979	1141.792	330.3641
1985	938.0228	175.6078
1986	912.2724	167.7736
1987	1122.234	291.7455
1989	456.4495	133.0012
2000	644.5036	204.9913
2003	1058.697	326.9192
2004	1203.548	207.1212
2005	1345.099	240.4967
2006	766.9149	207.952

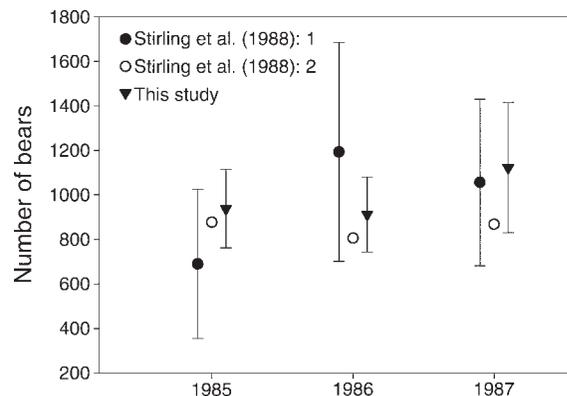


FIG. 3. Population estimates from 1985 to 1987 from Stirling et al. (1988) and the present study. Stirling et al. (1988) used two methods to estimate population size. The first method followed that of DeMaster et al. (1980) and shows the population estimate ± SD. The second method was the Fisher-Ford method (see Begon 1979), which does not provide a variance estimate. The most recent analysis (this study) reports population size ± SE.

TABLE 8. Extended.

Senescent adults		
Mean	95% CI _L	95% CI _U
NA	NA	NA
0.581	0.345	0.817
0.581	0.345	0.817
0.575	0.338	0.811
0.575	0.338	0.811
0.581	0.541	0.621
0.611	0.356	0.865
0.567	0.276	0.858
0.573	0.361	0.785
0.579	0.576	0.582
0.573	0.425	0.721
0.561	0.319	0.802
0.616	0.348	0.884
0.525	0.118	0.932

NB region, but they do verify that much of the area occupied by NB bears (Fig. 1) is beyond the range that we can reach by helicopter sampling (Amstrup et al. 2004). Because capture–recapture models cannot distinguish animals that are unavailable for capture from those that are dead, it is possible that such interannual movement of some individuals out of the principal sampling area could bias survival estimates low. Indeed, limited sampling during the 1990s indicated transient movements of some bears from our principal sampling area into the northern end of the NB region adjacent to

Prince Patrick Island (Fig. 1). This area, however, was not sampled in most years of this study because of budgetary limitations. If greater proportions of bears from the NB were unavailable for capture in many years of the study, it could explain differences between our estimates of apparent survival and those from the adjoining SB subpopulation, where such transience was recognized, but did not occur frequently enough to significantly influence estimates (Regehr et al. 2010). Further, the NB situation contrasts with sampling in Hudson Bay and some other areas where bears are trapped on land and are more uniformly available for sampling in summer and fall.

We found considerable variation among the survival rate estimates of bears in different age and sex classes within sampling periods (i.e., mid-1970s, mid-1980s, and 2000s). However, there was little variability among estimates for bears of the same age and sex classes in the different sampling periods. Tables 7 and 8 illustrate that survival rates estimated for different sex and age groups were relatively constant over the duration of our study. This suggests that the influence on survival of interannual or interdecadal variations in environmental factors, which may have occurred during this study, were below the level of influence that could be detected by our model-averaged estimates. It also suggests that the changes in sea ice habitats that have been observed in other regions, including the adjacent SB (Regehr et al. 2010), have not yet had a significant negative influence on polar bears in NB. Survival rate estimates of subadults and adults appeared to be more consistent

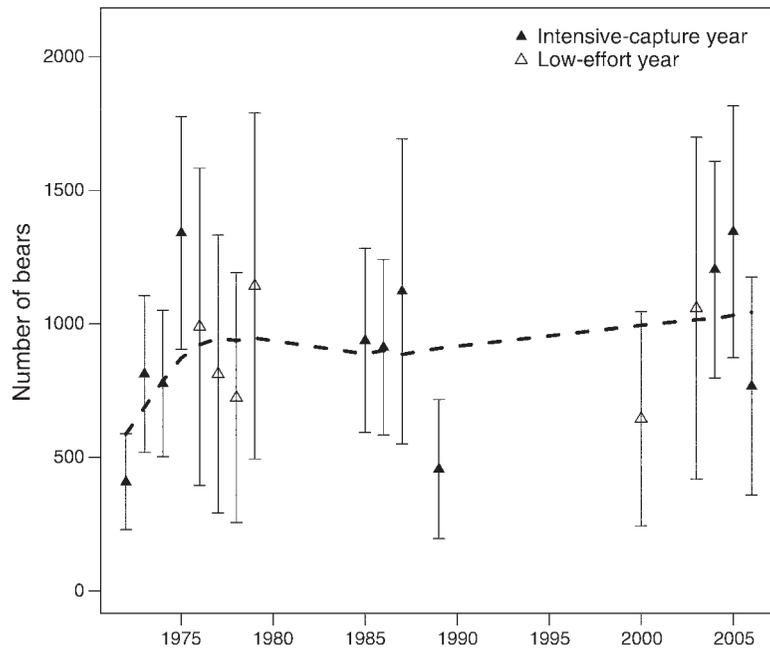


FIG. 4. Model-averaged estimates of abundance for the northern Beaufort Sea polar bear population during intensive-capture years vs. low-effort years. Bars indicate 95% confidence intervals that include model selection uncertainty. The fitted line was determined with Friedman’s Supersmoother in R (<http://cran.r-project.org>).

over time than did those for young and senescent animals. This is consistent with previous findings that very old and very young polar bears are the most vulnerable to changing ecological conditions. Regehr et al. (2007, 2010) found that the annual survival rates of prime adult females and males were higher than those of all other groups and were less affected by apparent fluctuations in ecological conditions.

Estimated survival rates for subadult, adult, and senescent adult males were consistently lower than rates for females in the same age groups. A similar pattern has also been reported for bears in the adjacent SB (Regehr et al. 2006, 2010) and in the more distant Western Hudson Bay (WH) (Regehr et al. 2007). Although a female-biased sex ratio is not uncommon among large mammals, the low estimates of model-averaged survival for males relative to females in NB may have been influenced by harvest. The harvest of polar bears in NB is strongly sex selective (2 males : 1 female), and guided trophy hunters, which include a portion of NB harvesters, seek the largest bears, assuring that adult males are taken more frequently. The sex ratio of all adult bears (≥ 5 years old) captured in NB and the Canadian portion of SB from 2003 to 2006 significantly differed from even (42.1:57.9; $\chi^2 = 11.27$, $P = 0.001$; Stirling et al. 2006), and the proportion of male bears over 10 years of age was also reduced in NB. This pattern parallels that in WH, corroborating the hypothesis that a sex-selective harvest can affect adult sex ratios and probably also has a differential effect on male and female survival rates, which may be harmful to the long-term health of a polar bear population (Derocher et al. 1997, McLoughlin et al. 2005, Molner et al. 2010).

An unexpected and unexplained anomaly in the survival calculations, which differed from the results of other polar bear population analyses (e.g., Obbard et al. 2007, Regehr 2007), was that the survival of COYs was consistently higher than that of yearlings. This is contrary to previously reported patterns (e.g., Amstrup and Durner 1995, Obbard et al. 2007, Regehr et al. 2007). Because this pattern is unlikely to be real, it probably reflects a consistent sampling bias. One possible bias is that much of the sampling through April and early May took place after females had weaned their 2.5-year-old cubs. If the probability of capture of these newly weaned subadults was lower than that of yearlings that were still traveling with their mother (and easier to track and capture because of being a group rather than a single bear), this could result in a consistent underrepresentation of young bears that had just passed through their second year of life.

Population size and trend

Previously only one study sought to directly estimate 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 (Begon 1979) to estimate population size from 1985 to

1987. The point estimates from the latter method were similar to estimates that we report here, and the confidence intervals from our current analysis indicate that these new estimates are not significantly different from the estimates derived by DeMaster et al. (1980); see Fig. 3.

We estimated population size for each of the three groups of years (1970s, 1980s, and 2000s) during which there was an intensive capture effort over most of the study area (Fig. 4). We believe that these estimates include almost all of the bears in NB. Limited sampling performed in the far northern part of the NB region suggested, however, that a small but unknown number of polar bears occurs there and may be less frequently available for capture in our main study area. If this is true, the estimates that we report here are biased low.

Although our averaged estimates of population size did not differ significantly over the three decades, other evidence suggests that the population could have gradually increased. 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 Canada in 1968 and the Marine Mammal Protection Act (1972) stopped aerial hunting in Alaska. In the decade or more that followed, the average age of both males and females increased from about 4 years to about 8 years. 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 percentage of bears 10 years of age or older had increased to 20–30% for males and slightly higher for females. This increase in the percentage of older animals parallels the increased average age of bears in the adjoining SB population, which was known to be associated with a population increase (Amstrup et al. 1986, Stirling 2002). Taken together, these data are consistent with a population increase at least through the 1970s and into the 1980s. Increased numbers of older animals were shown to coincide with population growth in the adjoining southern Beaufort Sea following the cessation of aerial hunting there (Amstrup et al. 1986). The dramatic increase in estimated numbers after the first year of our study (Fig. 4) probably reflects real population growth that was occurring at that time, as well as some sampling bias that occurred because of the increase in both the sample sizes and the area sampled during the first years of our study. Regehr et al. (2007) previously documented a similar impact of increased sampling numbers and area on population size estimates in the western Hudson Bay region.

Even though the estimates for the three periods were not statistically different, we also believe that the population size may have continued to increase slowly

into the decade of the 2000s. The low estimate of population size in 2006 (Table 9), which reduced the mean for the 2000s, should be viewed with caution. The capture and survival parameters for the last capture occasion are confounded in standard CJS models (Lebreton et al. 1992). The extent to which we may have compensated for this with use of individual covariates is not clear. More importantly, however, the empirical observations suggest that there was a major change in the distribution of bears in 2006. We obtained a smaller capture sample than in previous years, despite searching over a similar total number of kilometers of sea ice habitat in search of polar bears. Intensive studies in the adjacent SB region also indicated that changes in the distribution or availability may have reduced the local abundance of polar bears there in 2006 (Regehr et al. 2010), indicating the effect prevailed over the entire Beaufort Sea. If, as our observations suggest, the population estimate for 2006 is biased low, the estimates of ~1200–1300 in 2004 and 2005 may more accurately reflect the current number of polar bears in NB. Such an estimate suggests the possibility of some continued population growth through the end of our study.

Inuvialuit harvest of polar bears from the northern Beaufort Sea population

Between 1968 and the present, the annual quota for Inuvialuit hunters in NB was increased from 36 to 65 bears, 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). This has been well below the estimated sustainable harvest of 50–55 bears (Taylor et al. 1987). The low harvest, relative to maximum sustainable yield (MSY), may have been driven partly by difficult travel conditions for hunters and a reduced hunting effort in parts of the area. Although it appears that the level of annual harvesting in recent years has probably not reached its estimated MSY, the prospect of future reductions in MSY in response to anticipated deteriorating sea ice habitat in this region will require vigilant management of future harvests.

Population estimates in relation to minimum sea ice cover and future trends

In two other long-term studies of polar bears, changes in the timing of breakup, the distribution of the remaining sea ice, and the duration of the open-water period have been shown to be detrimental to survival and population size. In western Hudson Bay (WH), progressively earlier breakup of the sea ice, followed by several months of completely open water, forced bears to fast for increasingly long periods with progressively less stored fat reserves, resulting in a significant negative effect on the survival of juvenile, subadult, and senescent bears and a decline in total population size (Regehr et al. 2007). Similarly, at the southern limit of polar bear range, in southern Hudson Bay (SH), progressively earlier break up of the sea ice, followed by several

months of completely open water, has significantly extended the period through which bears must fast, resulting in significantly reduced body condition (Obbard et al. 2006). Because of the similarity to ecological conditions and the downward trend in body condition in the adjacent WH population, future declines in reproduction and population size have been predicted in SH (Stirling and Parkinson 2006).

In SB, when sea ice retreats to the north and open water forms along the coast in summer, polar bears move north because they need the sea ice platform from which they hunt their preferred seal prey, ringed seals. Historically, polar bears have preferred to remain on sea ice that is over shallow (<300 m) continental shelf waters (Durner et al. 2009), where productivity is higher and seals are more abundant (Stirling et al. 1982). Prolonged retreat of the sea ice beyond the continental shelf, has been linked to poorer growth and survival of young (Rode et al. 2010) and to poorer survival of adult females (Regehr et al. 2010). Similarly, declines in breeding rates, cub litter survival, body stature, and condition have also been significantly correlated with increasing duration of the ice-free period (Rode et al. 2010). These declines were not related to aboriginal harvesting because sustainable levels have not been exceeded (Brower et al. 2002). Because the duration of the open-water period in SB will only increase with climate warming (Amstrup et al. 2009), severe declines in population size have been projected to occur in SB in coming decades (Amstrup et al. 2008, Hunter et al. 2010). These patterns generally parallel similar trends that have been observed in more southerly portions of the polar bear range (Stirling et al. 1999, Obbard et al. 2006, Regehr et al. 2007), and corroborate the hypothesis that there may be a threshold of sea ice absence beyond which polar bears may not be able to persist (Molnar et al. 2010).

One of the most obvious, and probably most significant, ecological differences between NB and SB through most years of this study is that the sea ice adjacent to the coast and over the biologically productive continental shelf within the NB region did not melt completely each year (Fig. 1; see the Canadian Ice Service, Environment Canada for data *available online*).¹⁰ Thus the bears in NB probably had more extensive and continued access to seals during the summer than did those in SB, especially in the last decade. That difference, along with an annual harvest that has remained below sustainable limits, probably explains why the NB population has not experienced the problems recently observed in the neighboring SB. In some past years, Beaufort Sea ice was too heavy for too long to be ideal polar bear habitat (Amstrup et al. 1986, Stirling 2002). This suggests that some amelioration of harsh conditions may benefit bears in some circum-

¹⁰ (<http://www.ice.ec.gc.ca/IceGraph/IceGraph-GraphdesGlaces.jsf?id=11874&>)

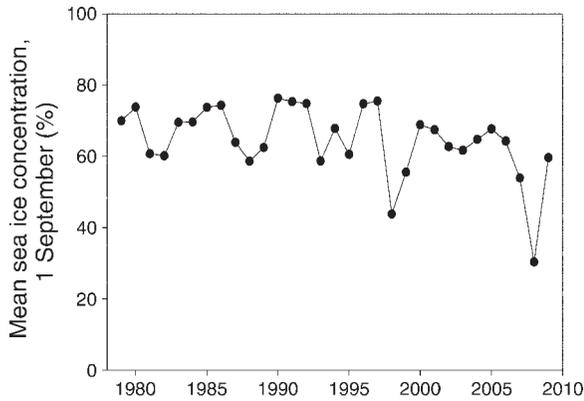


FIG. 5. Mean annual sea ice concentration of all sampling points ($n = 1063$) in the northern Beaufort Sea on 1 September, 1979–2009. Mean sea ice concentration was calculated by sampling the center of all 1063 raster cells that fell within the study area and calculating the average of the extracted sea ice concentration values.

stances. Although the ice conditions in the SB appear near, or may already have passed, the point at which polar bears could benefit from milder conditions, that threshold may not yet have been crossed in the NB. This seems the most likely explanation for the stable or possibly even increasing population that we observed over the last 30 years.

Although NB polar bears do not appear to have been harmed, and may even have benefited from sea ice trends of the past 30 years, this is most likely a transitory effect. The mean sea ice concentration at the September minimum has significantly declined over the period of our study (Fig. 5), and the portion of the sea ice of $\geq 50\%$ cover that remains over the continental shelf in summer has declined dramatically in recent years (Fig. 6). Available data indicate that polar bears tend to avoid areas where sea ice concentration is less than 50% (Stirling et al. 1999, Durner et al. 2009). We predict that if the amount and seasonal availability of the sea ice in NB continue to decline as projected (Comiso 2002,

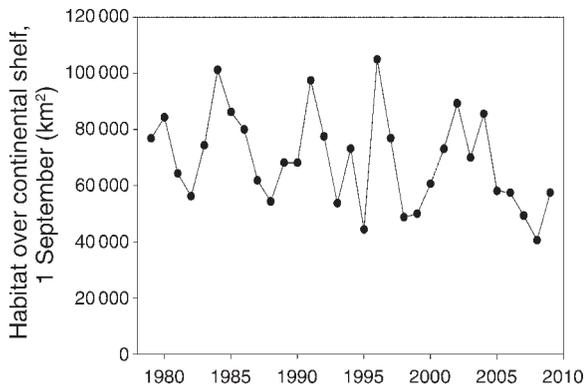


FIG. 6. Total annual area of polar bear habitat (i.e., all pixels with $>50\%$ sea ice concentration) over the continental shelf (waters <300 m deep) on 1 September, 1979–2009.

Stroeve et al. 2007), the population will decline along with that in the neighboring SB and the more distant WH. There is no evidence from anywhere in their current range that polar bears can persist in their current distribution or numbers without persistent sea ice (Amstrup et al. 2009, Molnar et al. 2010). The sea ice is “essential” habitat for polar bears, and just like any other animal, polar bears cannot fare well if their essential habitat is compromised or absent. Thresholds of persistence undoubtedly will differ across their current circumpolar distribution (Thiemann et al. 2008), but available data suggest that as long as sea ice continues to retreat, thresholds ultimately will be crossed and polar bears will be dramatically reduced throughout their range.

In the early stages of a sea ice-induced decline, reductions in the annual aboriginal harvest might forestall or minimize the rate of loss. Conversely, continuing harvest at rates similar to those of the past is likely to accelerate population decline, as it has in western Hudson Bay (Regehr et al. 2007). Therefore, future monitoring and reassessment of the status of the NB population, along with that of SB, should be undertaken at regular intervals. Quantitative comparisons between the current and future situations, made possible by continued monitoring and predictive modeling, would maximize the ability of managers and aboriginal hunters concerned about sustainable harvesting and minimizing the detrimental effects of offshore industrial activities to respond to future changes. They also would provide a sound basis for further quantifying and understanding the relationship between loss of sea ice and the population dynamics of other polar bear populations that occur at the periphery of the polar basin and for which population data are not available.

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