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

Polar Bear Population Status in Southern Hudson Bay, Canada

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Abbreviations, Acronyms, and Symbols

Abbreviations, Acronyms, and Symbols	Meaning
AIC	Akaike's Information Criterion
BCI	Body Condition Index
CJS	Cormack-Jolly-Seber model
COY	Cub-of-the-year
FB	Foxe Basin
GOF	Goodness-of-fit
SH	Southern Hudson Bay
USFWS	U.S. Fish and Wildlife Service
USGS	U.S. Geological Survey
WH	Western Hudson Bay
XZT	Telazol® and xylazine hydrochloride
ZT	Telazol®

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Abstract

The Southern Hudson Bay (SH) population of polar bears (*Ursus maritimus*) resides in a seasonal sea ice environment and is the most southerly population in the species' range. Therefore, SH polar bears may be among the first to show negative effects associated with climate warming and consequent loss of sea ice. Polar bears in the neighboring Western Hudson Bay (WH) population have declined significantly in body condition since the mid-1980s, and a recent study indicated that the size of the WH population declined by about 22% between 1987 and 2004. Similarly, SH bears have shown a significant decline in body condition since the mid-1980s, and an assessment of the current status of the SH population was therefore needed. We applied open population capture-recapture models to data collected from 1984-86 and 1999-2005 to estimate population size and survival. The size of the SH population appears to be unchanged from the mid-1980s (1984-1986: 641, 95% CI = 401, 881) vs. 2003-2005: 681 (95% CI = 401, 961). Point estimates of survival for subadults and adult females were 94% (95% CI = 68%, 100%) in 1984-1985 to 89% (95% CI = 79%, 99%) in 2003-2005, but imprecision exhibited by overlap of the confidence intervals prevented us from unequivocally concluding that this 5% decline in survival was not a chance occurrence. Similarly, a decline of 7% in survival was estimated for subadult and adult males over the same time period (male survival estimates = 88% (95% CI = 77%, 100%) in 1984-1985; 81% (95% CI = 66%, 96%), but again we could not unequivocally conclude that this decline was not chance. There was weak evidence of lower survival of cubs, yearlings, and senescent adults in the recent time period. This, combined with the evidence of significant declines in body condition for all age and sex classes, which were greatest for pregnant females and subadults, suggests this population may be under increased stress at this time. However, we did not find any clear association between survival and cub-of-the-year body condition, average body condition for the age class, or extent of ice cover in our data. This lack of association could be real or attributable to the coarse scale of our average body condition measure, or to limited sample size and few years of intensive sampling. That the WH population appears to be in decline, but the SH population does not, might be explained by changes to sea ice patterns which to date have been greater in the western half of Hudson Bay (breakup 10 days earlier per decade) than in the eastern and southern portions of Hudson Bay (breakup 5-8 days earlier per decade). However, if the trend in sea ice patterns (i.e., earlier melt and later freeze-up) continues in eastern and southern Hudson Bay, the SH population will likely respond similarly to the WH population and begin to decline.

Introduction

The U.S. Fish and Wildlife Service (USFWS) proposed listing the polar bear as a threatened species under the U.S. Endangered Species Act in January 2007 (USFWS 2007). To help inform their final decision, they requested that the U.S. Geological Survey (USGS) conduct additional analyses 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 from long-term studies of polar bears in Southern Hudson Bay, Canada. This

population is the southernmost population of polar bears and occurs within the seasonal ice ecoregion as defined by Amstrup et al. (2007).

Ecological change in the Arctic as a result of climatic warming may pose a significant threat to the conservation of polar bears (Lunn et al. 2002). Sea ice characteristics and dynamics differ among broad regions of the Arctic, resulting in regional differences in polar bear ecology. In their forecast of future status of polar bears worldwide, Amstrup et al. (2007) recognized four ecoregions based upon differences in historic and projected sea ice conditions. Predicted impacts of climatic warming may occur first for populations near the southern edge of the range in James Bay and Hudson Bay (Stirling and Derocher 1993, Arctic Climate Impact Assessment 2004, Derocher et al. 2004), which occur in the Seasonal Ice Ecoregion (Amstrup et al. 2007). In particular, earlier break-up of sea ice likely reduces opportunities for polar bears to feed and acquire stored reserves needed to sustain them during prolonged fasting during the ice-free season (Stirling et al. 1999) — a major ecological stressor for bears inhabiting Hudson Bay.

Polar bears in Hudson Bay are assigned to three sub-populations, Foxe Basin (FB), Western Hudson Bay (WH), and Southern Hudson Bay (SH) (Figure 1), based on a combination of tag returns from harvested bears, ice movement patterns, capture-recapture, and conventional and satellite radio-telemetry (Lunn et al. 2006). The SH population mainly summers on land in Ontario. In contrast to populations of polar bears at higher latitudes in the Archipelago Ecoregion of the Canadian Arctic and the two ecoregions of the Polar Basin, in the Hudson Bay system as well as in Davis Strait and Baffin Bay, the bears are forced ashore every summer because the ice melts completely each year (Etkin 1991, Wang et al. 1994a ,b; Stirling and Parkinson 2006). Second-year ice is rare and is restricted to northeast Hudson Bay when it occurs (Etkin and Ramseier 1993). Because currents flow counter-clockwise in Hudson Bay and prevailing winds are often north-westerly, remnant ice usually occurs latest in the year off the Ontario coast

(Etkin 1991, Saucier et al. 2004). The entire Bay is generally completely free of ice from mid-August or earlier to late October or later (Markham 1986, Wang et al. 1994a), and the Hudson Bay coast of Ontario is ice-free from mid-August until early December in most years (Gagnon and Gough 2005a). As a result, bears spend 4-5 months ashore until freeze-up in mid-November to early December (Stirling et al. 2004). Both the extent (Smith 1998, Parkinson et al. 1999) and duration of the sea-ice cover have been decreasing in Hudson Bay in recent decades (Etkin 1991, Stirling et al. 1999, Gough et al. 2004, Gagnon and Gough 2005a).

During the period ashore bears generally fast, surviving on adipose stores (Watts and Hansen 1987, Ramsay and Stirling 1988). However, when on land, polar bears in Hudson Bay and James Bay have been documented to feed on marine algae, terrestrial vegetation such as grasses, sedges, mosses, lichen, and berries of arctic blueberry (*Vaccinium uliginosum*) and crowberry (*Empetrum nigrum*), and flightless snow geese (*Anser caerulescens*) and other vertebrates (Russell 1975, Derocher et al. 1993). They may also feed opportunistically on such items as eggs of Canada geese (*Branta canadensis*) (Smith and Hill 1996), and have been recorded attempting to prey on caribou (*Rangifer tarandus)* (Brook and Richardson 2002). Along the Ontario coast in late summer and fall, polar bears have been observed to scavenge carcasses of beluga whale (*Delphinapterus leucas*), and to capture live ringed seals (*Phoca hispida*) and bearded seals (*Erignathus barbatus*) apparently stranded at low tide, and walrus (*Odobenus rosmarus*) on an off-shore haul-out (M. E. Obbard, unpublished data). Nevertheless, the significance to a bear's yearly energy budget of these sources obtained opportunistically during the ice-free season is not well understood, but is likely to not be significant at the population level (Amstrup 2003). The most important feeding period for bears in Hudson Bay is on the sea ice from early April to July when the major prey is ringed seals (Stirling and Archibald 1977, Stirling and Derocher 1993).

Once ashore, the bears in southern areas of

Hudson Bay are found along the coastlines of Manitoba and Ontario, on the islands of James Bay, and in inland areas (Jonkel et al. 1976; Stirling et al. 1977; Prevett and Kolenosky 1982; Derocher and Stirling 1990a; Kolenosky et al. 1992). Individual bears show a high degree of fidelity to general areas used for maternity denning (Ramsay and Stirling 1990, Lunn et al. 2004), and as summer refugia (Derocher and Stirling 1990a, Kolenosky et al. 1992, Stirling et al. 1999, Stirling et al. 2004). For example, of 1386 bears first captured in WH, the mean distance between consecutive captures was 62.3 ± 2.7 km for males (n = 678) and 46.0 ± 1.7 km for females (n = 708) (Stirling et al. 2004).

While onshore, polar bears are segregated by sex, age, and reproductive status. For example, in Ontario, pregnant females may move up to 100 km inland to construct a maternity den, though most maternity denning occurs closer to the coast (Kolenosky and Prevett 1983, Obbard and Walton 2004). Additional segregation occurs because adult male bears tend to aggregate on peninsulas, offshore spits and islands, and areas where there are elevated beach ridges (Latour 1981a, b, Derocher and Stirling 1990b); subadults and females with dependent young are also found along the coastal plain in Ontario though generally they avoid aggregations of adult males and are found in intervening habitat along the coast and inland (Prevett and Kolenosky 1982, Kolenosky et al. 1992, Lunn et al. 1997).

The size of the SH population was estimated to be 763 ± 323 animals based on a capture-recapture study conducted from 1984-86 (Kolenosky et al. 1992). This estimate was subsequently adjusted upwards to 1000 by the Polar Bear Technical Committee largely because the area away from the coast may have been under-sampled due to the difficulty of locating polar bears inland in the boreal forest and because areas in James Bay were not sampled (Lunn et al. 1998). Annual age-specific survival rates were also estimated for the 1984-86 period by Kolenosky et al. (1992).

The neighboring WH population (Figure 1) showed a significant decline in body condition and natality from 1981-1997 (Stirling et al. 1999,

Stirling and Parkinson 2006). A recent study estimated that the size of the WH population declined from 1194 (95% CI = 1020-1368) bears in 1987 to 935 (95% CI = 794-1076) in 2004 (Regehr et al. 2007). Demographic declines in western Hudson Bay were apparently associated with a 2-3°C rise in spring air temperatures over the past 50 years (Skinner et al. 1998, Gagnon and Gough 2005a), which have caused the sea ice to break up in the spring about 3 weeks earlier than it did 30 years ago (Gough et al. 2004, Stirling and Parkinson 2006).

Since the abundance estimate for SH was dated (1986), and declines in body condition and natality had been demonstrated for the neighboring WH population, the Ontario Ministry of Natural Resources began a study to monitor body condition of SH bears in 1999 and conducted an intensive capture-recapture effort from 2003-2005. Obbard et al. (2006) documented significant declines in body condition in all age and sex classes of bears for the period 2000-2005 compared to the 1984-1986 period (Figure 2). In the present study, we estimated demographic parameters (survival), size of the SH population, and factors associated with changes in these parameters. We were particularly interested in whether apparent changes in sea ice habitat and body condition were correlated with SH demographic parameters, as they appear to be in WH. We also compared estimated survival and abundance from 1999-2005 to 1984-1986 to assess trend. We utilized all available SH live capture-recapture data in our analysis.

Methods and Materials

Study Area

The study area extended along the Ontario coastline from Hook Point (~54° 50'N 82° 15'W) on north-western James Bay to the Hudson Bay coast at the Ontario–Manitoba border (~56°50'N 89° W) (Figure 3). In each year we searched for bears along the coastal strip including offshore spits and small islands, and in inland areas up to 40 km from the coast. The coastal zone included

tundra habitat in the most southern extent of continuous permafrost in Canada, and discontinuous permafrost with intervening fens. Forested areas farther inland from the coast were characterized by open stands of stunted black spruce (*Picea mariana*), tamarack (*Larix laricina)*, and white spruce (*P. glauca*). Forested areas occur closer to the shore of Hudson Bay in the western portion of the study area. Dry sites support open stands of white spruce with an ericaceous shrub layer and a ground cover of lichen (*Cladonia* spp., *Alectoria* spp., *Cetraria* spp.). Poorly drained sites are characterized by sedge (*Carex* spp.) and cottongrass (*Eriophorum* spp.) tussocks or sphagnum moss. Inland areas are a poorly drained region of unconsolidated glacial and postglacial deposits underlain by Palaeozoic limestone over Precambrian rock, with numerous bogs and shallow lakes (Rowe 1972).

Capture Methods

From 1984-1986, bears ≥1 year of age were captured by remote darting from a Bell 206L helicopter and immobilized using a mixture of ketamine hydrochloride and xylazine hydrochloride (Lee et al. 1981). Immobilization was reversed by intravenous injection of yohimbine hydrochloride (Ramsay et al. 1985). From 1999-2005, bears ≥1 were immobilized by darting from a Bell 206L-1 helicopter using Telazol® (ZT) (Stirling et al. 1989), or a mixture of Telazol® and xylazine hydrochloride (XZT) (Cattet et al. 2003). The xylazine in XZT immobilizations was reversed with atipamezole (Cattet et al. 2003). In all years, cubs-of-the-year (COYs) were immobilized using a jab pole.

The sex, reproductive status, and a series of standardized morphometric measures were collected from each bear. Straight-line body length was measured to the nearest cm as the dorsal straight-line distance from the tip of the nose to the caudal end of the last tail vertebra. All bears were measured while sternally recumbent with the back legs extended behind and bent forward at the knee, and the front legs forward and bent at the elbows to lie parallel to

the body. Total body mass was measured to the nearest 500 g either by suspending the bear from a spring-loaded weigh scale (1984-86), or from an electronic load cell scale (2000-05). During weighing, bears were placed in a semi-supportive sling and lifted by chain pulley until clear of the ground.

We calculated a Body Condition Index (BCI) value (Cattet et al. 2002) for each animal to use as a predictor of survival in capture-recapture models. This model predicts the standardized residual from the regression of observed body mass against body length and has a strong association with true body condition in polar bears, defined as the combined mass of fat and skeletal muscle relative to body size (Cattet et al. 2002). BCI is unbiased by body length enabling meaningful comparisons among age and sex classes of bears. Observed body mass data were missing for some bears in both the early and late periods. For these individuals we calculated an estimated body mass using the time-specific equations given in Cattet and Obbard (2005) that predict body mass from body length and axillary girth relationships, then we calculated BCI values based on the estimated body mass.

We extracted a vestigial premolar tooth from all animals, except known COYs and yearlings, for age determination (Calvert and Ramsay 1998). Tooth ages were unavailable for 22 bears from 1984–86 and 15 bears from 1999–2005 so an estimated age class was assigned to these animals based on straight-line body length (i.e., yearling, subadult [2-4 years], or adult [≥5 years]).

Capture effort varied among years. Intensive capture-recapture efforts were conducted from 1984–86 and again from 2003–2005. Lower effort occurred from 1999–2002 when the study had 2 objectives: to deploy satellite radio-collars on females accompanied by yearlings (and remove them 2 years later), and to monitor body condition of all age and sex classes. No capture efforts occurred from 1987–1998. During both intensive capture periods, some bears carried VHF or satellite radio collars, but collars were not used to locate bears and our analyses did not include any captures that were aided by

telemetry. During intensive capture periods all bears encountered were captured provided it was safe to do so. During both intensive capture-recapture periods animals were captured as far west as the Manitoba border. However, the area between longitude 88°W and the Ontario–Manitoba border is considered to be within the WH population boundary (Lunn et al. 2006) so those captures were excluded from this analysis.

Handling procedures were approved annually by the Animal Care Committee of the Ontario Ministry of Natural Resources and followed the guidelines of the American Society of Mammalogists (Committee for Field Methods in Mammalogy 1987), and the Canadian Council of Animal Care (1984).

Capture-recapture analysis

Data for each polar bear were summarized as individual capture histories and covariates. For example, bear number X16112 had a capture history of (1100000010), where 1 in the jth position of the history indicates capture and live release during sampling occasion j ($j = 1,2…10$) and a 0 indicates not captured during sampling occasion j. Multiple captures of an individual within a season were amalgamated and treated as a single capture (single 1) that year. The capture histories of a few bears that died as a result of handling were censored in our analyses (i.e., their deaths do not contribute to survival estimates). All other bears 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, sources of mortality included both natural and harvest mortality.

Capture histories were coded such that the gap in capture effort from 1987-1998 was treated as a single interval for survival estimation. Survival estimates for this interval were raised to the $1/12^{th}$ power (12th root, 12 = number of years in "gap") in order to place them on an annual basis. Polar bears can live longer than 12 years, and a few marked bears were captured before and after this interval, so inclusion of the early time period (1984-1986) and late time period (1999-2005) in

one analysis improved estimates over generating separate estimates for both periods, and provided a unified framework to investigate hypotheses related to differences in survival between the two periods.

We analyzed the SH capture-recapture data using Cormack-Jolly-Seber (CJS) models for open populations (Lebreton et al. 1992, McDonald and Amstrup 2001, Williams et al. 2002). The CJS model conditions on first capture (i.e., the initial capture is treated as a release) and estimates the probabilities of apparent survival (φ) and recapture (p) which are most likely to explain the observed capture history data assuming it came from an open population (Lebreton et al. 1992). We fit CJS models with a logit link function to relate model parameters to covariates, using R-language software that implemented the regression approach to capture-recapture (Amstrup et al. 2001, McDonald and Amstrup 2001, McDonald et al. 2005). The regression approach to capture-recapture is a parameterization of the CJS likelihood that ultimately fits the same models and produces the same parameter estimates as other parameterizations implemented in other software (e.g., Program MARK; Cooch and White 2005). Under the regression approach, variation in φ and p, including temporal and individual variation, are specified using covariate matrices with rows for individual animals and columns for time intervals (McDonald et al. 2005).

We completed the overall capture-recapture analysis in four steps. First, we evaluated the goodness-of-fit (GOF) of the SH data to the standard CJS model. Second, we identified combinations of individual, temporal, and environmental covariates that were likely to explain variation in φ and p based on polar bear biology and study design. Third, we constructed a set of candidate models and used a quasi-stepwise model selection procedure to identify well-supported combinations of covariates that explained variation in survival and recapture probabilities. Fourth, we derived model-average estimates of survival and population size. Each of these steps is described in turn below.

Goodness-of-fit

An assessment of GOF is required for valid model selection and for accurate estimation of parameter uncertainty (Choquet et al. 2005, Cooch and White 2005). We used program RELEASE (Burnham et al. 1987) to investigate patterns in the data, to quantify how well the standard Cormack-Jolly-Seber (CJS) model fit various subsets of the data, and to estimate the variance inflation factor ($\hat{c}$) that was subsequently used to adjust variance estimates and model selection criteria. The variance inflation factor was computed by summing chi-square statistics from the program RELEASE test components and dividing by the total degrees of freedom (e.g., Sendor and Simon 2003). We also used the parametric bootstrap (White and Burnham 1999) to evaluate the overall GOF of a model (described in Results) that allowed for major suspected sources of variation in φ and p. The GOF analysis did not detect any overdispersion in the SH data nor any heterogeneity that could not be explained with covariates; therefore, we set $\hat{c} = 1.0$ for all capture-recapture modeling.

Covariates

We used a variety of individual and time varying covariates to explain variation in survival and recapture probability (Table 1).

Age class—We defined 5 age classes based on previously established life history stages of polar bears (Derocher and Stirling 1992, Derocher and Stirling 1996, Amstrup 2003), and used time and individual varying covariates to model age effects on survival. The 5 age classes were cubs-of-the-year (*age0*; aged 0 years), yearlings (*age1*; aged 1 year), subadults (*age2*; aged 2 – 4 years), adults (*age3*; aged 5 – 20 years) and senescent animals (*age4*; aged ≥21 years). In addition, we investigated whether the relative difference in survival among age classes in SH mimicked that in the WH population. Based on the male-female and age class survival estimates of Regehr et al. (2007) for WH, we constructed a single time and individual varying covariate containing WH

survival rates to use as a covariate in the survival model (*WHage*).

Body Condition Index—We calculated individual BCI values (Cattet et al. 2002) for all bears captured (1984–86, $n = 417$; 1999–2005, $n = 640$), substituting estimated body mass for observed body mass where observed body mass was not available as described above, and used them to define two body condition covariates. Because CJS models condition on first capture and COYs were the youngest age class available for capture, the BCI of individual COYs (*BCIcoy*) was used as a covariate to explain individual variation in COY survival. Body mass of COYs has been shown to affect survival (Derocher and Stirling 1996). For other age classes, BCI could not be used as an individual covariate because it could not be measured when animals were not captured. Therefore, we created a second BCI covariate defined as the mean annual BCI for each sex and age class (*MeanBCI*) and evaluated whether this covariate predicted interannual variation in survival.

Period effects on survival— Due to sparse capture data in some years, we could not derive independent survival estimates for all years of the study. Therefore, we modeled survival as time invariant during the intervals defined by the different types of research activity (*yr84-85*, *yr1986*, *yr99-02*, *yr03-05*).

Ice condition (Break-up, Ice-Free, PMIce)— In a long-term study of polar bears in the neighboring WH population, Regehr et al. (2007) found that the date of spring sea ice breakup was the best predictor of interannual variation in survival for juvenile (0-1 year), subadult (2-4 year), and senescent-adult (≥20 year) polar bears. We developed temporal covariates using dates (as ordinal dates; International Organization for Standardization 2000) of break-up and freeze-up of the annual ice off the Ontario coast of Hudson Bay for 1984-2003 from Gagnon and Gough (2005*a*); W. Gough, University of Toronto (personal communication, 2007) provided dates for 2004 and 2005. We used data for Point 4 in Figure 1 of Gagnon and Gough (2005*a*: 371); break-up data were missing for Point 4 for 2002 and 2005 so we used data for Point 7 for those

years. We used December 16 (Day 350) as date of freeze-up for years with missing data (1994, 1997-1999). Break-up (*Break-up*) was defined as the date by which the melting ice covered only 50% of the water (Etkin 1991, Stirling et al.1999, Gough et al. 2004). Freeze-up was defined as the date by which the ice cover in the region had increased to cover 50% of the water. We determined the ice-free period (*Ice-Free*) as the number of days between break-up in spring and freeze-up the following fall (Table 2). We determined *PMIce* as the annual mean daily proportion of 25×25 km cells with greater than 50% ice concentration within the SH management zone calculated from daily passive microwave ice concentration values (D. Douglas, U.S. Geological Survey, personal communication).

We used the above environmental covariates to model both recapture probabilities and survival probabilities. We hypothesized that *Break-up* would affect capture probability since some age and sex classes of animals move inland after they come ashore (Derocher and Stirling 1990a, b), yet capture effort occurred at about the same time each year. Polar bears use sea ice as a platform to hunt seals so we assumed that reduced duration or quality of sea ice will affect a bear's nutritional status and possibly survival (Derocher and Stirling 1996, Stirling et al. 1999). Therefore, we hypothesized that *Ice-Free* and *PMIce* would affect survival because availability of ice affects a bear's ability to hunt for seals. We used *Ice-Free* rather than *Break-up* as a predictor of survival because of the recent evidence that break-up dates are earlier and freeze-up dates are becoming later in the eastern half of Hudson Bay (Gagnon and Gough 2005*a*). In their raw format, B*reak-up, Ice-free,* and *PMIce* were large numeric values, and to increase stability of the models, they were standardized by subtracting their respective means and dividing by their standard errors.

Post98—A covariate with time-invariant survival in all years prior to 1998 different from time-invariant survival after 1998 was included to test for a difference in survival since the earlier (1984 – 1986) capture-recapture study.

Effort— Capture effort was roughly equivalent during the early study period (1984-1986) and the late study period (2003-2005), was reduced during 1999-2002 while satellite radio-collars were deployed, and no captures occurred from 1987 to 1998. To model these suspected period effects on recapture probability we defined temporal covariates that allowed recapture probabilities to differ among the periods (i.e., were 1 during the period in question, and 0 otherwise: *effort.2, effort3.early, effort3.late,* and *effort.3*). These covariates fitted constant recapture parameters across years within the 4 effort periods. *Effort.3* forced capture probabilities to be equal during early and late periods, while including either *effort3.early* or *effort3.late* allowed different capture probability in each of the primary periods.

Period2— From 1999 to 2002, females accompanied by yearlings were targeted for capture in order to deploy satellite radio-collars to meet other study objectives. During this period, we hypothesized that adult females and their dependent young, (COYs and yearlings) had different capture probability than at other times in the study. The *period2* covariate was a 1 for all COYs, all yearlings, and adult females during 1999–2002, and 0 otherwise, in order to allow estimation of this effect.

Annual variation— Annual variation in recapture probabilities were modeled using nine $0 – 1$ indicator matrices delineating years (*year85, year86, year99, year00, year01, year02, year03, year04,* and *year05*). The initial capture probability in 1984 is not estimable, and when these effects were included, *year85* was omitted and used as the reference year.

Interactions— Several types of interaction effects were allowed in survival models we fitted. We constructed two interaction covariates based on age class and sex to accommodate the hypothesis that hunters target older males (*age234.sex* and *age1234.sex*). These covariates lumped survival of 2 or more age classes and allowed separate estimation of male and female survival. For example, when *age234.sex* was included in the survival model, survival of subadult, adult, and senescent males was

modeled as equal but different from other effects in the model. Another interaction covariate (*age34.sex*) allowed capture probability of older males to be different from other effects in the model. This covariate was hypothesized to be important because adult males travel more than other groups when females are in estrus, thus potentially increasing their probability of capture.

In addition to the above interactions, interactions between certain age class compositions (*age0, age01, age04,* and *age0124*) and *IceFree, PMIce, Post98, MeanBCI,* and annual variation were fitted during the last step of model selection (see below). These effects allowed for the effects on survival of environmental conditions and body condition to differ among age classes. For example, the interaction between *age01* and *IceFree* allowed for the hypothesis that an extended ice free period affected COY and yearling survival more severely than other (older) age classes.

Model selection

We used combinations of covariates, with both additive and interactive effects, for survival and recapture parameters to create a candidate set of CJS models. Because of the large number of combinations we wished to consider, an "all subsets" approach to model selection would not have been feasible. This approach to model selection would have required fitting 23184 models (i.e., 84 × 276 models). Instead, we opted for a quasi-stepwise approach to model selection in which we fixed either the survival or recapture probability model and varied the other. Then, in subsequent steps we selected the top (or top 2) models from previous steps to go forward. The quasi-stepwise model selection approach is summarized in Tables 3 and 4 and proceeded as follows:

Step 1. We fixed a general recapture (*p*) parameterization that was expected to be well supported based on the biology of the species and methods of capture. Here, we expected that recapture probability depended on: 1) whether capture occurred during 1999–2002

when an objective of the work was to deploy satellite radio-collars and so family groups including yearlings might be over-represented; 2) whether capture was during the intense capture-recapture periods (1984–86, or 2003–05); 3) whether a bear was a subadult; and 4) whether an adult or senescent bear was a male. Thus, our general model for recapture probability included effects of being an adult female, COY, or yearling during 1999-2002, being a subadult, being a male if an adult or senescent bear, and different levels of capture effort as described above (i.e., *p*(period2 + effort.2 + effort.3early + age.2 + age.34.sex); Table 3). Using this *p* parameterization we fit survival (*φ*) parameterizations representing all individual constraints (sex and age classes) and two types of temporal variation: time-constant and time-varying (Table 4);

Step 2. We selected the most supported survival model for each type of temporal variation. Using these two *φ* parameterizations we fit *p* parameterizations representing all individual constraints, with no time variation (i.e., time-constant models) (Table 3);

Step 3. We selected the top two supported *p* parameterizations from Step 2 and added temporal variation in *p* (Table 3);

Step 4. Using all previous fitted models, we selected the most supported parameterization for *p* and we fit models with all types of temporal variation in *φ* including appropriate interactions between temporal variation and individual constraints.

At each step in the model selection procedure, we selected among models using Akaike's Information Criterion (AIC) (Akaike 1981) corrected for small sample size (AICc).

Parameter estimates

We estimated survival and recapture probabilities as the AICc-weighted averages across all fitted models (Burnham and Anderson 2002). The CJS model produces estimates of

total apparent survival, which is the probability of remaining alive and not permanently emigrating from the study area (Lebreton et al. 1992).

We estimated population size during year j (N_j) using estimates of recapture probabilities derived from a particular CJS model and the Horvitz-Thompson estimator (McDonald and Amstrup 2001; Taylor et al. 2002; Williams et al. 2002). 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. Application of the Horvitz-Thompson estimator assumes that an un-equal probability sample of bears was obtained during each sampling occasion, and that the recapture probability model is correct for all bears ever captured 1 or more times.

The Horvitz-Thompson 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. Though the geographic extent of the bears with non-zero capture probability is difficult to assess, the pattern of capture effort implemented in each occasion when bears were on land, the distribution of locations (Figures 4, 5), and investigator experience leads us to conclude that our abundance estimates apply to the entire SH population between Hook Point and longitude 88°W on each occasion (i.e., all bears in the SH population had positive probability of capture every occasion). Low sample size is known to adversely affect Horvitz-Thompson size estimates. Consequently, size estimates were only reported during periods of intensive sampling effort.

Results

Captures

Capture-recapture information was available on 863 individual polar bears, 356 of which were captured during 1984-1986, 516 of which were captured from 1999-2005, and 9 of which were captured in both periods. The 356 bears observed during 1984-1986 were captured during a total of 417 events (Kolenosky et al. 1992). The 516 bears observed during 1999-2005 were captured during a total of 640 capture events. The geographic distribution of capture locations was similar among years and between intensive capture-recapture periods (Figures 4, 5), though the distribution of bears varies somewhat among years due to differences in sea ice dynamics (Stirling et al. 2004).

Goodness of fit

Program RELEASE applied to the entire SH dataset indicated minor lack of fit to the standard CJS model (overall $\chi^2 = 26.14$, df = 22), due entirely to component TEST3.SR. The directionality of this lack of fit suggested the lower future recapture rate of younger animals (Choquet et al. 2005). For a subset of the SH data that excluded COYs and yearlings, program RELEASE detected no lack of fit (overall $\chi^2 = 17.93$, df = 23) and estimated $\hat{c} = 0.78$.

To assess GOF using the parametric bootstrap in program MARK, we used a model with time-invariant survival for two age classes: COYs vs. all other polar bears. Recapture probabilities differed for 3 time periods: 1984-1986, 1999-2002, and 2003-2005. The deviance-based parametric bootstrap estimate of $\hat{c}$ for this model was 0.62 based on 1000 iterations. Because neither program RELEASE nor the parametric bootstrap detected overdispersion in the SH data, nor heterogeneity that could not be explained by covariates, we used $\hat{c} = 1.0$ for all capture-recapture modeling (Burnham and Anderson 2002).

Model selection

Step 1: Ninety-two survival models were fitted with the initial recapture model. After Step 1, the top 2 AICc-ranked models (combined AICc weight = 0.165) included the same individual constraint structure in φ, which included effects of being a COY or yearling, of being a senescent bear, and of being male (i.e.,

φ(Intercept + *age01* + *age4* + sexmales) and differed only in the form of temporal variation in φ, whether time-constant or varying among intervals (Table 5).

Step 2: Step 2 fit a total of 24 capture models, 12 with the top time constant φ model and 12 with the top time varying φ model (Table 3). After Step 2, the top 2 AICc-ranked models (combined AICc weight = 0.422) included the same structure for *p*, including effects of being an adult female, cub, or yearling during 1999 – 2002, and effect of being a cub or yearling, and an effect of being male if an adult or senescent bear (*period2* + *age01* + *age34.sex*). The 3rd-ranked and 4th-ranked (combined AICc weight = 0.243) models included a similar structure, but with a unique *p* for subadults (*period2* + *age01* + *age2* + *age34.sex*; see Table 5).

Step 3: Step 3 fitted a total of 24 additional capture models by combining the best 2 capture models from Step 2 with time varying effects of year, period, and breakup date. Survival models were the best time varying and time constant survival models from Step 1. Supported forms of temporal variation in *p* were: (1) annual variation (AICc weight = 0.238), and (2) a common, constant *p* in 1984–1986 and 2003–2005 and a different constant *p* in 1999–2002 (AICc weight = 0.093). The top ranked capture probability model, selected from the 48 models fit during Steps 2 and 3, included an effect of being an adult female or dependent offspring during 1999-2002, an effect of being a cub or yearling, an effect of being male if an adult or senescent bear, and annual variation (i.e., *p*[Intercept + period2 + age01 + age34.sex + yr1986 + yr1999 + yr2000 + yr2001 + yr2002 + yr2003 + yr2004 + yr2005]).

Step 4: Using the top ranked capture probability model, step 4 fitted 40 survival models that included interactions between age class and other effects, such as body condition, habitat measures (*PMIce* and *Ice-Free*), and period effects (*post98*). Following Step 4, all 187 models from Steps 1, 2, 3, and 4 were ranked to determine our final list of models. Only the top 20 models in the final ranking appear in Table 6. AICc weight of the top model was 0.237, and the combined AICc weight of the top 20 models was 0.944. Because the top model had relatively high AICc weight, model averaged estimates of survival and population size differed little from those obtained from the top model.

Survival Estimates

Model averaged estimates of survival appear in Table 7 and Figure 6. Estimates of survival of senescent adults ranged from 0.30 (males) to 0.60 (females). Estimates of COY and yearling survival were similar and ranged from 0.50 (males) to 0.75 (females). Survival of 2–4 years olds and adults were similar and ranged from 0.81 (males) to 0.93 (females). However, confidence intervals on the younger age classes were large (Figure 6), and we cannot be certain statistically that senescent survival is lower than COY and yearling survival. We can be reasonably certain statistically that survival of adults was higher than both COY and yearlings, and senescent adults (from top model, COY-yearling: Wald t ratio = –3.73, p = 0.0002; senescent: Wald t ratio = –4.31, p < 0.0001).

Survival of males was estimated to be lower than that of females (from top model, Wald t-ratio = –2.49; p = 0.0126). Although this result technically applies 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 included environmental or body condition covariates as predictors of interannual variation in survival were not supported by the data. The top model containing *Ice-Free* was ranked 37th and had a ΔAICc value of 10.5. The top model containing *PMIce* was ranked 44th and had a ΔAICc value of 11.3. The top model containing *MeanBCI* was ranked 51st and had a ΔAICc value of 12.2. The relationship between *BCIcoy* and cub survival had some support during Step 1, but was not one of the top 2 models, and did not propagate to subsequent steps. Following step 4, the top model containing *BCIcoy* was ranked 23rd and had a ΔAICc value of 8.30.

Models that allowed different survival rates

during early and late intensive sampling periods received some support in the data. Six of the top 10 models with ΔAICc values ≤ 4.0 contained the *yr84-85, yr1986,* and *yr99-02* effects (combined AICc weight = 0.332, or 43% of weight in top 10 models; Table 6). Model averaged estimates of survival for subadult and adult females declined from 0.936 (95% CI = 0.685, 1.00) in 1984-1985 to 0.892 (95% CI = 0.792, 0.993) in 2003-2005 (Table 7). Model averaged estimates of survival for subadult and adult males declined from 0.884 (95% CI = 0.767, 1.00) in 1984-1985 to 0.811 (95% CI = 0.662, 0.961) in 2003-2005 (Table 7). Estimated precision on these survival estimates was relatively high compared to other capture-recapture data sets (CV = 11% to 17%; calculated as 0.5 times the 95% confidence interval half width divided by the point estimate). Despite this, confidence intervals surrounding the point estimates were much bigger than the estimated decline in survival and this prevented us from unequivocally concluding that the observed declines of 5% and 7% in prime age female and male survival was not a random occurrence attributable to sampling effects. The top model containing *Post98* was ranked 53 and had a ΔAICc value of 12.4, implying that combination of survival in 1984-1985 with that in 1986–1999 was not justified by the data. This lack of support for *Post98* could be attributable to very sparse sample sizes and the long time interval between 1986 and 1999.

Models that included break up date as a predictor of capture probability received some support. The top model containing *Break-up* was ranked 7th with a ΔAICc value of 3.8. In this model, the coefficient of *Break-up* was positive, indicating higher capture probability for later break up dates, but was not significant (Wald t-ratio = 0.78, p = 0.44).

Abundance Estimates

Model averaged estimates of abundance, including model selection uncertainty, were similar between the periods 1984-1986 and 2003-2005 (Figure 7). The average number of bears estimated during 1984–1986 was 641 individuals (95% CI = 401, 881). The average number of bears estimated during 2003–2005 was 681 individuals (95% CI = 401, 961).

Discussion

Interpretation of Parameter Estimates

In our analyses, we used a weight of evidence approach (Burnham and Anderson 2002) to derive estimates of survival and population size by model-averaging over all models that were well supported by the data. Therefore, variance estimates represent both sampling uncertainty and model selection uncertainty.

To produce unbiased parameter estimates, capture-recapture models must adequately represent major sources of variation in the data (Williams et al. 2002). Un-modeled heterogeneity in recapture probabilities can introduce significant negative bias into estimates of population size (Carothers 1973), and can introduce a smaller progressive negative bias into estimates of survival (Devineau et al. 2006). In our quasi-stepwise model selection procedure, we focused on explaining variation in recapture probabilities using covariates for time, capture effort, sex and age (i.e., based on spatial segregation of polar bears in the study area), and sea ice breakup date. Individual variation in recapture probabilities associated with the extreme mobility of polar bears (Amstrup et al. 2000, Parks et al. 2006) was unlikely to be problematic, because capture efforts occurred during the ice-free period when polar bears were confined to a restricted area of the coast. Similarly, it is unlikely that non-random temporary emigration introduce bias into survival estimates because exchange with adjacent polar bear populations appears to be low, and SH polar bears exhibit a high degree of fidelity to the study area during the ice-free season (Stirling et al. 2004; M. E. Obbard, unpublished data). Finally, GOF tests did not find any evidence for heterogeneity in recapture probabilities, although small sample size may have resulted in low statistical power.

Survival

We found some evidence of a change in total apparent survival of subadults, adult females, and adult males between 1984-86 and 1999-2005, but variation was large and we cannot be certain that the declines we observed (5% and 7% for females and males, respectively) were real and not an artifact of the particular sample of bears we observed. However, a decline in survival of this magnitude is consistent with the hypothesis that the SH population is currently under stress, and that in time this decline would become more apparent. Beyond survival of prime age bears, there was weak evidence of a decline in survival of cubs-of-the-year and yearlings (Table 7, Figure 6) though this was not supported by any of the top models. Taken as a whole, the evidence in our dataset to support the hypothesis of a decline in survival between the mid-1980s and 2003-05 is equivocal.

In the neighboring WH population, Regehr et al. (2007) found that total apparent survival of adult females and males was stable from 1984-2004. However, survival of juvenile, subadult, and senescent adult bears was correlated with spring sea ice breakup date which varied among years, and occurred about 3 weeks earlier in 2004 than in 1984. Survival of these age classes declined with the date of sea ice break-up (i.e., earlier break-up resulted in reduced survival); as a result Regehr et al. (2007) proposed a causal association between earlier sea ice breakup due to climatic warming and decreased polar bear survival.

Stirling et al. (1999) noted a non-significant trend ($P = 0.07$) towards earlier sea ice breakup in western Hudson Bay for the period 1979-1998. Subsequently, Stirling et al. (2004) reported a statistically significant trend towards earlier breakup of sea ice off the Manitoba coast (but not off the Ontario coast) for the period 1971-2001. Focusing on an area north of the Ontario coast between longitude 89°W and Cape Henrietta Maria, Gough et al. (2004) documented a significant increase in the duration of the ice-free season in south-western Hudson Bay from 1971-2003, much of which was due to progressively earlier breakup of the sea ice. Breakup advanced on average by about 3 days per decade in south-western Hudson Bay during this period (Gough et al. 2004). In a more comprehensive analysis, Gagnon and Gough (2005*a*) found statistically significant trends toward earlier break-up of ice in James Bay, along the southern shore of Hudson Bay, and in western Hudson Bay, and towards later freeze-up in northern and north-eastern Hudson Bay during the period 1971–2003, in agreement with the projections from General Circulation Models (Gagnon and Gough 2005*b*). These studies provide strong evidence of a general trend towards a longer ice-free season over areas of Hudson Bay that are occupied by bears from the WH and SH populations during winter (Plante et al. 2001, Parks et al. 2006; M. E. Obbard, unpublished data). Trends towards earlier break-up dates are stronger for points in western areas of Hudson Bay off the coast of Manitoba where break-up is advancing by about 10 days per decade than for areas off the northern Ontario coast where an advance of 5-8 days per decade is suggested (Gagnon and Gough 2005*a*). This difference in rates of advance of break-up dates may explain why reductions in survival of juvenile, subadult and senescent polar bears were demonstrated for the WH population (Regehr et al. 2007), but were only weakly supported by our data (Table 7, Figure 6).

The effect of cub body condition (*BCIcoy*) on survival received some support during Step 1 of our model fitting exercise; however, this was not included in either of the top 2 models so did not carry forward to subsequent steps. This should be investigated in a post-hoc analysis since declines in survival are likely to be detected in this population following the demonstrated declines in body condition.

Population size and trend

Abundance in the Southern Hudson Bay population was unchanged between two intensive capture-recapture periods, which were separated by almost 20 years (1984–86 *vs.* 2003–05). This was so despite the evidence for a decline of 22%

in abundance for the neighboring Western Hudson Bay population over roughly the same period (i.e., 1987-2004; Regehr et al. 2007). Forested areas come close to the coast in the north-western section of the study area making sighting and capture of bears difficult. Also, an extensive fen system occurs east of the Sutton River inland from the coast which makes safe capture of bears found there difficult. Consequently, within the study area, there was likely some slight geographic heterogeneity in recapture probabilities associated with habitat features. However, these habitat features did not vary among years or between periods. Therefore, it is reasonable to assume that this bias in capture probability was constant among years and between periods, that no bears had a zero capture probability in all years (i.e., individual bears would not be found in these areas in all years), and as a result this bias did not affect our assessment of trend.

Kolenosky et al. (1992) estimated the size of the SH population (independent bears) at from 530 ± 90 (2SE) to 763 ± 323 (2SE), depending on analytical method used. Kolenosky et al. (1992) suggested that, including dependent young, a reasonable overall estimate of the population would be 900. However, Kolenosky et al. (1992) included animals captured as far west as the Manitoba border in their analysis. Here, in our re-analysis of data from 1984-86 and analysis of data from 2003-05 we restricted our capture sample to those animals captured east of longitude 88°W.

Following the results of the Kolenosky et al. (1992) study, the Polar Bear Technical Committee, considering that animals in James Bay were not sampled and that forested areas were likely under-sampled due to the difficulty of locating bears in these areas, adjusted the population estimate upwards to 1000 animals for management purposes (Lunn et al. 1998). Using a maximum sustained yield model (Taylor et al. 1987) to calculate the sustained yield from the SH population, Kolenosky et al. (1992) determined that an allowable harvest of 48 was sustainable from a population of 900 bears. During the 1970s and 1980s, the Ontario harvest

alone from the SH population averaged 20.8 animals, but since 1990 the Ontario harvest has averaged 8.8 animals (Obbard 2007). Total harvest for SH, including that from Nunavut and Quebec, has averaged about 45 in recent years (Lunn et al. 2006) and is apparently sustainable, suggesting a total population size of about 900-1000 animals in the SH management unit.

Some animals originally tagged in WH occur in the Nunavut harvest from the SH zone, that is, animals harvested by hunters from the community of Sanikiluaq on the Belcher Islands (F. Piugattuk, personal communication, August 2007), and some animals originally tagged in WH occur in the Quebec harvest (e.g., Stirling et al. 1977). Both the Nunavut and Québec harvests occur while bears are on the sea ice when there is some mixing of animals from both populations (Stirling et al. 2004), making it difficult to accurately describe the "population" the SH harvest is drawn from. Nevertheless, the majority of tag returns from the Nunavut and Québec harvests are of animals originally tagged in Ontario east of longitude 88°W or on islands in James Bay.

In the current designation of the boundaries of the SH population, bears occupying James Bay are included. Polar bears were not captured in James Bay south of Hook Point during either intensive capture period (Figures 3, 4, and 5). However, bears were captured on Akimiski Island and on North and South Twin Islands in 1997 and 1998 (M. E. Obbard and M. K. Taylor, unpublished data). The M_h Chao model for closed populations with small samples and heterogeneity as implemented in Program CAPTURE (Otis et al. 1978) provided an estimate of 110 (95% CI = 75, 195) for bears on these islands (M. E. Obbard and E. H. Howe, unpublished data). The average of 6 other M_o, M_t, M_b, M_h, and M_{bh} models for closed populations indicated a population size of 71.1 (95% CI = 56.6, 120.0) (M. E. Obbard and E. H. Howe, unpublished data). Crompton (2005) analyzed the genetic structure of bears from the Hudson Bay system and concluded that there was evidence of a distinctive James Bay cluster. This information suggests that 70-110 animals should

be added to our abundance estimate to provide an estimate of the total size of the SH population, including animals at risk of capture between longitude 88°W and Hook Point on James Bay.

Since a larger sample of marked animals now exists for animals captured between longitude 88°W and the Ontario—Manitoba border, future work should examine fidelity of these animals to summer areas, and harvest returns and re-capture information for these animals in order to refine our understanding of where the biologically relevant boundary between WH and SH should be located.

Future trend

In the adjacent western Hudson Bay polar bear population Stirling et al. (1999) documented declines in the body condition of adult male and adult female polar bears with cubs in relation to sea ice conditions. At the time there was no detectable trend in abundance of the population. However, subsequent analysis by Regehr et al. (2007) showed a significant decline in abundance between 1987 and 2004 suggesting a potential lag effect between declining body condition and subsequent population level effects.

The now documented declines in the body condition of individuals in SH, which were most dramatic for pregnant females and subadults (Obbard et al. 2006), have the potential to affect population recruitment, as lighter female polar bears produce smaller litters and lighter cubs (Derocher and Stirling 1994) that are less likely to survive (Derocher and Stirling 1996). Although a direct link has not been established between the survival of adult polar bears and body condition, Regehr et al. (2007) documented a significant correlation between the survival of juvenile, subadult, and senescent adult polar bears and the date of sea ice break-up in western Hudson Bay (i.e., earlier break-up resulted in reduced survival). Given the documented decline in the body condition of bears in western Hudson Bay in association with an increasingly early date of sea ice break-up (Stirling et al. 1999) it is reasonable to assume that changes in body condition could influence the survival of polar

bears. Indeed, in several large mammal species body mass has been shown to have a significant influence on subsequent survival (Albon et al. 1987; Baker and Fowler 1992; FestaBianchet et al. 1997). It appears that changes in environmental factors such as sea ice distribution and duration which are now well documented for southern and eastern Hudson Bay (Gagnon and Gough 2005a) have yet not resulted in unambiguous changes in survival or to a consequent reduction in population size in the SH population to this date.

Stirling and Parkinson (2006) predicted that trends towards earlier break-up and reduced body condition for SH bears will continue if projected warming trends continue in the future. If the body condition of polar bears in SH continues to decline, effects on reproduction will become evident. In addition, the declines in survival shown in the present study will become more pronounced. The net result will be a subsequent decline in the size of this population.

Acknowledgments

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Table 1. Individual and temporal covariates included in models of recapture probability (p) and apparent survival (φ), whether the covariate is expected to affect p or φ, and the type of effect allowed by the covariate. 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	φ	coys $\neq$ older bears
age1	φ	yrlgs $\neq$ other age classes
age2	p, φ	subads (aged 2–4 years) $\neq$ other age classes
age3	φ	adults (aged 5–20 years) $\neq$ other age classes
age4	φ	senescent animals (aged 21+) $\neq$ other age classes
age01	p, φ	coys = yrlgs $\neq$ other age classes
age23	φ	subads = ads $\neq$ other age classes
age234	φ	subads = ads = senescent $\neq$ other age classes
age1234	φ	yrlgs = subads = ads = senescent $\neq$ coys
age34	φ	ads = senescent $\neq$ other age classes
WHage	φ	relative differences in survival rates among age classes = those from Western Hudson Bay
sex	φ	M $\neq$ F
age234.sex	φ	subad M = ad M = senescent M $\neq$ other age classes in model
age1234.sex	φ	yrlg M = subad M = ad M = senescent M $\neq$ other age classes in model
age34.sex	p	ad M = senescent M $\neq$ other age classes in model
BCIcoy	φ	Body Condition Index (see text) of coys was related to φ of coys
Temporal Covariates		
IceFree	φ	Number of days between break-up and freeze-up. Break up defined below (*breakup*). Freeze-up defined as date in fall when ice cover in southern Hudson Bay increased past 50%. Values were standardized to mean of 0 and standard error of 1.
PMIce	φ	Annual mean daily proportion of 25km pixels in southern Hudson Bay with greater than 50% ice concentration. Values were standardized to mean of 0 and standard error of 1.
Post98	φ	constant 1984–1998 $\neq$ constant 1999–2005
MeanBCI	φ	The mean (within age/sex categories and years) of individual's body condition index values was related to survival of those age/sex classes in those years
yr84-85	φ	1984–1985 = 1985–1986 $\neq$ other intervals
yr1986	φ	constant 1986–1999 $\neq$ other intervals
yr99-02	φ	constant 1999–2002 $\neq$ other intervals
yr03-05	φ	constant 2003–2005 $\neq$ other intervals
year85	p	1985 $\neq$ other years
year86	p	1986 $\neq$ other years
year99	p	1999 $\neq$ other years
year00	p	2000 $\neq$ other years
year01	p	2001 $\neq$ other years
year02	p	2002 $\neq$ other years
year03	p	2003 $\neq$ other years
year04	p	2004 $\neq$ other years
year05	p	2005 $\neq$ other years
Breakup	p	Date in spring when ice concentration in southern Hudson Bay drops below 50%.
effort.2	p	constant 1999–2002 $\neq$ other years
effort.3early	p	constant 1984–1986 $\neq$ other years
effort.3late	p	constant 2003–2005 $\neq$ other years
effort.3	p	constant 1984–1986 = constant 2003–2005 $\neq$ other years
Period2	p	Coys, yrlgs, and adult F had different capture probabilities during 1999–2002.

Table 2. Dates of break-up and freeze-up of the sea ice, and annual number of ice-free days for southern Hudson Bay off the Ontario coast, 1983-2005. Source: 1983-2003—Gagnon and Gough (2005); 2004-05—Gough (personal communication).

YEAR	BREAK-UP DATE (ORDINAL DATE)	FREEZE-UP DATE (ORDINAL DATE)	ICE-FREE PERIOD (# DAYS)
1983	201	341	140
1984	187	320	133
1985	207	326	119
1986	202	321	119
1987	208	320	112
1988	206	332	126
1989	198	324	126
1990	169	330	161
1991	175	329	154
1992	222	327	105
1993	193	319	126
1994	185	350	165
1995	212	331	119
1996	189	336	147
1997	199	315	116
1998	195	315	120
1999	180	315	135
2000	192	336	144
2001	184	352	168
2002	218	323	105
2003	182	336	154
2004	194	333	139
2005	186	324	138

Table 3. Parameterizations considered for models of recapture probability, and the step in the model selection process during which parameterizations were fitted.

Capture Model #	Step	Regression Equation (all structures included intercepts)
0	1	Period2 + effort.2 + effort.3early + age2 + age34.sex
1	2	(intercept only) [a]
2	2	age2 + age34.sex [a]
3	2	age2 [a]
4	2	age34.sex [a]
5	2	age01 + age2 + age34.sex [a]
6	2	age01 + age34.sex [a]
7 – 12	2	Period2 + models 2 – 7[a]
13 – 16	3	Top 2 models from #1 through 12 + effort.2[a]
17 – 20	3	Top 2 models from #1 through 12 + effort.2 + effort.3early[a]
21 – 24	3	Top 2 models from #1 through 12 + breakup[a]
25 – 28	3	Top 2 models from #1 through 12 + annual variation[a]
29 – 32	3	Top 2 models from #1 through 12 + effort.2 + breakup[a]
33 – 36	3	Top 2 models from #1 through 12 + effort.2 + effort.3early + breakup
36	4	Top model from #1 through 35[b].

[a] Fitted with top time-varying and time-invariant survival models estimated from step1 (Table 4).
[b] Covariates in the survival model varied during step 4.

Table 4. Parameterizations considered for models of apparent survival and the step in the model selection process during which parameterizations were fitted.

Model #	Step	Regression Equation (all structures included intercepts)
1	1	(null)
2	1	WHage
3	1	age0 + age1 + age2 + age4
4	1	age01 + age2 + age4
5	1	age01 + age4
6	1	age01
7	1	age0 + age1 + age4
8	1	age0 + age1
9	1	age0 + age1 + age2
10	1	age01 + age2
11	1	age0
12 - 22	1	sex + models 1 - 11
23	1	age0 + age1 + age2 + age4 + age1234.sex
24	1	age0 + age1 + age4 + age1234.sex
25	1	age0 + age1 + age1234.sex
26	1	age0 + age1 + age2 + age1234.sex
27	1	age0 + age1234.sex
28	1	age01 + age2 + age4 + age234.sex
29	1	age01 + age4 + age234.sex
30	1	age01 + age234.sex
31	1	age01 + age2 + age234.sex
32 - 46	1	where age0 appeared above, replaced with age0 × BCIcoy
47 – 92	1	yr84_85 + yr1986 + yr99_02 + models 1 – 46
93 - 97	4	age0 interacted with each of (IceFree, PMIce, Post98, MeanBCI, and annual effects)
98 - 102	4	age01 interacted with each of (IceFree, PMIce, Post98, MeanBCI, and annual effects)
103 - 107	4	age04 interacted with each of (IceFree, PMIce, Post98, MeanBCI, and annual effects)
108 - 112	4	age012 interacted with each of (IceFree, PMIce, Post98, MeanBCI, and annual effects)
113 - 117	4	age0124 interacted with each of (IceFree, PMIce, Post98, MeanBCI, and annual effects)
118 - 122	4	Effects of (IceFree, PMIce, Post98, MeanBCI, and annual variation) restricted to age0 individuals
123 - 127	4	Effects of (IceFree, PMIce, Post98, MeanBCI, and annual variation) restricted to age0 and age1 individuals
128 – 132	4	Effects of (IceFree, PMIce, Post98, MeanBCI, and annual variation) restricted to age0 and age4 individuals
133 - 137	4	Effects of (IceFree, PMIce, Post98, MeanBCI, and annual variation) restricted to age0, age1, and age2 individuals
138 - 142	4	Effects of (IceFree, PMIce, Post98, MeanBCI, and annual variation) restricted to age0, age1, age2, and age4 individuals

Table 5. Results of individual steps during quasi- stepwise model selection (Int = intercept).

STEP	OBJECTIVE	OUTCOME
1	Identify appropriate models of individual heterogeneity in Phi	Phi structures carried forward to steps 2 & 3: 1. Int + age01 + age4 + sex 2. Int + age01 +age4 + sex + yr84–85 + yr1986 + yr99–02
2	Identify appropriate models of individual heterogeneity in p using the Phi structures from step 1.	p structures carried forward to step 3: 1. Int + Period2 + age01 + age34.sex 2. Int + Period2 + age01 + age2 + 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: 1. Int + period2 + age01 + age34.sex + yr1986 + yr1999 + yr2000 + yr2001 + yr2002 + yr2003 + yr2004 + yr2005
4	Identify appropriate models of temporal and individual variation in Phi by considering interactions, and using the top p structure from steps 2 and 3. Compare AICc across all fitted models.	See Table 6

Table 6. Model ranks, structures, ΔAICc values, AICc weights, number of model parameters for the top 20 AICc-ranked models of recapture and apparent survival probabilities of polar bears in the Southern Hudson Bay population, 1984–2005, after Step 4 of the model selection process. Models are sorted in ascending order of AICc values beginning with the model with the lowest AIC_c value.

RANK	P PARAMETERIZATION[A]	PHI PARAMETERIZATION	NUMBER OF PARAMETERS	DELTA AIC_C	AIC_C WEIGHT
1	Period2 + age01 + age34.sex + (years)[a]	age01 + age4 + sex	16	0.00	0.2357
2	Period2 + age01 + age34.sex + effort.2	age01 + age4 + sex + yr84-85 + yr1986 + yr99-02	12	1.877	0.0929
3	Period2 + age01 +age2 + age34.sex + (years)	age01 + age4 + sex	17	2.074	0.0842
4	Period2 + age01 + age34.sex + effort.2	age01 + age4 + sex	9	2.111	0.0826
5	Period2 + age01 + age34.sex + effort.2 + effort.3early	age01 + age4 + sex + yr84-85 + yr1986 + yr99-02	13	2.411	0.0712
6	Period2 + age01 + age34.sex + (years)	age01 + age4 + sex + yr84-85 + yr1986 + yr99-02	19	2.524	0.0672
7	Period2 + age01 + age34.sex + effort.2 + effort.3early + Breakup	age01 + age4 + sex + yr84-85 + yr1986 + yr99-02	14	3.871	0.0343
8	Period2 + age01 + age34.sex + effort.2 + Breakup	age01 + age4 + sex + yr84-85 + yr1986 + yr99-02	13	3.923	0.0334
9	Period2 + age01 + age2 + age34.sex + effort.2	age01 + age4 + sex + yr84-85 + yr1986 + yr99-02	13	3.938	0.0332
10	Period2 + age01 + age34.sex + effort.2 + Breakup	age01 + age4 + sex	10	4.001	0.0320
11	Period2 + age01 + age2 + age34.sex + effort.2	age01 + age4 + sex	10	4.121	0.0302
12	Period2 + age01 + age34.sex + effort.2 + effort.3early	age01 + age4 + sex	10	4.138	0.0300
13	Period2 + age01 + age2 + age34.sex + effort.2 + effort.3early	age01 + age4 + sex + yr84-85 + yr1986 + yr99-02	14	4.454	0.0256
14	Period2 + age01 + age2 + age34.sex + (years)	age01 + age4 + sex + yr84-85 + yr1986 + yr99-02	20	4.605	0.0238
15	Period2 + age01 + age34.sex + effort.2 + effort.3early + Breakup	age01 + age4 + sex	11	5.721	0.0136
16	Period2 + age01 + age2 + age34.sex + effort.2 + effort.3early + Breakup	age01 + age4 + sex + yr84-85 + yr1986 + yr99-02	15	5.917	0.0123
17	Period2 + age01 + age2 + age34.sex + effort.2 + Breakup	age01 + age4 + sex + yr84-85 + yr1986 + yr99-02	14	5.990	0.0119
18	Period2 + age01 + age2 + age34.sex + effort.2 + Breakup	age01 + age4 + sex	11	6.003	0.0118
19	Period2 + age01 + age2 + age34.sex + effort.2 + effort.3early	age01 + age4 + sex	11	6.160	0.0109
20	Period2 + age01 + age2 + age34.sex + effort.2 + effort.3early + Breakup	age01 + age4 + sex	12	7.749	0.0049

[a] Individual year effects (1986, 1987-1999, 2000, 2001, 2002, 2003, 2004, 2005) were included wherever "(years)" appears.

Table 7. Apparent survival rate estimates for SH polar bears, 1984-2004. Confidence intervals include estimation and model selection uncertainty.

|	Phi coy	95% CI	Phi yrlng	95% CI	Phi subad	95% CI	Phi ad	95% CI	Phi senescent	95% CI
Females										
1984	0.768	0.550 - 0.986	0.767	0.549 - 0.985	0.936	0.685 - 1.00	0.936	0.685 - 1.00	n/a*	n/a*
1985	0.768	0.550 - 0.986	0.767	0.549 - 0.985	0.936	0.685 - 1.00	0.936	0.685 - 1.00	0.591	0.254 - 0.928
1986	0.702	0.686 - 0.718	0.701	0.685 - 0.717	0.909	0.780 - 1.00	0.909	0.778 - 1.00	0.534	n/a*
1999	0.749	0.589 - 0.908	0.746	0.587 - 0.905	0.93	0.869 - 0.991	0.93	0.868 - 0.991	0.561	0.334 - 0.788
2000	0.748	0.589 - 0.908	0.746	0.587 - 0.905	0.93	0.869 - 0.991	0.93	0.869 - 0.991	0.561	0.334 - 0.788
2001	0.748	0.588 - 0.908	0.746	0.587 - 0.905	0.93	0.869 - 0.991	0.93	0.868 - 0.991	0.561	0.334 - 0.788
2002	0.749	0.589 - 0.908	0.746	0.587 - 0.905	0.93	0.869 - 0.991	0.93	0.869 - 0.991	0.561	0.334 - 0.788
2003	0.644	0.380 - 0.909	0.64	0.373 - 0.907	0.893	0.792 - 0.993	0.892	0.791 - 0.993	0.444	0.153 - 0.735
2004	0.645	0.380 - 0.909	0.64	0.373 - 0.907	0.893	0.792 - 0.993	0.892	0.791 - 0.993	0.444	0.153 - 0.735
Males										
1984	0.634	0.350 - 0.919	0.631	0.349 - 0.914	0.884	0.767 - 1.00	0.884	0.767 - 1.00	0.428	0.055 - 0.802
1985	0.635	0.350 - 0.919	0.631	0.349 - 0.914	0.884	0.767 - 1.00	0.884	0.767 - 1.00	0.428	0.055 - 0.802
1986	0.591	n/a*	0.593	n/a*	0.838	0.778 - 0.898	0.838	0.778 - 0.897	0.486	n/a*
1999	0.607	0.410 - 0.805	0.602	0.408 - 0.795	0.873	0.776 - 0.971	0.873	0.776 - 0.971	0.394	0.144 - 0.644
2000	0.607	0.410 - 0.804	0.602	0.408 - 0.795	0.873	0.776 - 0.971	0.873	0.776 - 0.971	0.394	0.144 - 0.644
2001	0.607	0.409 - 0.806	0.602	0.408 - 0.795	0.873	0.776 - 0.971	0.873	0.775 - 0.971	0.394	0.144 - 0.644
2002	0.607	0.410 - 0.805	0.602	0.408 - 0.796	0.874	0.776 - 0.971	0.874	0.776 - 0.971	0.394	0.144 - 0.645
2003	0.491	0.211 - 0.771	0.485	0.204 - 0.765	0.812	0.663 - 0.961	0.811	0.662 - 0.960	0.293	0.029 - 0.558
2004	0.492	0.211 - 0.772	0.485	0.204 - 0.766	0.812	0.663 - 0.961	0.811	0.662 - 0.961	0.293	0.029 - 0.588

* not-estimable
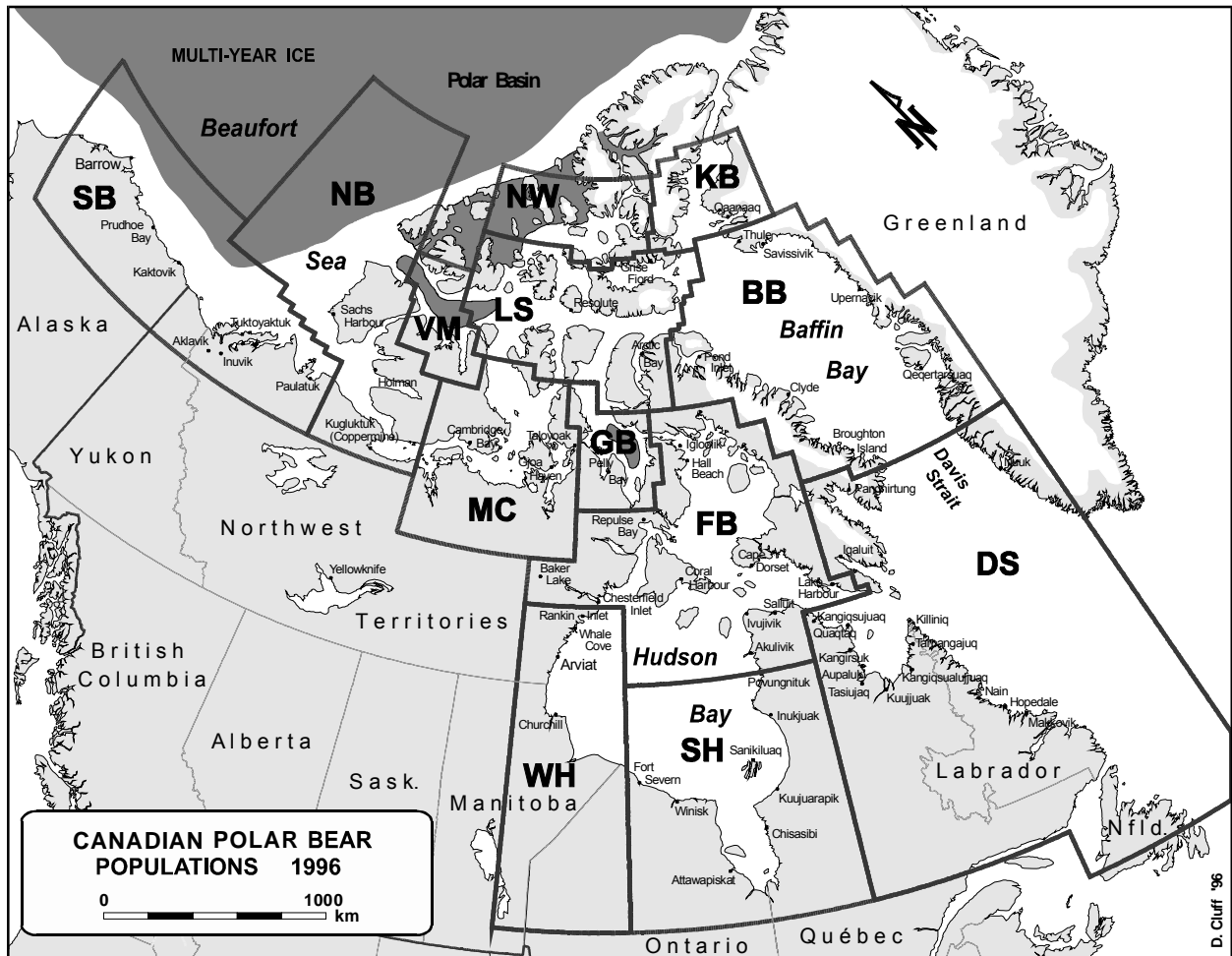
Figure 1. Polar bear subpopulations of Canada, and neighboring Alaska and Greenland. (SH = Southern Hudson Bay, WH = Western Hudson Bay, FB = Foxe Basin).
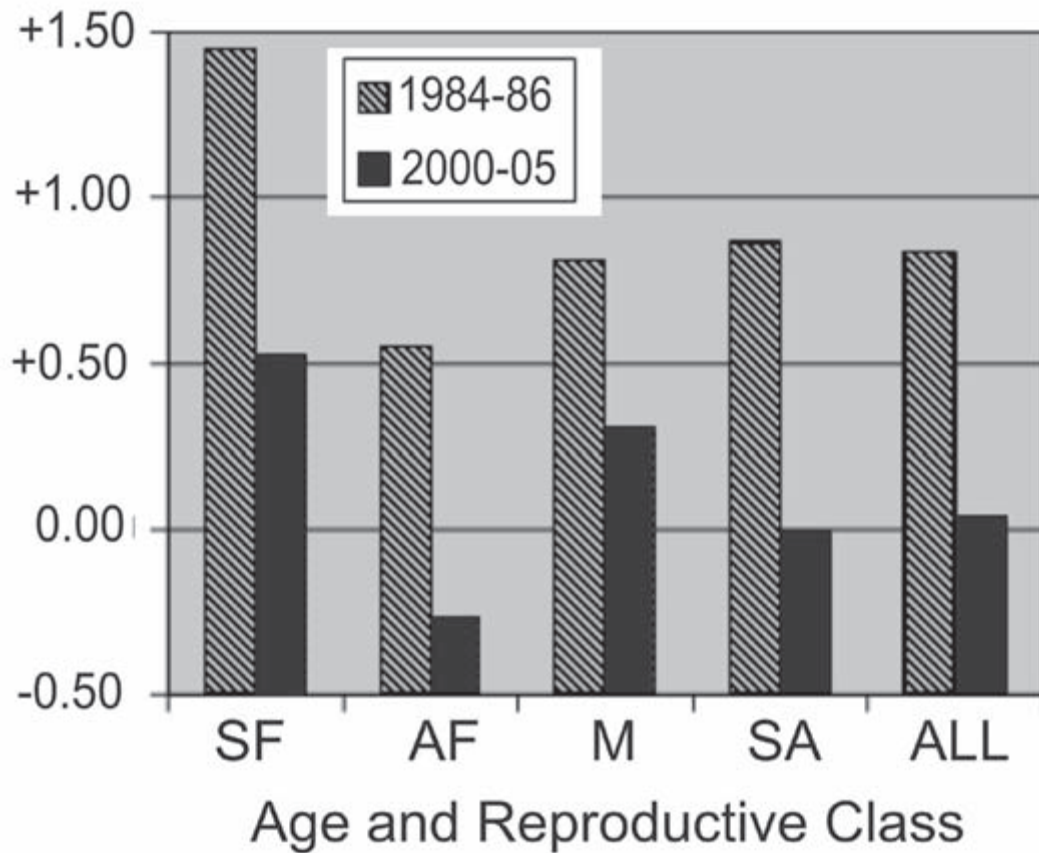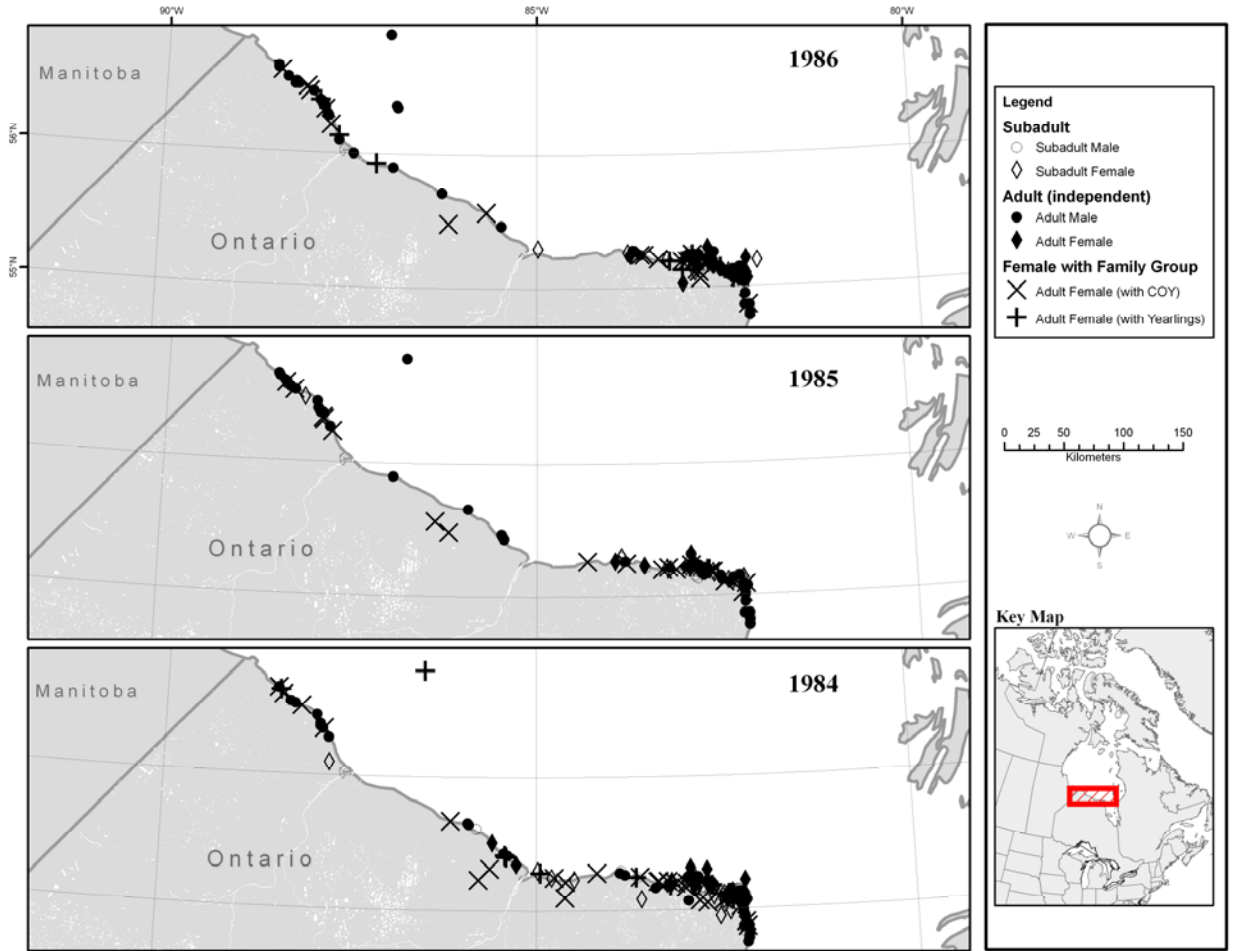
Figure 2. Mean Body Condition Index values (Cattet et al. 2002) for Southern Hudson Bay polar bears, 1984-1986 and 2000-2005. (SF = solitary adult females, AF = adult females with young, M = adult males, SA = subadults, ALL = all classes combined). Source: Obbard et al. (2006).
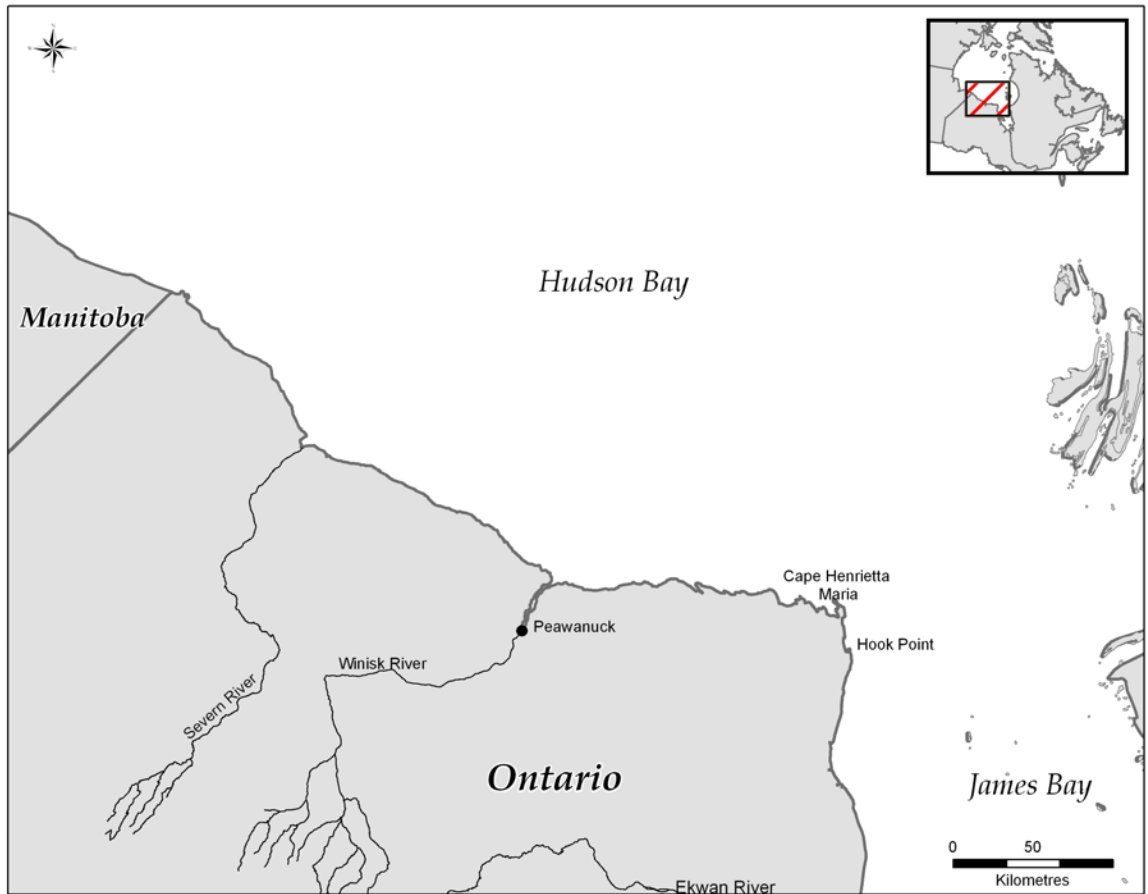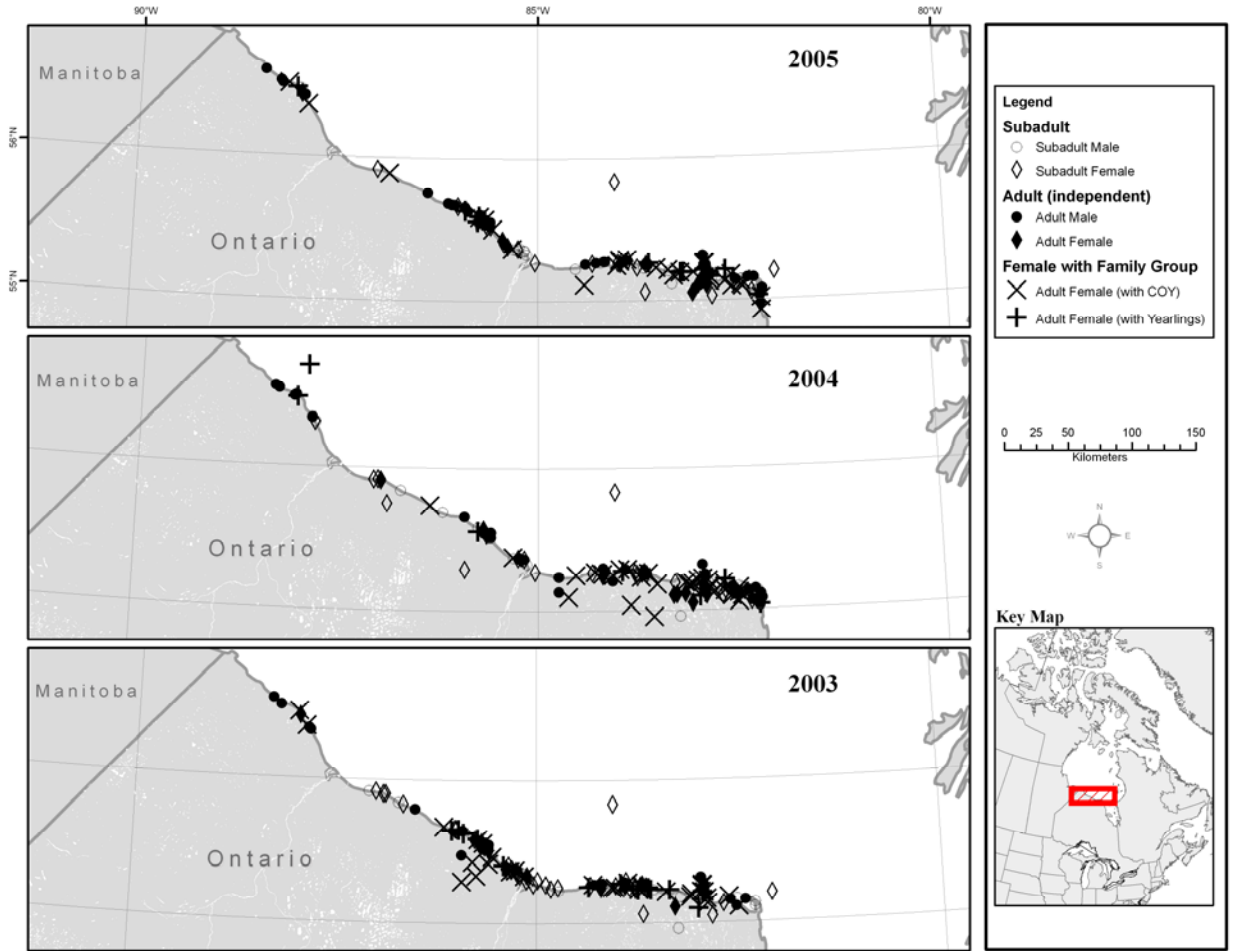
Figure 3. Study area along the Ontario coast from Hook Point on James Bay to the Ontario-Manitoba border.
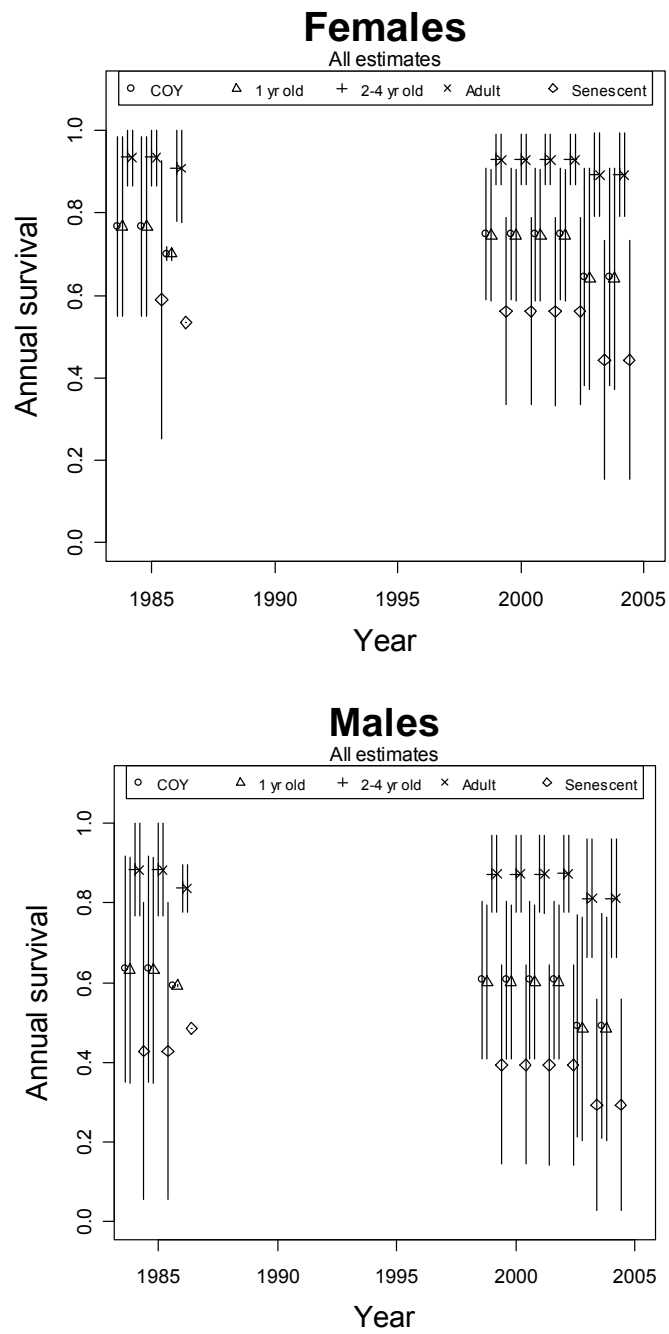
Figure 4. Distribution of captures during the 1984–86 intensive capture period.

Figure 5. Distribution of captures during the 2003–05 intensive capture period.

Figure 6. Model averaged estimates of age and sex structured survival for the Southern Hudson Bay polar bear population, 1984–86 and 2003–05. Bars are 95% confidence intervals and include both model selection and estimation uncertainty.
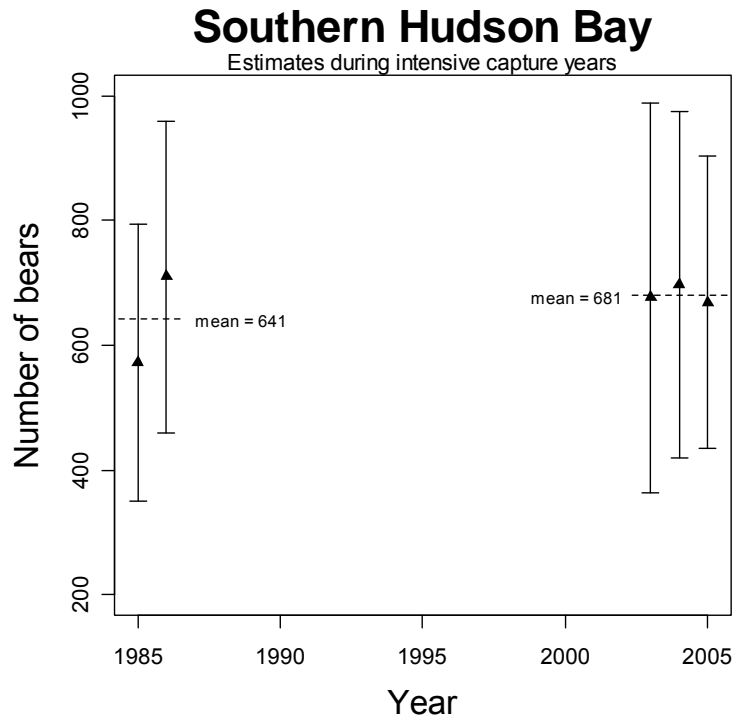
Figure 7. Model averaged estimates of the size of Southern Hudson Bay polar bear population, derived during years with intensive capture effort. Bars are 95% confidence intervals, and include both model selection and estimation uncertainty.