

**Demography and Population Assessment of Polar Bears in Western Hudson Bay,  
Canada**

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## SUMMARY

- We evaluated the population status and demography of the Western Hudson Bay (WH) polar bear subpopulation for the period 1984-2011, using live-recapture data from research studies and management actions, and dead-recovery data from the subsistence harvest in Nunavut.
- We used a Bayesian implementation of multistate capture-recapture models, coupled with a matrix-based demographic projection model, to integrate several types of data and to incorporate variation across the polar bear life cycle. This approach allowed the estimation a suite of vital rates, including both survival and reproduction, in a unified framework linked directly to estimating current and projecting future population trends.
- Survival of female polar bears of all age classes was correlated with sea ice conditions, with lower survival in years of early sea ice break-up. While this supports previous findings linking body condition, productivity, and status of WH polar bears to environmental changes associated with climatic warming, other productivity parameters were not linked to changes in the environmental variables that we examined.
- Survival of male polar bears of all age classes was not correlated with sea ice conditions, perhaps due to the over-riding effect of mortality from the male-biased subsistence harvest of polar bears in Nunavut.
- The 2011 population estimate for WH subpopulation based on capture-recapture analysis is 806 bears with 95% confidence intervals of 653-984. This is broadly consistent with the abundance estimate of 1,000 (95% CI = 715-1398) resulting from the 2011 aerial survey. The capture-recapture study point estimate is somewhat lower than the aerial survey estimate, likely due to differences in the size of the effective study population considered by each approach.
- The overall declining trend in size of the WH subpopulation over the period 1987-2004 was similar to the previous demographic evaluation (Regehr *et al.* 2007), suggesting consistency between the two analyses. However, point estimates differed slightly, with somewhat lower absolute values estimated using the updated statistical approach.
- This updated population assessment suggests that polar bear numbers in WH have been relatively stable over approximately the past decade. Female survival is the most important determinant of WH population growth, and the growth rate of the female segment of the population was estimated to be stable during 1991-2011 ( $\lambda = 1.02$ ; 95%CI = 0.98-1.06).
- As the estimate of female growth rate was derived from survival and reproductive rates, which are more robust than point estimates of population size, this value likely represents a reliable indicator of recent population trend.

## INTRODUCTION

Polar bears (*Ursus maritimus*) are distributed throughout the ice-covered waters of the circumpolar Arctic in 19 relatively discrete subpopulations (Obbard *et al.* 2010). As they depend on sea ice as a platform from which to hunt seals (Stirling and Derocher 2012), changes in the distribution and extent of sea ice and the patterns of freeze-up and break-up have the potential to significantly influence the population ecology of polar bears (Stirling and Derocher 1993, 2012; Derocher *et al.* 2004; Stirling and Parkinson 2006; Laidre *et al.* 2008). The impacts of a long-term warming trend in spring temperatures (Skinner *et al.* 1998; Gagnon and Gough 2005) on the dates of sea ice break-up and freeze-up in Hudson Bay have been well documented (Hochheim *et al.* 2010, 2011). These in turn impact body condition, reproduction, and population demography of polar bears in the Western Hudson Bay (WH) subpopulation (Stirling *et al.* 1999, 2004; Regehr *et al.* 2007). WH polar bears are spending progressively longer periods of time on land, due to documented trends towards earlier arrival onshore and later departure from land related to declines in the availability of sea ice (Cherry *et al.* 2013).

During the 1960s and 1970s, Inuit reported that the abundance of the WH subpopulation had increased (Tyrrell 2006; Nirlungayuk and Lee 2009), likely due to reduced hunting and disturbance following closure of the York Factory fur trading post, withdrawal of military personnel from Churchill, and the closure of hunting in Manitoba (Stirling *et al.* 1977; Derocher and Stirling 1995). Derocher and Stirling (1995) estimated the mean population size of the WH subpopulation for 1978-1992 to be  $1000 \pm 51$ . As this estimate was later considered to be conservative because the study had not included the southeastern portion of the range east of the Nelson River, the population size was later adjusted to 1200 for management purposes (Calvert *et al.* 1995; Wiig *et al.* 1995). Regehr *et al.* (2007) estimated that abundance had declined from about 1194 (95% CI = 1020, 1368) in 1987 to about 935 (95% CI = 794, 1076) in 2004. They found that survival rates of cubs, sub-adults, and old bears (>20 years) of both sexes were correlated with the date of sea ice break-up, and decreased 2-5% for each week that sea ice broke up earlier than average (Regehr *et al.* 2007).

In this report, we analyze data from the capture of free-ranging polar bears collected by Environment Canada and its partners for three decades, as part of a long-term research program on the ecology and status of polar bears in western Hudson Bay. Analysis of these data allows for quantification of relationships between environmental change and demography, an assessment of the health of this subpopulation by considering changes in key vital rates such as survival and productivity, and estimation of population size and trend to inform management decisions. Environment Canada, the US Fish and Wildlife Service, and the US Geological Survey undertook an updated demographic analysis for the WH subpopulation using seven additional years of data that were not available in previous analyses (Regehr *et al.* 2007, which included data through 2004). We used a hierarchical multistate capture-recapture model (e.g., Arnason 1972; Hestbeck *et al.* 1991; Kendall *et al.* 2006; Converse *et al.* 2009; Kéry and Schaub 2012), rather than the single-state model used previously. The multistate modeling framework involves specification of multiple states – in this case, life stages – which account for heterogeneity by allowing demographic parameters to vary between states. This model also allows for estimation of demographic parameters of primary interest, describing transitions between states. Our approach incorporated a broader range of data than previous analyses, and included sex, age, and reproductive status; data collected under multiple sampling protocols; data for bears that were captured and released alive; and data for bears that were harvested for subsistence purposes or killed for reasons of human safety. The hierarchical structure allowed us to more efficiently account for annual variation in parameters such as detection probability. The results of the estimation procedure were then used to construct a population model, using a Bayesian Population Viability Analysis (BPVA) approach (Wade 2002; Kéry and Schaub 2012; Servanty *et al.* in press) to project potential population outcomes under various sea-ice scenarios. The primary objectives were to:

1. estimate natural and total (i.e., including harvest and other human-caused mortality) survival rates, reproductive rates, population size, and population trend;
2. evaluate relationships between demographic parameters and environmental factors such as sea ice duration; and,

3. assess the potential impacts of changes in sea ice phenology on the status of polar bears in western Hudson Bay.

## **METHODS**

### ***Study area***

The current population boundaries of the WH subpopulation (Figure 1) are based on extensive records of capture, recapture, and harvest of tagged bears (Stirling *et al.* 1977; Derocher and Stirling 1990, 1995; Taylor and Lee 1995; Lunn *et al.* 1997). This subpopulation appears to be largely segregated geographically from the Southern Hudson Bay (SH) subpopulation to the southeast and the Foxe Basin (FB) subpopulation to the north during the open-water season, although all three subpopulations mix on the Hudson Bay sea ice during winter and spring (Stirling *et al.* 1977; Derocher and Stirling 1990; Stirling and Derocher 1993; Taylor and Lee 1995; Peacock *et al.* 2010).

### ***Field methods and data sources***

We analyzed live encounter and dead recovery data for WH polar bears collected from different sources. Environment Canada (EC) and University of Alberta personnel captured and released polar bears each year between late August and early October, as part of a long-term research program (e.g., Stirling *et al.* 1977; Ramsay and Stirling 1986, 1988; Derocher and Stirling 1990, 1995; Stirling *et al.* 1999). In each year, field crews attempted to evenly distribute sampling effort over the 12,000-km<sup>2</sup> EC study area between Churchill, Manitoba and the Nelson River (Figure 1; Area C). Polar bears were greatly concentrated relative to their dispersed winter distribution over the sea ice and were easily sighted against a snow-free background. Free-ranging bears were located by helicopter and captured using standard chemical immobilization techniques (Stirling *et al.* 1989). All polar bears observed were captured when it was safe to do so, except some pregnant females that took refuge in maternal dens excavated in the ground. Captured polar bears were individually marked using plastic ear tags and permanent tattoos on the inner surfaces of the upper lip. Each bear was temporarily marked with paint to avoid recapturing that individual the same season. A vestigial premolar was extracted from untagged animals older than one year for subsequent age determination

(Calvert and Ramsay 1988), and the age of cubs-of-the-year (COY; approximately 9 months old in autumn) was based on body size and dentition.

We also included data collected by the University of Saskatchewan within the EC study area from 1989-1996 using similar methods (e.g., Atkinson and Ramsay 1995; Cattet *et al.* 1997; Polischuk *et al.* 2002). Additional data were collected outside of the primary EC study area in some years. EC and the Ontario Ministry of Natural Resources captured bears between the Nelson River and the Manitoba-Ontario border (Figure 1; Area D) during 1984-1986 (EC and Ontario), 1994-1995 (EC) and 2003-2005 (EC and Ontario) and the Government of Nunavut (NU) captured bears along the Nunavut coast of western Hudson Bay (Figure 1; Area A) in 2007. To ensure that vital rates were estimated using a consistent study population, we only included live encounters outside the EC study area of polar bears previously captured within that area.

As part of the EC study, very high frequency (VHF) collars (Advanced Telemetry Systems, Isanti, MN or Telonics, Inc, Mesa, AZ) or satellite collars (Telonics, Inc.) were deployed on some adult females. Collars were not applied to subadult bears to avoid injury during growth, or to adult males as their necks are larger in circumference than their heads. Most VHF collars remained active for five years and satellite collars for two years. We derived the time-varying individual covariate *radio* to indicate when adult females were available for targeted recapture by radio telemetry, based on collar deployment information and expected battery life. This approach likely explained most individual heterogeneity in recapture probability resulting from live encounters of bears located by radio telemetry. It did not account for some yearlings located by radio telemetry in association with their mother's collar as we did not know *a priori* which collared females had dependent young, nor did it account for variation in battery life.

We also sampled bears captured by Manitoba Conservation (MB) staff near Churchill through the Polar Bear Alert Program (Kearney 1989). Polar bears were immobilized from the ground and either detained in a holding facility or transported out of Churchill, generally to coastal areas up to 50 km north. Some problem bears were subject to lethal removal. Marking and data collection procedures were similar to those used by EC. Previous analyses suggested that handling in Churchill was correlated with lower survival (Regehr *et al.* 2007), perhaps because bears seeking supplemental food in town were more likely to be in poor nutritional

condition (Lunn and Stirling 1985) or because bears frequenting Churchill had a greater chance of being killed by humans near communities. Handling in Churchill was also previously associated with higher recapture probability (Regehr *et al.* 2007), likely because polar bears handled there were more likely to return for potential food rewards, and were susceptible to capture by MB (Regehr *et al.* 2007). To account for this potential variation, we derived time-varying individual covariates following a live encounter by MB, as explained below.

All capture and handling methods were reviewed and approved annually by the EC Prairie and Northern Region Animal Care Committee and the University of Alberta BioSciences Animal Policy and Welfare Committee. Manitoba Conservation and Parks Canada Agency issued annual wildlife research permits under which these studies were conducted.

Additional data came from polar bears harvested each year as part of a legal, regulated subsistence hunt by Inuit living along the NU coast of western Hudson Bay (Figure 1; Area A; Derocher *et al.* 1997; Taylor *et al.* 2008). Biological samples and other information were obtained from harvested bears, and the identities of marked bears that were harvested were provided to EC.

We fitted models to a subset of the total data based on the following criteria. We considered data from 1984-2011 inclusive, for consistency with previous analyses (e.g., Regehr *et al.* 2007), and because EC and MB sampling protocols were consistent over these years. We excluded live captures from outside the annual sampling period of 1 August to 15 November, thus including approximately 95% of autumn live encounters, to better meet the assumption of instantaneous sampling common to live capture-recapture models for open populations (Williams *et al.* 2002). If an individual had more than one live encounter in a year with differences in state in each encounter (e.g., had a live cub in one encounter but not in another), we used the earlier encounter to define the bear's state. If a known female was encountered but identities of her dependent young were unknown (e.g., during a visual encounter of a family group located by radio telemetry), we used the field-estimated age class of the dependent young to inform the state of the adult female (e.g., a female with cubs-of-the-year versus a female without), and did not otherwise include the dependent young in the dataset.



We assigned numeric ages to 16 yearlings and two-year-olds that lacked tooth-derived age information, based on their field-estimated age class. We assigned numeric ages to 66 older bears lacking age information, based on the median tooth-derived age of other bears captured on the same sampling occasion with the same field-estimated age class (subadult or adult) and degree of tooth wear (subjective index 1-3).

We handled dead recoveries in two ways. First, individual capture histories were right-censored following inadvertent deaths during capture, so these removals did not affect parameter estimates. Second, we included a “human-caused mortality” state for purposeful human-caused removals (i.e., bears in the NU harvest and problem bears killed by MB). Dead recoveries that occurred after the start of the sampling period in calendar year  $j$  were assigned to the human-caused mortality state in calendar year  $j+1$ , which ensured that estimates of human-caused mortality included bears first marked in year  $j$  and subsequently removed in the same year. Since capture-recapture models estimate demographic parameters based on capture histories of individually-identified animals, we only included dead recovery data for polar bears that had been previously encountered and marked in the EC study area after 1984.

### ***Sea ice***

We examined trends in sea ice concentration in the Western Hudson Bay subpopulation management zone from 1979-2012 using passive microwave satellite imagery (resolution 25 x 25 km) from the National Snow and Ice data Center in Colorado (NASA Team algorithm) which provides daily sea ice cover concentrations to the nearest percentage (Cavalieri *et al.* 2012). Sea ice imagery was sampled each day using 381 sampling points that provided complete coverage of the Western Hudson Bay management zone (Figure 1). The mean ice concentration average over all 381 pixels was calculated for each day of the year to determine the average ice concentration within the management zone. From these data we derived three sea ice metrics: i) break-up date: defined as the ordinal date at which spring sea ice reached 50% sea ice concentration and stayed below that concentration for at least three consecutive days, ii) freeze-up date: the ordinal date at which autumn sea ice reached 50% sea ice concentration and remained above that concentration for at least three consecutive days, and iii) ice decay: the slope of an ordinary least squares regression of the rate of sea ice loss from 1

May of each year until the Western Hudson Bay management zone was completely ice free in the same year, expressed as a percentage.

### ***Multistate model structure***

We developed separate multistate structures for males and females (Figures 2-4), and all analyses were conducted separately for each sex due to the large size of the datasets. Transitions among states (Figures 2-4) are represented by arrows and depend on five types of parameters (Table 1). Female cubs (Figure 2) can first enter the dataset as cubs of the year (~9-month old cubs dependent on their mother; abbreviated as FC). One year later, conditional on their survival  $S$ , these cubs will have either become independent (i.e., weaned; F1I) with probability  $W$  or remained dependent on their mother (F1D) with probability  $1-W$ . Three subsequent classes reflect annual age increases (F2, F3, F4) and transitions between these states are deterministic, conditional on survival. Females F4 state (i.e., at 4+ years of age) transition the following year into 1 of 3 adult states, conditional on survival, including females with no cubs (FnY), with probability  $1-B$  where  $B$  is defined as breeding probability. Conditional on breeding, with probability  $B$ , females can be observed in autumn with 2 cubs (i.e., twins, with probability  $T$ ; F2Y) or with a single cub (with probability  $T$ ; F1Y). Adult bears in the state FnY include a mix of females without dependent young, and females with one or more yearlings, which may be either dependent (and so would be observed if the mother is observed) or independent (and may or may not be observed, independent of the mother). Including a female-with-yearling state would require accounting for state uncertainty (Pradel 2005), in order to appropriately account for stochasticity in the weaning process and resulting uncertainty in survival of yearlings. However, this inclusion would have resulted in a model structure that was too complex for our purposes.

The state structure for males is substantially simpler (Figure 3), and includes states analogous to FC, F1I, and F1D (MC, M1I, and M1D, respectively). Beyond the age of 21 months (i.e., states M1D and M1I), all males, conditional on survival, enter an adult male state (MA).

With the inclusion of mortality information, both female and male multistate structures include 2 death states (Figure 4), either of which can be entered from any live state, conditional on mortality ( $1-S$ ). These include an observable death state (FoD and MoD, for females and

males respectively), which bears enter with probability  $H$ , given mortality, indicating the probability that mortality was human-caused (either through hunting or management removals). We assume that all bears entering this state are detected, given the requirements for reporting bears taken in these ways. Bears can also enter an unobservable dead state (FuD and MuD), if their mortality is not due to a human cause, with probability  $1-H$ .

Survival,  $S$ , reflects annual apparent survival, the probability that an individual survives and remains on the study area from year  $t$  to year  $t+1$ . Weaning,  $W$ , is the probability that, conditional on survival, an individual in a cub state (FC or MC) in year  $t$  has weaned and entered state F1I or M1I by year  $t+1$ . Breeding probability,  $B$ , is the probability that a female bear without a cub at the previous time step produces a cub that survives to 9 months of age. Twinning probability,  $T$ , is the probability, conditional on breeding, that a female produces 2 (or, in very rare cases, 3) young that survive to 9 months of age. Harvest probability,  $H$ , is the probability, that, conditional on mortality, mortality was caused by a human, through hunting or management removal.

### ***Modeled covariates***

We tested a variety of covariates and effects which described polar bear biology, environmental conditions, or aspects of study design. Covariates were used together with the state structure in the life-cycle graphs to explain temporal, group, and individual variation in the parameters (Table 2). In some cases, age effects were fully represented by states in the life-cycle graph (e.g., states FC through F5 reflect annual ages for female from COY through five-year-old). In other cases, more detailed age effects were identified within a state (e.g., age effects were identified within state MA, which includes all males 33 mo. and older; Table 2). Overall age structure was similar to or more detailed than previous analyses (Regehr *et al.* 2007) and varied among the parameters  $S$ ,  $B$ ,  $H$ ,  $T$  and  $W$ . Furthermore, we included interactions between age structure and environmental covariates, to allow for differing effects of ice conditions on bears of different ages.

### ***Model fitting***

We fitted the models using MCMC simulations in a Bayesian analytical context (e.g., McCarthy 2007; Royle and Dorazio 2008). We chose standard vague prior distributions for the

parameters as appropriate. Three MCMC chains with random initial values were generated, with convergence assessed based on a Gelman and Rubin statistic between 1 and 1.1 (Gelman 1996; Gelman and Hill 2007). The simulations were performed using JAGS 3.3.0 (Plummer 2003). The R package rjags (Plummer 2013) was used to call JAGS and export results to R 2.14.2 (R Development Core Team 2012). We used empirical means and 95% Bayesian credible intervals (95% BCI) to summarize posterior distributions.

We used program RELEASE (Burnham *et al.* 1987) to evaluate how well the Cormack-Jolly-Seber (CJS) capture-recapture model for open populations fit a subset of the data that excluded human-caused removals and animals captured using radio telemetry. When applied to four strata consisting of females  $\leq 4$  years, females  $\geq 5$  years, males  $\leq 4$  years, and males  $\geq 5$  years, the summed chi-square statistics divided by the total degrees of freedom estimated a variance inflation factor (*chat*) of 0.94 ( $\chi^2 = 446.8$ ,  $df = 474$ ). Similar to previous analyses (Regehr *et al.* 2007), this suggests that a standard CJS model provides an adequate fit to the data when partitioned to allow sex- and age-based variation in survival and recapture probabilities. Because the multistate models used here were more general than the standard CJS model (e.g., they allowed additional variation as a function of reproductive state), we concluded that at the most general multistate model fit the data well and therefore used *chat* = 1.0 for model selection.

### ***Model selection and parameter estimation***

We used the deviance information criterion (DIC) for model selection, and completed model selection for each parameter in a stepped fashion (Tables 3, 4). In all cases, we used a general model for detection probability,  $p$ , which included state and age effects, random time effects, and effects to account for sightings in Churchill, and for radios (females only). We then used a step-by-step model selection approach to select the most-supported model structure for one parameter while using a structure with state and age effects for the other parameters that had not yet been evaluated. This approach focused on evaluating potential relationships between environmental conditions and polar bear vital rates, a primary objective of the analysis. By fitting a relatively small number of general models, we allowed for major sources of variation in the data based on *a priori* hypotheses about biology and study design, while

reducing the number of models we ran. The latter was necessary because the MCMC simulations were computationally intensive for the large WH dataset, requiring approximately 400 hours and 200 hours to fit a female or male model, respectively. For males, we first selected the best model structure for survival, then human-caused mortality, and then weaning. For females we first selected the best model structure for survival, then human-caused mortality, breeding, twinning, and finally weaning.

We derived abundance estimates from the top-ranked models using the Horvitz-Thompson (HT) estimator, similar to Regehr *et al.* (2007) but extended to the Bayesian framework. This approach estimates population size at time  $t$  by dividing an indicator variable for each individual (0 or 1, depending on whether the individual was captured and released alive at time  $t$ ) by the estimated recapture probability for that individual, and summing the results over all individuals. Variance estimation reflected uncertainty in both annual sample size and the estimates of recapture probability, producing point estimates of population size with accompanying Bayesian Credibility Intervals. Because multistate models condition on first capture and therefore do not produce estimates of  $p$  for COYs, which are by definition first-time captures, we estimated the number of COYs at each sampling occasion based on the number of adult females with one or two COYs (state F1Y and F2Y).

### ***Population projection modeling***

We developed a post-breeding Leslie matrix population projection model (Caswell 2000) based on the female and male life cycle graphs (Figures 2, 3) to estimate population growth rate ( $\lambda$ ) using the survival and reproductive parameters from the multistate capture-recapture modeling. This approach has the advantage of basing demographic projections on the full polar bear life cycle, using a suite of vital rates estimated in a unified modeling framework, and including the potential effects of environmental covariates on parameters. We projected the population so as to account for parametric uncertainty, demographic stochasticity, and annual stochasticity. Parametric uncertainty was accounted for through inclusion of the full sampling distribution as represented by the samples in the MCMC chains. Demographic uncertainty was accounted through inclusion of Markov trials for each of the demographic processes (survival, weaning, breeding, etc.) and annual stochasticity was accounted for through variation in

environmental covariates. We built two separate projection models, one using the top-ranked model, and one using a global model that included all hypothesized effects.

We initialized population projections using the mean state and age composition of the population for the three-year period 1985-1987, during which sample sizes were the largest, as calculated from the capture samples and estimates of  $p$  from the most-supported model using the Horvitz-Thompson estimator. This proportional composition was applied to the starting year for a given projection by multiplying by the estimated number of females and males in that year. To evaluate the population-level effects of potential changes in environmental conditions, we ran the population model under three different sea ice scenarios. First, we sampled from the entire time series (1984-2010) of sea ice variables, with replacement, for each 50-yr run of the population model. We sampled in a manner to retain the natural correlations in the sea ice variables (i.e., if a break-up date was selected for year  $t$ , the corresponding freeze-up date was selected as well). Second, we ran a ‘good’ sea ice scenario, which included the sea ice variables sampled from the 1984-2010 time series using the upper 50% quantile of *break-up* (i.e., later sea ice break-up), the lower 50% quantile of *freeze-up* (i.e., earlier freeze-up), and the lower 50% quantile of *ice.decay* (i.e., slow ice decay). These conditions are likely to maximize the time available for polar bears to forage on the sea ice and thus represent favorable environmental conditions. Last, we ran a ‘poor’ sea ice scenario, which included sea ice variables sampled from opposite quantiles to those used in the “good years” scenario, to represent ice conditions that previous studies have suggested are likely to have negative effects on polar bears.

## RESULTS

The modeled subset of WH data consisted of individual capture histories for 3,034 polar bears, including 6,224 live encounters (62 of which were incidental removals) and 519 purposeful human-caused removals. Of the live encounters, 493 were bears aged one year or older which were targeted for capture by radio telemetry. The capture of COYs, whether by standard search or aided by radio telemetry, did not directly contribute to estimates of recapture probability because multistate models condition on first capture. The covariate

*telemetry* provided coverage for approximately 75% of radio telemetry encounters, suggesting that it explained most of the individual variation in  $p$  associated with radio telemetry.

Approximately 34% of individual bears were encountered by MB at some point and, therefore, had non-zero entries in the two *Churchill* covariates.

### **Sea ice**

Changes in sea ice chronology on western Hudson Bay over the period 1979-2012 showed significant shifts towards earlier break-up in the spring and later freeze-up in the autumn (Figure 5). The date of sea ice break-up has been occurring 5.5 days earlier per decade ( $t = -3.359$ ,  $p = 0.002$ ) and varied from 2 June to 11 July, with a mean of 22 June (SE = 1.8 days). The date of sea ice freeze-up has been occurring 4.1 days later per decade ( $t = 2.655$ ,  $p = 0.013$ ) and varied from 10 November to 16 December, with a mean of 28 November (SE = 1.6 days).

Over the last decade (2001-2010), however, while the date of sea ice break-up has varied between 4 June and 2 July, there has been no significant trend in break-up date over time (linear regression,  $p = 0.584$ ). Similarly, the date of sea ice freeze-up has varied between 23 November and 9 December but there was no significant trend over time (linear regression,  $p = 0.132$ ).

### **Model selection**

For female polar bears, step-wise model selection led to the most-supported model M3 (Table 5) with survival (S) as a function of state and age effects (COY, yearling dependent, yearling independent to 4 yr, 5-19 yr without COY, 5-19 yr with COY,  $\geq 20$  yr without COY, and  $\geq 20$  yr with COY ) and the time-varying covariates *break-up*, *freeze-up*, and the interaction between *break-up* and *freeze-up*; time-constant human-caused mortality (H) as a function of state and age effects (COY and dependent yearling, independent yearling to 4 yr,  $\geq 5$  yr without COY, and  $\geq 5$  yr with COY); time-constant breeding (B) as a function of state and age effects (4 yr, 5-9 yr, 10-19 yr, and  $\geq 20$  yr); and time-constant twinning (T) and weaning (W) probabilities with no state or age structure.

For male polar bears, model selection led to the most-supported model M1 (Table 6) with time-constant survival (S) as a function of state and age effects (COY, yearling dependent, yearling independent to 4 yr, 5-9 yr, 10-19 yr,  $\geq 20$  yr); time-constant human-caused mortality

(H) as a function of state and age effects (COY and dependent yearling, independent yearling to 4 yr, 5-9 yr, and  $\geq 10$  yr); and time-constant weaning (W) probabilities with no state or age structure. All models used the general structure for recapture probability ( $p$ ) as described in the Methods.

### ***Parameter estimates***

For female polar bears, total apparent survival ( $S$ ) varied with time as a function of sea ice conditions (Figure 6, a representative graph for adult females 5-19 years old and without COY). The strongest sea ice relationship was between earlier break-up and lower survival for all age classes (Figure 7, a representative graph for adult females 5-19 years old with cubs-of-the-year and independent females 1-4 years old). This is consistent with Regehr *et al.* (2007); although that analysis found support for negative effects of break-up on survival for non-prime adult polar bears only, while the current analysis indicates that the survival of prime-adult females also reflects ice conditions. The difference between these findings is likely due to the more explicit state structure of the multistate models, and the inclusion of additional data (e.g., captures by radio telemetry), which improved our ability to model variation in  $S$  and  $p$ , and therefore likely improved statistical power to detect ecologically-meaningful relationships in the data. For example, recapture probabilities for adult females aged 5-19 years old without COY (and without a radio collar or previous capture in Churchill) were 0.11, compared to 0.37 for females with COY. This supports the hypothesis of lower  $p$  for pregnant adult females that may seek refuge in maternal dens and therefore be less susceptible to capture.

For male bears, the model selection process supported time-constant survival. Although previous analyses indicated effects of sea ice on survival for some age classes of male bears, the current lack of support of ice effects is likely the result of directly incorporating human-caused removals into our analysis; specifically, the relatively high rates of human-caused mortality for males. As males are preferentially taken in the sex-selective subsistence harvest of the WH subpopulation, a sufficient number are likely killed by humans each year to dampen fluctuations in natural survival due to environmental variation, making these fluctuations difficult to detect.



Time-invariant estimates of  $S$  were derived for female bears using the MCMC chains from model M3 without the coefficients associated with sea ice covariates (i.e., using the intercept and state and age coefficients only). This allowed for comparison of survival among states and age classes, and with time-invariant estimates of  $S$  from the most supported model M1 for males (Table 7). Similar to previous analyses (Regehr *et al.* 2007), we found evidence for increasing survival with age, followed by senescent declines for bears  $\geq 20$  years old. There was no indication of differences in adult female survival as a function of reproductive status, with the exception of higher  $S$  for senescent-adult females with cubs compared to senescent-adult females without cubs. Estimates of total apparent survival were generally similar for females and males, with male survival lower for most age classes, likely due to the effects of the sex-selective harvest.

### ***Estimates of human-related mortality***

The probability of having been purposefully killed by a human, conditional on death for any reason ( $H$ ), varied by sex and age (Table 8). For females, independent yearlings through four-year-olds exhibited the highest  $H$ . For males, young adults aged 5-9 years exhibited the highest  $H$ , followed by independent yearlings through four-year-olds. These patterns are consistent with previous work suggesting that younger bears, particularly males, are most likely to encroach upon human settlements and thus risk being killed for defense (Lunn and Stirling 1985), and are disproportionately represented in the subsistence harvest (Derocher *et al.* 1997; Peacock *et al.* 2010). The relatively high estimates for  $H$  for some sex and age classes suggest that a large component of overall mortality for some segments of the WH subpopulation is due to human-caused removals. For example, the parameter  $H = 0.73$  for young adult males (5-9 years) can be interpreted as follows: for every 100 young adult males that die each year for any reason, approximately 73 of them were purposefully killed by humans.

### ***Probability of breeding***

Estimates of breeding probability for adult females were time-constant and did not vary as a function of sea ice conditions. Breeding probability exhibited an age-related increase followed by a senescent decline in reproduction (Table 9). The probability of producing twins ( $T$ ) was also time-constant over the course of the study, and constant across states and ages, at

0.47 (95% BCI = 0.43-0.52). The probability of weaning (W) for COYs was time-constant at 0.22 (95% BCI = 0.14-0.40) for females and 0.28 (95% BCI = 0.18-0.41) for males.

### ***Subpopulation abundance estimates***

Abundance estimates for the WH subpopulation (Figure 8) were derived using the HT estimator applied to estimates of  $p$  for the most supported models M3 for females and M1 for males. The estimate of abundance declined from 1184 polar bears (95% CI: 993-1411) in 1987 to 806 bears (95% CI = 653-984) in the final year of the study, 2011. Although there was variation in the annual abundance point estimates from 2004-2011 (range: 670 (95% CI: 531-834 in 2008) to 806 (95% CI: 653-984 in 2011)), there was no significant trend (Figure 8).

Although the population estimates predicted by the updated modeling approach are lower than previous estimates in Regehr *et al.* (2007) proper inference can only be made within each of the models. To assess any difference between the two modeling approaches, we compared the general trend in point estimates of population size in this study and Regehr *et al.* (2007), based on the mean geometric observed population growth rate, which is calculated by exponentiating the mean of log abundance for sequential sampling occasions (Humbert *et al.* 2009). Using this approach, the mean observed population growth rate for the period 1987-2004 for the current study is 0.974, compared to 0.981 based on point estimates of population size from Regehr *et al.* (2007). This similarity indicates consistency between the two analyses. A more detailed comparison of point estimates of population size, on an annual basis, is complicated by statistical uncertainty and differences in the datasets and modeling approaches. Although the current estimate of abundance in 2011 is lower than the estimate of 935 (95% CI = 794-1076) for the year 2004 from Regehr *et al.* (2007), comparison of these numbers is not valid. The appropriate comparison would be between estimates taken from the recent analysis, thus comparing the 2011 estimate of 806 with the new 2004 estimate of 742 (95% CI = 630-872), which are not significantly different (Figure 8). However, we also used matrix-based population projection models to produce more robust estimates of population growth rate for the past decade, based on estimates of survival and other vital rates from the multistate models (see the section *Population projection model*).

### ***Population projection model***

To develop a robust, unbiased estimate of population growth in WH, we used matrix-based projection models to estimate population growth rate ( $\lambda$ ) over different time-frames and environmental conditions. These estimates are derived from estimates of  $S$  and other vital rates estimated from the multistate models, and because estimates of  $S$  are less susceptible to bias than point estimates of population size, estimates of  $\lambda$  likely represent the most robust capture-recapture assessment of the trend of the WH subpopulation.

For the current analysis, we focused on estimating  $\lambda$  for the female segment of the population, due to the critical importance of female bears to reproduction and population growth. For the female segment of the WH subpopulation, we estimated  $\lambda = 1.02$  (95% CI = 0.98-1.06) for the period 1991-2010. This is based on the most-supported female model M3 and likely represents the most reliable assessment of population trend, suggesting that the female population remained stable or increased very slightly during this period. Although this estimate reflects both natural and purposeful human-caused mortality, it applies to females only and does not reflect potentially lower  $\lambda$  for male bears due to the effects of male-biased harvest mortality, as suggested by lower estimates of  $S$  for males and females. For comparison, a similar estimate of  $\lambda = 1.02$  (95% CI = 0.98-1.06) was derived from the more general female model that included ice effects on the reproductive parameters  $B$ ,  $W$ , and  $T$ . This suggests that estimates of  $\lambda$  are robust to the model selection process, and that the most-supported model did not exclude, on statistical grounds, potential biologically-meaningful environmental effects of reproductive parameters.

We also projected population size forward in time for the female segment of the population, and for females and males together (i.e., the total population), under two assumptions for future sea ice conditions (Table 10). This represents a sensitivity analysis with regard to the expected trend of the WH subpopulation, given a range of hypothetical future sea ice conditions. This approach assumed that the relationship between ice covariates and population parameters as estimated from the 1984-2011 data remained stationary, as did all other factors (e.g., the level of human-caused removals). For the combined female and male projections, we used parameter estimates of a male model that included sea ice effects, to reflect their potential biological importance, despite sea ice covariates not being supported

during the model selection procedure. If future sea ice conditions are ‘good’ for polar bears, as represented by the favourable upper half of sea ice conditions observed from 1984-2010, the long-term population growth rate is estimated to be approximately  $\lambda = 1.02$ , or 2% population growth per year. Similarly, if sea ice conditions are ‘poor’ for polar bears, long-term population growth rate is estimated to be approximately  $\lambda = 0.97$ , representing a 3% population decline per year.

## **DISCUSSION**

### ***Population trend***

Assessments of the status of the Western Hudson Bay subpopulation of polar bears have been undertaken by analyzing almost 30 years of demographic data, in support of population conservation and harvest management. Demographic analysis of this long-lived species is increasingly important, as long-term declines in availability of sea-ice habitat associated with changing climates add to the complexity of management decisions. This level of information has enabled the development of detailed population models to assess changes in population size and other vital rates. We used Bayesian implementation of multistate capture-recapture models, coupled with a matrix-based demographic projection model, to integrate population data and environmental variables, and to incorporate variation across the polar bear life cycle.

The updated analysis presented in this report shows that the size of the WH subpopulation has declined overall since capture-recapture studies began in the mid-1980s, and has been relatively stable over the last decade (Figure 8). The major driver of population change for female polar bears was the timing of sea ice break-up and formation, which influenced the survival of all age categories of females. We found no evidence of changes in fecundity or productivity related to sea ice conditions for females in WH. In contrast, the survival of male polar bears was primarily determined by their age class, likely linked to higher level of hunting mortality in males than females. These results underscore the value of considering environmental factors within demographic population models in order to identify causative mechanisms.

The long-term response of polar bears to climate change is expected to vary in time and space, both among and within subpopulations (Amstrup *et al.* 2010). This study represents the highest-resolution analysis of polar bear demography to date, providing insight into how such changes occur, and confirming the linkage between sea ice conditions and polar bear survival, and thus population trend. As the model predicts, the lack of negative trend in spring sea ice break-up date from 2001-2011 apparently resulted in sufficient natural growth within the female segment of the population to maintain female numbers in the context of environmental variation and harvest. This period of relative stability in sea ice conditions allowed sufficient productivity that the level of human-caused removals of females was sustainable over this decade. Evidence for the dependence of the WH subpopulation on sea ice conditions, combined with forecasts of decreasing duration and extent of ice cover in southern and western Hudson Bay from regional climate models, suggests that the long-term population trend is likely to be negative. However, these results also suggest that the WH population is able to respond positively when climatic and sea ice conditions improve.

### ***Population abundance***

It is important to estimate the actual number of polar bears within the WH subpopulation (e.g., point estimates of population size) to support key harvest management decisions. Abundance can be estimated using different approaches, such as capture-recapture analysis and aerial surveys, which provide slightly different temporal and spatial perspectives and require careful consideration of the different assumptions and caveats involved. Because capture-recapture studies provide extensive long-term biological data on marked individuals, they permit robust estimation of population parameters and investigation of the relationships among vital rates, environmental conditions and population status. Although Bayesian multistate modeling and demographic projections allowed us to develop robust estimates of population trend, estimates of abundance developed using this framework may be influenced by the site fidelity of individuals and by the effective coverage of the capture-recapture sampling area.

The demographic modeling approach used is robust to differences in the area sampled among years, and allows for an estimation of population size for a specific year across the

entire sampling area, rather than just the area specifically monitored that year. However, the point estimate will be negatively biased if bears permanently leave the sampling area, as they will have wrongly been assigned as having died. This may be the case for bears in Area D, east of the Nelson River (Figure 1), where capture-recapture sampling did not occur after 2005, if those bears exhibit high seasonal fidelity to areas outside the main capture-recapture sampling area. This bias would result in point estimates of the size of the WH subpopulation that are lower than those from aerial surveys. Future research should address the potential for distributional shifts within the WH subpopulation during the autumn that may affect this bias (Towns *et al.* 2010; Atkinson *et al.* 2012; Cherry *et al.* 2013), using geo-spatial analysis of capture locations and movement data from radio-collared bears.

In addition, we note that the estimates of total apparent survival used in matrix models represent the cumulative probability of remaining alive and of not permanently emigrating from the study population. Thus, these estimates may include an emigration component, which should be balanced by an opposing immigration component in the projection models (if such immigration exists) to accurately represent overall population change. Future analyses will evaluate matrix-based estimates of population growth rate for the entire 1984-2011 period, and assess potential changes in polar bear movements with respect to the sampling area over time.

Comparison of the 2011 point estimate of 806 (95% CI = 653-984) from this study with the estimate of 1,000 (95%CI = 715-1398) from the 2011 aerial survey (Atkinson *et al.* 2012) requires careful interpretation. The aerial survey likely provides an accurate “snapshot” estimate of the total number and distribution of polar bears in the WH management area at the time of the survey. This differs somewhat from the point estimate of population size from capture-recapture models, which represents the group of bears with a non-zero probability of moving through the capture-recapture sampling area over a multiple-year period (considered the “superpopulation”; e.g., Williams *et al.* 2002).

The overall difference in point estimates of 2011 population size from the two approaches is not large, as evidenced by overlap in their confidence intervals. However, given apparent differences, it is useful to consider which estimate might be more appropriate to

consider in decisions related to harvest management. Results of a 2007 capture program, a 2010 pilot aerial survey, and the 2011 comprehensive aerial survey along the Kivalliq coast of Nunavut north of Churchill (Peacock and Taylor 2007; Atkinson *et al.* 2012), did not suggest that EC's capture-recapture studies had missed a significant segment of the WH subpopulation of relevance to harvest management north of the Manitoba border. Thus, the higher point estimate of population size from the recent aerial survey of WH may represent inclusion of bears with fidelity to the southeastern portion of the WH management area which, if unlikely to enter the EC capture-recapture study area, may also be unlikely to use the Kivalliq coast and be exposed to harvest in Nunavut.

### ***Influence of sea ice conditions on survival***

We found that survival of female polar bears in all age classes was correlated with sea ice conditions, with lower survival in years of early break-up. This is consistent with previous studies that linked body condition, productivity, and status of WH polar bears to changes in duration of sea ice cover associated with climatic warming (e.g., Stirling *et al.* 1999; Regehr *et al.* 2007). Continuing reduction of sea ice extent and duration would represent a significant threat to polar bears (Stirling and Derocher 1993; Derocher *et al.* 2004; Molnár *et al.* 2010; Peacock *et al.* 2010; Molnár *et al.* 2011; de la Guardia *et al.* 2013), as population sustainability would be largely dependent on survival and productivity of adult females.

Trends of declining sea ice duration and declines in polar bear survival and reproduction have also been documented in the Baffin Bay (Peacock *et al.* 2012) and Southern Beaufort Sea (Regehr *et al.* 2010; Rode *et al.* 2010) subpopulations. In areas such as Hudson Bay, where seasonal sea ice dynamics result in extended ice-free periods, polar bears transition between positive (on ice, feeding) and negative (on shore, fasting) energy states. Longer periods on shore will result in greater negative impacts on energy budgets and consequently, on survival and productivity (Molnár *et al.* 2010, 2011).

Despite the growing body of literature on the effects on marine mammals of climate change, sea ice change, and subsequent shifts within Arctic marine ecosystems (e.g. Ferguson *et al.* 2005, Laidre and Heide-Jørgensen 2005; Kovacs and Lydersen 2008; Laidre *et al.* 2008; Wiig *et al.* 2008; Molnár *et al.* 2010, 2011; Stirling and Derocher 2012), our ability to detect and

to understand how such ecosystem changes will affect polar bears in the WH subpopulation is limited. Thus, while the availability of ringed seals, the main prey of polar bears in Hudson Bay, will be negatively affected by climate change (Ferguson *et al.* 2005), it is unclear how and at what rate these changes will further impact polar bears.

### ***Influence of harvest on survival***

Although Regehr *et al.* (2007) found effects of changes in duration of sea ice on survival of dependent, juvenile, and senescent male polar bears, and in our analysis we found that survival of female bears was a function of sea ice conditions, we found that the survival of male bears of all age classes was not correlated with sea ice conditions. This may be related to the direct incorporation of human-caused mortality in this analysis. Nunavut has a sex-selective, male-biased subsistence harvest of polar bears (Taylor *et al.* 2008). Young male bears are not only disproportionately represented in the harvest (Derocher *et al.* 1997; Peacock *et al.* 2010), but are also most likely to encroach upon human settlements and thus risk being killed for defense reasons (Lunn and Stirling 1985). Young males had a high value (0.73) for *H* (human-caused mortality) (Table 8). Thus, the number of male bears killed by humans may be sufficiently large to dampen any fluctuations in natural survival due to environmental variation, making them difficult to detect. In addition, male polar bears may be more buffered from environmental fluctuations compared to females. Molnár *et al.* (2010) used dynamic energy budget models to predict survival, and estimated that only 3-6% of adult male polar bears in western Hudson Bay would die of starvation before the end of a 120-day fasting period, but that this would increase to 28%-48% before the end of a 180-day fasting period. This suggests that fully-grown adult males have lower energetic demands while on land, and may be the group least impacted by changing sea ice conditions experienced to date.

### ***Influence of sea ice conditions on productivity and body condition***

We did not find that reproduction was correlated with varying sea ice conditions over the period 1984-2011. However, comparisons of observations of mean litter size in FB, SH, and WH in the early 2000s (Peacock *et al.* 2010) and more recently (Atkinson *et al.* 2012) indicate that WH subpopulation is less productive. The relatively low number of cubs recorded during the 2011 WH aerial and coastal surveys was noted by Atkinson *et al.* 2012.



The late spring - early summer period is critical for polar bears, as it is during this time that they accumulate at least two-thirds of the energy that they require for the entire year (Stirling and Øritsland 1995). It is suggested that changes in body condition of adult males, adult females with cubs and solitary adult females (Stirling *et al.* 1999), and declines in mass of solitary adult females (Stirling and Parkinson 2006), reflect the amount of time that bears have spent on the sea ice prior to coming ashore. Our analysis did not include such morphometric covariates. Rode *et al.* 2013 examined body size, condition, and recruitment of polar bears in two adjacent subpopulations - Chukchi Sea and Southern Beaufort Sea - during a period of declining sea ice habitat. They found differing responses and concluded that declines in sea ice extent did not completely explain observed population productivity, and suggested that polar bears may show complex and non-linear responses to climate change.

Integrating population information from multiple sources at different spatial and temporal scales is necessary to effectively understand the status and trend Canada's polar bear subpopulations. The strength of the multistate modeling approach used here is the ability to assess linkages between changes in vital rates, environmental correlates and population trend. This allows the processes underlying population change to be identified, allowing for the development of appropriate management actions. The strong demographic linkage between sea ice conditions and female survival in WH polar bears enables effective forecasting of the outcome of different management scenarios and their implications for subsequent changes in population size, and confirms the sensitivity of the population trends in Western Hudson Bay to changes in sea ice conditions.

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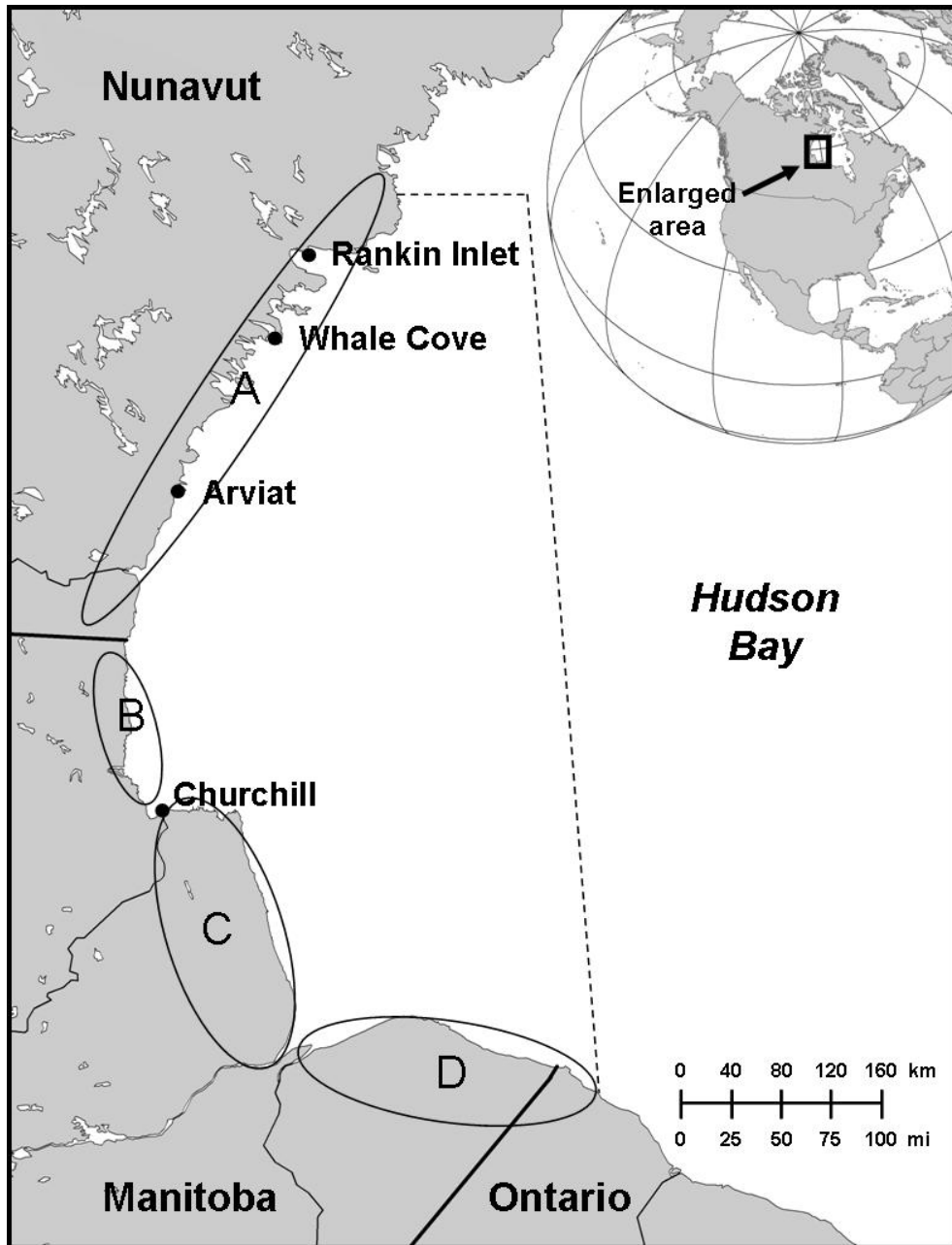
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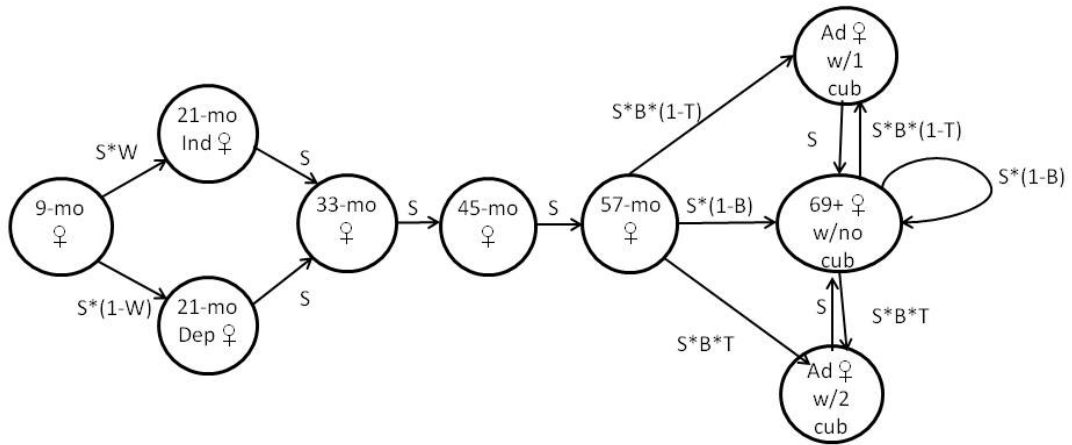
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**Figure 1.** Map of Hudson Bay showing the management boundary of the Western Hudson Bay polar bear subpopulation (dashed line) and areas of research and survey effort. Most of the capture-recapture data come from animals handled in Area C, with limited captures in Area B. Geographic coverage for capture-recapture data was extended to include Area D in 1984-86, 1994-95, and 2003-05. The 2011 aerial survey covered the Areas A, B, C, and D.

## Female compartment



S: Survival

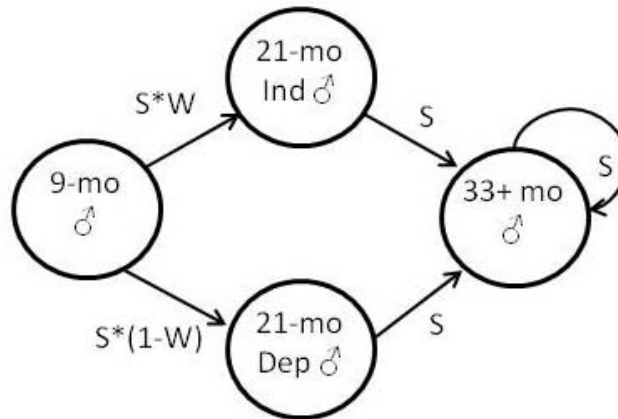
W: Probability to have an independent yearling given that a female had a 9-month old cub last year

B: Probability to reproduce and to have at least one surviving cub of 9 months old

T: Probability to have another cub given that a female have one cub

**Figure 2.** Multistate model structure – female compartment.

## Male compartment

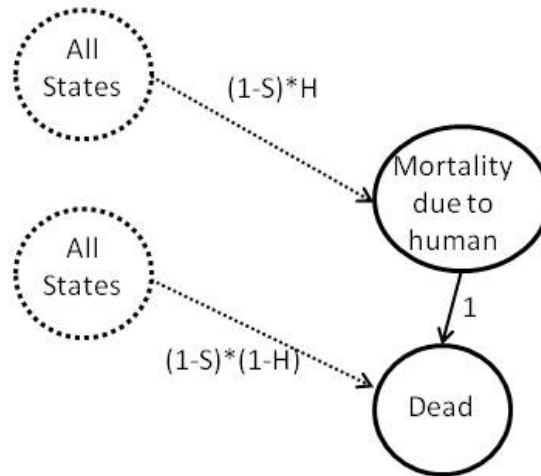


S: Survival

W: Probability to have an independent yearling given that a female had a 9-month old cub last year

**Figure 3.** Multistate model structure – male compartment.

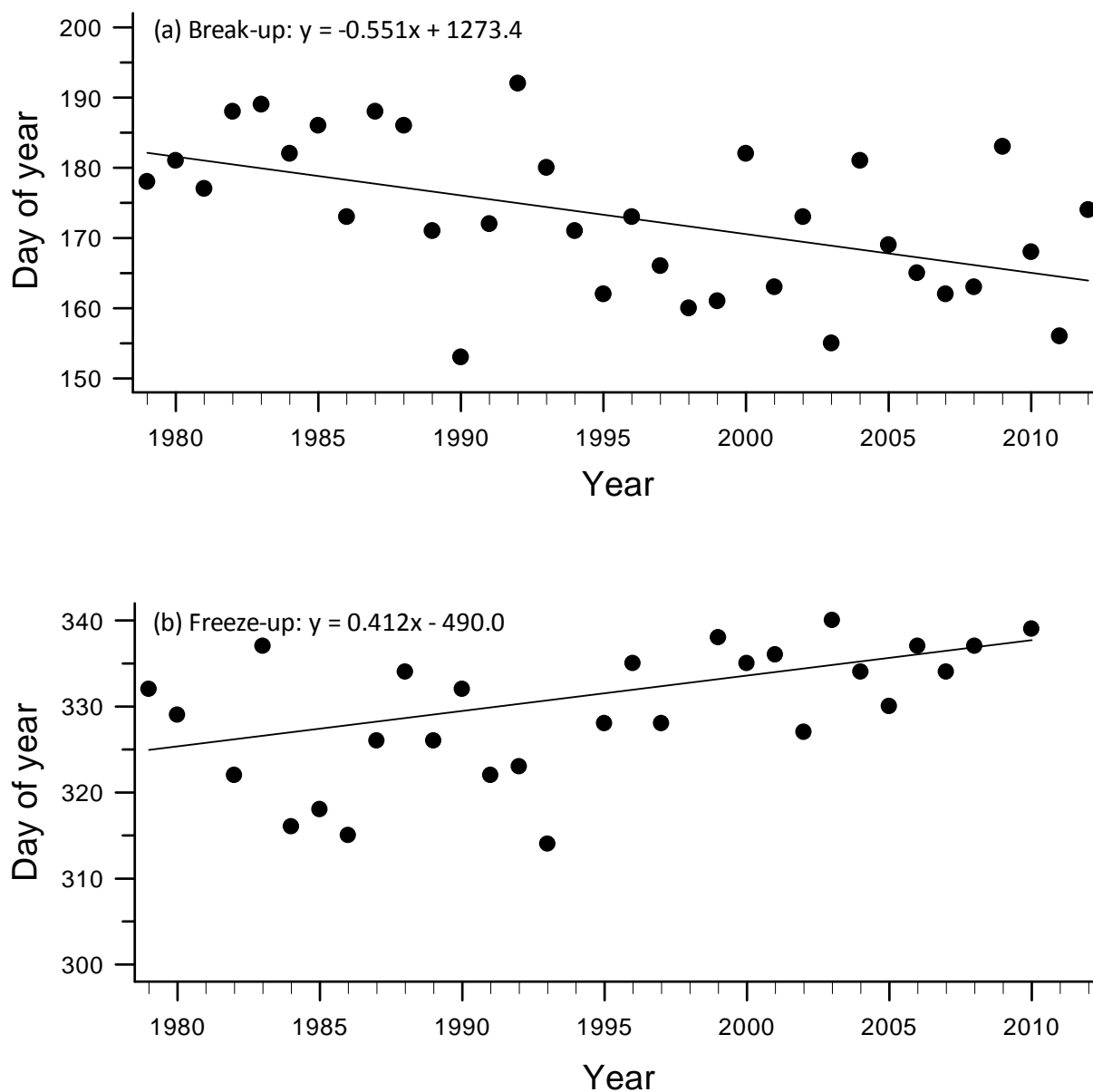
# Mortality



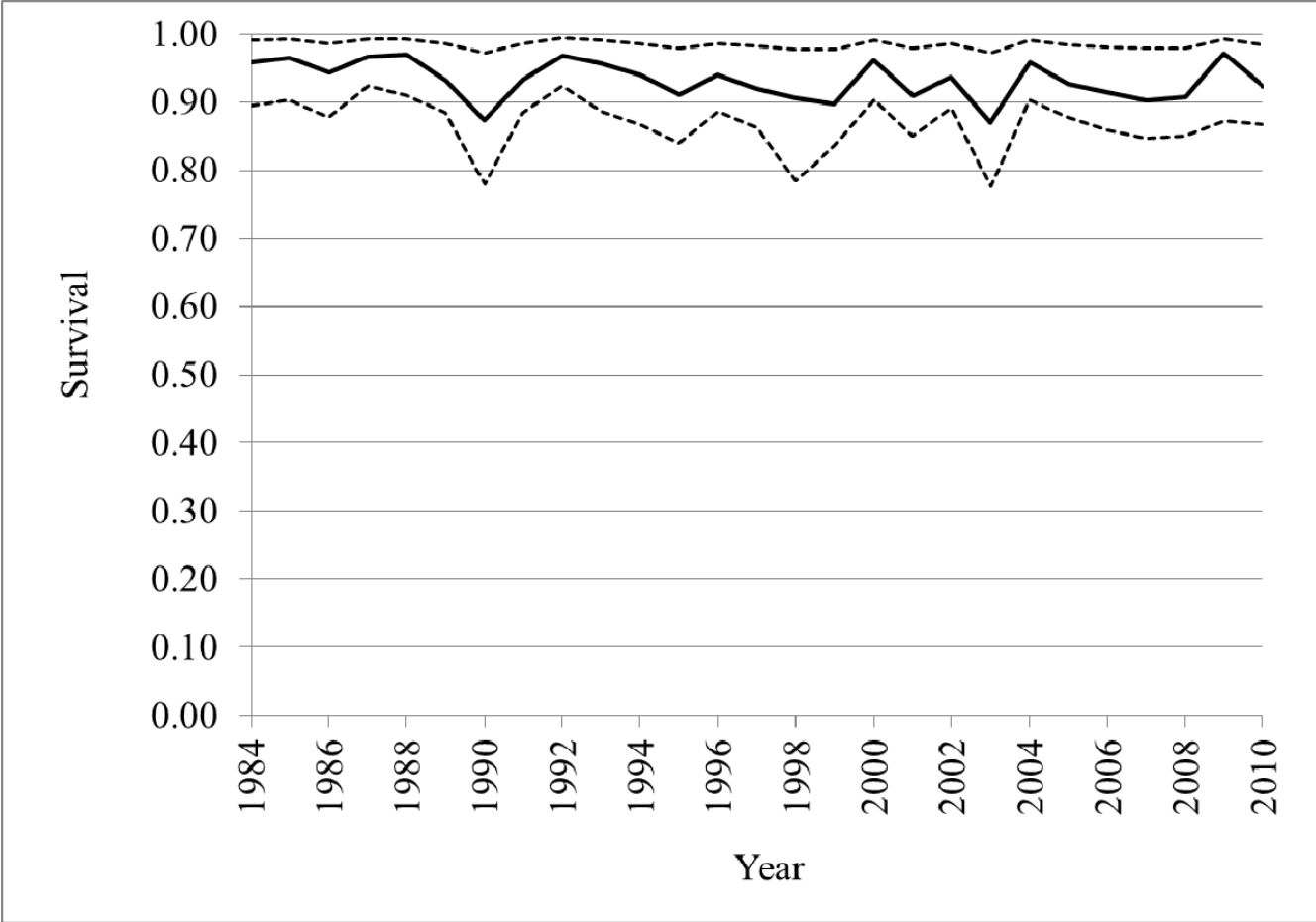
S: Survival

H: Probability to die from human causes given that the individual is dead

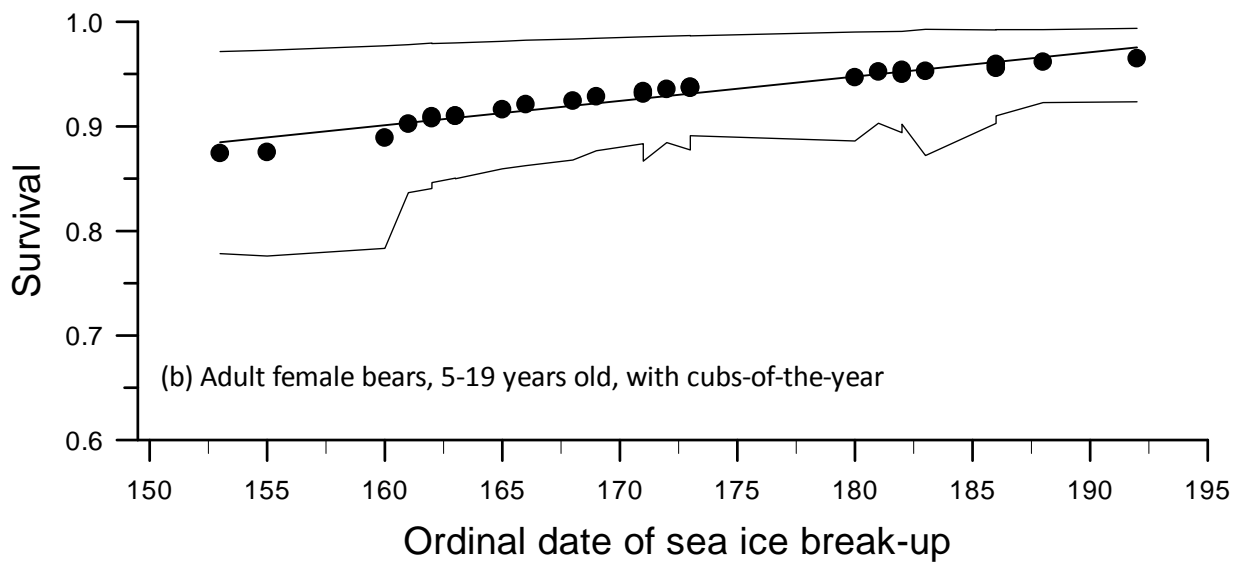
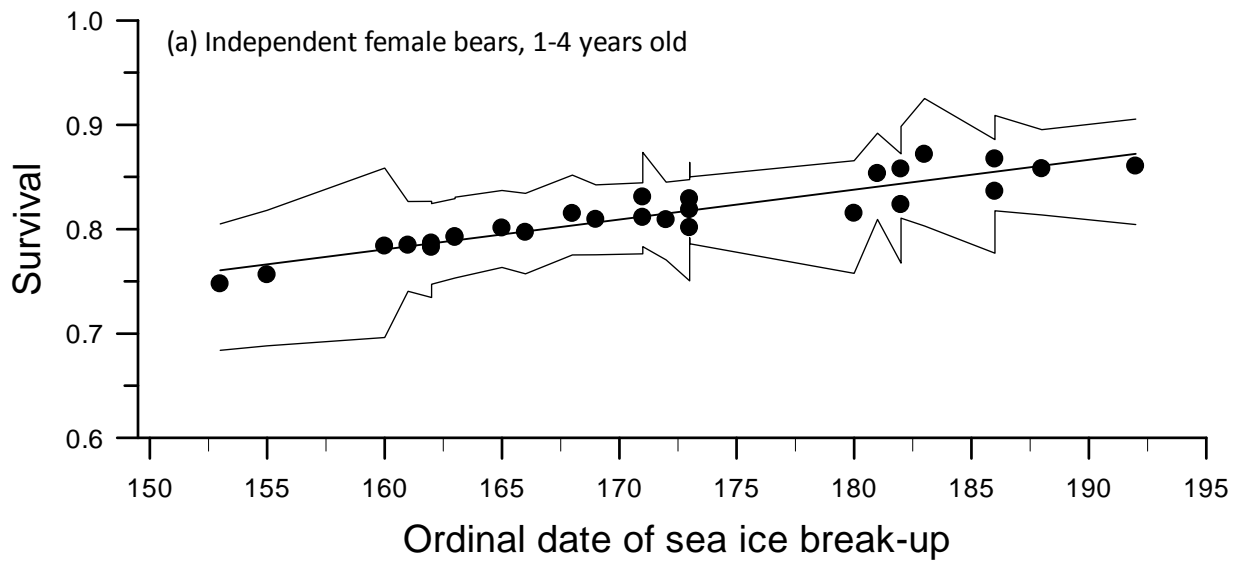
**Figure 4.** Multistate model structure – mortality.



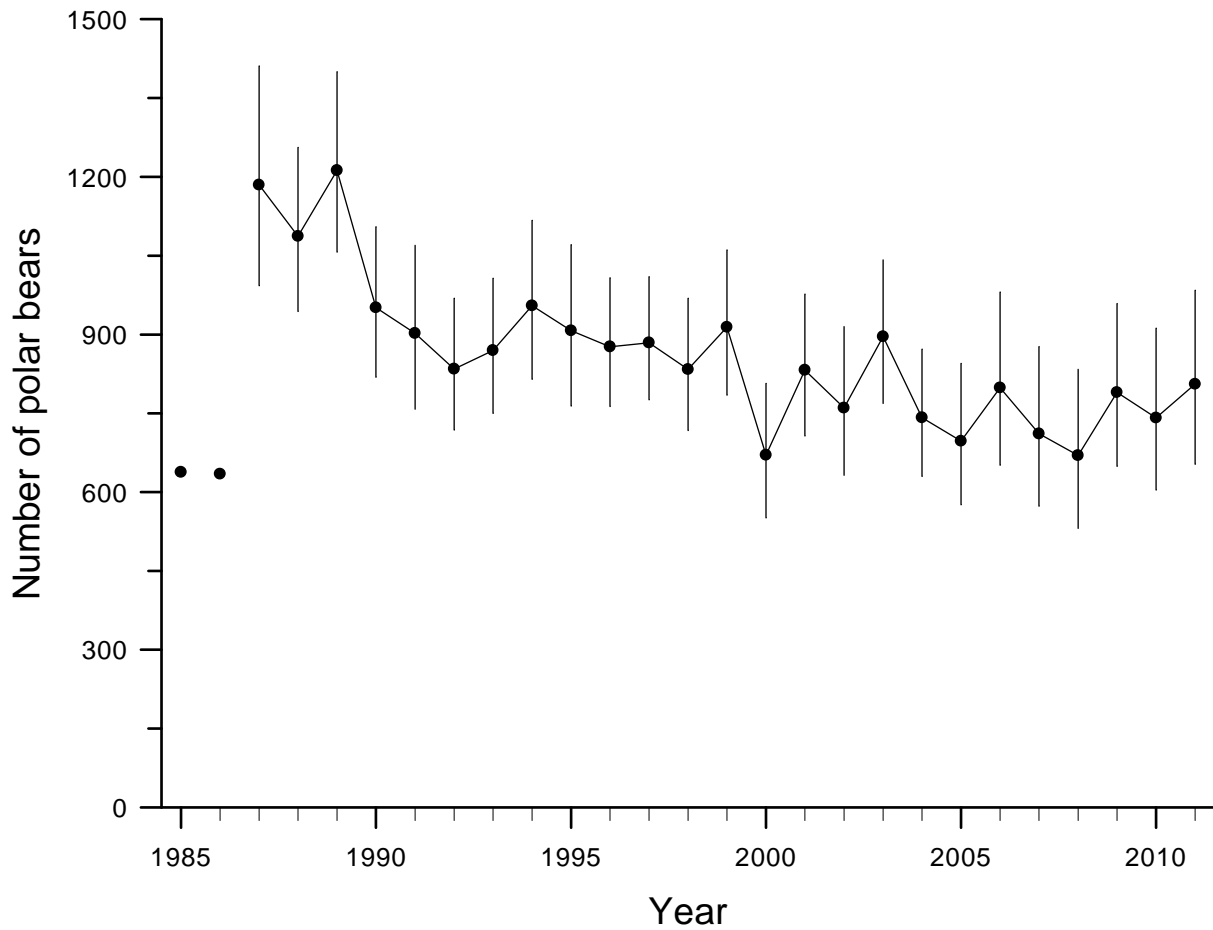
**Figure 5.** Date of (a) sea ice break-up (50% sea ice concentration) in spring and (b) sea ice freeze-up (50% sea ice concentration) in autumn in western Hudson Bay from 1979-2012, estimated from passive microwave satellite imagery (data source: National Snow and Ice Data Center, Boulder, Colorado; <http://nsidc.org>).



**Figure 6.** Total apparent survival for adult females aged 5-19 years old and without COYs, estimated from live-recapture and dead-recovery data for the Western Hudson Bay polar bear subpopulation from 1984-2011 using multistate capture-recapture models. This study showed that interannual variation in survival is a function of sea ice conditions.



**Figure 7.** Survival rates of (a) independent female polar bears 1-4 years old and (b) adult female bears 5-19 years old with cubs-of-the-year in relation to date of sea ice break-up, western Hudson Bay, 1984-2011.



**Figure 8.** Estimated population size, derived by applying a Horvitz-Thompson estimator to recapture probabilities estimated from live-recapture and dead-recovery data for the Western Hudson Bay polar bear subpopulation from 1984-2011, using multistate capture-recapture models. Point estimates of abundance and 95% confidence intervals are shown for 1987–2011 only, because the 1985–1986 point estimates were biased by incomplete sampling of the core study area and are not comparable (Regehr *et al.* 2007).



Table 1. Parameters estimated from live-recapture and dead-recovery data for the Western Hudson Bay polar bear subpopulation for 1984-2011, using multistate capture-recapture models based on the life-cycle graphs in Figures 2-4.

Parameter	Description
<i>S</i>	Total apparent survival: the probability that an individual alive in the autumn of year <i>t</i> survives to the autumn of year <i>t</i> +1 and does not permanently emigrate from the study population
<i>W</i>	Weaning: the probability that a dependent 9 mo. cub in the autumn of year <i>t</i> (state FC or MC) becomes an independent yearling in the autumn of year <i>t</i> +1 (state F1I or M1I), conditional on survival
<i>B</i>	Breeding: the probability that an adult female gives birth in the spring of year <i>t</i> and that at least one member of a litter survives until the autumn of year <i>t</i> .
<i>T</i>	Twinning: the probability that two or more members of a litter survive until autumn, conditional on the adult female giving birth in the spring, and at least one member of the litter survives until autumn
<i>H</i>	Human-caused mortality: the probability that an individual that dies in the interval <i>t</i> to <i>t</i> +1 was purposefully killed by a human (e.g., subsistence harvest or defense kill), conditional upon dying by any cause
<i>p</i>	Recapture: the probability that an individual was captured and released alive on sampling occasion <i>t</i> , conditional on being alive and not having permanently emigrated from the study population

Table 2. Covariates and effects used to explain variation in parameters estimated from live-recapture and dead-recovery data for the Western Hudson Bay polar bear subpopulation for 1984-2011.

Covariate or effect	Description
<i>age.male</i> effects	Additional age effects within the adult male state MA consisting of subadults (2-4 yr), young adults (5-9 yr), prime adults (10-19 yr), and senescent adults ( $\geq 20$ yr).
<i>age.female</i> effects	Additional age effects within the adult female states (FnY, F1Y, F2Y) consisting of young adults (5-9 yr), prime adults (10-19 yr), and senescent adults ( $\geq 20$ yr).
<i>churchill</i>	Individual and time-varying covariate. The value was 0 if an individual had never been captured around the community of Churchill, and 1 for all sampling occasions following the first capture around Churchill.
<i>telemetry</i>	Individual and time-varying covariate, applied only to adult females $\geq 5$ years. The value was 1 if a female was equipped with a functional radio collar and available for recapture using VHF or satellite telemetry, and 0 otherwise.
<i>breakup</i>	Julian date for calendar year t on which sea ice extent in the Western Hudson Bay management area declined below 50% coverage.
<i>freezeup</i>	Julian date for calendar year t on which sea ice extent in the Western Hudson Bay management area increased to above 50% coverage.
<i>ice.decay</i>	Absolute value in calendar year t for the slope of the ice decay function between Julian dates XXXX and YYYY.

Table 3. Stepped model selection, female polar bears.

First step: Setting up the first model with which we're going to do the comparison	
Model notation	Effects included in the probability of recapture
M1	$p = f(\text{State/age effect} + \text{Churchill recap} + \text{telemetry} + \text{time random effect})$ $S = f(\text{State/age effect})$ $H = f(\text{State/age effect})$ $B = f(\text{State/age effect})$ T, W
Second step: Selection of the best model for survival	
Model notation	Effects included in survival
M2	$S = f(\text{State/age effect} + \text{break-up})$
M3	$S = f(\text{State/age effect} + \text{Break-up} + \text{Freeze-up} + \text{Break-up} * \text{Freeze-up})$
M4	$S = f(\text{State/age effect} + \text{Break-up} + \text{Ice decay} + \text{Break-up} * \text{Ice decay})$
Third step: Selection of the best model for the probability of dying due to human causes	
Model notation	Effects included in the probability of dying due to hunting
M5	$H = f(\text{State/age effect} + \text{Churchill hunting})$
Fourth step: Selection of the best model for the probability to reproduce and have an alive 9mo old cub	
Model notation	Effect included in the probability to reproduce and have an alive 9mo old cub
M6	$B = f(\text{State/age effect} + \text{break-up})$
M7	$B = f(\text{State/age effect} + \text{break-up} + \text{ice decay} + \text{break-up} * \text{ice decay})$
Fifth step: Selection of the best model for the probability of twinning	
Model notation	Effect included in the probability of twinning
M8	$T = f(\text{State/age effect} + \text{break-up})$
Sixth step: Selection of the best model for the probability of weaning	
Model notation	Effect included in the probability of weaning
M9	$W = f(\text{break-up})$

Table 4. Stepped model selection, male polar bears.

First step: Setting up the first model with which we're going to do the comparison	
Model notation	Effects included in the different parameters
M1	$p = f(\text{State/age effect} + \text{Churchill recap} + \text{time random effect})$ $S = f(\text{State/age effect})$ $H = f(\text{State/age effect})$ $W$
Second step: Selection of the best model for survival	
Model notation	Effects included in survival
M2	$S = f(\text{State/ age effect} + \text{break-up})$
M3	$S = f(\text{State/age effect} + \text{Break-up} + \text{Freeze-up} + \text{Break-up} * \text{Freeze-up})$
M4	$S = f(\text{State/ age effect} + \text{Break-up} + \text{Ice decay} + \text{Break-up} * \text{Ice decay})$
Third step: Selection of the best model for the probability of dying due to human causes	
Model notation	Effects included in the probability of dying due to hunting
M5	$H = f(\text{State/age effect} + \text{Churchill hunting})$
Fourth step: Selection of the best model for the probability of weaning	
Model notation	Effect included in the probability of weaning
M6	$W = f(\text{break-up})$

Table 5. Selection of most-supported model for female polar bears using deviance information criterion (DIC). A general model for recapture probability was used that included state and age effects; random time effects; effects to account for sightings in Churchill; and effects due to radio telemetry. Additional parameters were added using a step-by-step model selection approach.

First step: Selection of the best model for survival					
Model notation	Effect included in survival while using the best model for probability of recapture	Dev female	Var dev/2	DIC Gelman	Delta DIC
M3	State + age effect + Break-up + Freeze-up + Break-up * Freeze-up	18326.73	2145.889	20472.62	
M4	State + age effect + Break-up + Ice decay + Break-up * Ice decay	18318.63	2276.129	20594.76	122.14
M2	State + age effect + break-up	18319.73	2344.892	20664.62	192
M1	Stage + age effect	18337.45	2399.979	20737.43	264.81
Second step: Selection of the best model for the probability of dying due to human causes					
Model notation	Effect included in probability of hunting while using the best model for probability of recapture and survival (model M3)	Dev female	Var dev/2	DIC Gelman	Delta DIC
M3	State + age effect	18326.73	2145.889	20472.62	
M5	State + age effect + Churchill covariate	18319.38	2341.344	20660.73	188.11
Third step: Selection of the best model for the probability of reproducing					
Model notation	Effect included in probability of reproducing while using the best model for probability of recapture, survival and hunting (model M3)	Dev female	Var dev/2	DIC Gelman	Delta DIC
M3	State + age effect	18326.73	2145.889	20472.62	
M7	State + age effect + break-up + ice decay + break-up*ice decay	18317.48	2199.88	20517.36	44.74
M6	State + age effect + break-up	18322.36	2460.246	20782.61	309.99
Fourth step: Selection of the best model for the probability of twinning					
Model notation	Effect included in probability of twinning while using the best model for probability of recapture, survival, hunting and reproducing (model M3)	Dev female	Var dev/2	DIC Gelman	Delta DIC
M3	State + age effect	18326.73	2145.889	20472.62	
M8	State + age effect + break-up	18323.47	2493.004	20816.48	343.86
Fifth step: Selection of the best model for the probability of weaning					
Model notation	Effect included in probability of twinning while using the best model for probability of recapture, survival, hunting, reproducing and twinning	Dev female	Var dev/2	DIC Gelman	Delta DIC
M3	State + age effect	18326.73	2145.889	20472.62	
M9	State + age effect + break-up	18324.16	2301.032	20625.19	152.5699

Table 6. Selection of most-supported model for male polar bears using deviance information criterion (DIC). A general model for recapture probability was used that included state and age effects; random time effects; and effects to account for sightings in Churchill. Additional parameters were added using a step-by-step model selection approach.

First step: Selection of the best model for survival					
Model notation	Effect included in survival while using the best model for probability of recapture	Dev male	Var dev/2	DIC Gelman	Delta DIC
M1	State/age effect	13143.31	1533.99	14677.3	
M3	State + age effect + Break-up + Freeze-up + Break-up * Freeze-up	13143.66	1552.334	14695.99	18.69
M2	State + age effect + break-up	13146.44	1632.879	14779.32	102.02
M4	State + age effect + Break-up + Ice decay + Break-up * Ice decay	13155.33	1735.959	14891.29	213.99
Second step: Selection of the best model for the probability of dying due to human causes					
Model notation	Effect included in probability of hunting while using the best model for probability of recapture and survival (model M1)	Dev male	Var dev/2	DIC Gelman	Delta DIC
M1	State + age effect	13143.31	1533.99	14677.3	
M5	State + age effect + Churchill covariate	13154.41	1565.002	14719.41	42.11
Third step: Selection of the best model for the probability of weaning					
Model notation	Effect included in probability of weaning while using the best model for probability of recapture, survival and hunting (model M1)	Dev male	Var dev/2	DIC Gelman	Delta DIC
M1	State + age effect	13143.31	1533.99	14677.3	
M6	State + age effect + break-up	13143.91	1623.598	14767.5	90.2

Table 7. Estimates of time-invariant total apparent survival ( $S$ ), estimated from live-recapture and dead-recovery data for the Western Hudson Bay polar bear subpopulation 1984-2011 using multistate capture-recapture models. Age classes represent a combination of state structure and age effect covariates.

Age class	Female		
	$S$ (mode)	95% CI lower	95% CI upper
COY (9 mo.)	0.56	0.48	0.66
Yearling (dependent)	0.71	0.61	0.81
Yearling (independent) to 4 yr	0.82	0.79	0.85
5-19 yr without COY	0.94	0.92	0.96
5-19 yr with COY	0.94	0.89	0.99
$\geq 20$ yr without COY	0.77	0.71	0.82
$\geq 20$ yr with COY	0.89	0.73	0.99

Age class	Male		
	$S$ (mode)	95% CI lower	95% CI upper
COY (9 mo.)	0.52	0.46	0.58
Yearling (dependent)	0.79	0.71	0.87
Yearling (independent) to 4 yr	0.75	0.72	0.77
5-9 yr	0.93	0.91	0.95
10-19 yr	0.90	0.88	0.91
$\geq 20$ yr	0.72	0.67	0.76

Table 8. Estimates of the probability of having been purposefully killed by a human, condition on death ( $H$ ), estimated from live-recapture and dead-recovery data for the Western Hudson Bay polar bear subpopulation 1984-2011 using multistate capture-recapture models. Age classes represent a combination of state structure and age effect covariates.

Age class	$H$ (mode)	Female	
		95% CI lower	95% CI upper
COY (9 mo.) and yearling (dependent)	0.05	0.03	0.07
Yearling (independent) to 4 yr	0.28	0.22	0.35
≥ 5 yr without COY	0.08	0.05	0.11
≥ 5 yr with COY	0.15	0.08	0.99

Age class	$H$ (mode)	Male	
		95% CI lower	95% CI upper
COY (9 mo.) and yearling (dependent)	0.05	0.03	0.08
Yearling (independent) to 4 yr	0.44	0.38	0.49
5-9 yr	0.73	0.58	0.91
≥ 10 yr	0.24	0.20	0.29



Table 9. Estimates of the probability of giving birth and having at least one member of a litter survive until autumn ( $B$ ), estimated from live-recapture and dead-recovery data for the Western Hudson Bay polar bear subpopulation 1984-2011 using multistate capture-recapture models. Age classes represent a combination of state structure and age effect covariates.

Age class	$B$ (mode)	Female	
		95% CI lower	95% CI upper
4 yr	0.04	0.02	0.10
5-9 yr	0.24	0.18	0.31
10-19 yr	0.31	0.25	0.39
$\geq 20$ yr	0.27	0.20	0.36

Table 10. Future population growth rate, from matrix-based population projection models using parameters estimated from live-recapture and dead-recovery data for the Western Hudson Bay polar bear subpopulation 1984-2011 using multistate capture-recapture models.

Population segment	Future sea ice conditions	Future time frame (years)	Population growth rate ( $\lambda$ )	Lower 95% CI	Upper 95% CI
female	good	10	1.02	0.98	1.05
female	good	20	1.02	0.99	1.04
female	good	50	1.02	1.00	1.05
female	poor	10	0.97	0.85	1.02
female	poor	20	0.96	0.85	1.01
female	poor	50	0.97	0.92	1.01
female and male	good	10	1.02	0.99	1.05
female and male	good	20	1.02	0.99	1.05
female and male	good	50	1.02	0.99	1.05
female and male	poor	10	0.96	0.85	1.01
female and male	poor	20	0.96	0.88	1.01
female and male	poor	50	0.97	0.92	1.01