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

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SUMMARY

- We evaluated the demography and population status 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 polar bears harvested for subsistence purposes or removed during human-bear conflicts.

- 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 sampling uncertainty, and demographic and environmental stochasticity across the polar bear life cycle. This approach allowed for estimation of a suite of vital rates, including survival and reproduction. These vital rates were used to parameterize a Bayesian population model to evaluate population trends and project potential population outcomes under different environmental scenarios.

- Survival of female polar bears of all age classes was significantly correlated with sea ice conditions; particularly with the timing of sea ice break-up in the spring and formation in the fall and the interaction of the two. This is consistent with previous findings linking body condition and survival of WH polar bears to environmental changes associated with climatic warming and supports the ecological dependence of polar bears on the availability of sea ice.

- Survival of male polar bears was not correlated with sea ice conditions. This was likely because a higher proportion of mortality for males was caused by humans rather than by natural factors. For example, approximately 73% of mortality for young male bears (i.e., 5-9 years old) was due to direct human-caused removals, largely because of sex selectivity in the subsistence harvest.

- The declining trend in size of the WH subpopulation over the period 1987-2004 was similar to a previous analysis (Regehr *et al*. 2007), suggesting consistency between the two demographic evaluations. Point estimates of abundance were somewhat lower using the updated statistical approach. It is important to recognize that the analyzed data were not collected in a manner that is optimal for estimating abundance and that the goal of the current analysis was to estimate vital rates and demographic trends.

- Estimates of population growth rate were also derived using a Bayesian population model based on estimated survival and reproductive rates from the multistate capture-recapture model. For the recent decade 2001-2011, the growth rate of the female segment of the population was 1.02 (95% CI = 0.98-1.06). Apparently stable to positive population growth for females may be due in large part to nonlinearity (i.e., short-term stability) in the long-term observed and forecasted trend toward earlier sea ice break-up in western Hudson Bay.

- The 2011 abundance estimate from this analysis was 806 bears with a 95% Bayesian

credible interval of 653-984. This is lower than, but broadly consistent with, the abundance estimate of 1,030 (95% confidence interval = 745-1406) from a 2011 aerial survey (Stapleton *et al.* 2014). The capture-recapture and aerial survey approaches have different spatial and temporal coverage of the WH subpopulation and, consequently, the effective study population considered by each approach is different.

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 influence the population ecology of polar bears (Stirling and Derocher 1993, 2012; Derocher *et al*. 2004; Stirling and Parkinson 2006; Laidre *et al*. 2008; Rode *et al*. 2010, 2012, 2013). 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 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 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 ± 51. As this estimate was considered to be conservative because the study had not included the southeastern portion of the range east of the Nelson River (Figure 1), 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).

As part of a collaborative effort between Environment Canada, the US Fish and Wildlife Service, and the US Geological Survey, we analyzed 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 the subpopulation by considering changes in key vital rates such as survival and reproductive rates, and estimation of the size and trend of the effective study population, as defined by the extent and timing of capture-recapture sampling, to inform management decisions. Our analysis included seven additional years of data (2005-2011) that were not available in previous analyses (Regehr *et al*. 2007). 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 can more effectively account for heterogeneity by allowing demographic parameters to vary between states. This model also allows for estimation of demographic parameters of primary interest, such as survival and reproductive rates, which describe transitions between states. Our approach incorporated a broader range of data than previous analyses: data for bears that were captured and released alive under multiple sampling protocols, for both research and management purposes, and data for bears that were harvested for subsistence purposes or killed for reasons of human safety. The multistate model allowed us to explicitly consider the sex, age, and reproductive status of bears and the hierarchical structure allowed us to more efficiently account for annual variation in parameters such as detection probability. We used the results of this estimation procedure to construct a population model, using a Bayesian Population Viability Analysis (BPVA) approach (i.e., demographic inputs to the viability analysis come from the Bayesian estimation procedure; Wade 2002; Kéry and Schaub 2012; Servanty *et al*. 2014), to project potential population outcomes under different sea-ice scenarios. The primary objectives were to:

1. estimate survival rates, rates of mortality directly attributable to humans, reproductive rates, population size, and population trend;
2. evaluate relationships between demographic parameters and sea ice availability; and,
3. assess the potential impacts of changes in sea ice availability on the status of the WH subpopulation.

METHODS

Study area

The current 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 to some degree 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 that were collected from different sources from 1984-2011. Each year between late August and early October, Environment Canada (EC) and the University of Alberta captured and released polar bears in a 12,000 km^2 area between Churchill, Manitoba and the Nelson River (Figure 1; Area C) 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). Although there was limited geographic coverage in the sampling effort within this area in 1984-1986, the annual sampling effort was more evenly distributed since 1987 (Regehr *et al*. 2007). Additional sampling by EC occurred in the area between Churchill and the Manitoba-Nunavut border (Figure 1; Area B) in 1999, and 2005-2011; and, between the Nelson River and the Manitoba-Ontario border (Figure 1; Area D) in 1984-1986, 1994-1995, and 2003-2005.

In the autumn when research occurred, 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 during fieldwork were captured when it was safe to do so, except for 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 age determination (Calvert and Ramsay 1988) whereas the aging of cubs-of-the-year (COY; approximately 9 months old in autumn) and yearling cubs (approximately 21 months old in autumn) was based on body size and dentition.

Very high frequency (VHF) collars (Advanced Telemetry Systems, Isanti, MN or Telonics, Inc., Mesa, AZ; use of product names does not imply endorsement by the US or Canadian governments) 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. However, active collars did not guarantee recapture, so capture probability for this group was expected to be <1. We derived the time-varying individual covariate *telemetry* to indicate when adult females were likely to be available for targeted recapture by telemetry, based on collar deployment information and expected battery life. This approach was expected to account for most individual heterogeneity in recapture probability resulting from live encounters of bears located by telemetry. It did not account for some yearlings located by telemetry in association with their mother's collar because we did not know *a priori* which collared females had dependent young, nor did it account for variation in battery life or collar retention.

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.

We also included data that were collected by other agencies using similar methods: in Area C by University of Saskatchewan in 1989-1996 (e.g., Atkinson and Ramsay 1995; Cattet *et al*. 1997; Polischuk *et al*. 2002); in Area D by Ontario Ministry of Natural Resources in 1984-1986 and 2003-2005; and, along the Nunavut coast of western Hudson Bay (Figure 1; Area A) by the Government of Nunavut in 2007. To ensure that vital rates were estimated using a consistent study population, we only included live encounters of polar bears outside the study area (Area C) if they had been previously captured within it.

We also included data on 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 therefore be susceptible to recapture by MB (Regehr *et al*. 2007). To account for this potential variation, we derived a time-varying individual covariate, *Churchill*, which was set to 0 prior to and including the sampling occasion on which a bear was first captured by MB and set to 1 on all subsequent sampling occasions.

Finally, 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 research-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, for consistency with previous analyses (e.g., Regehr *et al*.

2007), and because EC and MB sampling protocols were relatively 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 a different state in each encounter (e.g., had a dependent cub in one encounter but not in another), we used the earlier encounter to define the bear's state (when a female has dependent cubs, observation of the female is expected to guarantee observation of the cubs as well). 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 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 (i.e., ignored in the analysis) 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 (for which we estimated a transition probability) 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 were encountered and marked in the study area after 1984.

Sea ice

We evaluated trends in sea ice availability 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 (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 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% concentration and stayed below that concentration for at least three consecutive days (Etkin 1991; Stirling *et al*. 1999; Gagnon and Gough 2005; Stirling and Parkinson 2006), ii) freeze-up date: the ordinal date at which autumn sea ice reached 50% concentration and remained above that concentration for at least three consecutive days, and iii) ice decay: the absolute value of 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. Correlations between these 3 variables were weak with the exception of the correlation between break-up date and ice decay, which was -0.93. However, we included both break-up date and ice decay in the models to determine which might be a better predictor of demographic parameters, via model selection as described below. We also included interactions between break-up and freeze-up date in some models to account for the potential interactive effect of having both an early break-up and a late freeze-up (for example) in a given year, and break-up and ice decay to account for the potential interactive effect of both the timing and rate of sea ice break-up.

Multistate model structure

We developed separate multistate structures for males and females (Figures 2-4). Transitions among states are represented by arrows and depend on five types of parameters (Table 1). Female bears (Figure 2) can first enter the dataset when they are as young as cubs of the year (~9-mo 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 (i.e., the bear must get older) conditional on survival. Females in the F4 state (i.e., at 4+ years of age) transition the following year into one of three adult states, conditional on survival. Conditional on not breeding, with probability 1-*B* where *B* is defined as breeding probability, females transition into the female with no cubs (FnY) state. 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 1-*T*; F1Y). We emphasize that breeding is defined here as the probability of having at least one cub that survives to autumn, and so is the product of the probabilities of giving birth to at least one cub and of having at least one of the cubs produced survive to autumn. 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) to appropriately represent stochasticity in the weaning process and resulting uncertainty in survival of yearlings. As including this state would have resulted in a model structure that was prohibitively complex, it was preferable for our purposes to not include it and accept some heterogeneity in the FnY state. A consequence of this approach is that *B* represents an average breeding probability for all adult females in states F4 and FnY, some of which (e.g., the females with yearlings in FnY) were not likely physiologically capable of being pregnant in that year.

The state structure for males is 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., beyond 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*, conditional on 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 high adherence to reporting requirements for bears taken under the regulated subsistence harvest (Stirling and Prestrud 1994; Peacock *et al*. 2011; Vongraven and Peacock 2011) or for management purposes. 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 in 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 rare cases, 3) young that survive to 9 months of age.

Model fitting

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). Age effects were partially represented by states in the life-cycle graph (states FC through F4 reflect annual ages for females, and states MC, M1I, and M1D reflect annual ages for males). For states that included multiple ages (MA, F1Y, F2Y, and FnY) more detailed age effects were included within the states. The structure of these age effects is described in 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. Sea ice covariates were transformed to a standard normal distribution before inclusion in the model.

The large size of the data set made it impractical to analyze as a single unit, so all analyses were conducted separately for females and males. We fitted the models using Markov chain Monte Carlo (MCMC) simulations in a Bayesian analytical context (e.g., McCarthy 2007; Royle and Dorazio 2008). We chose standard vague prior distributions for the parameters.

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 telemetry. When applied to four strata consisting of females ≤ 4 years, females ≥ 5 years, males ≤ 4 years, and males ≥ 5 years, the summed chi-square statistics divided by the total degrees of freedom estimated a variance inflation factor ($\hat{c}$) of 0.94 (χ^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 the most general multistate model would also fit the data well and therefore did not include a variance inflation factor in analyses.

Model selection and parameter estimation

We used the deviance information criterion (DIC) calculated as Gelman's approximation (Gelman *et al*. 2004) 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 the *telemetry* (females only) and *Churchill* covariates. We then used a step-by-step model selection approach to select the most-supported model structure for one parameter while using a general structure with state and age effects for the 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 (computationally intensive) models we ran. 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 abundance at time *t* by dividing an indicator variable for each individual (equal to 1 if the individual was captured at time *t*, and equal to 0 otherwise) by the estimated recapture probability for that individual, and summing the results over all individuals. This Bayesian-based approach allowed for an estimation of variance that accounted for the variation in both annual sample size and recapture probability and allowed us to estimate the uncertainty around population size. 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) and the mean litter size for females in state F2Y (2.04 COYs, because this state included a few females with triplet litters). We calculated population trend, in terms of the mean geometric observed population growth rate, based on abundance estimates. This was achieved by exponentiating the mean of the ratios of the natural log of abundance for sequential sampling occasions (Humbert *et al*. 2009).

Population projection modeling

We developed a post-breeding matrix-based population projection model (Caswell 2000) based on the female and male life cycle graphs (Figures 2, 3) to both estimate and project population growth rate (λ) using the survival and reproductive parameters from the multistate capture-recapture modeling. This approach uses the suite of vital rates estimated from the multistate model framework, including the potential effects of environmental covariates on parameters, and allows us to project population growth under varying environmental conditions. We projected the population so as to account for sampling uncertainty, demographic stochasticity, and environmental stochasticity. Sampling uncertainty was accounted for through inclusion of the full sampling distribution as represented by the samples

in the MCMC chains. Demographic stochasticity was accounted for through inclusion of binomial trials for each of the demographic processes (survival, weaning, breeding, etc.) and environmental stochasticity was accounted for by selecting, at each time step in the population projection, the estimated set of demographic parameters corresponding to the sea ice variables at that time step. We built two separate projection models, one using parameter estimates from the top-ranked model identified by the model selection procedure described above, and one using a global model that included all hypothesized effects. This provided a general assessment of the sensitivity of population projections to the structure of the estimation model.

We initialized population projections using the mean state and age composition of the population for the three-year period 1985-1987, 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 'high' sea ice scenario, which included the sea ice variables sampled from the 1984-2010 time series using the values from those years that met each of 3 conditions: they were in 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 represent years with relatively high availability of sea ice and thus represent favorable environmental conditions for polar bears with respect to their ability to access prey. Last, we ran a 'low' sea ice scenario, which included sea ice variables sampled from opposite quantiles to those used in the 'high' 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 that were targeted for capture by telemetry. The covariate *telemetry* provided coverage for approximately 75% of telemetry encounters, suggesting that it explained most of the individual variation in *p* associated with radio and satellite telemetry. Approximately 34% of individual bears were encountered by MB at some point and, therefore, had non-zero entries in the *Churchill* covariates used to model variation in *p* and *H*.

Sea ice

Changes in sea ice chronology on western Hudson Bay over the period 1979-2012 showed a significant trend 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), the date of sea ice break-up varied between 4 June and 2 July but did not exhibit a significant trend (linear regression, p = 0.584). Similarly, the date of sea ice freeze-up varied between 23 November and 9 December without a significant trend (linear regression, p = 0.132).

Model selection

For female polar bears, 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, ≥ 20 yr without COY, and ≥ 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, ≥ 5 yr without COY, and ≥ 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 ≥ 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, and ≥ 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 ≥ 10 yr); and time-constant weaning (*W*) probabilities with no state or age structure.

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 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). Recapture probabilities for adult females varied by state: females aged 5-19 years old without COY (and without a radio collar or previous capture in Churchill) had $p = 0.11$, compared to $p = 0.37$ 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.

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). While we found evidence for increasing survival with age, followed by senescent declines for bears ≥ 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 older adult females with cubs compared to older adult females without cubs. Estimates of total apparent survival were lower for all age classes of independent males than for independent females, likely due to the effects of the sex-selective harvest.

Estimates of human-caused mortality

The probability of having been purposely killed by a human, conditional on dying (*H*), varied by sex and age (Table 8). For females, independent yearlings through 4-yr-olds exhibited the highest *H*. For males, young adults aged 5-9 years exhibited the highest *H*, followed by independent yearlings through 4-yr-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 (Lunn and Stirling 1985), and are disproportionately represented in the subsistence harvest due to a sex-selective management approach (Derocher *et al*. 1997; Taylor *et al*. 2008; Peacock *et al*. 2010). The relatively high estimates of *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, *H* = 0.73 for young adult males (5-9 years), indicating that for every 100 young adult males that die each year, approximately 73 of them were purposely killed by humans.

Reproductive parameters

Estimates of breeding probability for adult females were time-constant and did not vary as a function of sea ice conditions. Breeding probability increased with adult female age, followed by a senescent decline for females ≥20 years old (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.

Abundance of the effective study population

Abundance estimates from the capture-recapture study apply to an effective study population defined as animals with a non-negligible probability of occurring in the study area during autumn sampling (i.e., the "superpopulation" per Kendall *et al*. 1997). This definition includes animals with long-term fidelity to the study area that were randomly outside of this area in any given year, but does not include animals that had high fidelity to other areas and were consequently unlikely to ever enter the study area or our capture sample. We derived abundance estimates (Figure 8) using the HT estimator applied using estimates of *p* for the

most supported models; M3 for females and M1 for males. The estimate of overall abundance declined from 1185 polar bears (95% CI: 993-1411) in 1987 to 806 bears (95% CI = 653-984) in 2011. Although there was variation in the annual abundance estimates from 2004-2011, the period of time since the previous demographic assessment of the WH population, there was no clear trend (Figure 8).

Although the abundance estimates from the updated modeling approach for the years 1987-2004 are lower than previous estimates in Regehr *et al*. (2007), proper inference can only be made within each of the models. The mean observed population growth rate for the period 1987-2004 for the current study is 0.973, compared to 0.981 based on point estimates of population size from Regehr *et al*. (2007). This indicates a consistent evaluation of population trend between the two analyses. A more detailed comparison of point estimates of population size, on an annual basis, is complicated by differences in the datasets and the modeling approaches. In particular, small changes in how *p* is modeled can result in large changes in the abundance estimates, because abundance estimates produced in this way are highly sensitive to heterogeneity in capture (Williams *et al*. 2002). 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 tenuous. A more reliable indicator of recent trend is the mean observed population growth rate, which is 1.01 over the years 2004-2011.

Population projection model

As an additional and complementary approach for understanding population trends (Sandercock and Beissinger 2002) and also for projecting trends under different possible sea ice scenarios, we used matrix-based population projection models to estimate population growth rate based on estimates of survival and other vital rates from the multistate models.

We used post-breeding matrix-based projection models to model population growth rate (λ) over different time-frames (i.e., past and future) and over a variety of possible environmental conditions. These estimates are, therefore, derived from estimates of *S* and other vital rates from the multistate models.

For the current analysis, we focused on estimating λ for the female segment of the population, due to the critical importance of female bears to reproduction and population

growth. For females, we estimated λ = 1.02 (95% CI = 0.98-1.06) for the period 2001-2010. This is based on the most-supported female model M3 and likely represents the most reliable assessment of recent population trend, suggesting that the female population remained stable or increased slightly during the last decade. Although this estimate reflects both natural and purposeful human-caused mortality, it applies to females only and does not reflect potentially lower λ for male bears due to the effects of male-biased harvest mortality, as suggested by higher estimates of *H* for males compared to females (the mean observed population growth rate for the entire population over the 2001-2010 period, calculated from the abundance estimates as described above, was 0.99). For comparison, a similar estimate of λ = 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 λ for females are robust to the model selection process and that the most-supported model did not exclude, on statistical grounds, potential biologically-meaningful effects on reproductive parameters of the limited number of sea ice metrics that we evaluated.

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 projected trend of the WH subpopulation, given a range of relevant but hypothetical future sea ice conditions. This approach assumed that the relationship between ice covariates and demographic parameters as estimated from the 1984-2011 data will remain stable, as would other factors such as the level of human-caused removals. For the combined female and male projections, we used parameter estimates from a male model that included sea ice effects on survival, as in females, to reflect their potential biological importance, despite sea ice covariates not being supported during the model selection procedure. If future sea ice conditions are 'high', as represented by a subset of sea ice conditions observed from 1984-2010, the long-term population growth rate is estimated to be approximately λ = 1.02, or 2% population growth per year. Similarly, if sea ice conditions are 'low', long-term population growth rate is estimated to be approximately λ = 0.97, representing a 3% population decline per year.

DISCUSSION

Population trend

Our updated analysis suggested that the growth rate of the WH subpopulation has, overall, been negative 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 was correlated from year-to-year with survival of all age and reproductive categories of females, but not with annual reproductive rates (cub production and survival to first autumn). In contrast, the survival of male polar bears was not closely linked to sea ice, but was instead primarily a function of their age class. This may be a result of higher rates of direct human-caused mortality in males than females, which from year-to-year are based on management decisions rather than environmental variation and may lead to compensatory effects due to density dependence or the selective removal of animals in poorer nutritional conditions. These results underscore the importance of considering environmental factors within demographic population models in order to account for important drivers of demographic rates.

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; IUCN/SSC Polar Bear Specialist Group 2013) and case studies continue to improve our understanding of the complexity of the species' response to ecological change (Peacock *et al*. 2012; Rode *et al*. 2012, 2013). This study represents one of the longest-term and highest-resolution analyses of polar bear demography to date, providing insight into how demographic changes may occur and providing additional evidence for linkages between sea ice conditions and polar bear survival. The matrix projection model results suggest that the lack of a negative trend in spring sea ice break-up date from 2001-2010 resulted in a stable female population, and this was generally supported by the relatively stable abundance estimates, suggesting consistency between these two different (but not independent) methods of inference. It is likely that this period of relative stability in sea ice conditions allowed for sufficient survival and reproduction that human-caused removal 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 (Joly *et al*. 2011), suggests that the long-term population trend is likely to be negative. However, our results suggest that the WH population is able to respond positively when climatic and sea ice conditions improve; assuming that the abundance and availability of prey populations also respond similarly. This highlights the sensitivity of population projections to assumptions about future environmental conditions and the relationships linking the environmental conditions to vital rates.

The estimates of total apparent survival used in matrix models represent the probability of remaining alive and in the study area. Permanent emigration out of the study area will result in estimates of apparent survival that are lower than natural survival, which may introduce negative bias into population projections if not compensated by including estimates of immigration into the study area. Temporary movement out of the study area can also result in biased survival estimates in some cases (Kendall *et al*. 1997). The degree to which movements have introduced bias into survival estimates in our case is not known, but the strong site fidelity of these bears during autumn (Derocher and Stirling 1990; Stirling *et al*. 2004; Cherry *et al*. 2013), combined with periodic captures of bears outside the study area (e.g., in Area D) likely minimizes these effects.

Abundance of the effective study population

It is important to estimate both the actual number of polar bears within the WH subpopulation (e.g., point estimates of population size) and the trend in numbers over time (i.e., population growth rate) to inform harvest management decisions. Abundance can be estimated using different approaches, such as capture-recapture analysis and aerial surveys, which provide different temporal and spatial perspectives and involve different assumptions and caveats. The estimates of abundance developed using the current capture-recapture framework are defined with respect to the effective study population – which may be different than the population as defined from biological or management perspectives – and depend on the spatial coverage of the capture-recapture sampling area, the timing of capture-recapture sampling, and the movement of animals in and out of this area over multiple years. Estimates of abundance from capture-recapture studies may also be influenced by other factors resulting

in un-modeled capture heterogeneity, which can introduce bias that is generally negative (Schaub *et al*. 2004). Although we do not know the degree to which our abundance estimates may be biased, we do not think it was a significant factor in this analysis because the estimated *p*-values were reasonably high and because we tried to minimize the potential effects of capture heterogeneity by including several covariates (*telemetry*, *Churchill*) and both state and age effects in the models.

Previous capture-recapture analyses for the WH subpopulation (Lunn *et al*. 1997; Regehr *et al*. 2007) considered estimates of abundance to reflect the population as defined from a biological or management perspective, which was based on earlier observations that relatively few polar bears exhibited consistently high fidelity to areas of the coast that were outside of the primary study area but still within the WH management boundary (Derocher and Stirling 1990; Stirling *et al*. 2004). However, a recent aerial survey (Stapleton *et al*. 2014) found evidence for significant numbers of bears located outside the EC sampling area to the east of the Nelson River in 2011, and estimated a larger size for the population of polar bears inhabiting the WH management area. Comparison of the 2011 point estimate of 806 (95% CI = 653-984) from this study with the estimate of 1030 (95% CI = 754-1406) from the 2011 aerial survey 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 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 (a much smaller area than that covered by the aerial survey; defined as the "superpopulation"; e.g., Williams *et al*. 2002). Furthermore, the 2011 population size estimates from the two approaches cannot definitively be said to be different, as evidenced by overlap in their confidence intervals. We suggest that considering results from the capture-recapture and aerial surveys together, keeping the strengths and limitations of each method in mind, provides a more complete picture of the distribution, status, and trend of the WH population.

Influence of sea ice conditions on survival

We found that survival of female polar bears in all age classes was correlated with the

timing of sea ice break-up, freeze-up, and the interaction of break-up and freeze-up. This is consistent with previous studies that linked body condition 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 the WH subpopulation (Stirling and Derocher 1993, 2012; Derocher *et al*. 2004; Molnár *et al*. 2010; Peacock *et al*. 2010; Molnár *et al*. 2011; Castro de la Guardia *et al*. 2013) because population growth rate for polar bears and similar long-lived animals depends primarily on survival and productivity of adult females (e.g., Hunter *et al*. 2010).

Trends of declining sea ice duration and declines in polar bear survival and reproduction have also been documented in the Southern Beaufort Sea subpopulation (Regehr *et al*. 2010; Rode *et al*. 2010). Correlations between sea ice and body condition in the Baffin Bay and Davis Strait subpopulations suggest environmental conditions can limit the nutritional status and productivity of polar bear populations (Rode *et al*. 2012), although the role of density effects are poorly understood, especially in Davis Strait where polar bear abundance has increased (Peacock *et al*. 2013). Environmental limitation itself is a natural and ubiquitous phenomenon required to maintain populations within the range of environmental carrying capacity; it becomes a conservation concern when carrying capacity exhibits long-term declines such as appears to be the case for the WH and Southern Beaufort Sea subpopulations. In the Chukchi Sea subpopulation, polar bears appear to have maintained body condition and reproduction over a 20-year period despite large declines in sea ice (Rode *et al*. 2013), possibly due to high biological productivity, the relatively recent advent of ice-free days in preferred polar bear habitats over the continental shelf, or density effects associated with previously high levels of human-caused removals. In the Northern Beaufort Sea and SH subpopulations, demographic analyses suggested equivocal or absent support for relationships between survival and ice conditions, respectively, although concerns remain regarding the likelihood of negative effects of continued sea ice loss on polar bears in both subpopulations (Stirling *et al*. 2011; Obbard *et al*. 2007). 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; Castro de la Guardia *et al*. 2013).

Despite the growing body of literature on marine mammal responses to 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), predicting long-term demographic changes is difficult. The relationships we detected between sea ice and polar bears in western Hudson Bay may change over time. For example, there may be critical thresholds for the length of the fasting period, which for WH polar bears is determined by sea ice conditions, beyond which bears cannot accumulate sufficient body fat to survive and reproduce (Robbins *et al*. 2012). Furthermore, while the availability of ringed seals, the main prey of polar bears in Hudson Bay, is likely to be negatively affected by climate change (Ferguson *et al*. 2005), there are insufficient data available to assess how or at what rate these and other changes at lower trophic levels will further impact polar bears (Stirling and Derocher 2012). We suggest that variability in relationships between sea ice and polar bear population status that have been estimated to date, as well as uncertainty about the future form of such relationships, does not diminish long-term concerns (e.g., Amstrup *et al*. 2008; Stirling and Derocher 2012) based on forecasts of continued sea ice loss (Holland *et al*. 2006; Zang and Walsh 2006; Stroeve *et al*. 2007, 2012) and the fundamental reliance of polar bears on sea ice as a platform from which to access energy-rich marine prey (Amstrup 2003). Case studies such as the current analyses are key to understanding the complexities of such relationships and providing managers with the information necessary to develop conservation plans that reflect both nearer-term variation and longer-term concerns.

Influence of sea ice and harvest on male polar bear 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, we did not detect a relationship between survival of male bears and sea ice conditions. There are a number of possible explanations. First, in recent years these relationships may have relaxed given relatively stable sea ice conditions. Second, the current approach of modeling female and male data separately

may have improved our ability to detect sex-specific effects. Third, the direct inclusion of detailed data on human-caused mortality may have had an impact on the estimation of these effects. In particular, the number of male bears killed by humans (the probability of a dead male bear having died due to direct human causes ranged from 0.24 to 0.73, depending on age; Table 8) may be sufficiently large to incur compensatory effects that dampen fluctuations in natural survival due to environmental variation, making relationships between survival and sea ice difficult to detect. Harvest occurs primarily in the autumn as bears move northward along the coast of western Hudson Bay in anticipation of freeze-up. The selection for males in the harvest, combined with the tendency for nutritionally stressed bears to approach human settlements where they are exposed to harvest, could effectively remove a large proportion of younger males that otherwise would have been susceptible to natural mortality in the coming winter, thus making harvest at least partially non-additive to natural mortality. In addition, larger adult male polar bears may be more buffered from environmental fluctuations compared to females because of the extra energetic demands on females raising cubs. Based on body mass and fat content of WH polar bears collected in the 1980s and 1990s, Robbins *et al*. (2012) estimated that adult males can spend twice as long fasting (240 days) as lactating females (120 days) before starvation occurs. This suggests that fully-grown adult males have lower size-specific 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 reproduction

We did not find that reproduction was correlated with varying sea ice conditions over the period 1984-2011. This may have been influenced by heterogeneity in the breeding probability of FnY individuals, as they included both single adult females that were potentially pregnant and able to produce COY the following year and adult females with dependent yearlings that were unlikely to be pregnant. This state simplification was necessary to avoid building a model including state uncertainty, which would have significantly increased the number of unobservable stages to consider. It would have likely decreased statistical power to detect patterns in survival, the primary driver of population dynamics for polar bears, and raised identifiability problems (Gimenez *et al*. 2009). Consequences of this approach may have

been reduced ability to detect temporal variation in breeding probability (*B*), as well as a nuanced interpretation of *B*. As *B* was estimated for a mixed group of females that included some individuals that were physiologically incapable of being pregnant, due to their continued care for yearlings, the parameter cannot be interpreted directly as the probability of breeding for single adult females. These issues should not introduce bias into estimates of *B* or overall estimates of population growth rate from matrix projection models, although use of time-constant *B* might slightly obscure temporal patterns in population growth rate over the course of the study. We also note that effects on breeding probability may be inherently more difficult to detect, because breeding probability is estimated from a smaller group of bears (only those bears in the FnY state) and so may have less statistical precision, whereas survival is estimated for all bears. Comparisons of observations of mean litter size in FB, SH, and WH in the early 2000s (Peacock *et al*. 2010) and more recently (Stapleton *et al*. 2014) indicate that the WH subpopulation is currently less productive. The relatively low number of cubs recorded during the 2011 WH aerial and coastal surveys was noted by Stapleton *et al*. (2014).

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 that are influenced by factors such as biological productivity. We recommend that future research efforts consider incorporating a mechanistic energetics model within the demographic framework used to project future population status (e.g., Molnár *et al*. 2010).

Integrating population information from multiple sources at different spatial and

temporal scales is necessary to effectively understand the status and trend in 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 provides additional evidence of the sensitivity of the population trends in Western Hudson Bay to changes in sea ice conditions.

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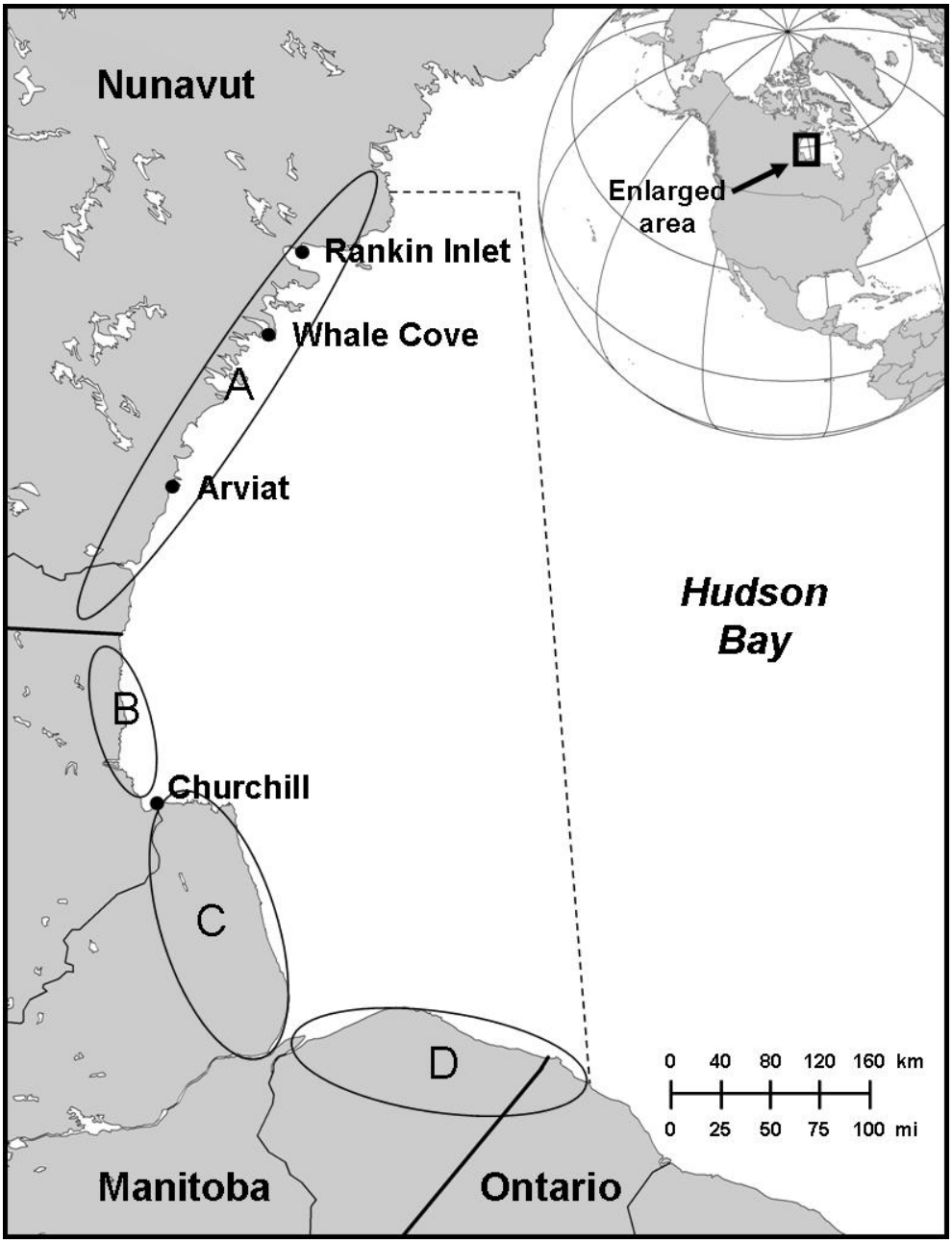

Figure 1. Map of Hudson Bay showing the management boundary of the Western Hudson Bay polar bear subpopulation (dashed line) and areas of research and survey effort. Most of the capture-recapture data come from animals handled in Area C (study area), with limited captures in Area B. Geographic coverage for capture-recapture data was extended to include Area D in 1984-86, 1994-95, and 2003-05 for animals that had first been captured in Areas B and C. The 2011 aerial survey covered the Areas A, B, C, and D (Stapleton *et al.* 2014).

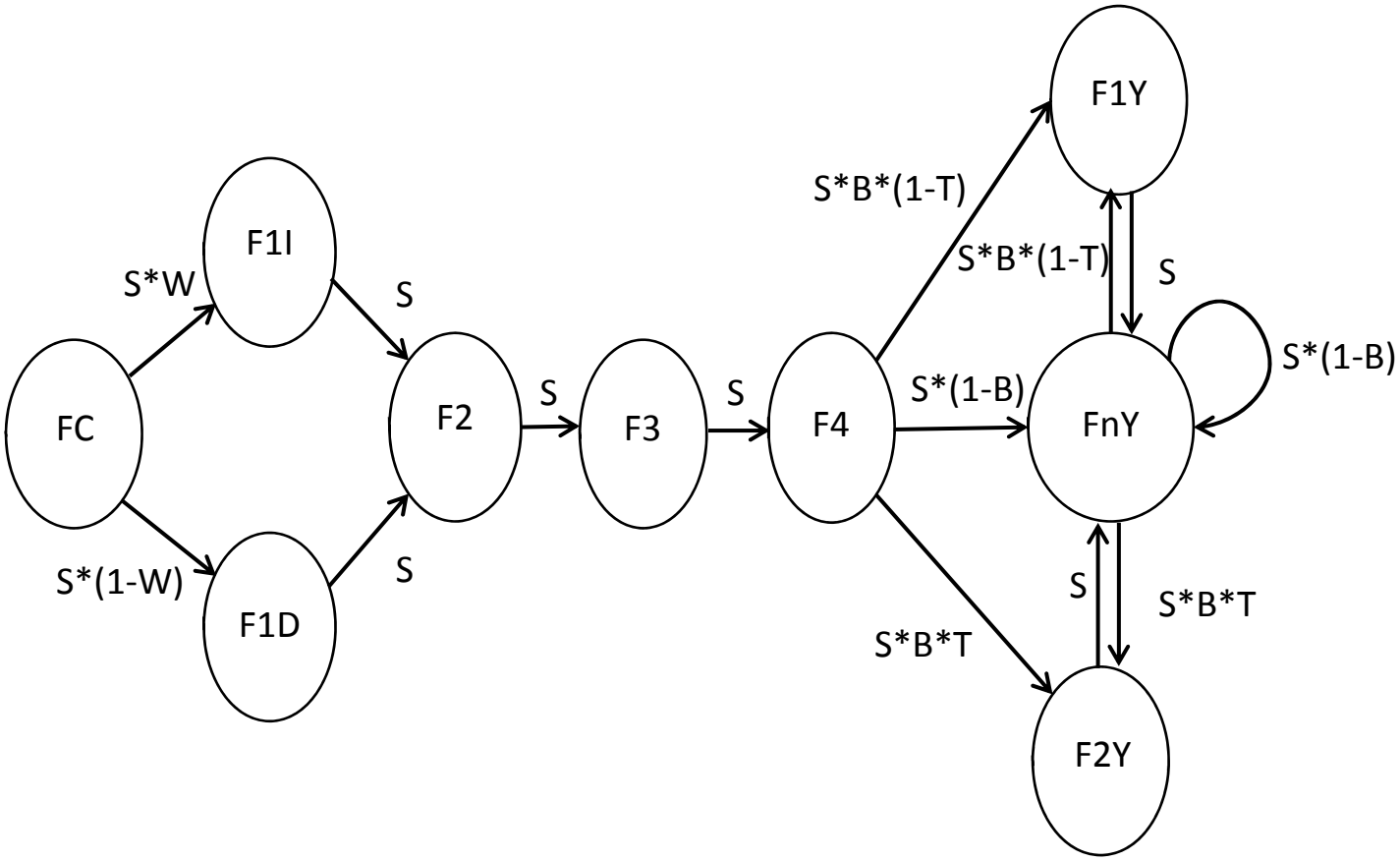

Figure 2. Multistate model structure for the female compartment. Parameters are defined in Table 1.

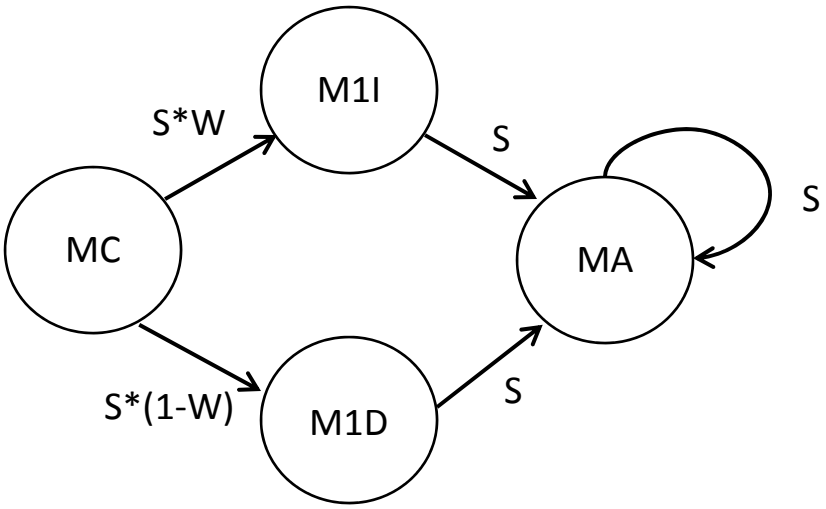

Figure 3. Multistate model structure for the male compartment. Parameters are defined in Table 1.

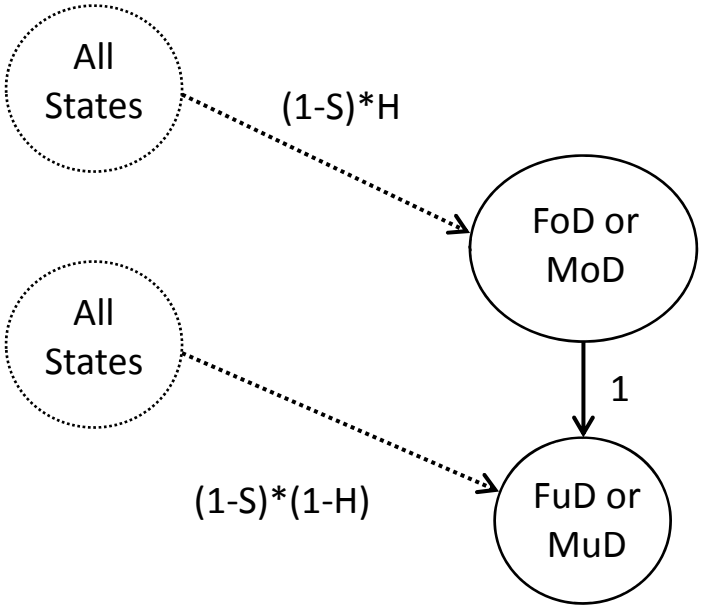

Figure 4. Multistate model structure for mortality. Parameters are defined in Table 1.

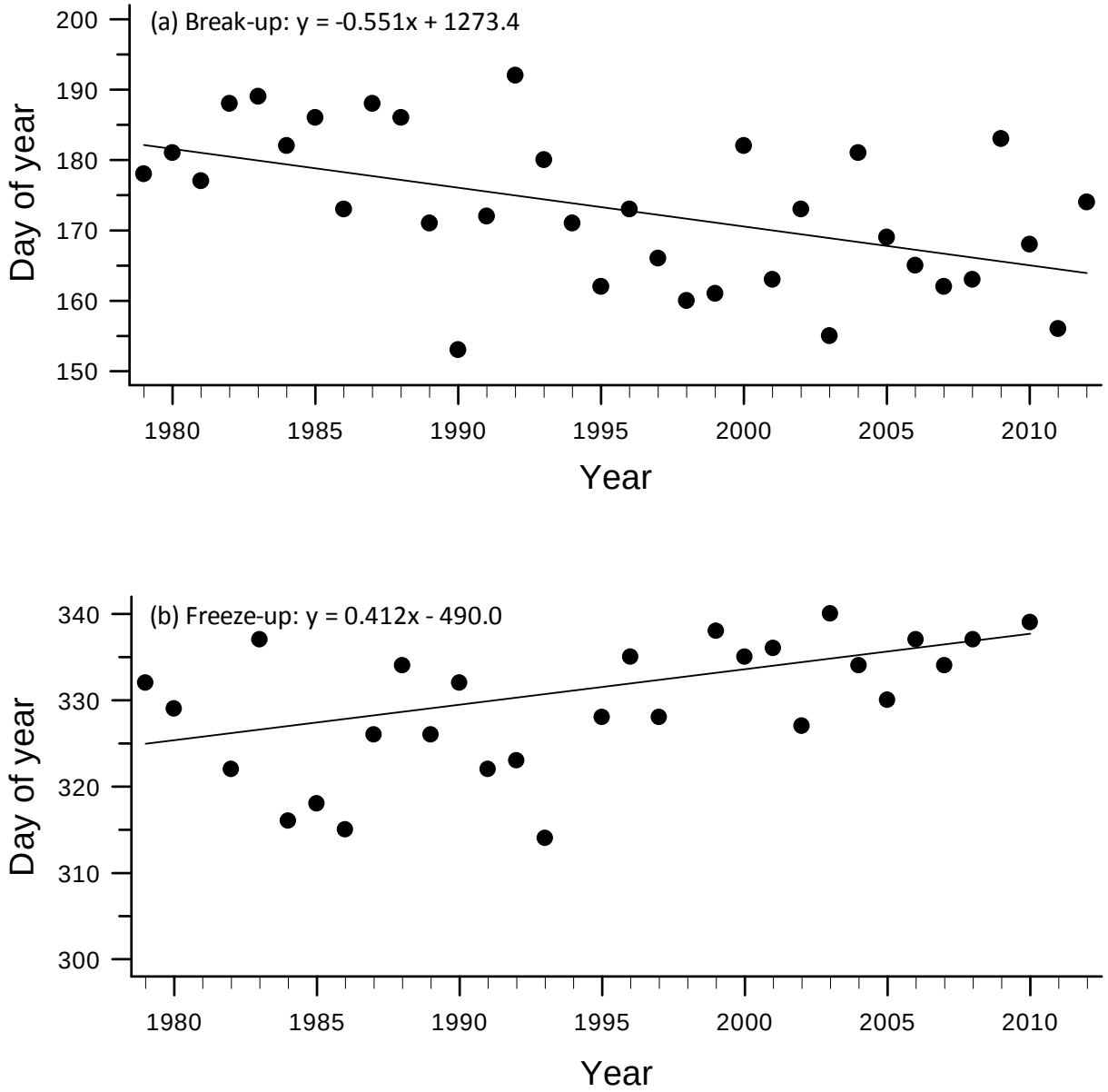

Figure 5. Date of (a) sea ice break-up (50% sea ice concentration) in spring and (b) sea ice freeze-up (50% sea ice concentration) in autumn in western Hudson Bay from 1979-2012, estimated from passive microwave satellite imagery (data source: National Snow and Ice Data Center, Boulder, Colorado; http://nsidc.org).

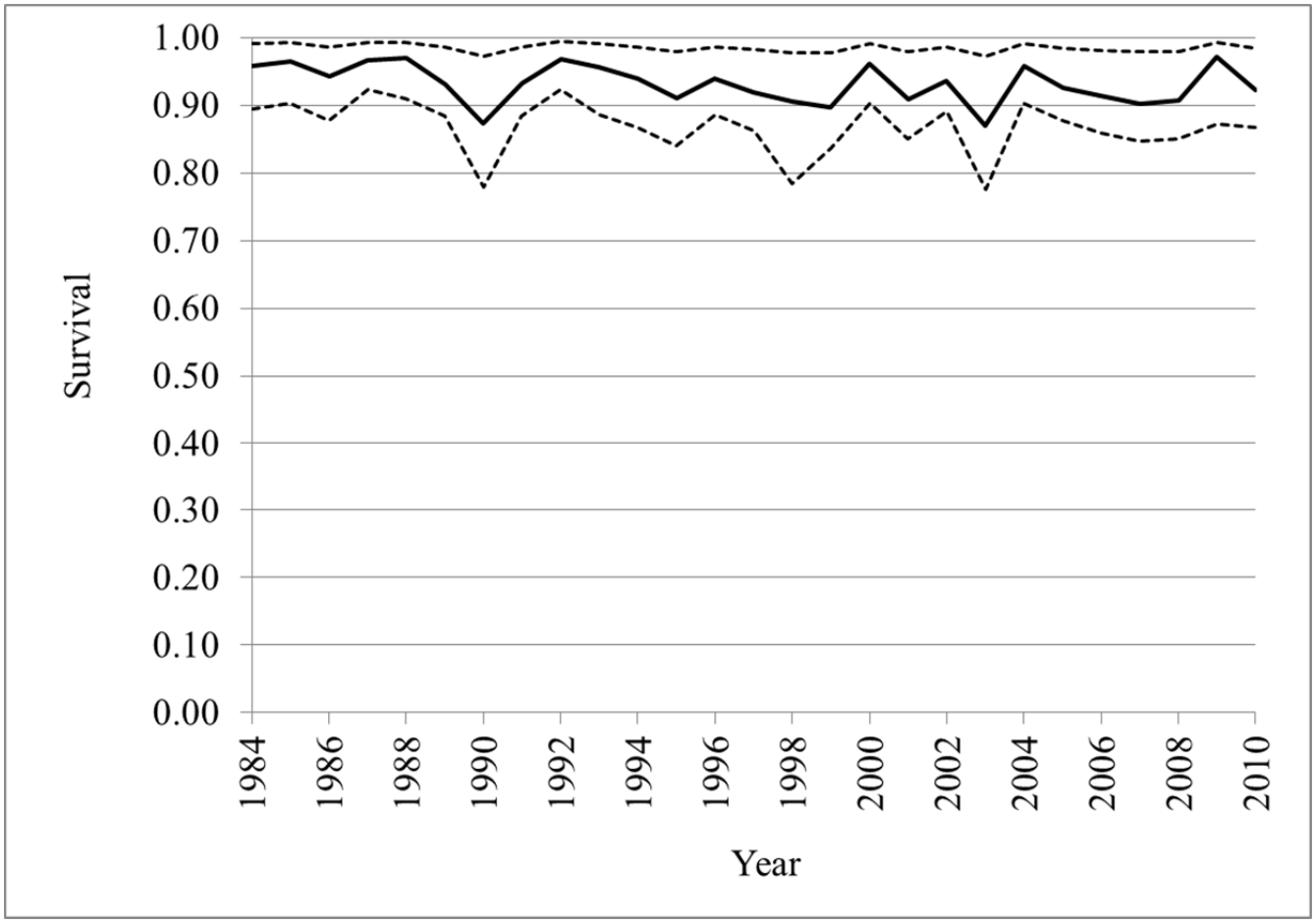

Figure 6. Total apparent survival for adult females aged 5-19 years old and without COYs, estimated from live-recapture and dead-recovery data for the Western Hudson Bay polar bear subpopulation from 1984-2011 using multistate capture-recapture models. This study showed that interannual variation in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

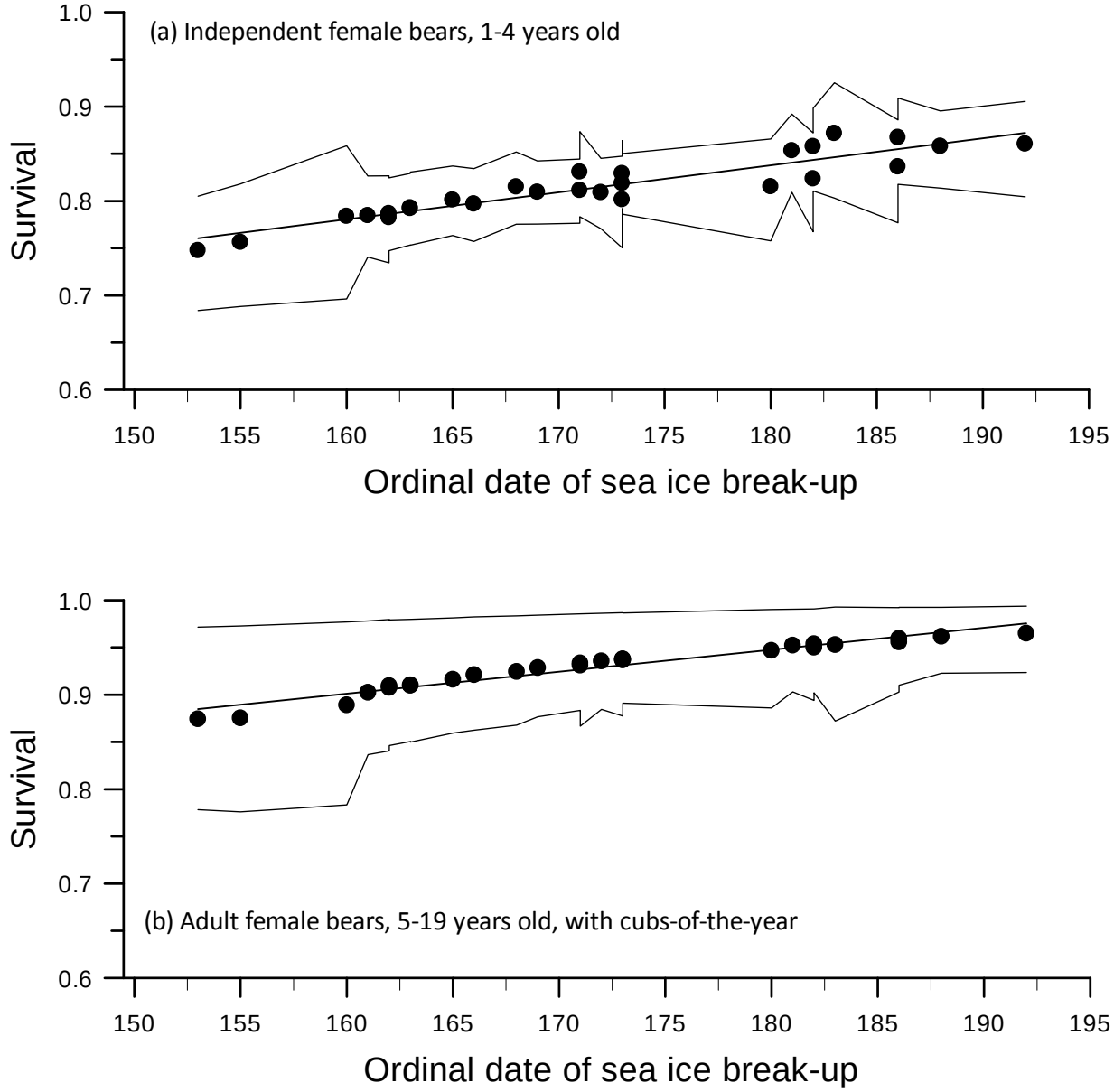

Figure 7. Survival rates of (a) independent female polar bears 1-4 years old and (b) adult female bears 5-19 years old with cubs-of-the-year in relation to date of sea ice break-up, western Hudson Bay, 1984-2011.

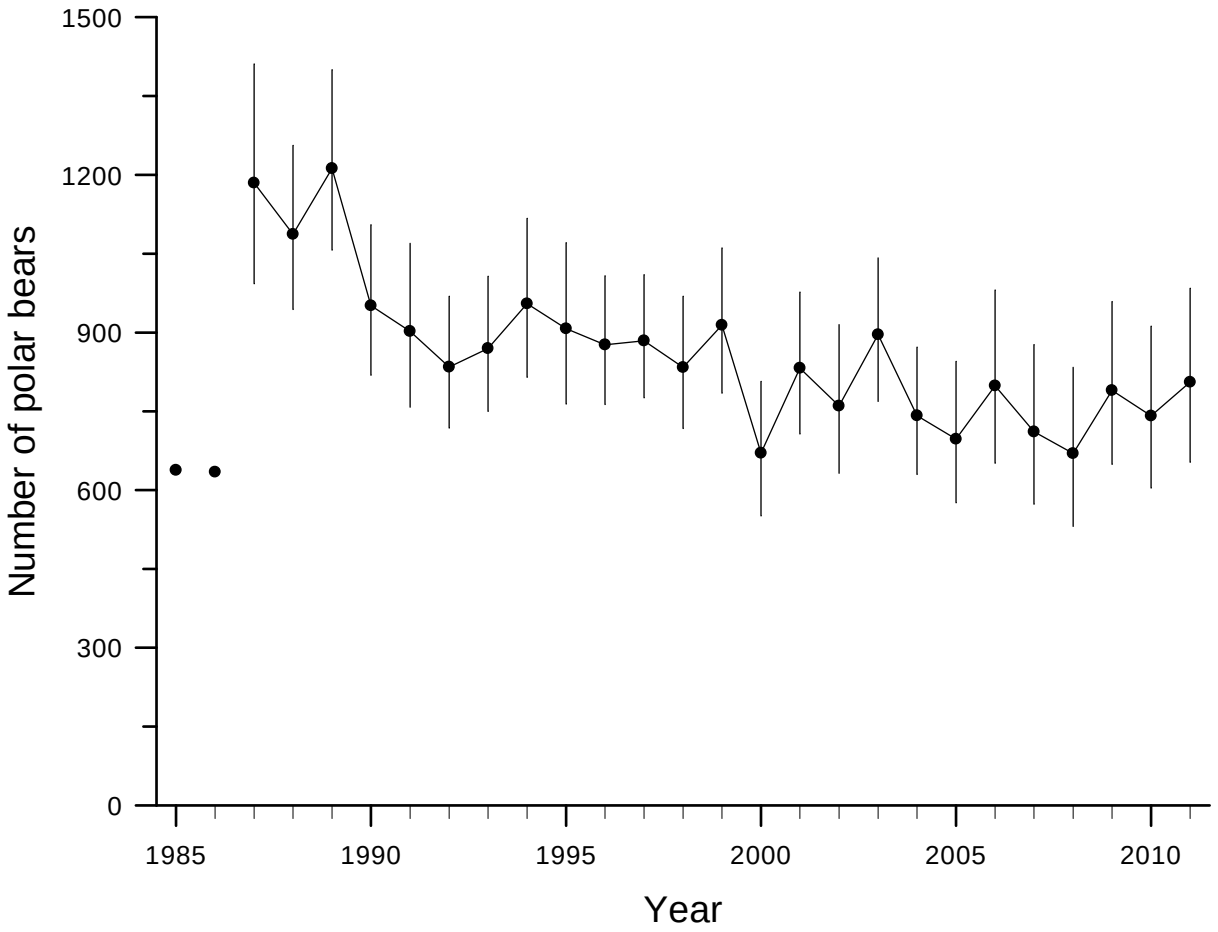

Figure 8. Estimated population size, derived by applying a Horvitz-Thompson estimator using recapture probabilities estimated from live-recapture and dead-recovery data for the Western Hudson Bay polar bear subpopulation from 1984-2011, using multistate capture-recapture models. Point estimates of abundance 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
S	Total apparent survival: the probability that an individual alive in the autumn of year *t* survives to the autumn of year *t+1* and does not permanently emigrate from the study population
W	Weaning: the probability that a dependent 9 mo. cub in the autumn of year *t* (state FC or MC) becomes an independent yearling in the autumn of year *t+1* (state F1I or M1I), conditional on survival
B	Breeding: the probability that an adult female gives birth in the spring of year *t* and that at least one member of a litter survives until the autumn of year *t*
T	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
H	Human-caused mortality: the probability that an individual that dies in the interval *t* to *t+1* was purposely killed by a human (e.g., subsistence harvest or defense kill)
p	Recapture: the probability that an individual was recaptured and released alive on sampling occasion *t*, 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
age.male 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 (≥ 20 yr).
age.female 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 (≥ 20 yr).
churchill	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.
telemetry	Individual and time-varying covariate, applied only to adult females ≥ 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.
break-up	Julian date for calendar year *t* on which sea ice extent in the Western Hudson Bay management area declined below 50% coverage.
freeze-up	Julian date for calendar year *t* on which sea ice extent in the Western Hudson Bay management area increased to above 50% coverage.
ice decay	Absolute value in calendar year *t* for the slope of the ice decay function between May 1 and the date on which the Western Hudson Bay management area is completely ice-free.
random time	A random effect of year, included only in the model of detection probability.

Table 3. Stepped model selection for 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(State/age effect + Churchill recap + telemetry + random time) S = f(State/age effect) H = f(State/age effect) B = f(State/age effect) T, W
Second step: Selection of the best model for survival	
Model notation	Effects included in survival
M2	S = f (State/age effect + Break-up)
M3	S = f (State/ age effect + Break-up + Freeze-up + Break-up * Freeze-up)
M4	S = f (State/ age effect + Break-up + Ice decay + Break-up * 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 (State/age effect + Churchill hunting)
Fourth step: Selection of the best model for the probability to reproduce and have a live 9mo old cub	
Model notation	Effect included in the probability to reproduce and have a live 9mo old cub
M6	B = f(State/age effect + Break-up)
M7	B = f(State/age effect + Break-up + Ice decay + Break-up * 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(State/age effect + 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(Break-up)

Table 4. Stepped model selection for 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(State/age effect + Churchill recap + random time)
	S = f(State/age effect)
	H = f(State/age effect)
	W
Second step: Selection of the best model for survival	
Model notation	Effects included in survival
M2	S = f(State/ age effect + Break-up)
M3	S = f (State/age effect + Break-up + Freeze-up + Break-up * Freeze-up)
M4	S = f (State/ age effect + Break-up + Ice decay + Break-up * 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(State/age effect + 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(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 (see also Table 3).

First step: Selection of the best model for survival					
Model	Effects included in survival	Deviance	(Variance deviance)/2	DIC	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 human-related mortality					
Model	Effects included in human-related mortality while using the best model for survival (model M3)	Deviance	(Variance deviance)/2	DIC	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 breeding					
Model	Effects included in probability of breeding while using the best model for survival and human-related mortality (model M3)	Deviance	(Variance deviance)/2	DIC	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	Effects included in probability of twinning while using the best model for probability of survival, human-related mortality and probability of breeding (model M3)	Deviance	(Variance deviance)/2	DIC	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	Effects included in probability of weaning while using the best model for survival, human-related mortality, probabilities of breeding and twinning (model M3)	Deviance	(Variance deviance)/2	DIC	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 (see also Table 4).

First step: Selection of the best model for survival					
Model	Effects included in survival	Deviance	(Variance deviance)/2	DIC	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 human-related mortality					
Model	Effects included in human-related mortality while using the best model for survival (model M1)	Deviance	(Variance deviance)/2	DIC	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	Effects included in probability of weaning while using the best model for survival and human-related mortality (model M1)	Deviance	(Variance deviance)/2	DIC	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.

	Female		
Age class	*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
≥ 20 yr without COY	0.77	0.71	0.82
≥ 20 yr with COY	0.89	0.73	0.99

	Male		
Age class	*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
≥ 20 yr	0.72	0.67	0.76

Table 8. Estimates of the probability of human-related mortality conditional 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.

	Female		
Age class	*H* (mode)	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

	Male		
Age class	*H* (mode)	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.

	Female		
Age class	*B* (mode)	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
≥ 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 (λ)	Lower 95% CI	Upper 95% CI
female	high	10	1.02	0.98	1.05
female	high	20	1.02	0.99	1.04
female	high	50	1.02	1.00	1.05
female	low	10	0.97	0.85	1.02
female	low	20	0.96	0.85	1.01
female	low	50	0.97	0.92	1.01
female and male	high	10	1.02	0.99	1.05
female and male	high	20	1.02	0.99	1.05
female and male	high	50	1.02	1.00	1.05
female and male	low	10	0.96	0.85	1.01
female and male	low	20	0.96	0.88	1.01
female and male	low	50	0.97	0.92	1.01