

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/316322637>

Lunn, N.J., Servanty, S., Regehr, E.V., Converse, S.J., Richardson, E., Stirling, I. Population dynamics of an apex predator near the southern edge of its distribution – impacts of...

Article · January 2016

CITATIONS

0

READS

190

1 author:



[Ian Stirling](#)

University of Alberta

318 PUBLICATIONS **15,123** CITATIONS

[SEE PROFILE](#)

Demography of an apex predator at the edge of its range: impacts of changing sea ice on polar bears in Hudson Bay

NICHOLAS J. LUNN,^{1,6} SABRINA SERVANTY,^{2,3} ERIC V. REGEHR,⁴ SARAH J. CONVERSE,³
EVAN RICHARDSON,¹ AND IAN STIRLING^{1,5}

¹Wildlife Research Division, Science & Technology Branch, Environment and Climate Change Canada,
CW405 Biological Sciences Centre, University of Alberta, Edmonton, Alberta T6G2E9 Canada

²Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, Colorado 80523 USA

³Patuxent Wildlife Research Center, US Geological Survey, 12100 Beech Forest Road, Laurel, Maryland 20708 USA

⁴Marine Mammals Management, US Fish and Wildlife Service, 1011 East Tudor Road, Anchorage, Alaska 99503 USA

⁵Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G2E9 Canada

Abstract. Changes in the abundance and distribution of wildlife populations are common consequences of historic and contemporary climate change. Some Arctic marine mammals, such as the polar bear (*Ursus maritimus*), may be particularly vulnerable to such changes due to the loss of Arctic sea ice. We evaluated the impacts of environmental variation on demographic rates for the Western Hudson Bay (WH), polar bear subpopulation from 1984 to 2011 using live-recapture and dead-recovery data in a Bayesian implementation of multistate capture–recapture models. We found that survival of female polar bears was related to the annual timing of sea ice break-up and formation. Using estimated vital rates (e.g., survival and reproduction) in matrix projection models, we calculated the growth rate of the WH subpopulation and projected population responses under different environmental scenarios while accounting for parametric uncertainty, temporal variation, and demographic stochasticity. Our analysis suggested a long-term decline in the number of bears from 1185 (95% Bayesian credible interval [BCI] = 993–1411) in 1987 to 806 (95% BCI = 653–984) in 2011. In the last 10 yr of the study, the number of bears appeared stable due to temporary stability in sea ice conditions (mean population growth rate for the period 2001–2010 = 1.02, 95% BCI = 0.98–1.06). Looking forward, we estimated long-term growth rates for the WH subpopulation of ~1.02 (95% BCI = 1.00–1.05) and 0.97 (95% BCI = 0.92–1.01) under hypothetical high and low sea ice conditions, respectively. Our findings support previous evidence for a demographic linkage between sea ice conditions and polar bear population dynamics. Furthermore, we present a robust framework for sensitivity analysis with respect to continued climate change (e.g., to inform scenario planning) and for evaluating the combined effects of climate change and management actions on the status of wildlife populations.

Key words: abundance; Bayesian; climate change; Hudson Bay, Canada; multistate capture–recapture; polar bear (*Ursus maritimus*); population growth rate; reproduction; sea ice; survival; *Ursus maritimus*.

INTRODUCTION

Environmental conditions shape ecosystems and influence the evolution of life-history strategies. While many species are adapted to interannual variation in environmental conditions, in recent decades, increased variation coupled with rapid warming has impacted the earth's physical and biological systems (IPCC [Intergovernmental Panel on Climate Change] 2014). Sensitivity and resilience to climate change is expected to vary across species (Bellard et al. 2012), and species that are slow to adapt or highly specialized appear particularly vulnerable (Davies et al. 2004, Pacifici et al. 2015).

Polar bears (*Ursus maritimus*) are distributed throughout the ice-covered waters of the circumpolar Arctic and

rely on sea ice as a platform from which to hunt seals, their primary prey (Stirling and Øritsland 1995, Laidre et al. 2008, Thiemann et al. 2008). Although polar bears still occupy much of their historic range (PBSG [IUCN/SSC Polar Bear Specialist Group] 2015), the Arctic has been warming more rapidly than the global average, and the loss of Arctic sea ice is accelerating (Comiso 2002, Stroeve et al. 2012b). The unidirectional nature of sea ice loss, caused by anthropogenic forcing of the climate system, has raised long-term conservation concerns for Arctic marine mammals including polar bears (Wiig et al. 2008, Kovacs et al. 2011, Stirling and Derocher 2012, Derocher et al. 2013, Laidre et al. 2015).

Changes in the extent, character, and phenology of sea ice have the potential to influence the population ecology of polar bears (Stirling and Derocher 2012). Although declines in sea ice have been linked to declines in body condition, reproduction, survival, or abundance

Manuscript received 7 July 2015; revised 30 November 2015; accepted 1 December 2015. Corresponding Editor: P. Dayton.

⁶E-mail: nick.lunn@canada.ca

in several polar bear subpopulations (e.g., Obbard et al. 2006, Regehr et al. 2007, 2010, Peacock et al. 2012), similar relationships are not yet apparent for other subpopulations that have also experienced sea ice declines (Obbard et al. 2007, Stirling et al. 2011, Rode et al. 2014). Geographic variation in population ecology may reflect differences in biological productivity, differences in the magnitude and history of sea ice declines, and complex ecological interactions within and across trophic levels (Amstrup et al. 2010, Rode et al. 2014, Bromaghin et al. 2015). Improved understanding of relationships between environmental conditions and population dynamics is necessary to develop conservation and management plans that reflect both nearer-term variation and longer-term concerns.

The data required to develop such an understanding are lacking for most Arctic marine mammals. One exception is the ongoing research program on polar bears in western Hudson Bay, Canada (e.g., Stirling et al. 1977, 1999, Ramsay and Stirling 1988, Derocher and Stirling 1995, Regehr et al. 2007), where individually marked, free-ranging bears have been studied over three decades, providing an unparalleled opportunity to assess the demographic response of a marine mammal to climate change. The Western Hudson Bay (WH) subpopulation occurs near the southern limit of the species' range (PBSG [IUCN/SSC Polar Bear Specialist Group] 2015). Increasing spring temperatures in the region have resulted in trends toward earlier sea ice break-up and later freeze-up (Gagnon and Gough 2005, Stirling and Parkinson 2006, Hochheim et al. 2010), forcing WH polar bears to spend progressively longer periods on land (Cherry et al. 2013). Longer ice-free periods have been linked to declines in body condition, reproduction, survival, and abundance (Derocher and Stirling 1995, Stirling et al. 1999, Regehr et al. 2007). Regehr et al. (2007) estimated that abundance of the WH subpopulation declined by 22% from 1194 in 1987 to 935 in 2004; and that survival rates of cubs, subadults, and old bears (>20 years) declined 2–5% for each week earlier than average that the sea ice broke up. More recent studies have used energetic models to suggest that declines in productivity and population viability are likely to occur under predicted scenarios of sea ice loss (Molnár et al. 2010, 2011, 2014, Robbins et al. 2012). However, studies to date have not coupled estimated relationships between environmental variation and demographic rates with robust methods to project population responses as a function of future environmental conditions.

To address concerns about the impacts of sea ice loss on the WH subpopulation of polar bears, we undertook an analysis of data collected under multiple sampling and management protocols over the period 1984–2011. We estimated vital rates, and the relationships between vital rates and environmental conditions, using a Bayesian implementation of multistate capture–recapture models. These models allow for the specification of

biological or physiological states that can explain additional variation in the data by allowing demographic parameters to differ among states (Arnason 1972, Hestbeck et al. 1991, Kendall et al. 2006). Multistate models may thus allow a more powerful and higher-resolution assessment of the demographic consequences of environmental variation than single-state capture–recapture models (e.g., Regehr et al. 2007).

We used the long-term data set of individually marked WH polar bears and a Bayesian implementation of a multistate model (Converse et al. 2009, Kéry and Schaub 2012) to evaluate demography of the WH polar bear subpopulation, 1984–2011. Our specific objectives were to (1) estimate demographic parameters (e.g., survival rates, rates of mortality due to direct human-caused removals, reproductive rates, population size and its trend), (2) evaluate relationships between demographic parameters and sea ice conditions, and (3) project potential population outcomes under different sea ice scenarios, using a Bayesian Population Viability Analysis (Wade 2002, Kéry and Schaub 2012, Servanty et al. 2014).

METHODS

Study area

Hudson Bay (Fig. 1) is a relatively shallow inland sea that is ice-covered in winter and ice-free in summer (Hochheim et al. 2010). Based on extensive capture and harvest records of marked bears (Stirling et al. 1977, Taylor and Lee 1995), three subpopulations of polar bears are recognized in Hudson Bay; Foxe Basin (FB), Southern Hudson Bay (SH), and Western Hudson Bay (Peacock et al. 2010). During the open-water season, the WH subpopulation appears to be largely segregated from the SH subpopulation to the southeast and the FB subpopulation to the north, although all three mix to some degree on the sea ice during winter and spring (Stirling et al. 1977, Derocher and Stirling 1990, Peacock et al. 2010).

WH polar bears come onshore ~21–28 d after sea ice coverage drops to 30–50% (Stirling et al. 1999, Cherry et al. 2013) and exhibit strong fidelity to terrestrial summering areas, where they segregate by sex, age, and reproductive status: adult males remain along the coast, pregnant females and females accompanied by young move into an interior denning area, and subadult bears are generally distributed throughout the core summering area (Stirling et al. 1977, Derocher and Stirling 1990, Cherry et al. 2013). Although the WH management unit is considerably larger than the core summering area (Fig. 1, Area C), relatively few polar bears show consistent fidelity to regions outside of Area C (Derocher and Stirling 1990, Stirling et al. 2004, but see Stapleton et al. 2014). Polar bears return to the sea ice when it reforms in November or December, except pregnant females, who remain onshore, give birth in terrestrial dens, and return to the sea ice in late February and March (Stirling et al. 1977, Ramsay and Andriashek 1986).

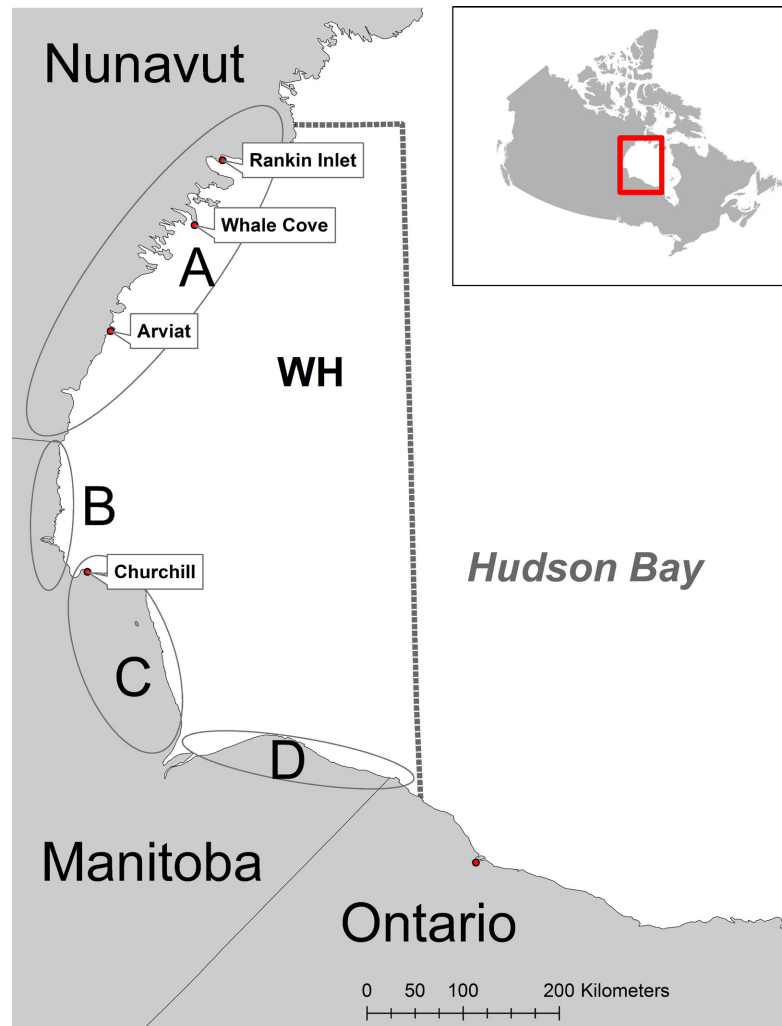


FIG. 1. Map of Hudson Bay, Canada showing the management boundary of the Western Hudson Bay polar bear (*Ursus maritimus*) subpopulation (dashed line) and areas of research and survey effort. Most of the capture-recapture data come from animals handled in Area C (core summering area). Geographic coverage for capture-recapture data was extended to include Area B in 1999 and 2005–2011 and Area D in 1984–1986, 1994–1995, and 2003–2005 for animals that had first been captured in Area C. The 2011 aerial survey covered the Areas A, B, C, and D (Stapleton et al. 2014).

Field methods and data sources

We analyzed live-encounter and dead-recovery data collected from multiple sources from 1984 to 2011. Each year between late August and early October, Environment Canada (EC) captured and released polar bears in Area C as part of ongoing, long-term research (e.g., Ramsay and Stirling 1988, Derocher and Stirling 1995, Stirling et al. 1999). The geographic distribution of sampling within this area was limited from 1984 to 1986 and was relatively evenly distributed since 1987 (Regehr et al. 2007). Additional sampling occurred in Area B in 1999 and 2005–2011 and in Area D in 1984–1986, 1994–1995, and 2003–2005.

During live-encounter research, free-ranging bears were located by helicopter, captured using standard

chemical immobilization techniques (Stirling et al. 1989), and individually marked using numbered ear tags and permanent tattoos. A vestigial premolar was extracted for age determination (Calvert and Ramsay 1988) from previously unmarked bears older than 1 yr. Aging of cubs-of-the-year (COY, ~9 months old in autumn) and yearling cubs (~21 months old in autumn) was based on body size and dentition. 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.

Very high frequency (VHF) radio collars (Advanced Telemetry Systems, Isanti, Minnesota, USA; Telonics, Mesa, Arizona, USA) or satellite radio collars (Telonics) were deployed on some adult females as part of the

long-term research. Most VHF collars remained active for 5 yr and satellite collars for 2 yr. To account for the influence of radio collars on detection probabilities, we derived a time-varying individual covariate, telemetry, to indicate when adult females were potentially available to be recaptured by telemetry, based on collar deployment date and battery life (Table 1); this was used in the modeling of detection probability. This approach did not account for some yearling cubs located by telemetry in association with their mother's collar because we did not know a priori which collared females had dependent young.

We also included data collected using similar methods to EC by University of Saskatchewan in 1989–1996 in Area C (e.g., Atkinson and Ramsay 1995); Ontario Ministry of Natural Resources in 1984–1986 and 2003–2005 in Area D; and Government of Nunavut in 2007 in Area A. To ensure that vital rates were estimated for a consistent study population, we only included live encounters of polar bears outside the core summering area (Area C) if they had been previously captured within it.

In addition to research data, we also included data from problem bears captured by Manitoba Conservation (MB) near the community of Churchill (Kearney 1989). Marking and data collection procedures were similar to those used by EC. Previous analyses suggested that handling in Churchill was correlated with lower survival and higher recapture probability (Regehr et al. 2007). To account for such effects, we derived a time-varying individual covariate, Churchill, which was set to zero prior to and including the sampling occasion on which a bear was first captured by MB and set to one on all subsequent sampling occasions (Table 1). This covariate was used in models of both detection probability and human-caused mortality.

Finally, we used data from research-marked polar bears taken as part of a legal, regulated subsistence harvest along the coast of western Hudson Bay in Area A (Derocher et al. 1997, Taylor et al. 2008).

Prior to analyses, we extracted a subset of the total data available based on criteria designed to achieve consistency with previous analyses and minimize heterogeneity. We considered data from 1984 to 2011 because EC and MB sampling protocols were relatively consistent over these years (see Regehr et al. 2007). We only included live captures that occurred within the period of 1 August to 15 November (~95% of total autumn live encounters) to minimize mortality or movements with respect to the core summering area within sampling periods. If an individual was encountered more than once in a year, but with different capture states (see *Multistate model structure*), 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., 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

TABLE 1. Covariates and effects used to explain variation in parameters estimated from live-recapture and dead-recovery data for the Western Hudson Bay, polar bear (*Ursus maritimus*) 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 zero if an individual had never been captured around the community of Churchill (Manitoba, Canada), and one for all sampling occasions following the first capture around Churchill.
Telemetry	Individual and time-varying covariate, applied only to adult females ≥ 5 yr. 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 of the slope of an ordinary least-squares regression of sea ice concentration against date from 1 May until the date on which the Western Hudson Bay management area was completely ice-free.
Random time	A random effect of year, included only in the detection probability.

adult female (i.e., a female with cubs-of-the-year vs. a female without) and did not otherwise include the dependent young in the data set.

We assigned numeric ages to 16 yearlings and 2-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 that was correlated with age for known-age bears).

We handled dead recoveries in two ways. First, individual capture histories were right-censored following inadvertent deaths during capture, so these infrequent removals did not affect parameter estimates. Second, we

included a “human-caused mortality” state for purposeful human-caused removals (i.e., harvested bears and problem bears). 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. We only included dead-recovery data for bears that were marked and encountered in the core summering area after 1984.

Sea ice

We used ArcInfo (Environmental Systems Research Institute, Redlands, California, USA) to extract sea ice concentrations from 25×25 km resolution passive microwave satellite raster imagery (NASA Team algorithm; Cavalieri et al. 1996, 2012) obtained from the National Snow and Ice Data Center (Boulder, Colorado, USA) for 1979–2011. Each grid cell in the imagery has an associated sea ice concentration value, which is an estimate of the fractional amount of sea ice covering that cell (Cavalieri et al. 1996). We calculated daily mean sea ice concentrations from 381 grid cells that provided complete coverage of the WH management zone. Three sea ice metrics were derived from the daily mean sea ice concentration: (1) break-up, the ordinal date in the spring on which sea ice reached and remained below 50% concentration for at least three consecutive days (Etkin 1991, Gagnon and Gough 2005, Stirling and Parkinson 2006); (2) freeze-up, the ordinal date in the autumn on which sea ice reached and remained above 50% concentration for at least three consecutive days; and (3) ice decay, the absolute value of the slope of an ordinary least squares regression of sea ice concentration against date from 1 May until the date on which the WH management zone was completely ice free. Correlations among these three variables were weak, with the exception of break-up and ice decay, for which the correlation coefficient was -0.93 .

Multistate model structure

We developed separate multistate model structures for males (four states) and females (nine states), where states represented age and reproductive status (Fig. 2). Transitions among states were defined by five demographic parameters. Female bears (Fig. 2a) could first enter the model as COY (~9-month-old cubs dependent on their mother; abbreviated FC). One year later, conditional on survival with probability S , these cubs either became independent (weaned; F1I) with probability W or remained dependent on their mother (F1D) with probability $1 - W$. Three subsequent states reflected annual age increases (F2, F3, F4) and transitions between these states were deterministic (i.e., the bear must get older), conditional on survival. Females in the F4 state transitioned the following year into one of three reproductive states, conditional on survival. Females

that did not breed (with probability $1 - B$) transitioned into the adult female with no cubs (FnY) state. Conditional on breeding, with probability B , females could be observed in autumn with two cubs in state F2Y with probability T or with a single cub in state F1Y with probability $1 - T$ (we make the reasonable assumption that any dependent cub will be seen if its mother is seen). Breeding was therefore defined as the product of the probabilities of giving birth to at least one cub in the spring and of having at least one cub survive until autumn. We assumed that bears in the state FnY were able to transition the next year to state F1Y or F2Y with probability B , although the FnY state actually included some bears that were incapable of this transition. In particular, any female that had dependent young in the previous spring, when copulations occur, could not produce a cub the following spring. While this could be determined in the case of bears that were observed with a dependent yearling, other bears may have had dependent young in the previous spring but not at the time of sampling, because their yearling weaned or died, or their cub died. Dealing with this complexity formally would have required increasing the model complexity to account for state uncertainty (Pradel 2005). While our approach allowed us to retain a simpler model structure, it introduced heterogeneity into the FnY state and meant that B represented an average breeding probability for all adult females without dependent cubs.

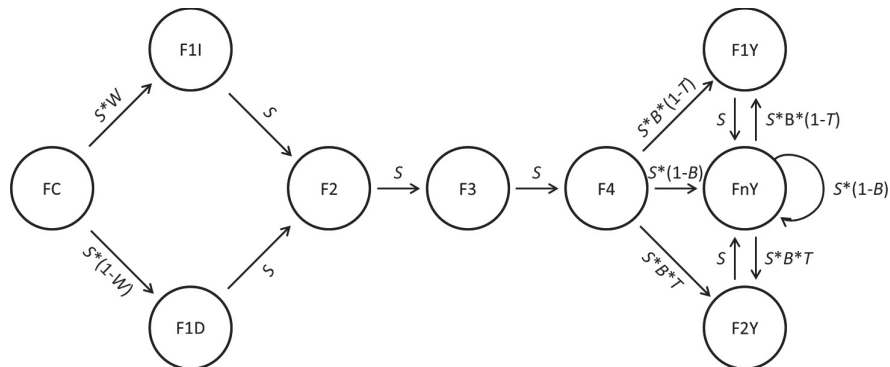
The state structure for males was simpler (Fig. 2b) and included states analogous to FC, F1I, and F1D (MC, M1I, and M1D, respectively). Beyond the age of 21 months, all males, conditional on survival, entered an adult state (MA). Using a single adult state did not preclude consideration of age-related variation within this state through the use of individual covariates, as described subsequently.

Female and male multistate structures included two death states (Fig. 2c), either of which could be entered from any live state, conditional on mortality ($1 - S$). The parameter S represented total apparent survival, the cumulative probability of remaining alive and in the core summering area. The two death states included an observable dead state (FoD, females; MoD, males), which bears entered with probability H , the probability that mortality was human-caused; and an unobservable dead state (FuD and MuD), with probability $1 - H$, if mortality was not human-caused. We assumed that all bears killed by humans were reported because of high compliance with reporting requirements for bears taken under the regulated subsistence harvest (Peacock et al. 2011) or for management purposes.

In summary, five types of demographic parameters controlled transitions among states: apparent survival probability (S ; probability of surviving and remaining in the core summering area), breeding probability (B ; probability that a female gives birth and at least one cub survives to autumn), twinning probability (T ; probability that a female that breeds has at least two cubs

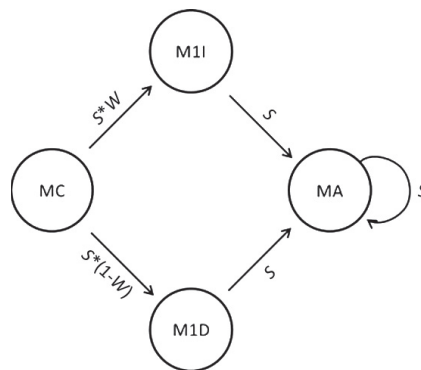
(a)

Females



(b)

Males



(c)

Mortality

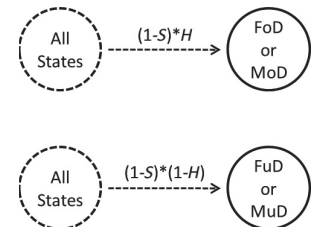


FIG. 2. Multistate model structure for (a) female polar bears, (b) male polar bears, and (c) mortality. Parameters are defined in Section: Multistate model structure.

that survive to autumn), weaning probability (W ; probability of a 9-month cub becoming independent by the following year), and probability that mortality is human-caused (H).

Model fitting and parameter estimation

We constructed candidate models that used the state structure in the life-cycle graphs along with covariates to represent temporal, group, or individual-based variation in demographic parameters based on polar bear biology, environmental conditions, and study design (Table 1). Age effects were represented by the state structure and, for states that included bears of multiple ages (MA, F1Y, F2Y, and FnY), through the use of individual covariates. We allowed for an interaction between age structure and environmental covariates to evaluate differing effects of ice conditions on bears that were either younger than 5 yr or older than 20 yr vs. those that were between the ages of 5 and 19 yr (i.e., prime-aged bears; Regehr et al. 2007). Sea ice covariates were

standardized by subtracting their mean and dividing by their standard deviation.

We completed model selection for each parameter in a stepped fashion (details in Appendix S1) based on deviance information criterion (DIC) calculated with Gelman's approximation (Gelman et al. 2004). In all steps, we used a general model for detection probability, p , which included state and age effects, random annual effects, and the telemetry (females only) and Churchill covariates. The stepped approach was used to select the top-ranked model structure for one demographic parameter, while using the selected structure for any parameters that had already been evaluated, and a general structure with state and age effects for the demographic parameters that had not yet been evaluated. By doing so, we focused on evaluating major sources of variation in the data based on a priori hypotheses about polar bear biology and study design, while reducing the number of computationally intensive models to fit. For females, we first selected the best model structure for survival (S), then human-caused mortality (H), breeding (B), twinning (T),

and finally weaning (W). For males, we first selected the best model structure for S , then H , and then W . A stepped model selection procedure is not guaranteed to find the globally optimal model, but evaluating all possible models is often, as in this case, infeasible due to the large number of possible models. A stepped strategy has been shown to provide reliable parameter estimates (Doherty et al. 2012).

The large size of the data set made it necessary to conduct analyses separately for females and males. We fitted 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). Computations were performed using JAGS 3.3.0 (Plummer 2003). The package rjags (Plummer 2013) was used to call JAGS and export results to the R computing environment (Version 2.14.2; R Development Core Team 2012). We used means and 95% Bayesian credible intervals (95% BCI) to summarize posterior distributions.

We used program U-CARE (Choquet et al. 2009) to evaluate goodness-of-fit for the multistate model. U-CARE tests the JollyMove model; a generalized multistate model with state memory, in which encounter probability can be a function of the previous state. We treated age groups as states in the analysis to account for both state and age structure in the model.

Abundance estimation

Estimates of abundance from open-population capture–recapture models apply to an effective study population defined as animals with a non-negligible probability of occurring in the study area during 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 it in any given year, but does not include animals with fidelity to other areas that were unlikely to be included in the capture sample.

We derived abundance estimates using capture probability estimates from our top-ranked multistate models for females and males. We estimated abundance at time t by fitting a Bayesian model in which counts of a given age/state group captured, and the MCMC-generated samples from the posterior distribution of detection probability (p) for that group, are treated as data in the model. Counts are modeled as binomially distributed with index N (equal to population size for that age/state group) and probability p . N is modeled as a Poisson variable, with the mean of the Poisson given an uninformative gamma-distributed prior (i.e., $a = 0.001$, $s = 0.001$). This approach resulted in estimates of abundance that reflected variation in both annual sample size

and detection probability. Because multistate models condition on first capture and therefore do not produce estimates of p for COYs, which were necessarily 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 as calculated from encounter histories (2.04 COYs, because this state included a few females with triplet litters).

Population projection modeling

We developed a post-breeding matrix-based population model (Caswell 2000) based on the female and male life cycle graphs (Fig. 2a,b) to estimate population growth rate using estimates of demographic parameters from the multistate capture–recapture models. This approach incorporates potential relationships between environmental covariates and demographic parameters and therefore allows population projections to be performed under various assumptions about environmental conditions. Our population projections reflected multiple types of uncertainty. Sampling uncertainty was accounted for through inclusion of the full parameter sampling distributions as represented by the samples in the MCMC chains. Demographic stochasticity was accounted for through inclusion of binomial trials for each demographic process (survival, 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 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 3-yr period 1985–1987, as calculated from captures in those years and detection probabilities in the top-ranked model. All projections retained observed correlations among sea ice variables (e.g., if break-up date was selected for year t , the corresponding freeze-up date was also selected). To summarize status of the WH subpopulation, we calculated the geometric mean of estimated annual population growth rates over periods of interest. We first ran the population model forward under observed sea ice conditions for a 20-yr period starting from 1991 through 2010.

We also evaluated population-level effects of hypothetical environmental conditions by projecting the 2011 population size forward in time 50 yr, under two sea ice scenarios. First, we ran a high sea ice scenario using values of sea ice variables sampled from the 1984–2010 time series that 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 relatively high availability of sea ice and

thus favorable environmental conditions for polar bears. Second, 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 (e.g., Stirling et al. 1999, Regehr et al. 2007, Molnár et al. 2010, 2011) have suggested may have negative effects on polar bears. All projections retained observed correlations among sea ice variables (e.g., if break-up date was selected for year t , the corresponding freeze-up date was also selected).

RESULTS

The modeled subset of WH data consisted of individual capture histories for 3034 polar bears, including 6224 live encounters and 519 purposeful human-caused removals. Of the live encounters, 493 were bears that were targeted for capture by telemetry. The covariate telemetry provided coverage for ~75% of telemetry encounters, suggesting that it explained most variation in p associated with radio and satellite telemetry. Approximately 34% of individual bears were encountered by MB at some point and, therefore, had nonzero entries in the Churchill covariates used to model variation in p and H .

All component GOF tests for both males and females were nonsignificant (Test WBWA females, $\chi^2 = 74.4$, $df = 138$; test WBWA males, $\chi^2 = 56.5$, $df = 74$; test

3G.SR females, $\chi^2 = 88.9$, $df = 199$; test 3G.SR males, $\chi^2 = 80.1$, $df = 122$; test 3G.SM females, $\chi^2 = 158.3$, $df = 461$; test 3G.SM males, $\chi^2 = 186.6$, $df = 332$) except for tests of immediate trap-dependence (test M.ITEC females, $G^2 = 39.6$, $df = 9$; Test M.ITEC males, $G^2 = 146.9$, $df = 37$) and longer-term trap-dependence (Test M.LTEC females, $G^2 = 8.3$, $df = 1$; Test M.LTEC males, $G^2 = 46.5$, $df = 14$). However, these goodness-of-fit tests cannot integrate individual covariates. We designed individual covariates expressly to deal with an anticipated problem of trap response (e.g., Churchill and telemetry covariates, Table 1) and, therefore, accepted the general model as a reasonable fit and did not include an over-dispersion parameter.

Sea ice

Sea ice phenology for western Hudson Bay over the period 1979–2011 showed a significant trend toward earlier break-up and later freeze-up (Fig. 3). The date of break-up has advanced 5.5 d per decade ($t = -3.359$, $P = 0.002$) and varied from 2 June to 11 July, with a mean of 22 June (standard error [SE] = 1.8 d). The date of freeze-up has been occurring 4.1 d 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 d). Over the last decade of our study (2001–2010), the mean date of break-up was 18 June (SE = 2.8 d) and varied between 4 June and 2

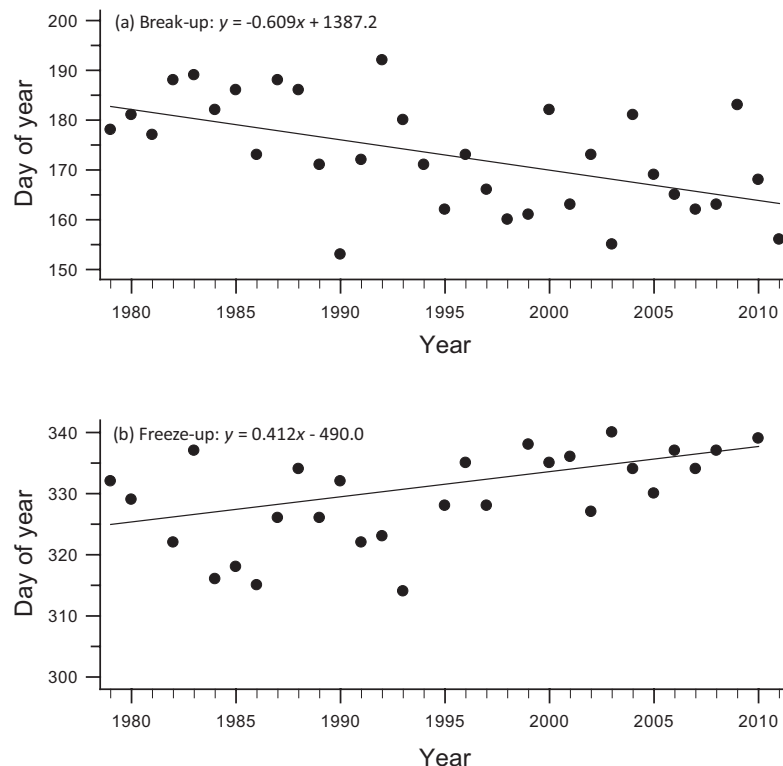


FIG. 3. Date of (a) sea ice break-up (50% sea ice concentration) in spring and (b) sea ice freeze-up (50% sea ice concentration) in autumn in western Hudson Bay from 1979 to 2011, estimated from passive microwave satellite imagery (data source: National Snow and Ice Data Center, Boulder, Colorado, USA).

July, but there was no significant trend (linear regression, $P = 0.584$). Similarly, over the last decade the mean date of freeze-up was 2 December (SE = 1.5 d) and varied between 23 November and 9 December but with no significant trend (linear regression, $P = 0.132$).

Model selection

For female polar bears, the top-ranked model M3 (Table 2) included survival (S) as a function of state and age effects (COY, dependent yearling, independent yearling 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 and freeze-up, including their interaction; 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, the top-ranked model M1 (Table 3) included time-constant survival (S) as a function of state and age effects (COY, dependent yearling, independent yearling 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.

Survival and recapture probabilities

For female polar bears, total apparent survival (S) varied with time as a function of sea ice conditions (Fig. 4, Appendix S2). The strongest relationship was between earlier break-up and lower survival for all age classes (e.g., Fig. 5). Recapture probabilities for adult females varied by state: females aged 5–19 yr old without COY (and without a radio collar or previous capture in Churchill) had capture probabilities ranging, across years, from $p = 0.07$ (95% BCI = 0.05–0.11) to $p = 0.20$ (95% BCI = 0.15–0.28), compared to $p = 0.27$ (95% BCI = 0.18–0.40) and $p = 0.56$ (95% BCI = 0.43–0.67) for females with COY. This supports the hypothesis of lower p for females without cubs, some of which may be pregnant and seeking refuge in maternal dens and therefore less susceptible to capture. Females wearing a radio collar or previously captured in Churchill have an increased probability of recapture (Appendix S2).

We also derived time-invariant estimates of S for female bears (Table 4) by using the intercept, and state

TABLE 2. Selection of top-ranked model for female polar bears using deviance information criterion (DIC).

Model	Selection	Deviance	$\sigma^2_{(\text{deviance})}/2$	DIC	Δ_{DIC}
First step: best model for survival: effects included in survival					
M3	state + age effect + break-up + freeze-up + break-up \times freeze-up	18326.73	2145.89	20472.62	
M4	state + age effect + break-up + ice decay + break-up \times ice decay	18318.63	2276.13	20594.76	122.14
M2	state + age effect + break-up	18319.73	2344.89	20664.62	192.00
M1	state + age effect	18337.45	2399.98	20737.43	264.81
Second step: best model for human-related mortality: effects included in human-related mortality while using best model for survival (model M3)					
M3	state + age effect	18326.73	2145.89	20472.62	
M5	state + age effect + Churchill	18319.38	2341.34	20660.73	188.11
Third step: best model for the probability of breeding: effects included in probability of breeding while using best model for survival and human-related mortality (model M3)					
M3	state + age effect	18326.73	2145.89	20472.62	
M7	state + age effect + break-up + ice decay + break-up \times ice decay	18317.48	2199.88	20517.36	44.74
M6	state + age effect + break-up	18322.36	2460.25	20782.61	309.99
Fourth step: best model for the probability of twinning: effects included in probability of twinning while using best model for survival, human-related mortality and probability of breeding (model M3)					
M3	state + age effect	18326.73	2145.89	20472.62	
M8	state + age effect + break-up	18323.47	2493.00	20816.48	343.86
Fifth step: best model for the probability of weaning: effects included in probability of weaning while using best model for survival, human-related mortality, and probabilities of breeding and twinning (model M3)					
M3	state + age effect	18326.73	2145.89	20472.62	
M9	state + age effect + break-up	18324.16	2301.03	20625.19	152.57

Notes: 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 Appendix S1).

TABLE 3. Selection of top-ranked model for male polar bears using deviance information criterion (DIC).

Model	Selection	Deviance	$\sigma^2_{(\text{deviance})}/2$	DIC	Δ_{DIC}
First step: best model for survival: effects included in survival					
M1	state + age effect	13143.31	1533.99	14677.30	
M3	state + age effect + break-up + freeze-up + break-up \times freeze-up	13143.66	1552.33	14695.99	18.69
M2	state + age effect + break-up	13146.44	1632.88	14779.32	102.02
M4	state + age effect + break-up + ice decay + break-up \times ice decay	13155.33	1735.96	14891.29	213.99
Second step: best model for human-related mortality: effects included in human-related mortality while using best model for survival (model M1)					
M1	state + age effect	13143.31	1533.99	14677.30	
M5	state + age effect + Churchill	13154.41	1565.00	14719.41	42.11
Third step: best model for probability of weaning: effects included in probability of weaning while using best model for survival and human-related mortality (model M1)					
M1	state + age effect	13143.31	1533.99	14677.30	
M6	state + age effect + break-up	13143.91	1623.60	14767.50	90.20

Notes: 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 Appendix S1).

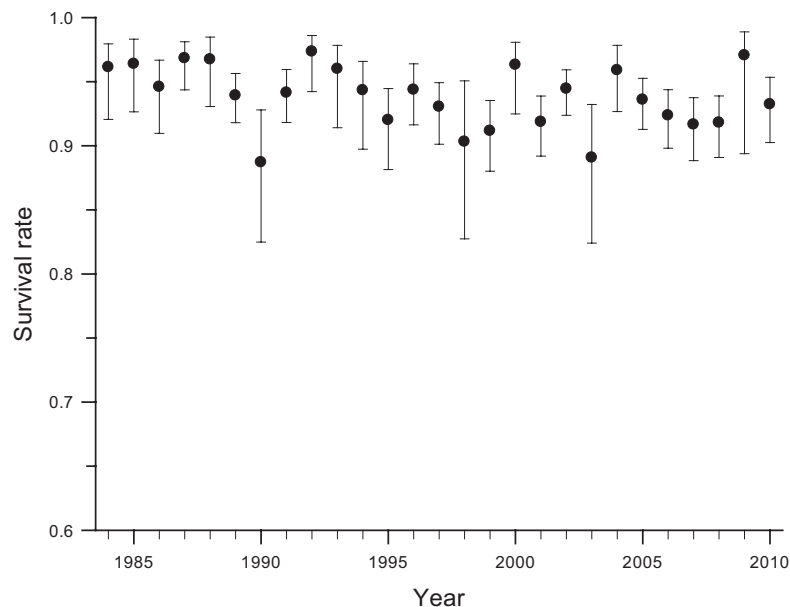


FIG. 4. Estimated apparent survival for adult females aged 5–19 yr old and without cubs-of-the-year, estimated from live-recapture and dead-recovery data for the Western Hudson Bay polar bear subpopulation from 1984 to 2011 using multistate capture–recapture models. Error lines shown are 95% Bayesian credible intervals.

and age coefficients of the MCMC chains from model M3. This allowed for comparison of survival among states and age classes, with time-invariant estimates of S from the top-ranked model M1 for males. We found evidence for increasing survival with age, followed by senescent declines for bears ≥ 20 yr old, but no evidence for differences in adult female survival as a function of reproductive status (with the exception of higher S for older adult females with COY, compared to older adult females without COY).

For male polar bears, estimates of S were time-constant and did not vary as a function of sea ice conditions. Point estimates of S were lower for all age classes of independent males than for independent females, likely due to the effects of the sex-selective harvest (Table 4). Similar to females, recapture probabilities of males varied by state. The lowest observed recapture probability for male bears without a history of capture in Churchill was $p = 0.13$ (95% BCI = 0.09–0.18) in 2008 for adult males. The highest estimate for male bears

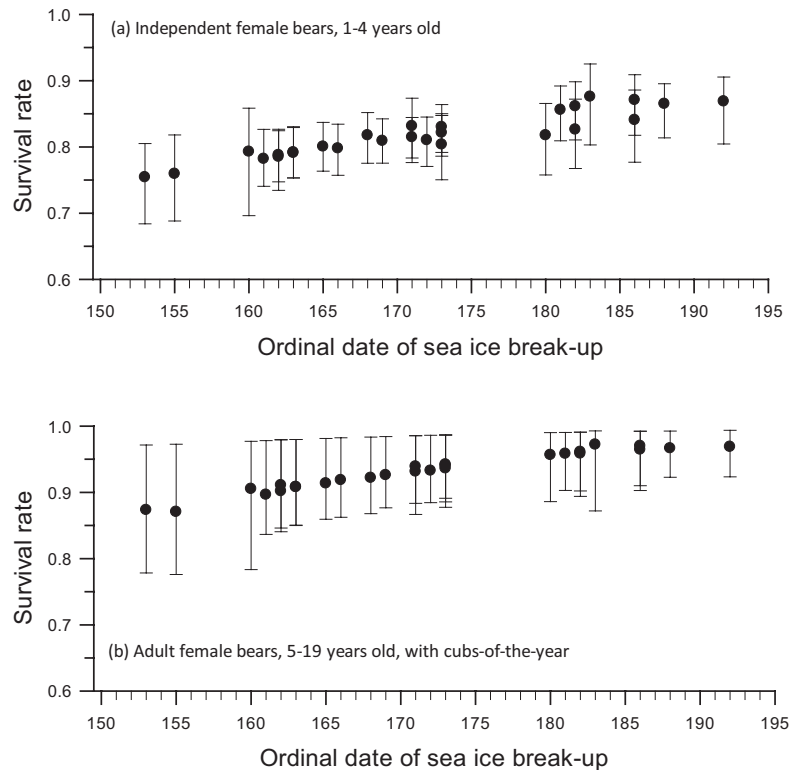


FIG. 5. Estimated annual apparent survival rates for (a) independent female polar bears 1–4 yr old, and (b) adult female bears 5–19 yr old with cubs-of-the-year, plotted against sea ice breakup date, from the top-ranked multistate model for the Western Hudson Bay polar bear subpopulation. Multiple estimates on the same break-up date represent multiple years when break-up date was the same. Discrepancy between multiple estimates on a single break-up date is due to differences in freeze-up date, as both break-up and freeze-up date appeared in the top-ranked model.

TABLE 4. 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 class	S (mode)	95% BCI _L	95% BCI _U
Female polar bears			
COY (9 months)	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 polar bears			
COY (9 months)	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

Notes: Age classes represent a combination of state structure and age effect covariates. BCI_L and BCI_U represent the lower and upper Bayesian credible intervals, respectively.

without a history of capture in Churchill was $p = 0.55$ (0.41–0.71) in 1985 for dependent yearlings. For both young and adult male bears, previous capture in Churchill was associated with an increase in subsequent capture probability (Appendix S2).

Human-caused mortality

For polar bears that died, the probability that death was due to direct human-caused removal (H) varied by sex and age (Table 5). For females, independent yearlings through 4-yr-olds exhibited the highest H . For males, young adults aged 5–9 yr exhibited the highest H , followed by independent yearlings through 4-year-olds. Estimates of H suggest that a significant component of mortality for some segments of the WH subpopulation was human-caused removals. For example, $H = 0.73$ for young adult males (5–9 yr) suggested that ~73 of every 100 young adult males that died were the result of subsistence harvest or management actions.

Reproductive parameters

Estimates of breeding probability did not vary as a function of sea ice conditions. Breeding probability increased with age, followed by a senescent decline for

TABLE 5. 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 class	H (mode)	95% BCI _L	95% BCI _U
Female polar bears			
COY (9 months) 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 polar bears			
COY (9 months) 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

Note: Age classes represent a combination of state structure and age effect covariates.

TABLE 6. 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 class	B (mode)	95% BCI _L	95% BCI _U
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

Note: Age classes represent a combination of state structure and age effect covariates.

females ≥20 yr old (Table 6). The probability of producing twins (T) was time-constant at 0.47 (95% BCI = 0.43–0.52) over the course of the study, and constant across states and ages. The probability of weaning (W) for yearlings 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

We derived annual abundance estimates (Fig. 6) from the top-ranked models for males and females. Overall abundance declined from 1185 polar bears (95% BCI = 993–1411) in 1987 to 806 bears (95% BCI = 653–984) in 2011. Since 2004, the last year of the previous demographic assessment (Regehr et al. 2007), there was no apparent trend in abundance (Fig. 6). The estimate of abundance for 2004 from the current study (742, 95% BCI = 630–872) is lower, although with overlapping confidence intervals, than the 2004 estimate (935, 95% CI = 794–1076) from Regehr et al. (2007).

Population projections

We focused matrix-based population modeling on the female segment of the subpopulation due to its critical importance for reproduction. Population growth rate for females, based on parameter estimates from Model M3, was 1.02 (95% BCI = 0.98–1.06) over the period 2001–2010 and only 0.99 (95% BCI = 0.96–1.02) over the previous 10-yr period 1991–2000. These estimates, which reflect both natural and direct human-caused mortality, suggest that the female population increased slightly during the most recent decade, and was slightly declining prior to that. We estimated a similar population growth rate of 1.02 (95% BCI = 0.98–1.06) over the period 2001–2010 using the more general female model that included ice effects on the reproductive parameters B , W , and T , suggesting that model-based estimates of population growth rate were not sensitive to the model selection process. A matrix model including both females and males estimated a population growth rate of 1.01 (95% BCI = 0.98–1.05) for 2001–2010, and 0.97 (95% BCI = 0.95–1.00) for 1991–2000, suggesting similar trends but likely with larger declines in the total population during the 1990s.

We projected population size forward, for females only and the total population, under scenarios for high and low future sea ice conditions. For females, we used parameter estimates from both the top-ranked model M3, and estimates from the more general female model (Table 7). For males, we used parameter estimates from model M3 that included sea ice effects on survival (similar to females), to reflect the potential biological importance of sea ice despite the lack of statistical support for such covariates in the model selection procedure. For females and males together, the 50-yr model-based population growth rate was 1.02 (95% BCI = 1.00–1.05) under high sea ice conditions, and 0.97 (95% BCI = 0.92–1.01) under low sea ice conditions. Results were similar for female-only projections (Table 7). All projections reflected an assumption that relationships between sea ice and vital rates, as estimated during this study, would remain stationary into the future.

DISCUSSION

Understanding complex relationships between polar bear population dynamics, environmental conditions, and other factors are necessary to assess population status and develop conservation and management plans that reflect both nearer-term variation and longer-term concerns. The current study represents the longest-term and highest-resolution assessment of polar bear demography to date, providing evidence for the fundamental dependence of polar bears on sea ice as well as the influence of internal climate variability (Kay et al. 2011, Swart et al. 2015) on short-term trends in sea ice conditions and, thus, on population status.

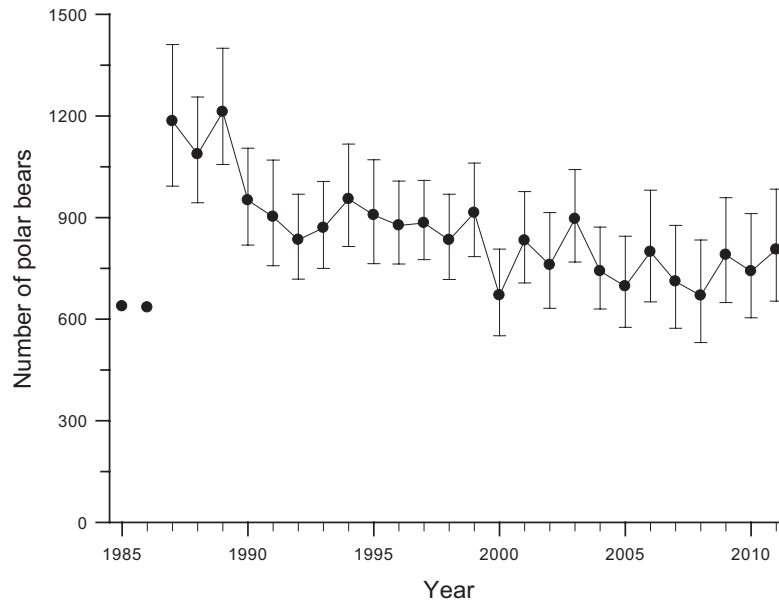


FIG. 6. Estimated population size, derived using recapture probabilities estimated for the Western Hudson Bay polar bear subpopulation from 1984 to 2011, using multistate capture–recapture models. Point estimates of abundance and 95% credible intervals are shown for 1987–2011 only because the 1985–1986 point estimates were biased by incomplete sampling of the core summering area and are not comparable (Regehr et al. 2007).

TABLE 7. 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 (yr)	Population growth rate	95% BCI _L	95% BCI _U
Female (global model)	high	50	1.03	1.00	1.05
Female (global model)	low	50	0.97	0.91	1.01
Female	high	50	1.02	1.00	1.05
Female	low	50	0.97	0.92	1.01
Female and male	high	50	1.02	1.00	1.05
Female and male	low	50	0.97	0.92	1.01

Note: Parameter estimates come from the top-ranked model in the model-selection routine (described in Section: Model fitting and parameter estimation and Appendix S1) except where global model is noted; in those cases the most general estimation model was used.

Influence of sea ice conditions on polar bear survival

Survival rate is a primary driver of population trend for long-lived species such as polar bears (Eberhardt 1990). In our analysis, the survival of female polar bears in all age classes was correlated with timing of sea ice break-up, freeze-up, and their interaction, which 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). 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) energetic states. Although some polar bears may take advantage of terrestrial food sources or beach-cast

marine mammal carcasses, their availability and caloric content are generally limited (Rode et al. 2015). Thus, beyond certain critical thresholds, longer periods on shore are expected to result in greater negative impacts on energy budgets and consequently on survival and productivity (Molnár et al. 2010, Robbins et al. 2012, Castro de la Guardia et al. 2013).

In contrast to females, sea ice variables considered in our analysis were not related to annual variation in total apparent survival of male bears. Although previous studies (e.g., Regehr et al. 2007) led us to expect similar relationships for females and males, there are several possible explanations for the current finding. First, direct inclusion of data on human-caused removals within the analytical framework assigned harvest-based mortality more accurately. The relatively high number of male

bears whose death was due to direct human-caused mortality (Table 5) may have been sufficiently large that compensatory effects dampened fluctuations in natural survival, making a potential underlying relationship 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. Young adult males aged 5–9 years exhibited the highest H , followed by independent yearling through 4-year-old males. These patterns are consistent with previous studies suggesting that younger bears, particularly males, are most likely to encroach upon human settlements and thus risk being killed (Lunn and Stirling 1985, Kearney 1989, Towns et al. 2009), and are disproportionately represented in the subsistence harvest due to a sex-selective management approach (Derocher et al. 1997, Taylor et al. 2008). Thus, direct human-caused mortality could effectively remove a significant proportion of younger males that otherwise would have been susceptible to natural mortality in the coming winter, making harvest at least partially compensatory to natural mortality. Second, Robbins et al. (2012) estimated that while on land adult males can spend twice as long fasting (240 days) as lactating females (120 days) before starvation occurs and, therefore, males may have been less impacted by changing sea ice conditions experienced to date.

Influence of sea ice conditions on reproduction

We did not find that interannual variation in reproduction was correlated with sea ice conditions. We had expected to see such a result on the grounds that reproduction should be relatively sensitive to environmental variation, especially compared to adult survival (Pfister 1998). Thus, it is somewhat surprising to have detected an effect of sea ice on adult survival but not on any parameters related to reproduction. This result may have been influenced by heterogeneity in the breeding probability of individuals in state FnY, which included both single females that were potentially pregnant and able to produce COY the following year, and females with dependent yearlings that would not be pregnant. We used a simplified model structure to avoid state uncertainty, which likely would have decreased parameter identifiability (Gimenez et al. 2009) and statistical power to detect patterns in survival, a primary objective of our analysis. Consequences of our approach include potentially reduced ability to detect temporal variation in breeding probability (B). We also note that effects of sea ice on breeding probability may be inherently difficult to detect because this parameter is estimated from the relatively small number of bears in the FnY state, whereas survival is estimated from all bears.

Despite lack of evidence in the current analysis for a direct relationship between sea ice and reproduction in our analysis, other evidence does indicate a relationship between sea ice and reproductive output in this

population (Stirling et al. 1999) and other populations (e.g., Regehr et al. 2010, Rode et al. 2010). With more data and different modeling approaches (e.g., integrated population models; Besbeas et al. 2002) it may be possible to document such an effect in future.

There is a growing body of literature linking sea ice extent and duration and various polar bear demographic parameters (e.g., Regehr et al. 2007, 2010, Rode et al. 2010, 2012, 2014, Bromaghin et al. 2015), although similar linkages have not yet been detected in other subpopulations (Obbard et al. 2007, Stirling et al. 2011, Peacock et al. 2013). During late spring and early summer, polar bears accumulate at least two-thirds of the energy they require for the entire year (Stirling and Øritsland 1995). Declining body condition in WH polar bears and, subsequently, reproduction, survival, and abundance (Derocher and Stirling 1995, Stirling et al. 1999, Regehr et al. 2007) likely reflect the amount of time that bears have spent on the sea ice prior to coming ashore. However, our analysis did not directly include covariates related to body size or nutritional condition. Rode et al. (2014) 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 more complex and nonlinear responses to climate change that are influenced by factors such as biological productivity.

Abundance of the effective study population

In our analyses, estimates of total apparent survival represented the probability of remaining alive and in the core summering area. Permanent emigration out of this area will result in estimates of apparent survival that are lower than natural survival, which can introduce negative bias into population projections if not accounted for. Nonrandom, temporary movement out of the core summering area can also result in biased survival estimates (Kendall et al. 1997). The degree to which movements may have introduced bias into our estimates of survival is unknown, although strong site fidelity of WH bears during autumn (Derocher and Stirling 1990, Stirling et al. 2004, Cherry et al. 2013), combined with captures of bears outside the core summering area (in three consecutive years of sampling during three different time periods) likely minimizes such effects. Harvested bears in our data set were harvested outside the EC study area, and so conceivably could include individuals that were permanent emigrants from the study area. This could complicate the interpretation of parameter H in our multistate models. However, we think it unlikely, given the seasonal movements of bears, and the relative proximity of the harvest area and the EC study area relative to individual polar bear movements, that a

meaningful number of animals could have emigrated far enough to be permanently outside the study area but still within the harvest area.

The estimates of abundance developed here are defined with respect to the effective study population, which depends on the spatial coverage and timing of the capture–recapture sampling area, and movement of animals in and out of this area over multiple years. Estimates of abundance from capture–recapture studies may also be influenced by the degree to which assumptions of the modeling approach were met, including the potential for unmodeled heterogeneity in recapture probabilities that tend to introduce negative bias (Schaub et al. 2004). We suggest that negative bias in our estimates of the size of the effective study population was likely small, due to relatively high values of p (Pollock et al. 1990), and use of covariates (telemetry, Churchill), state and age effects, and random temporal effects to explain heterogeneity in model parameters.

To determine the degree to which the effective study population represents the WH subpopulation, as considered from a biological or management perspective, requires auxiliary information. Previous capture–recapture analyses (Lunn et al. 1997, Regehr et al. 2007) suggested close alignment among populations of interest, based on observations that relatively few polar bears exhibited consistent fidelity to areas outside of the core summering 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 a significant number of bears located in Area D in 2011, and consequently estimated a larger number of total polar bears within the WH management area (Fig. 1). Comparison of the 2011 point estimate of 806 (95% BCI = 653–984) from this study with the estimate of 1030 (95% CI = 754–1406) from the 2011 aerial survey requires careful interpretation because the two studies provide different temporal and spatial perspectives and involve different assumptions and caveats (e.g., Williams et al. 2002, Buckland et al. 2007). The aerial survey provides a “snapshot” estimate of the distribution and abundance of polar bears when the survey was flown. This differs from the point estimate of abundance from a capture–recapture model, which uses individually identified animals to estimate the number of bears with a nonzero probability of moving through a sampling area over multiple years. In light of these considerations and the overlapping confidence intervals between the two abundance estimates, we suggest that the results of both survey methods, keeping in mind their strengths and limitations, provide a complimentary and largely consistent understanding of the distribution, status, and trend of the WH subpopulation.

Population trend

The Hudson Bay marine ecosystem has experienced physical (e.g., Gagnon and Gough 2005, Hochheim et al.

2010) and biological (e.g., Stirling et al. 1999, Ferguson et al. 2005, Regehr et al. 2007, Gaston et al. 2012) changes over the past 3–4 decades. As a possible response, our analysis indicated a decline in the size of the effective study population from 1185 bears (95% BCI = 993–1411) in 1987 to 806 bears (95% BCI = 653–984) in 2011. In the most recent decade of our study (2001–2010), the matrix-based growth rate for the total WH subpopulation was 1.01 (95% BCI = 0.98–1.05), suggesting a period of population stability associated with stability in sea ice conditions that influence female survival rates. In the preceding decade, 1991–2000, the population appeared to be declining with a growth rate of 0.97 (95% BCI = 0.95–1.00).

The relationship between sea ice conditions and polar bear survival is likely mediated by both direct (e.g., availability of sea ice as a platform for hunting) and indirect (e.g., effects of sea ice on the population dynamics of prey species) mechanisms. Reduced production, survival, and recruitment of ringed seals (*Pusa hispida*) in the 1990s were thought to be due to less favorable environmental conditions (Ferguson et al. 2005, Chambellant et al. 2012). In areas such as Hudson Bay, where ringed seals form a large part of the diet of polar bears (Thiemann et al. 2008), environmental carrying capacity for polar bears appears to be correlated with ringed seal abundance (Stirling and Øritsland 1995). Thus, the decline in size of the WH polar bear subpopulation through the 1990s may reflect poor reproductive performance of ringed seals during the same period. Although environmental conditions may have improved for ringed seals in the 2000s (Ferguson et al. 2005, Chambellant 2010), the population trend for polar bears during this period appears relatively stable and may reflect the increasingly limited ability of polar bears to access ringed seals due to earlier sea break-up.

The matrix projection model results suggest that the lack of trend in break-up date from 2001 to 2010 resulted in a stable population, and this was generally consistent with point estimates of abundance for the effective study population. Thus, it appears likely that survival and reproduction were sufficient to maintain the population and support human-caused removal levels over this decade. However, because population growth rate for polar bears depends primarily on survival and productivity of adult females (e.g., Hunter et al. 2010) and because of evidence for the dependence of WH polar bears on sea ice (Stirling et al. 1999, Regehr et al. 2007, this study), the long-term trend for this subpopulation is likely to be negative (Derocher et al. 2004, Molnár et al. 2010, Castro de la Guardia et al. 2013) considering forecasts of decreasing duration and extent of sea ice cover in southern and western Hudson Bay (Joly et al. 2011, Castro de la Guardia et al. 2013).

Our findings suggest that the WH subpopulation is capable of responding positively to shorter-term (2–10 year) periods of stability or improvement in sea ice conditions, which are expected to occur with decreasing magnitude

and frequency under continued anthropogenic forcing of the climate system (Kay et al. 2011, Swart et al. 2015). Furthermore, positive population responses are dependent on sufficient prey availability and the requirement that sea ice conditions have not reached a critical threshold beyond which polar bears are unable to accumulate sufficient energy reserves to survive the ice-free period (Molnár et al. 2010). These findings emphasize the importance of understanding and incorporating the complexities of relationships between vital rates and environmental conditions in demographic assessments for management and conservation planning (Regehr et al. 2015), while highlighting the sensitivity of such assessments to variation and uncertainty in future environmental conditions.

Despite a growing body of literature on responses of marine mammals to climate change, sea ice change, and subsequent shifts within Arctic marine ecosystems (e.g., Ferguson et al. 2005, Laidre and Heide-Jørgensen 2005, Post et al. 2013, Laidre et al. 2015), predicting long-term demographic change remains difficult. Relationships between sea ice conditions and polar bears in western Hudson Bay may change over time. Furthermore, while availability of ringed seals in Hudson Bay is likely to be negatively affected by climate change (Ferguson et al. 2005), there are insufficient data to assess how changes at lower trophic levels will affect polar bears (Stirling and Derocher 2012). We suggest that such uncertainty should not diminish long-term conservation concerns for the species (Tynan and DeMaster 1997, Derocher et al. 2004, Stirling and Derocher 2012), which are based on forecasts of continued sea ice loss (Holland et al. 2006, Stroeve et al. 2007, 2012a) and the fundamental dependence of polar bears on sea ice as a platform from which to access energy-rich marine prey (Amstrup 2003). Similarly, long-term trends in environmental conditions, and qualitative or coarse-resolution models of future population status (e.g., Amstrup et al. 2008, 2010), may not be suitable tools for addressing local management questions over shorter timeframes (e.g., setting of subsistence harvest levels) or for understanding how climate change and management actions interact to affect population viability (Regehr et al. 2015).

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). The strong demographic linkage between sea ice conditions and female survival in WH polar bears would enable effective forecasting of the outcome of different management scenarios and their implications for subsequent changes in population size. Overall, our study provides additional evidence of the sensitivity of polar bears to changes in sea ice conditions, and presents an improved analytical framework that can provide greater resolution for understanding demographic responses of polar bears to climate change in a rapidly warming Arctic.

ACKNOWLEDGMENTS

We thank the Governments of Manitoba, Nunavut, and Ontario, Canada, and the University of Saskatchewan for permission to use their data. Financial and logistical support of field research was provided by Busch Entertainment Corporation/Sea World, Care for the Wild International, the Churchill Northern Studies Centre, Earth Rangers Foundation, Environment Canada, the Isdell Family Foundation, Manitoba Conservation, National Fish and Wildlife Foundation, Natural Sciences and Engineering Research Council, Nunavut Wildlife Research Trust Fund, Parks Canada Agency, Quark Expeditions, Schad Foundation, US Fish and Wildlife Service, Wildlife Media Inc., World Wildlife Fund Arctic Programme, and World Wildlife Fund Canada. Financial and logistical support for data analysis was provided by the U.S. Fish and Wildlife Service, USGS Patuxent Wildlife Research Center, and the Colorado Cooperative Fish and Wildlife Research Unit. Many thanks to the numerous co-workers, field assistants, and helicopter crews who made it possible to collect three decades of data under challenging field conditions and our appreciation goes to L. L. Bailey, W. A. Link, J. D. Nichols, J. A. Royle, and M. C. Runge for helpful discussions and support during data analysis. This paper benefitted from useful comments on earlier drafts by R. D. Elliot, E. A. Krebs, J. D. Nichols, K. Rode, M. C. Runge, and two anonymous reviewers.

The findings and conclusions in this paper are those of the authors and do not necessarily represent the views of Environment Canada or the US Fish and Wildlife Service. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States or Canadian governments.

LITERATURE CITED

- Amstrup, S. C. 2003. Polar bear, *Ursus maritimus*. Pages 587–610 in G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Mammals of North America: biology, management, and conservation. The Johns Hopkins University Press, Baltimore, Maryland, USA.
- Amstrup, S. C., B. G. Marcot, and D. C. Douglas. 2008. A Bayesian network modeling approach to forecasting the 21st century worldwide status of polar bears. Pages 213–268 in E. T. DeWeaver, C. M. Bitz, and L.-B. Tremblay, editors. Arctic sea ice decline: observations, projections, mechanisms, and implications. Geophysical Monograph Series 180. American Geophysical Union, Washington, DC, USA.
- Amstrup, S. C., E. T. DeWeaver, D. C. Douglas, B. G. Marcot, G. M. Durner, C. M. Bitz, and D. A. Bailey. 2010. Greenhouse gas mitigation can reduce sea-ice loss and increase polar bear persistence. *Nature* 468:955–958.
- Arnason, A. N. 1972. Parameter estimates from mark-recapture experiments on two populations subject to migration and death. *Researches on Population Ecology* 13:97–113.
- Atkinson, S. N., and M. A. Ramsay. 1995. The effects of prolonged fasting on the body composition and reproductive performance of pregnant female polar bears (*Ursus maritimus*). *Functional Ecology* 9:559–567.
- Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters* 15:365–377.
- Besbeas, P., S. N. Freeman, B. J. T. Morgan, and E. A. Catchpole. 2002. Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics* 58:540–547.
- Bromaghin, J. F., T. L. McDonald, I. Stirling, A. E. Derocher, E. S. Richardson, E. V. Regehr, D. C. Douglas, G. M. Durner, T. Atwood, and S. C. Amstrup. 2015. Polar bear population

- dynamics in the southern Beaufort Sea during a period of sea ice decline. *Ecological Applications* 25:634–651.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2007. Advanced distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford, UK.
- Calvert, W., and M. A. Ramsay. 1988. Evaluation of age determination of polar bears by counts of cementum growth layer groups. *Ursus* 10:449–453.
- Castro de la Guardia, L., A. E. Derocher, P. G. Myers, A. D. Terwisscha van Scheltinga, and N. J. Lunn. 2013. Future sea ice conditions in western Hudson Bay and consequences for polar bears in the 21st century. *Global Change Biology* 19:2675–2687.
- Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology* 81:619–627.
- Cavalieri, D. J., C. L. Parkinson, P. Gloersen, and H. J. Zwally. 1996, updated yearly. Sea ice concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS passive microwave data [1979–2011]. NASA National Snow and Ice Data Center Distributed Active Archive Center, Boulder, Colorado, USA.
- Cavalieri, D. J., C. L. Parkinson, N. DiGirolamo, and A. Ivanoff. 2012. Intersensor calibration between F13 SSMI and F17 SSMIS for global sea ice data records. *IEEE Geoscience and Remote Sensing Letters* 9:233–236.
- Chambellant, M. 2010. Hudson Bay ringed seal: ecology in a warming climate. Pages 137–158 in S. H. Ferguson, L. L. Loseto, and M. L. Mallory, editors. *A little less Arctic: top predators in the world's largest northern inland sea*. Springer, New York, New York, USA.
- Chambellant, M., I. Stirling, W. A. Gough, and S. H. Ferguson. 2012. Temporal variations in Hudson Bay ringed seal (*Phoca hispida*) life-history parameters in relation to environment. *Journal of Mammalogy* 93:267–281.
- Cherry, S. G., A. E. Derocher, G. W. Thiemann, and N. J. Lunn. 2013. Migration phenology and seasonal fidelity of an Arctic marine predator in relation to sea ice dynamics. *Journal of Animal Ecology* 82:912–921.
- Choquet, R., J.-D. Lebreton, O. Gimenez, A.-M. Reboulet, and R. Pradel. 2009. U-CARE: utilities for performing goodness of fit tests and manipulating CAPture-REcapture data. *Ecography* 32:1071–1074.
- Comiso, J. C. 2002. A rapidly declining Arctic perennial ice cover. *Geophysical Research Letters* 29:1956.
- Converse, S. J., W. L. Kendall, P. F. Doherty Jr, and P. G. Ryan. 2009. Multistate models for estimation of survival and reproduction in the Grey-Headed Albatross (*Thalassarche chrysostoma*). *The Auk* 126:77–88.
- Davies, K. F., C. R. Margules, and J. F. Lawrence. 2004. A synergistic effect puts rare, specialized species at greater risk of extinction. *Ecology* 85:265–271.
- Derocher, A. E., and I. Stirling. 1990. Distribution of polar bears (*Ursus maritimus*) during the ice-free period in western Hudson Bay. *Canadian Journal of Zoology* 68:1395–1403.
- Derocher, A. E., and I. Stirling. 1995. Temporal variation in reproduction and body mass of polar bears in western Hudson Bay. *Canadian Journal of Zoology* 73:1657–1665.
- Derocher, A. E., I. Stirling, and W. Calvert. 1997. Male-biased harvesting of polar bears in western Hudson Bay. *Journal of Wildlife Management* 61:1075–1082.
- Derocher, A. E., N. J. Lunn, and I. Stirling. 2004. Polar bears in a warming climate. *Integrative and Comparative Biology* 44:163–176.
- Derocher, A. E., et al. 2013. Rapid ecosystem change and polar bear conservation. *Conservation Letters* 6:368–375.
- Doherty, P. F., G. C. White, and K. P. Burnham. 2012. Comparison of model building and selection strategies. *Journal of Ornithology* 152(Supplement 2):317–323.
- Eberhardt, L. L. 1990. Survival rates required to sustain bear populations. *Journal of Wildlife Management* 54:587–590.
- Etkin, D. A. 1991. Break-up in Hudson Bay: its sensitivity to air temperatures and implications for climate warming. *Climatological Bulletin* 25:21–34.
- Ferguson, S. H., I. Stirling, and P. McLoughlin. 2005. Climate change and ringed seal (*Phoca hispida*) recruitment in western Hudson Bay. *Marine Mammal Science* 21:121–135.
- Gagnon, A. S., and W. A. Gough. 2005. Trends in dates of ice freeze-up and break-up over Hudson Bay, Canada. *Arctic* 58:370–382.
- Gaston, A. J., P. A. Smith, and J. F. Provencher. 2012. Discontinuous change in ice cover in Hudson Bay in the 1990s and some consequences for marine birds and their prey. *ICES Journal of Marine Science* 69:1218–1225.
- Gelman, A. 1996. Inference and monitoring convergence. Pages 131–143 in W. R. Gilks, S. Richardson, and D. J. Spiegelhalter, editors. *Markov Chain Monte Carlo in practice*. Chapman and Hall, London, UK.
- Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, New York, New York, USA.
- Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. Bayesian data analysis, 2nd edition. Chapman & Hall/CRC, Boca Raton, Florida, USA.
- Gimenez, O., B. J. T. Morgan, and S. P. Brooks. 2009. Weak identifiability in models for mark-recapture-recovery data. Pages 1055–1067 in D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. *Modeling demographic processes in marked populations*. Springer, New York, New York, USA.
- Hestbeck, J. B., J. D. Nichols, and R. Malecki. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. *Ecology* 72:523–533.
- Hochheim, K., D. G. Barber, and J. V. Lukovich. 2010. Changing sea ice conditions in Hudson Bay, 1980–2005. Pages 39–51 in S. H. Ferguson, L. L. Loseto, and M. L. Mallory, editors. *A little less Arctic: top predators in the world's largest northern inland sea*. Springer, New York, New York, USA.
- Holland, M. M., C. M. Bitz, and B. Tremblay. 2006. Future abrupt reductions in the summer arctic sea ice. *Geophysical Research Letters* 33:L23503.
- Hunter, C. M., H. Caswell, M. C. Runge, E. V. Regehr, S. C. Amstrup, and I. Stirling. 2010. Climate change threatens polar bear populations: a stochastic demographic analysis. *Ecology* 91:2883–2897.
- IPCC [Intergovernmental Panel on Climate Change]. 2014. Climate change 2014: impacts, adaptation, and vulnerability. Part A: global and sectoral aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Joly, S., S. Senneville, D. Caya, and F. J. Saucier. 2011. Sensitivity of Hudson Bay Sea ice and ocean climate to atmospheric temperature forcing. *Climate Dynamics* 36:1835–1849.
- Kay, J. E., M. M. Holland, and A. Jahn. 2011. Inter-annual to multi-decadal Arctic sea ice extent trends in a warming world. *Geophysical Research Letters* 38:L15708.
- Kearney, S. R. 1989. The polar bear alert program at Churchill, Manitoba. Pages 83–92 in M. Bromley, editor. *Bear-people conflicts: proceedings of a symposium on management strategies*. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.

- Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78:563–578.
- Kendall, W. L., P. B. Conn, and J. E. Hines. 2006. Combining multistate capture-recapture data with tag recoveries to estimate demographic parameters. *Ecology* 87:169–177.
- Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, San Diego, California, USA.
- Kovacs, K. M., C. Lydersen, J. E. Overland, and S. E. Moore. 2011. Impacts of changing sea-ice conditions on Arctic marine mammals. *Marine Biodiversity* 41:181–194.
- Laidre, K. L., and M. P. Heide-Jørgensen. 2005. Arctic sea ice trends and narwhal vulnerability. *Biological Conservation* 121:509–517.
- Laidre, K. L., I. Stirling, L. F. Lowry, Ø. Wiig, M. P. Heide-Jørgensen, and S. H. Ferguson. 2008. Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecological Applications* 18(Supplement):S97–S125.
- Laidre, K. L., et al. 2015. Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conservation Biology* 29:724–737.
- Lunn, N. J., and I. Stirling. 1985. The significance of supplemental food to polar bears during the ice-free period of Hudson Bay. *Canadian Journal of Zoology* 63:2291–2297.
- Lunn, N. J., I. Stirling, D. Andriashek, and G. B. Kolenosky. 1997. Re-estimating the size of the polar bear population in Western Hudson Bay. *Arctic* 50:234–240.
- McCarthy, M. A. 2007. Bayesian methods for ecology. Cambridge University Press, Cambridge, UK.
- Molnár, P. K., A. E. Derocher, G. W. Thiemann, and M. A. Lewis. 2010. Predicting survival, reproduction, and abundance of polar bears under climate change. *Biological Conservation* 143:1612–1622.
- Molnár, P. K., A. E. Derocher, T. Klanjscek, and M. A. Lewis. 2011. Predicting climate change impacts on polar bear litter size. *Nature Communications* 2:186.
- Molnár, P. K., A. E. Derocher, G. W. Thiemann, and M. A. Lewis. 2014. Corrigendum to “Predicting survival, reproduction and abundance of polar bears under climate change” [Biol. Conserv. 143 (2010) 1612–1622]. *Biological Conservation* 177:230–231.
- Obbard, M. E., M. R. L. Cattet, T. Moody, L. R. Walton, D. Potter, J. Inglis, and C. Chenier. 2006. Temporal trends in the body condition of Southern Hudson Bay polar bears. Climate Change Research Information Note 3, Ontario Ministry of Natural Resources, Sault Ste. Marie, Ontario, Canada.
- Obbard, M. E., T. L. McDonald, E. J. Howe, E. V. Regehr, and E. S. Richardson. 2007. Polar bear population status in Southern Hudson Bay, Canada. Administrative Report, US Geological Survey, Reston, Virginia, USA.
- Pacifici, M., et al. 2015. Assessing species vulnerability to climate change. *Nature Climate Change* 5:215–225.
- PBSG [IUCN/SSC Polar Bear Specialist Group]. 2015. Summary of polar bear population status as per 2014. <http://pbsg.npolar.no/en/status/status-table.html>.
- Peacock, E., A. E. Derocher, N. J. Lunn, and M. E. Obbard. 2010. Polar bear ecology and management in Hudson Bay in the face of climate change. Pages 93–115 in S. H. Ferguson, L. L. Loseto, and M. L. Mallory, editors. A little less Arctic: top predators in the world's largest northern inland sea. Springer, New York, New York, USA.
- Peacock, E., A. E. Derocher, G. W. Thiemann, and I. Stirling. 2011. Conservation and management of Canada's polar bears (*Ursus maritimus*) in a changing Arctic. *Canadian Journal of Zoology* 89:371–385.
- Peacock, E., J. Laake, K. L. Laidre, E. W. Born, and S. N. Atkinson. 2012. The utility of harvest recoveries of marked individuals to assess polar bear (*Ursus maritimus*) survival. *Arctic* 65:391–400.
- Peacock, E., M. K. Taylor, J. Laake, and I. Stirling. 2013. Population ecology of polar bears in Davis Strait, Canada and Greenland. *Journal of Wildlife Management* 77:463–476.
- Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences* 95:213–218.
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*, March 20–22, Vienna, Austria.
- Plummer, M. 2013. Package rjags: Bayesian graphical models using MCMC. Version 3.10. <http://sourceforge.net/projects/mcmc-jags/files/>.
- Pollock, K. H., J. D. Nichols, J. E. Hines, and C. Brownie. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107.
- Post, E., U. S. Bhatt, C. M. Bitz, J. F. Brodie, T. L. Fulton, M. Hebblewhite, J. Kerby, S. J. Kutz, I. Stirling, and D. A. Walker. 2013. Ecological consequences of sea-ice decline. *Science* 341:519–524.
- Pradel, R. 2005. Multievent: an extension of multistate capture-recapture models to uncertain states. *Biometrics* 61:442–447.
- R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Ramsay, M. A., and D. S. Andriashek. 1986. Long distance route orientation of female polar bears (*Ursus maritimus*) in spring. *Journal of Zoology* 208:63–72.
- Ramsay, M. A., and I. Stirling. 1988. Reproductive biology of female polar bears (*Ursus maritimus*). *Journal of Zoology, London* 214:601–634.
- Regehr, E. V., N. J. Lunn, S. C. Amstrup, and I. Stirling. 2007. Effects of earlier sea ice breakup on survival and population size of polar bears in western Hudson Bay. *Journal of Wildlife Management* 71:2673–2683.
- Regehr, E. V., C. M. Hunter, H. Caswell, S. C. Amstrup, and I. Stirling. 2010. Survival and breeding of polar bears in the southern Beaufort Sea in relation to sea ice. *Journal of Animal Ecology* 79:117–127.
- Regehr, E. V., R. R. Wilson, K. D. Rode, and M. C. Runge. 2015. Resilience and risk – a demographic model to inform conservation planning for polar bears. Open-File Report 2015-1029. US Geological Survey, Reston, Virginia, USA.
- Robbins, C. T., C. Lopez-Alfaro, K. D. Rode, Ø. Tøien, and O. L. Nelson. 2012. Hibernation and seasonal fasting in bears: the energetic costs and consequences for polar bears. *Journal of Mammalogy* 93:1493–1503.
- Rode, K. D., S. C. Amstrup, and E. V. Regehr. 2010. Reduced body size and cub recruitment in polar bears associated with sea ice decline. *Ecological Applications* 20:768–782.
- Rode, K. D., E. Peacock, M. Taylor, I. Stirling, E. W. Born, K. L. Laidre, and Ø. Wiig. 2012. A tale of two polar bear populations: ice habitat, harvest, and body condition. *Population Ecology* 54:3–18.
- Rode, K. D., E. V. Regehr, D. C. Douglas, G. Durner, A. E. Derocher, G. W. Thiemann, and S. M. Budge. 2014. Variation in the response of an Arctic top predator

- experiencing habitat loss: feeding and reproductive ecology of two polar bear populations. *Global Change Biology* 20:76–88.
- Rode, K. D., C. T. Robbins, L. Nelson, and S. C. Amstrup. 2015. Can polar bears use terrestrial foods to offset lost ice-based hunting opportunities? *Frontiers in Ecology and the Environment* 13:138–145.
- Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Academic Press, San Diego, California, USA.
- Schaub, M., O. Gimenez, B. R. Schmidt, and R. Pradel. 2004. Estimating survival and temporary emigration in the multi-state capture-recapture framework. *Ecology* 85:2107–2113.
- Servanty, S., S. J. Converse, and L. L. Bailey. 2014. Demography of a reintroduced population: moving toward management models for an endangered species, the whooping crane. *Ecological Applications* 24:927–937.
- Stapleton, S., S. Atkinson, D. Hedman, and D. Garshelis. 2014. Revisiting Western Hudson Bay: using aerial surveys to update polar bear abundance in a sentinel population. *Biological Conservation* 170:38–47.
- Stirling, I., and A. E. Derocher. 2012. Effects of climate warming on polar bears: a review of the evidence. *Global Change Biology* 18:2694–2706.
- Stirling, I., and N. A. Øritsland. 1995. Relationships between estimates of ringed seal (*Phoca hispida*) and polar bear (*Ursus maritimus*) populations in the Canadian Arctic. *Canadian Journal of Fisheries and Aquatic Sciences* 52:2594–2612.
- Stirling, I., and C. L. Parkinson. 2006. Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. *Arctic* 59:261–275.
- Stirling, I., C. Jonkel, P. Smith, R. Robertson, and D. Cross. 1977. The ecology of the polar bear (*Ursus maritimus*) along the western coast of Hudson Bay. Occasional Paper 33, Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Stirling, I., C. Spencer, and D. Andriashek. 1989. Immobilization of polar bears (*Ursus maritimus*) with Telazol® in the Canadian Arctic. *Journal of Wildlife Diseases* 25:159–168.
- Stirling, I., N. J. Lunn, and J. Iacozza. 1999. Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. *Arctic* 52:294–306.
- Stirling, I., N. J. Lunn, J. Iacozza, C. Elliott, and M. Obbard. 2004. Polar bear distribution and abundance on the Southwestern Hudson Bay Coast during open water season, in relation to population trends and annual ice patterns. *Arctic* 57:15–26.
- Stirling, I., T. L. McDonald, E. S. Richardson, E. V. Regehr, and S. C. Amstrup. 2011. Polar bear population status in the northern Beaufort Sea, Canada, 1971–2006. *Ecological Applications* 21:859–876.
- Stroeve, J., M. M. Holland, W. Meier, T. Scambos, and M. Serreze. 2007. Arctic sea ice decline: faster than forecast. *Geophysical Research Letters* 34:L09501.
- Stroeve, J. C., V. Kattsov, A. Barrett, M. Serreze, T. Pavlova, M. Holland, and W. N. Meier. 2012a. Trends in Arctic sea ice extent from CMIP5, CMIP3 and observations. *Geophysical Research Letters* 39:L16502.
- Stroeve, J. C., M. C. Serreze, M. M. Holland, J. E. Kay, J. Malanik, and A. P. Barrett. 2012b. The Arctic's rapidly shrinking sea ice cover: a research synthesis. *Climatic Change* 110:1005–1027.
- Swart, N. C., J. C. Fyfe, E. Hawkins, J. E. Kay, and A. Jahn. 2015. Influence of internal variability on Arctic sea-ice trends. *Nature Climate Change* 5:86–89.
- Taylor, M., and J. Lee. 1995. Distribution and abundance of Canadian polar bear populations – a management perspective. *Arctic* 48:147–154.
- Taylor, M. K., P. D. McLoughlin, and F. Messier. 2008. Sex-selective harvesting of polar bears *Ursus maritimus*. *Wildlife Biology* 14:52–60.
- Thiemann, G. W., S. J. Iverson, and I. Stirling. 2008. Polar bear diets and Arctic marine food webs: insights from fatty acid analysis. *Ecological Monographs* 78:591–613.
- Towns, L., A. E. Derocher, I. Stirling, N. J. Lunn, and D. Hedman. 2009. Spatial and temporal patterns of problem polar bears in Churchill, Manitoba. *Polar Biology* 32:1529–1537.
- Tynan, C. T., and D. P. DeMaster. 1997. Observations and predictions of Arctic climate change: potential effects on marine mammals. *Arctic* 50:308–322.
- Wade, P. R. 2002. Bayesian population viability analysis. Pages 213–238 in S. R. Beissinger, and D. R. McCullough, editors. *Population viability analysis*. University of Chicago Press, Chicago, Illinois, USA.
- Wiig, Ø., J. Aars, and E. W. Born. 2008. Effects of climate change on polar bears. *Science Progress* 91:151–173.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. *Analysis and management of animal populations*. Academic Press, San Diego, California, USA.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1890/15-1256/supinfo>