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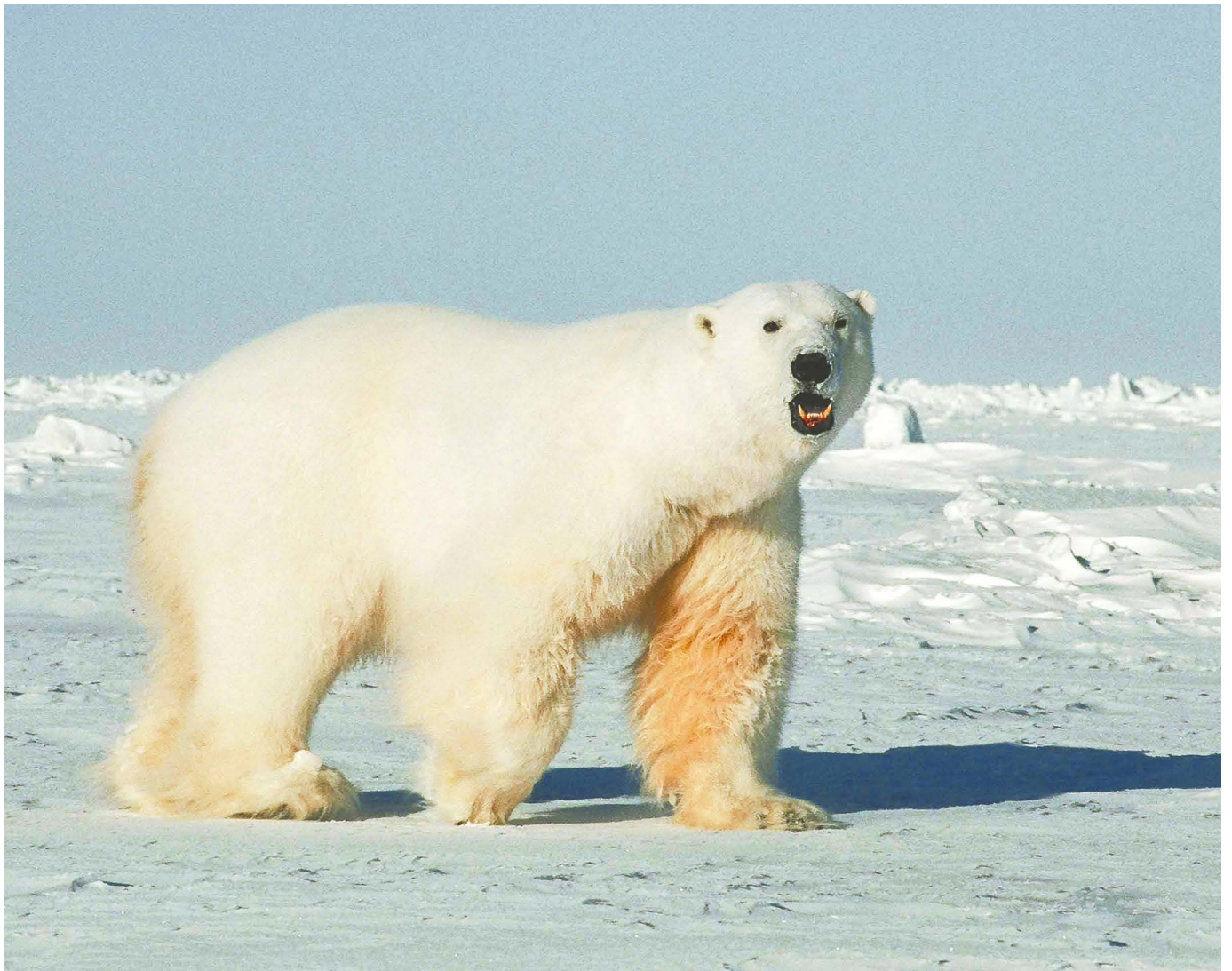
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# Polar bear population dynamics in the southern Beaufort Sea during a period of sea ice decline

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**Abstract.** In the southern Beaufort Sea of the United States and Canada, prior investigations have linked declines in summer sea ice to reduced physical condition, growth, and survival of polar bears (*Ursus maritimus*). Combined with projections of population decline due to continued climate warming and the ensuing loss of sea ice habitat, those findings contributed to the 2008 decision to list the species as threatened under the U.S. Endangered Species Act. Here, we used mark–recapture models to investigate the population dynamics of polar bears in the southern Beaufort Sea from 2001 to 2010, years during which the spatial and temporal extent of summer sea ice generally declined. Low survival from 2004 through 2006 led to a 25–50% decline in abundance. We hypothesize that low survival during this period resulted from (1) unfavorable ice conditions that limited access to prey during multiple seasons; and possibly, (2) low prey abundance. For reasons that are not clear, survival of adults and cubs began to improve in 2007 and abundance was comparatively stable from 2008 to 2010, with ~900 bears in 2010 (90% CI 606–1212). However, survival of subadult bears declined throughout the entire period. Reduced spatial and temporal availability of sea ice is expected to increasingly force population dynamics of polar bears as the climate continues to warm. However, in the short term, our findings suggest that factors other than sea ice can influence survival. A refined understanding of the ecological mechanisms underlying polar bear population dynamics is necessary to improve projections of their future status and facilitate development of management strategies.

**Key words:** abundance; Arctic; climate warming; Cormack-Jolly-Seber; demographic modeling; Horvitz-Thompson; mark–recapture; sea ice; survival; *Ursus maritimus*.

## INTRODUCTION

The polar bear (*Ursus maritimus*) is a universally recognized symbol of the Arctic. Polar bears prefer sea ice concentrations exceeding 50% in the shallow, productive waters over the continental shelf (Sakshaug 2004, Durner et al. 2009), where ice provides a platform from which polar bears can efficiently hunt marine mammals (see Plate 1). Their primary prey are ringed (*Pusa hispida*) and bearded (*Erignathus barbatus*) seals, although diet varies regionally with prey availability (Thiemann et al. 2008, Cherry et al. 2011).

Polar bears are vulnerable to the loss of sea ice, which is projected to induce substantial declines in abundance by mid-century (Amstrup et al. 2008, Hunter et al. 2010)

unless global greenhouse gas levels are reduced (Amstrup et al. 2010). Global temperatures will rise as atmospheric greenhouse gas concentrations increase (Pierrehumbert 2011), and the Arctic has warmed at twice the global rate (IPCC 2007), in part due to positive feedback mechanisms referred to as Arctic Amplification (Serreze and Francis 2006, Perovich and Polashen-ski 2012). Since the advent of satellite observations in 1979, the spatial extent of Arctic sea ice during the autumn ice minimum declined by over 12% per decade through 2010 (Stroeve et al. 2012), a rate of loss greater than predicted by climate models (Stroeve et al. 2007, Overland and Wang 2013). Coastal areas are experiencing longer ice-free periods (Markus et al. 2009), and the remaining ice is increasingly composed of thin, first-year ice (Maslanik et al. 2007, 2011) with greater potential for rapid melt in subsequent years (Stroeve et al. 2012). Projections of global warming and sea ice loss led to the species being listed as threatened under the U.S. Endangered Species Act in 2008, increasing global awareness of its status, and elevating the importance

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of monitoring by circumpolar nations (Vongraven et al. 2012).

Amstrup et al. (2008) introduced a classification of polar bear habitat into ecoregions based on broad seasonal patterns of sea ice dynamics that is useful for understanding regional differences in polar bear ecology (Fig. 1). However, populations sharing an ecoregion may experience localized combinations of environmental and ecological conditions that elicit different responses. For example, in the seasonal ice ecoregion (Fig. 1), where sea ice melts completely in summer and forces all bears ashore until ice re-forms in autumn, reduced access to prey during prolonged ice-free periods is negatively affecting the status of some populations (Stirling et al. 1999, Regehr et al. 2007, Rode et al. 2012), while high prey abundance may be forestalling declines in other populations (Peacock et al. 2013). In the divergent ice ecoregion (Fig. 1), polar bears still have access to some ice all year, although its availability over the continental shelf during summer and autumn is increasingly limited (Markus et al. 2009). Despite extensive sea ice loss throughout the divergent ice ecoregion (Markus et al. 2009, Stammerjohn et al. 2012), an expansive continental shelf and high productivity may have enabled the Chukchi Sea population to maintain condition and recruitment more effectively than the neighboring southern Beaufort Sea (SBS) population (Rode et al. 2014).

The SBS population is one of 19 recognized worldwide (Obbard et al. 2010), and it has been studied more intensively than most. The population is thought to have been overharvested prior to the passage of the U.S. Marine Mammal Protection Act in 1972 (Amstrup et al. 1986), and to have generally increased in abundance thereafter through the late 1990s (Amstrup et al. 2001). Estimates from the mid-2000s suggested that abundance had stabilized and possibly declined (Regehr et al. 2006).

Recent investigations of the SBS population have revealed early indications of the effects of climate-induced changes in the characteristics and availability of sea ice. Fischbach et al. (2007) documented a shift in the distribution of maternal dens from multiyear pack ice to terrestrial locations, perhaps in response to the reduced availability of ice suitable for denning (Amstrup and Gardner 1994). The summer retreat of sea ice from continental-shelf waters now forces polar bears to either remain with the remnant ice in the central Polar Basin or move to land; both options are hypothesized to reduce fitness compared to historical patterns of habitat availability and use. Although most SBS polar bears currently remain with the sea ice, a growing proportion of the population is utilizing terrestrial habitat (Schliebe et al. 2008; USGS, *unpublished data*) and accessing remains of subsistence-harvested bowhead whale (*Balaena mysticetus*) carcasses (Herreman and Peacock 2013). The increasing distance between shore and the summer pack ice increases the potential for long-distance swimming (Pagano et al. 2012), which elevates

susceptibility to adverse weather (Monnett and Gleason 2006) and is energetically expensive (Durner et al. 2011). Nutritional stress also appears to be increasing (Cherry et al. 2009, Rode et al. 2014), and may be responsible for observations of reduced body size, growth, and survival of young (Rode et al. 2010, 2014). Regehr et al. (2010) associated reduced ice over the continental shelf in 2004 and 2005 with reductions in survival (Amstrup and Durner 1995, Amstrup et al. 2001).

We investigated the population dynamics of SBS polar bears from 2001 to 2010 using Cormack-Jolly-Seber (CJS) mark-recapture models (Lebreton et al. 1992, Amstrup et al. 2005) to (1) determine whether low survival rates reported for 2004 and 2005 (Regehr et al. 2010) persisted into subsequent years, (2) assess the recent trend in abundance, and (3) refine our understanding of the relationship between sea ice and polar bear survival. The spatial and temporal extent of sea ice over the continental shelf generally declined during this period, and we evaluated the utility of measures of ice availability to explain temporal patterns in survival. Our findings provide new information on population status, as well as insights into the ecological mechanisms underlying population dynamics of polar bears.

## METHODS

### *Study area*

The Beaufort Sea (Fig. 1), unlike most marginal seas in the Polar Basin, has a narrow continental shelf with a steep shelf-break that plunges to some of the deepest waters of the Arctic Ocean (Jakobsson et al. 2008). Pacific waters enter the Arctic Ocean via the Bering Strait and the remnant of the Alaska Coastal Current flows eastward along the shelf (Schulze and Pickart 2012). Nearshore waters carry substantial freshwater inputs, including terrestrial carbon and nitrogen, from the Mackenzie River and numerous smaller river systems (Dunton et al. 2006). Offshore, the anti-cyclonic Beaufort Gyre (Proshutinsky et al. 2002, Giles et al. 2012) and the Transpolar Drift Stream (Serreze et al. 1989) govern sea ice motion basin-wide.

During spring, primary production in the SBS is dominated by ice algae (Horner and Schrader 1982). Wind-induced current reversals and storm events pump nutrient-rich basin waters onto the continental shelf, supporting production throughout the year and seeding the algal bloom the following year (e.g., Sigler et al. 2011, Tremblay et al. 2011, Schulze and Pickart 2012, Pickart et al. 2013a, b). Climate warming is increasing primary productivity (Tremblay et al. 2011, Nicolaus et al. 2012, Pickart et al. 2013a) and altering its composition (Lasternas and Agustí 2010). Open water at the interface of land-fast ice and pack ice is an additional source of primary production (Palmer et al. 2011), and these areas are important for numerous Arctic species (Stirling 1997). Zooplankton are thought to underutilize primary production in Arctic ecosystems, thereby favoring a rich benthos (Grebmeier et al. 2006,

Logerwell et al. 2011). Arctic cod (*Boreogadus saida*) are the most abundant fish in pelagic waters (Jarvela and Thorsteinson 1999, Parker-Stetter et al. 2011). Ringed and bearded seals are resident year-round (Stirling et al. 1982, Frost et al. 2004), while beluga (*Delphinapterus leucas*) and bowhead whales migrate into the SBS during summer (Luque and Ferguson 2009, Ashjian et al. 2010). Polar bears are an apex predator of this food web, which may be sensitive to perturbation due to its simple structure and strong interspecific dependencies (Banašek-Richter et al. 2009).

#### Data sources

U.S. Geological Survey (USGS) researchers captured polar bears in the U.S. portion (Alaska) of the SBS (Fig. 1) from approximately late March to early May annually from 2001 to 2010. The communities of Barrow, Deadhorse, and Barter Island (Kaktovik) were used as operational bases each year, excluding Barrow in 2001 and Barter Island in 2006. Helicopters were used to search the sea ice for polar bears, ranging as far as ~160 km from the coast. Bears were immobilized with Telazol (Pfizer Animal Health, New York, New York, USA) administered with projectile syringes fired from a helicopter (Stirling et al. 1989) and given lip tattoos and ear tags with unique identification numbers. Satellite radio collars were affixed to a subset of adult females captured, except in 2010. Captures were generally nonselective with respect to sex and age class, although females wearing radio collars were often targeted to facilitate collar retrieval. Field procedures were approved by the independent USGS Alaska Science Center Animal Care and Use Committee.

Researchers from Environment Canada (EC) and the University of Alberta (UA) conducted mark-recapture activities in the Canadian portion of the population range (Fig. 1) using similar methods in April and May from 2003 to 2006. The combined efforts of USGS, EC, and UA resulted in the distribution of capture effort throughout the majority of the SBS population range in those years. UA researchers continued to capture polar bears in Canada from 2007 to 2010, although subadults and females were preferentially targeted, and capture effort did not extend into the easternmost portion of the study area. Animal welfare committees of EC and UA approved bear capture and handling protocols in Canada.

We modeled the population dynamics of SBS polar bears using two combinations of data. The first data set (USGS) was compiled from USGS captures in the United States portion of the study area. Capture methods were consistent throughout the study period, and these data were therefore expected to provide the most reliable assessment of trends in survival and abundance, although estimates were applicable only to the portion of the population available for capture within the United States. The second data set (USA and Canada [USCA]), was compiled from the data collected

by all three entities. The USCA data had greater spatial coverage and the potential to produce estimates germane to the entire SBS population. However, the geographic and temporal discontinuities in capture effort and differential selectivity for age and sex classes in some years presented modeling challenges, especially with respect to estimation of recapture probabilities and abundance.

#### Mark-recapture modeling

We estimated the survival and abundance of SBS polar bears using open-population Cormack-Jolly-Seber (CJS) models (Lebreton et al. 1992, Amstrup et al. 2005), similar to several previous mark-recapture investigations of polar bear populations (e.g., Amstrup et al. 2001, Regehr et al. 2007, 2010, Taylor et al. 2008, Stirling et al. 2011). Multiple observations of an individual within a calendar year were amalgamated into a single capture record for that year and the history of annual capture indicators was constructed for each animal. We used information on harvests of marked bears to terminate subsequent modeling of their capture histories.

CJS models are composed of sub-models for survival and recapture probabilities, which are typically expressed as linear functions of explanatory variables (covariates) via a logistic link function (Lebreton et al. 1992). Covariates were either single variables or groups of related variables that were employed simultaneously, so we used a single term to reference either case (Table 1; Appendix A). We utilized the regression parameterization of CJS models (McDonald and Amstrup 2001, Amstrup et al. 2005) because of the flexibility with which it incorporates covariates. Parameters of the logistic functions were estimated using maximum likelihood. Survival and recapture probabilities were estimated from the parameters of the logistic functions, and abundance estimates were derived from the estimated recapture probabilities using the Horvitz-Thompson estimator (Horvitz and Thompson 1952, McDonald and Amstrup 2001).

#### Survival probability models

We constructed survival models from combinations of covariates representing age and sex class effects and forms of temporal structure, and modeled survival probabilities separately for each age class (Table 2). Four age classes were defined: cub (Age0), yearling (Age1), subadult (2 to 4 years old, Age2), and adult (>4 years old, Age3), categories similar to those used in other investigations (e.g., Regehr et al. 2010, Stirling et al. 2011). Survival models also incorporated one of four forms of temporal variation: temporal stratification (TS-sur), a cubic function of year (Time-cubic), and two measures of sea ice availability. Data were too sparse to independently estimate an annual survival probability for each age class, but the covariates TS-sur and Time-cubic provided flexibility to model temporal variation

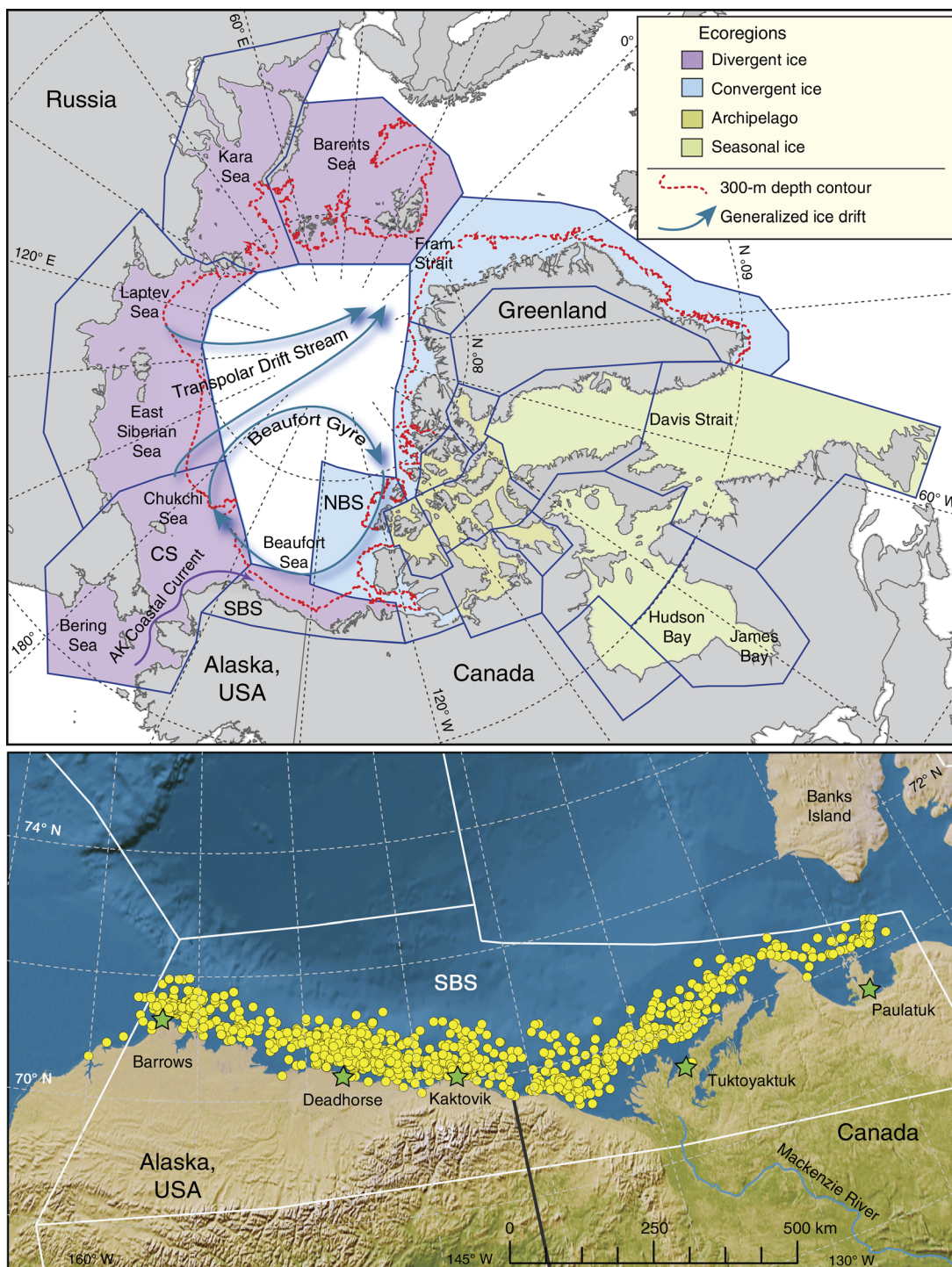


FIG. 1. The upper panel contains a map of the Polar Basin, showing peripheral seas, predominate currents, and ecoregions based upon characteristics of sea ice dynamics. Solid blue lines show the boundaries of polar bear populations recognized by the International Union for the Conservation of Nature, Polar Bear Specialist Group (<http://pbsg.npolar.no/en/status/population-map.html>). The lower panel shows the range of the southern Beaufort Sea polar bear (*Ursus maritimus*) population defined by the International Union for Conservation of Nature, with a modified western boundary per Amstrup et al. (2008), and locations of polar bear captures from 2001 to 2010 (yellow circles). Abbreviations are: AK, Alaska, USA; NBS, northern Beaufort Sea; and CS, Chukchi Sea.



TABLE 1. Covariates and covariate groups used to model polar bear (*Ursus maritimus*) survival and recapture probabilities, with a brief description, the associated degrees of freedom (df), the data set (USGS, USCA, or both), and component of the CJS model ( $\phi$ , survival, or  $p$ , recapture) in which each covariate was used.

| Covariate group | Description   | df | Data | Model        |
|-----------------|---|----|------|--------------|
| Age0            | a cub, age 0  | 1  | both | $\phi$       |
| Age01.23Fem     | a cub or yearling, or subadult or adult female            | 1  | both | $p$          |
| Age01.3Fem      | a cub or yearling, or adult female                        | 1  | both | $p$          |
| Age1            | a yearling, age 1 yr                                      | 1  | both | $\phi$       |
| Age2            | a subadult, age 2–4 yr                                    | 1  | both | $\phi$ , $p$ |
| Age2Fem         | a subadult female   | 1  | both | $\phi$ , $p$ |
| Age3            | an adult, age >4 yr                                       | 1  | both | $\phi$ , $p$ |
| Age3Fem         | an adult female   | 1  | both | $\phi$ , $p$ |
| BI2006          | a home stratum of Barter Island in 2006                   | 1  | both | $p$          |
| CA              | a home stratum of Canada                                  | 1  | USCA | $p$          |
| Cap-procliv     | a summarization of prior capture history                  | 1  | both | $p$          |
| Eff-CA          | effort strata in Canada; low, medium, and high            | 3  | USCA | $p$          |
| Eff-US          | effort strata in the USA; low, medium, and high           | 3  | both | $p$          |
| Home            | indicator of home stratum                                 | 3  | both | $p$          |
| Melt-season     | length of the melt-season each year                       | 1  | both | $\phi$       |
| Radio           | indicator of an active collar                             | 1  | both | $p$          |
| Search          | hours searching for bears in the USA and Canada           | 1  | USCA | $p$          |
| Search-US       | hours searching for bears in the USA                      | 1  | USGS | $p$          |
| Summer-habitat  | area of optimal ice habitat each year                     | 1  | both | $\phi$       |
| Time            | separate probability for each year                        | 9  | both | $p$          |
| Time-cubic      | linear, quadratic, and cubic functions of time            | 3  | both | $\phi$       |
| TS-sur          | temporal strata for U.S. and Canada survival              | 3  | both | $\phi$       |
| UA              | sex and age covariates for University of Alberta captures | 3  | USCA | $p$          |
| US              | indicator of U.S. home strata                             | 1  | both | $p$          |

Notes: The covariates comprising each group are defined in Appendix A. Abbreviations are: USGS, U.S. Geological Survey; USCA, USA and Canada; and CJS, Cormack-Jolly-Seber.

using fewer parameters (e.g., Stoklosa and Huggins 2012, Peacock et al. 2013, Thorson et al. 2013). We constructed the ice covariate Summer-habitat by summing monthly indices of the area ( $\text{km}^2$ ) of optimal polar bear habitat over the SBS continental shelf (Durner et al. 2009) for July through October of each year (Fig. 2). We expected this covariate to be informative because it was based on the availability of habitat preferred by radio-collared polar bears. The ice covariate Melt-season measured the time between the melt and freeze onset in the Beaufort Sea each summer (Inner Melt Length; Fig. 2; Markus et al. 2009, Stroeve et al. 2014), obtained courtesy of Dr. Julianne Stroeve (National Snow and Ice Data Center, University of Colorado, *personal communication*). We included Melt-season because it covered a broader geographic region than Summer-habitat and the two covariates were not highly correlated ( $r = -0.68$ ). The means and standard deviations of the ice covariates from 2001 to 2010 were used to normalize their values before analysis.

#### Recapture probability models

Recapture models incorporated covariates for sex and the four age classes. We constrained recapture probabilities of cubs and yearlings to equal those of adult females because family groups were captured simultaneously (Age01.3Fem). We constructed a group of time-varying indicator covariates (UA) to model potential discontinuities in Canadian recapture probabilities after 2006, because UA researchers targeted females and subadults and expended less capture effort from 2007 to 2010.

Recapture models incorporated two nonparametric forms of temporal structure, either constant through time or a separate probability for each year (Time). In addition, we constructed covariates to model temporal variation arising from heterogeneity in capture effort. The hours spent searching for polar bears in the United States each year was recorded by USGS (Search-US). The total hours

TABLE 2. Covariate structure and associated degrees of freedom (df) used to model survival probabilities for each age class.

| Age class | Covariate structure   | df |
|-----------|---|----|
| Cub       | Age0 $\times$ TS-sur  | 3  |
| Cub       | <b>Age0 + Age0 <math>\times</math> Time-cubic</b>           | 4  |
| Cub       | Age0 + Age0 $\times$ Summer-habitat                         | 2  |
| Cub       | Age0 + Age0 $\times$ Melt-season                            | 2  |
| Yearling  | Age1 $\times$ TS-sur  | 3  |
| Yearling  | <b>Age1 + Age1 <math>\times</math> Time-cubic</b>           | 4  |
| Yearling  | Age1 + Age1 $\times$ Summer-habitat                         | 2  |
| Yearling  | Age1 + Age1 $\times$ Melt-season                            | 2  |
| Subadult  | Age2 $\times$ TS-sur + Age2Fem                              | 4  |
| Subadult  | <b>Age2 + Age2 <math>\times</math> Time-cubic + Age2Fem</b> | 5  |
| Subadult  | Age2 + Age2 $\times$ Summer-habitat + Age2Fem               | 3  |
| Subadult  | Age2 + Age2 $\times$ Melt-season + Age2Fem                  | 3  |
| Adult     | Age3 $\times$ TS-sur + Age3Fem                              | 4  |
| Adult     | <b>Int + Age3 <math>\times</math> Time-cubic + Age3Fem</b>  | 5  |
| Adult     | Int + Age3 $\times$ Summer-habitat + Age3Fem                | 3  |
| Adult     | Int + Age3 $\times$ Melt-season + Age3Fem                   | 3  |

Notes: A “+” denotes an additive model, and “ $\times$ ” denotes a covariate interaction. The adult component contains an overall mean (Int) when only continuous temporal covariates are included. See Table 1 for descriptions of covariate abbreviations. Some covariates consisted of multiple related covariates that were always used jointly; definitions are provided in Appendix A. Covariate structures in boldface type were used to assess goodness-of-fit.

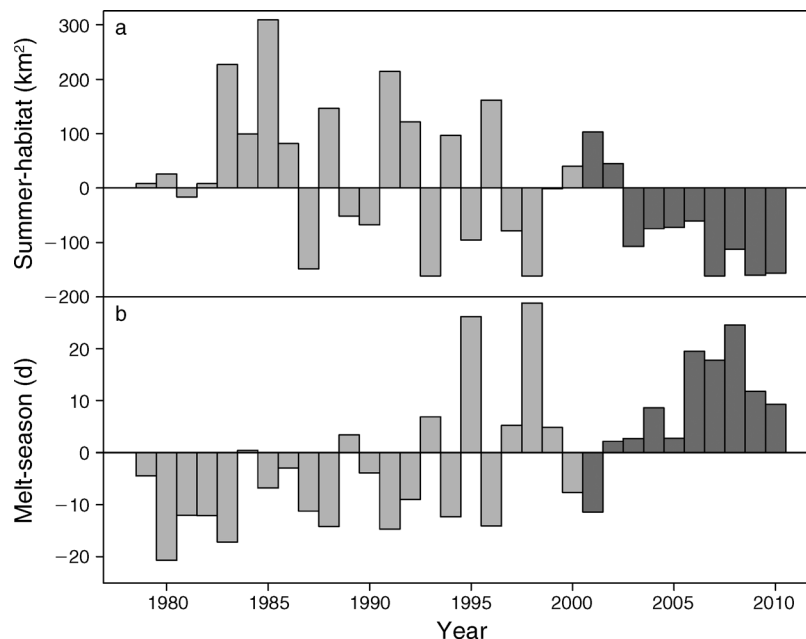


FIG. 2. Anomalies (difference from the mean) of the two sea ice covariates from 1979 to 2010. Normalized values from 2001 to 2010 (dark gray) were used to model polar bear survival probabilities: (a) Summer-habitat, and (b) Melt-season. Summer-habitat was constructed by summing monthly indices of the area ( $\text{km}^2$ ) of optimal polar bear habitat over the SBS continental shelf (Durner et al. 2009) for July through October of each year, and Melt-season measured the time between the melt and freeze onset in the Beaufort Sea each summer.

spent flying in Canada was recorded, and we assumed 60% of flight hours were spent actively searching for polar bears, a percentage derived from USGS flight records. We added the resulting approximation of Canadian search hours to USGS search hours to construct a measure of effort for the entire study area (Search). In addition, we stratified annual search hours in the United States and Canada into low, medium, and high effort categories (Eff-US, Eff-CA), which Stirling et al. (2011) found useful.

We incorporated geographic structure into some models because recapture probabilities vary within the study area (Amstrup et al. 2001). We assigned individuals to a home stratum based on the proximity of their mean capture longitude to the four operational bases (Fig. 1), and used stratum assignments to construct four indicator covariates: Barrow, Deadhorse, Barter Island, and Canada (Home). These covariates reflected coarse variation in recapture probabilities among regions, rather than distinct locations as would be used in multistate models (White et al. 2006). We collapsed the Home covariates into two covariates corresponding to country (US, CA) for some models. In addition, we used an indicator covariate (BI2006) to accommodate the lack of effort from the Barter Island base in 2006.

Two covariates improved model fit so greatly that we included them in all recapture models. The first (Radio) indicated whether a bear was wearing an active radio during the sampling period each year. Instrumented bears were often targeted for sampling to evaluate their condition and retrieve radios, and could therefore have

elevated recapture probabilities; similar covariates have been used by other researchers (e.g., Amstrup et al. 2001, Regehr et al. 2010, Stirling et al. 2011). The second covariate (Cap-procliv) modeled potential recapture heterogeneity unexplained by other covariates, using an individual's prior capture history as a measure of its current tendency to be recaptured (Appendix F), indirectly accounting for individual characteristics, such as behavior, that are difficult to quantify.

We constructed models of recapture probability from combinations of four age and sex class effects and eight covariate combinations representing temporal and geographic (abiotic) structure (Tables 3 and 4).

#### Modeling strategies

We formed CJS models from combinations of survival and recapture sub-models (Tables 2–4). We utilized the plausible combinations (PC) strategy (Bromaghin et al. 2013), with an Akaike's information criterion ( $\text{AIC}_c$ ) model weight (Burnham and Anderson 2002) of 2.5% as an inclusion threshold, to objectively base inference on a reduced model space. Simulation results (Bromaghin et al. 2013) suggest its performance is similar to that of the “all combinations” strategy recommended by Doherty et al. (2012).

We utilized R version 3.0.3 (R Development Core Team 2013) for data manipulation and version 2.14 of the R package mra (*available online*)<sup>9</sup> to estimate model

<sup>9</sup> <http://cran.r-project.org/web/packages/mra/index.html>



TABLE 3. Covariate structure and associated degrees of freedom (df) used to model recapture probabilities for the USGS data set.

| Source  | Covariate structure                                      | df |
|---------|--|----|
| Age–sex | ...  | 0  |
| Age–sex | Age2   | 1  |
| Age–sex | Age01.23Fem  | 1  |
| Age–sex | <b>Age01.3Fem + Age2 + Age2Fem</b>                       | 3  |
| Abiotic | Int + Radio + Cap-procliv                                | 3  |
| Abiotic | Eff-US + Radio + Cap-procliv                             | 5  |
| Abiotic | Int + Hunt-US + Radio + Cap-procliv                      | 4  |
| Abiotic | Home × US + BI2006 + Radio + Cap-procliv                 | 5  |
| Abiotic | Time + Radio + Cap-procliv                               | 11 |
| Abiotic | Eff-US + Home × US + BI2006 + Radio + Cap-procliv        | 7  |
| Abiotic | Int + Hunt-US + Home × US + BI2006 + Radio + Cap-procliv | 6  |
| Abiotic | <b>Time + Home × US + BI2006 + Radio + Cap-procliv</b>   | 13 |

*Notes:* Covariates associated with temporal and geographic structure are collectively referred to as Abiotic. A “+” denotes an additive model and “×” denotes a covariate interaction. The abiotic component contains an overall mean (Int) when only continuous temporal covariates are included. See Table 1 for descriptions of covariate abbreviations. Some covariates consisted of multiple related covariates that were always used jointly; definitions are provided in Appendix A. An ellipsis signifies that no parameters were used to model different recapture probabilities for sex and age classes; all sex and age classes had the same recapture probability. Covariate structures in boldface type were used to assess goodness-of-fit.

parameters (function `F.cjs.estim`), using the Horvitz-Thompson estimator of abundance (Horvitz and Thompson 1952, McDonald and Amstrup 2001), and compute model-averaged estimates based on  $AIC_c$  model weights (function `F.cr.model.avg`).

We evaluated estimation precision using bootstrap resampling (Chernick 1999), drawing bootstrap samples of capture histories and individual covariates at random with replacement. For each sample, we implemented the PC strategy to select models, estimate the parameters of all selected models, and compute model-averaged estimates (Burnham and Anderson 2002) of recapture, survival, and abundance. Because of the computational burden of this approach, we drew 100 bootstrap samples. We bias-corrected (Chernick 1999) the model-averaged estimates, so their means equaled the original model-averaged estimates, and constructed nonpara-

metric 90% confidence intervals as the 5th and 95th quantiles of the corrected bootstrap estimates.

$AIC_c$  is a relative measure of model suitability, so confidence in the interpretation of  $AIC_c$  statistics is enhanced if at least one model provides a reasonable approximation to the data. For each data set, we selected one of the most flexible models and assessed goodness-of-fit using tests implemented in the R package `mra` (function `F.cjs.gof`), which are derived from procedures common in logistic regression (Hosmer and Lemeshow 2000, Sakar and Midi 2010).

We assessed the importance of covariates using summed  $AIC_c$  model weights (Burnham and Anderson 2002). However, because uninformative covariates accumulate weight when used in combination with informative covariates (Doherty et al. 2012, Bromaghin et al. 2013), we summed weights on the basis of covariate

TABLE 4. Covariate structure and associated degrees of freedom (df) used to model recapture probabilities for the USCA data set.

| Source  | Covariate structure  | df |
|---------|--|----|
| Age–sex | UA   | 3  |
| Age–sex | Age2 + UA  | 4  |
| Age–sex | Age01.23Fem + UA   | 4  |
| Age–sex | <b>Age01.3Fem + Age2 + Age2Fem + UA</b>                              | 6  |
| Abiotic | Int + Radio + Cap-procliv  | 3  |
| Abiotic | Int + Hunt + Radio + Cap-procliv                                     | 4  |
| Abiotic | Time + Radio + Cap-procliv   | 11 |
| Abiotic | Home + BI2006 + Eff-CA.1 × CA + Radio + Cap-procliv                  | 7  |
| Abiotic | Int + Hunt + Home + BI2006 + Eff-CA.1 × CA + Radio + Cap-procliv     | 8  |
| Abiotic | <b>Time + Home + BI2006 + Eff-CA.1 × CA + Radio + Cap-procliv</b>    | 15 |
| Abiotic | Eff-US × US + Eff-CA × CA + Radio + Cap-procliv                      | 8  |
| Abiotic | Eff-US × US + Home × US + BI2006 + Eff-CA × CA + Radio + Cap-procliv | 10 |

*Notes:* Covariates associated with temporal and geographic structure are collectively referred to as Abiotic. A “+” denotes an additive model, and “×” denotes a covariate interaction. The abiotic component contains an overall mean (Int) when only continuous temporal covariates are included. See Table 1 for descriptions of covariate abbreviations. Some covariates consisted of multiple related covariates that were always used jointly; definitions are provided in Appendix A. Covariate structures in boldface type were used to assess goodness-of-fit.

combinations (Tables 2–4), rather than individual covariates (Burnham and Anderson 2002).

#### *Complementary analyses to investigate potential bias*

Aspects of animal movement and their availability for capture are important considerations in mark–recapture modeling. A pulse of permanent emigration, or temporary emigration near the end of a study, can produce the type of decline in apparent survival reported by Regehr et al. (2010). Although the population level effect of permanent emigration is equivalent to death (e.g., Nichols 2005), understanding population dynamics requires differentiating between them. Similarly, because only the nearshore regions of SBS polar bear habitat can be searched by helicopter (Fig. 1), heterogeneity in habitat preference, temporary emigration, and the nonrandom distribution of individuals could bias parameter estimates. For these reasons, we analyzed available location data from radio-collared female polar bears for signs of pulsed emigration or nonrandom movement that might aid interpretation of parameter estimates.

Abundance estimates in CJS models are derived from recapture probabilities using the Horvitz-Thompson estimator (Horvitz and Thompson 1952, McDonald and Amstrup 2001). Because un-modeled heterogeneity in recapture probabilities can bias abundance estimates, we investigated the reliability of estimated abundance trends by comparing them to simulated abundance projections based on estimated survival probabilities, which are comparatively robust to recapture heterogeneity (Carothers 1979, Abadi et al. 2013), but also see Peñaloza et al. (2014). The projections incorporated a measure of cub production similar to litter production rate (Ramsay and Stirling 1988) and breeding success (Wiig 1998).

## RESULTS

### *Data summary*

The USGS data contained information on 715 individual bears that were captured a total of 1049 times (Appendix B). Information on the harvests of 21 marked bears was used to censor their capture histories. The USCA data contained information on 1086 individuals captured a total of 1590 times, and capture histories of 38 bears were censored following their harvests. The number of bears captured annually ranged from 75 to 148 individuals in the USGS data, and from 97 to 291 individuals in the USCA data set (Table 5). The proportion of captured bears that were marked increased during the initial years and stabilized approximately midway through the investigation (Table 5). Additional capture statistics are provided in Appendix B.

### *Model selection and goodness-of-fit*

The PC model selection strategy (Bromaghin et al. 2013) with the USGS data resulted in the retention of 60

TABLE 5. The number of southern Beaufort Sea polar bears captured ( $N$ ), and the number ( $M$ ) and percentage (%) that were previously marked, by year in the USGS and USCA data sets.

| Year | USGS |     |      | USCA |     |      |
|------|------|-----|------|------|-----|------|
|      | $N$  | $M$ | %    | $N$  | $M$ | %    |
| 2001 | 135  | ... | ...  | 135  | ... | ...  |
| 2002 | 118  | 36  | 30.5 | 118  | 36  | 30.5 |
| 2003 | 107  | 28  | 26.2 | 167  | 32  | 19.2 |
| 2004 | 148  | 39  | 26.4 | 291  | 64  | 22.0 |
| 2005 | 96   | 37  | 38.5 | 251  | 81  | 32.3 |
| 2006 | 90   | 40  | 44.4 | 150  | 64  | 42.7 |
| 2007 | 80   | 29  | 36.3 | 116  | 53  | 45.7 |
| 2008 | 88   | 35  | 39.8 | 108  | 49  | 45.4 |
| 2009 | 112  | 52  | 46.4 | 157  | 80  | 51.0 |
| 2010 | 75   | 38  | 50.7 | 97   | 45  | 46.4 |

Note: The first year of tagging was 2001, and recaptures could not occur until 2002 (indicated with ellipses).

survival probability models and 20 recapture probability models. The estimation algorithm failed to converge for one combination of survival and recapture models (for survival, Int + Age3 × Melt-season + Age3Fem + Age2 × Melt-season + Age2Fem + Age1 × Melt-season + Age0 × TS-sur; and for recapture, Time + Age01.23Fem + Radio + Cap-procliv). The model selected to evaluate goodness-of-fit contained 34 parameters (covariate structures listed in boldface type in Tables 2 and 3). The results of goodness-of-fit tests did not raise concerns regarding inadequate model fit. The Osius-Rojek test could not be evaluated (it returned a “not-a-number” code), but the Hosmer-Lemeshow test was not significant ( $P = 0.690$ ), and the Receiver Operating Characteristic (ROC) curve displayed acceptable discrimination (0.736).

For the USCA data, the PC model selection strategy resulted in 47 survival probability models and 4 recapture probability models being selected for further consideration. The model selected to assess goodness-of-fit contained 39 parameters (covariate structures listed in boldface type in Tables 2 and 4). Based on that model, the Osius-Rojek test was moderately significant ( $P = 0.036$ ), but the Hosmer-Lemeshow test was not ( $P = 0.276$ ) and the Receiver Operating Characteristic (ROC) curve displayed acceptable discrimination (0.727), providing no compelling evidence of inadequate model fit.

### *Survival and recapture probabilities*

Model-averaged estimates of survival based on the USGS data differed among age classes and varied through time (Fig. 3, Table 6). Survival of adult bears was high from 2001 through 2003, substantially reduced from 2004 through 2007, and higher but below historical levels in 2008 and 2009 (Amstrup and Durner 1995, Amstrup et al. 2001). Point estimates for males were slightly higher than for females, though confidence intervals broadly overlapped. Model weight was distributed across all forms of temporal structure for adults,

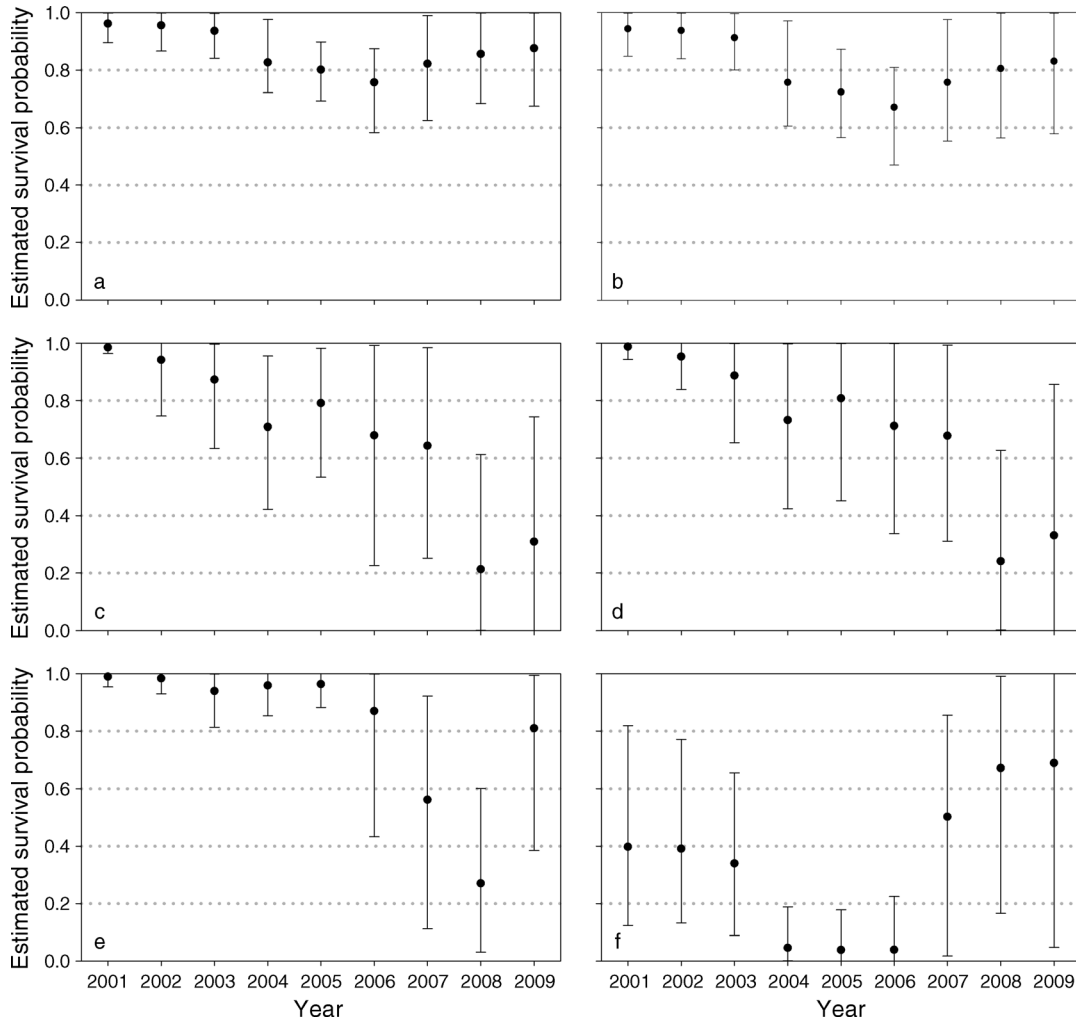


FIG. 3. Model-averaged estimates of annual polar bear survival probability by age class and sex for the U.S. Geological Survey (USGS) data set: (a) adult males, (b) adult females, (c) subadult males, (d) subadult females, (e) yearlings, and (f) cubs. Error bars represent 90% bias-corrected bootstrap confidence intervals based on 100 replications.

TABLE 6. Total corrected Akaike's information criterion ( $AIC_c$ ) model weight associated with covariate structures of survival probability models, by age class, based on the USGS data set.

| Age class | Covariate structure                           | Weight |
|-----------|---|--------|
| Cub       | Age0 $\times$ TS-sur                          | 0.781  |
| Cub       | Age0 + Age0 $\times$ Time-cubic               | 0.219  |
| Yearling  | Age1 + Age1 $\times$ Melt-season              | 0.424  |
| Yearling  | Age1 + Age1 $\times$ Time-cubic               | 0.245  |
| Yearling  | Age1 + Age1 $\times$ Summer-habitat           | 0.215  |
| Yearling  | Age1 $\times$ TS-sur                          | 0.117  |
| Subadult  | Age2 + Age2 $\times$ Time-cubic + Age2Fem     | 0.536  |
| Subadult  | Age2 + Age2 $\times$ Melt-season + Age2Fem    | 0.402  |
| Subadult  | Age2 $\times$ TS-sur + Age2Fem                | 0.047  |
| Subadult  | Age2 + Age2 $\times$ Summer-habitat + Age2Fem | 0.015  |
| Adult     | Age3 $\times$ TS-sur + Age3Fem                | 0.443  |
| Adult     | Int + Age3 $\times$ Time-cubic + Age3Fem      | 0.229  |
| Adult     | Int + Age3 $\times$ Melt-season + Age3Fem     | 0.210  |
| Adult     | Int + Age3 $\times$ Summer-habitat + Age3Fem  | 0.118  |

*Notes:* Covariate structures with a weight  $<0.01$  are excluded. A "+" denotes an additive term, and " $\times$ " denotes a covariate interaction. The adult component contains an overall mean (Int) when only continuous temporal covariates are included. See Table 1 for descriptions of covariate abbreviations. Some covariates consisted of multiple related covariates that were always used jointly; definitions are provided in Appendix A.



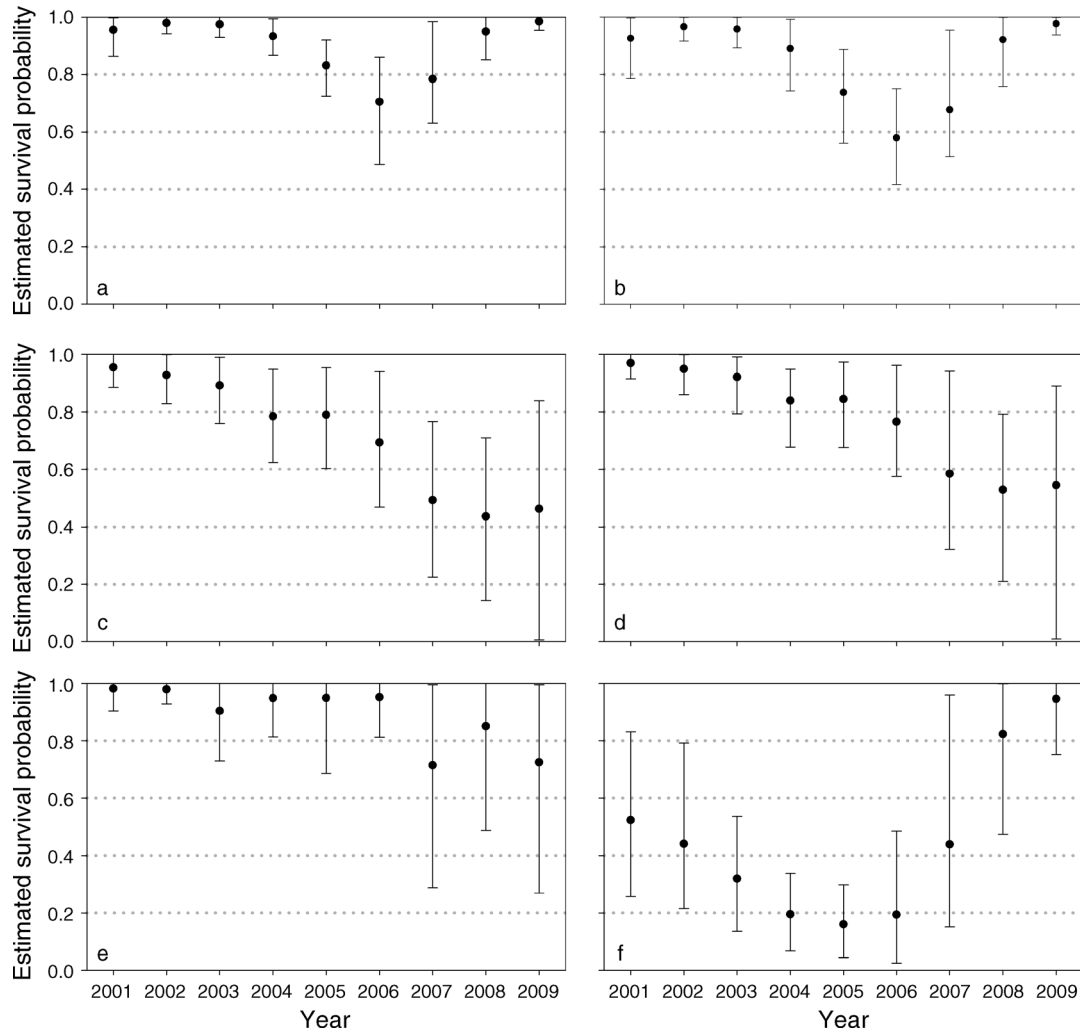


FIG. 4. Model-averaged estimates of annual polar bear survival probability by age class and sex for the USCA and Canada (USCA) data set: (a) adult males, (b) adult females, (c) subadult males, (d) subadult females, (e) yearlings, and (f) cubs. Error bars represent 90% bias-corrected bootstrap confidence intervals based on 100 replications.

though temporal stratification (TS-sur) accumulated the most  $AIC_c$  model weight ( $w = 0.443$ ). Survival of subadults generally declined, although confidence intervals were broad. Most of the weight for subadults was accumulated by covariate structures incorporating Time-cubic ( $w = 0.536$ ) or Melt-season ( $w = 0.402$ ). Estimates of yearling survival were high during the first half of the study, but lower and more variable in the later years. Model weight for yearlings was distributed across all forms of temporal structure, with Melt-season accumulating the greatest weight ( $w = 0.424$ ). Survival of cubs displayed a temporal pattern similar to that of adults, though the mid-study decline and the rebound in the last years were more exaggerated. The covariates TS-sur ( $w = 0.781$ ) and Time-cubic ( $w = 0.219$ ) accumulated all the weight for cubs.

Model-averaged estimates of survival probabilities based on the USCA data were similar to those obtained with the USGS data (Fig. 4, Table 7). The survival of

adults was lower in 2006 and 2007, but higher in 2008 and 2009, compared to the USGS estimates (Fig. 3). The temporal pattern in estimates of cub survival was similar to the pattern obtained with the USGS data, but survival estimates were higher in 2004–2006 and 2008–2009. The form of temporal variation accumulating the most weight for both adults and cubs incorporated the Time-cubic covariate ( $w = 0.883$  and  $w = 0.872$ , respectively). For subadult bears, the top covariate structure ( $w = 0.458$ ) included temporal stratification (TS-sur). This differs somewhat from results obtained with the USGS data, although subadult survival rate estimates trended downward in both cases. The Summer-habitat covariate accumulated the most model weight ( $w = 0.583$ ) for yearlings.

Model-averaged estimates of recapture probabilities and total model weights associated with covariate combinations for both data sets are presented in Appendix C.

TABLE 7. Total AIC<sub>c</sub> model weight associated with covariate structures of survival probability models, by age class, based on the USCA data set.

| Age class | Covariate structure                    | Weight |
|-----------|--|--------|
| Cub       | Age0 + Age0 × Time-cubic               | 0.872  |
| Cub       | Age0 × TS-sur                          | 0.128  |
| Yearling  | Age1 + Age1 × Summer-habitat           | 0.583  |
| Yearling  | Age1 + Age1 × Melt-season              | 0.242  |
| Yearling  | Age1 × TS-sur                          | 0.145  |
| Yearling  | Age1 + Age1 × Time-cubic               | 0.030  |
| Subadult  | Age2 × TS-sur + Age2Fem                | 0.458  |
| Subadult  | Age2 + Age2 × Melt-season + Age2Fem    | 0.239  |
| Subadult  | Age2 + Age2 × Time-cubic + Age2Fem     | 0.208  |
| Subadult  | Age2 + Age2 × Summer-habitat + Age2Fem | 0.095  |
| Adult     | Int + Age3 × Time-cubic + Age3Fem      | 0.883  |
| Adult     | Int + Age3 × Melt-season + Age3Fem     | 0.071  |
| Adult     | Age3 × TS-sur + Age3Fem                | 0.046  |

Notes: Covariate structures with a weight <0.01 are excluded. A “+” denotes an additive term, and “×” denotes a covariate interaction. The adult component contains an overall mean (Int) when only continuous temporal covariates are included. Some covariates consisted of multiple related covariates that were always used jointly; definitions are provided in Appendix A.

### Abundance

Annual abundance estimates based on the USGS data, applicable to the Alaskan portion of the study area, ranged from 376 bears in 2009 to 1158 in 2004 (Fig. 5a). We suspect estimates in the first two years, particularly 2002, were negatively biased by the absence of capture effort from Barrow in 2001, which may have caused an overestimate of recapture probability in 2002 (Appendix C: Figs. C1–C3). In addition, the mixing of marked and unmarked individuals may have been incomplete during the initial years of the study (Appendix D: Fig. D2). The unusually large number of bears captured in 2004 (Table 5) produced a seemingly large estimate with a wide confidence interval. Even though there is uncertainty regarding abundance levels in these years, the broader pattern of a decline in abundance during the middle of the study followed by relative stability at the end of the study was consistent with patterns in survival.

Abundance estimates based on the USCA data ranged from 464 bears in 2002 to 1607 in 2004 (Fig. 5b). As with the USGS data, we suspect estimates for the initial years of the investigation were less reliable than those in the latter years, particularly because no capture effort occurred in Canada before 2003 and our models were not robust to this deficiency. Considering this uncertainty in the earliest estimates, the temporal pattern in abundance resembled that of the USGS estimates and was consistent with patterns in survival. The correlation between USGS and USCA abundance estimates was 0.84 across all years and 0.86 excluding 2002.

### Complementary analyses to investigate potential bias

Analyses of location data from radio-collared females produced no strong evidence that temporary emigration or non-random movement negatively biased estimates of survival (Appendix D). An exact test of the hypothesis that equal proportions of collared bears were available for capture each year was not significant ( $P = 0.990$ ),

implying that a pulse of permanent emigration did not occur in the middle of the investigation. We did, however, find indications of nonrandom movement between nearshore and offshore habitats among consecutive years. Although such nonrandom movement can bias estimates of recapture and survival probabilities, our data are consistent with conditions in which bias in survival probabilities is small (modest state transition probabilities; Kendall et al. 1997, Schaub et al. 2004).

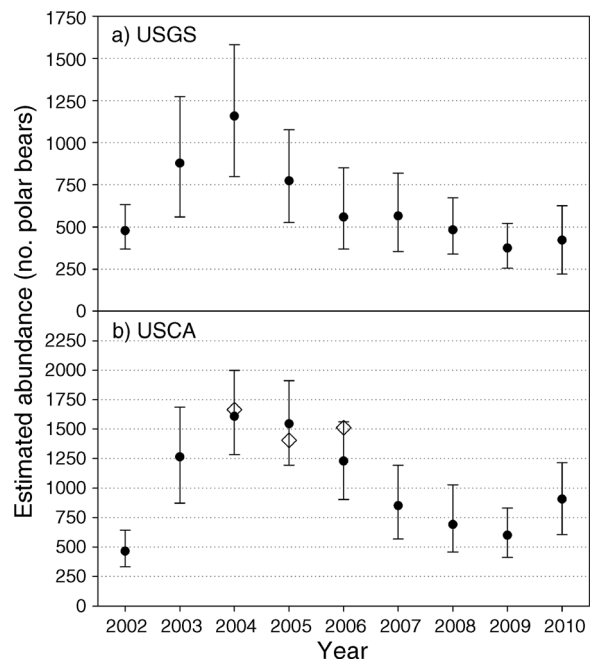


FIG. 5. Model-averaged estimates of polar bear abundance based on (a) the USGS data set and (b) the USCA data set. Error bars represent 90% bias-corrected confidence intervals based on 100 bootstrap samples. Prior estimates (Regehr et al. 2006) are shown for comparative purposes (open diamonds in panel [b]).



PLATE 1. Large male polar bear (*Ursus maritimus*) on the sea ice of the southern Beaufort Sea. Photo credit: U.S. Geological Survey, Alaska Science Center.

The results of population projections were largely consistent with the estimated trends in abundance (Appendix E). Projected abundance increased during the initial years of the study, though more slowly than suggested by the abundance estimates, supporting our conjecture that abundance estimates in the earliest years were negatively biased. Projected abundance declined through the middle of the study, and then stabilized. The correlation between abundance estimates and the projections based on the USGS data set was 0.85 across all years and 0.90 excluding 2002; the corresponding correlations for the USCA data set were 0.89 and 0.95.

## DISCUSSION

### *Methodological effectiveness*

We constructed covariates to account for multiple sources of heterogeneity in recapture probabilities that could otherwise bias survival and abundance estimates (Abadi et al. 2013). Recapture probabilities were allowed to vary by sex and age class. Covariates indexed both capture effort and nonparametric temporal structure, and geographic covariates accounted for previously discovered regional differences in recapture probabilities (Amstrup et al. 2001). The covariate Cap-procliv (Appendix F) indirectly accounted for potential sources of heterogeneity we could not measure. Collectively, these covariates accounted for several known or potential sources of heterogeneity, and any bias originating from un-modeled heterogeneity is likely to

be small compared to the temporal variation in survival and abundance estimates.

We found no compelling evidence that emigration or nonrandom movement meaningfully biased estimates. Neither analysis of movement data (Appendix D), nor patterns in recapture rates (Appendix B) revealed a pulse of permanent emigration that could explain the mid-study decline in survival. Similarly, a pulse of immigration followed shortly by permanent emigration, which could explain the high USGS abundance estimate in 2004 and the mid-study decline in survival, is unlikely to have occurred given joint consideration of movement data and recapture rates. The most likely sources of immigrants are the neighboring northern Beaufort and Chukchi Seas (Fig. 1), but large-scale immigration from these regions seems unlikely because their ecological conditions are thought to be more favorable than in the SBS (e.g., Stirling et al. 2011, Rode et al. 2014). In addition, our estimates did not exhibit the decline in apparent survival near the end of the investigation that is indicative of temporary emigration (e.g., Langtimm 2009, Kendall et al. 2013). Analyses of movement data suggested that Markovian dependency in the probability of being available for capture between consecutive years remains a potential source of bias (Schaub et al. 2004). However, we view these results with some caution because of the small sample sizes and prior evidence that bears prefer ice in waters over the narrow continental shelf (Durner et al. 2009). Further, there is no reason to suspect that behavior leading to nonrandom movement



during the spring capture season changed during the investigation, implying that trends in survival and abundance would not be appreciably affected even if some bias is present. In summary, although we are aware of the potential influence of temporary emigration and nonrandom movement, we believe any bias from these sources is likely to be small compared to the magnitude of temporal variation and trends in survival and abundance estimates.

We believe that the assumptions of the Horvitz-Thompson abundance estimator (Horvitz and Thompson 1952, McDonald and Amstrup 2001) were satisfied. Covariates were utilized to model several known and potential sources of heterogeneity in recapture probabilities, so there is no reason to suspect they are systematically biased. The CJS model conditions on initial captures and estimates subsequent recapture probabilities, while the Horvitz-Thompson estimator applies estimated recapture probabilities to both initial captures and recaptures (McDonald and Amstrup 2001). A behavioral response to initial capture that lowers recapture probabilities therefore has the potential to positively bias abundance estimates. However, our capture methods largely preclude such a behavioral response. Bears are often located by following fresh tracks in snow. There are patches of rough ice in which bears could attempt to hide, if they were not being tracked, but we have not observed hiding behavior. Most bears move away as the helicopter approaches, though some display curiosity or aggression toward it. In addition, we are unaware of any information that suggests our abundance estimates are unrealistically high.

#### *Insights into ecological mechanisms*

The previously reported low survival of SBS polar bears in 2004 and 2005 (Regehr et al. 2010) continued into 2007, at levels substantially less than earlier estimates for this population (Amstrup and Durner 1995, Amstrup et al. 2001). Annual survival of cubs during that period was estimated to be  $<0.2$  based on the USCA data and near zero with the USGS data. Indeed, only 2 of 80 cubs in the USGS data observed from 2003 to 2007 are known to have survived to an older age class (Appendix B: Fig. B1). Such poor recruitment, combined with reduced survival of other age classes, must have substantially impacted abundance, and our abundance estimates declined accordingly during those years. Estimated survival of adults and cubs from both data sets began to improve in 2007, with estimates based on the USCA data suggesting a somewhat stronger recovery, although confidence intervals overlap broadly. This potential divergence may be an early indication of regional differences in ecosystem function and polar bear response that may become more apparent as the Arctic continues to warm.

Several independent sources of information are consistent with reduced survival during the middle of

the study period. Cherry et al. (2009) found physiological indications of nutritional stress to be two to three times greater in 2005 and 2006 than in the 1980s. Regehr et al. (2006) reported observations of starvation during this period, and unusual incidents of polar bears stalking and killing other bears occurred in 2004 (Amstrup et al. 2006). Stirling et al. (2008) reported a case of cannibalism and several instances of polar bears penetrating unusually thick ice barriers to reach ringed seal lairs between 2003 and 2007, predatory behavior that is energetically inefficient and a likely indication of nutritional stress. A similar instance of ice penetration was observed in the SBS in 1975 (Stirling et al. 2008), during a period of low seal production and reduced polar bear cub survival throughout the Canadian portion of the Beaufort Sea (Stirling 2002). Similar low productivity of ringed seals and reduced survival of polar bear cubs were documented in the Canadian portion of the Beaufort Sea again in the mid-1980s (Smith 1987, Stirling 2002).

Factors leading to improved survival beginning in 2007 are difficult to identify, but there are indications of a transition at this time. Pilfold et al. (2014) reported a shift in the distribution of seal kill sites among land-fast and pack ice between the periods 2003–2006 and 2007–2011, and more kill sites were located in the latter period. The pattern and occurrence of open-water lead systems and ice deformation within the central Beaufort Sea changed in 2006 (Mahoney et al. 2012). Similarly, Melling et al. (2012) reported unusual atmospheric and oceanographic conditions in the Beaufort Sea during 2007. Ringed seal productivity within Amundsen Gulf in the eastern SBS was low in 2005 and 2006, but improved in 2007 (Harwood et al. 2012), although this was attributed to localized ice conditions and is not thought to be indicative of the low ringed seal production broadly observed in the 1970s and 1980s (Stirling 2002). Potential linkages between these indicators of a transition in the 2006–2007 time frame and polar bear survival may become apparent as our understanding of Arctic ecology improves.

Improved survival after 2007 might be partially attributable to either density-dependent mechanisms or the altered characteristics or behavior of surviving individuals. Reduced competition for limited resources resulting from lower abundance may have increased survival at the end of the study period. Similarly, consecutive years of unfavorable conditions may have eliminated the less fit individuals from the population, with the survivors collectively displaying seemingly enhanced survival. Finally, some individuals may have adopted behavior that increased their survival. For example, a growing proportion of the population utilizes terrestrial habitat after ice retreats from the continental shelf in summer (USGS, *unpublished data*). These bears have access to subsistence-harvested bowhead whale carcasses at discrete locations along the Alaskan coast (Herreman and Peacock 2013), an energy-rich alterna-

tive food source (Bentzen et al. 2007) that may enhance survival. Bears utilizing terrestrial habitat in summer may also have earlier access to seals in autumn. Land-fast ice begins to form over coastal waters earlier than the expanding pack ice provides bears summering on perennial ice deep in the Polar Basin with access to continental shelf waters. Such behavioral tendencies are likely to be adopted by dependent young and may therefore become increasingly common.

Subadults, unlike adults and cubs, did not display increased survival during the latter years of our investigation. Newly independent and inexperienced individuals are likely to be less efficient hunters, and less capable of competing for limited resources or retaining control of kills, than adults (Stirling 1974), and may be more susceptible to unfavorable conditions. Subadults are also less likely to utilize crowded feeding sites such as bowhead whale remains. Sea ice covariates were more strongly associated with the survival of subadults than adults, which is consistent with findings that the body condition of growing bears is more closely linked to ice conditions than that of older bears (Rode et al. 2010). The lack of an improvement in subadult survival may be, in part, a residual effect of poor conditions in prior years. Yearlings that survived to subadult status during years of low survival may have been in inadequate condition to survive independently. Regardless of cause, the status of subadults in the SBS population merits monitoring, because their continued low survival could ultimately lead to further declines in abundance.

Polar bears depend on sea ice for several aspects of their life history, and multiple characteristics of sea ice can be expected to influence their vital rates, potentially via mechanisms that are complex and nonlinear (e.g., Ellis and Post 2004, Tyler et al. 2008, Derocher et al. 2013). The duration of ice-absence from the continental shelf is thought to directly affect polar bear condition and vital rates through reduced access to prey (Regehr et al. 2010, Rode et al. 2010, 2012). Observations of polar bears and seal kills in low-concentration, unconsolidated ice (Chukchi Sea in 2009, SBS in 2010; S. C. Amstrup, G. M. Durner, and E. V. Regehr, *unpublished field observations*) testify to the high value of sea ice in biologically productive shelf waters. However, other aspects of sea ice are undoubtedly important. Extensive ice rubble and rafted floes during winter and spring are thought to have led to past declines in polar bear productivity in the SBS (Stirling et al. 1976, Amstrup et al. 1986, Stirling 2002), as well as during our investigation (Stirling et al. 2008). The increased frequency and severity of storms (Sepp and Jaagus 2011, Thomson and Rogers 2014) combined with thinner and more mobile pack ice (Spreen et al. 2011), both consequences of climate warming, are likely to result in a greater prevalence of deformed ice in winter and spring that may result in lower quality ringed seal birth lair habitat and subsequent reductions in reproductive success.

Similarly, continued warming may increase the frequency of unsuitable snow and ice conditions for maintenance of ringed seal lairs (Stirling and Smith 2004, Hezel et al. 2012). The increased vulnerability of ringed seal pups to predation could temporarily enhance polar bear survival, though it would likely also lead to subsequent reductions in prey abundance. Finally, access to terrestrial denning sites can be limited by ice conditions (Derocher et al. 2011).

Despite the known importance of sea ice, measures of ice availability did not fully explain short-term demographic patterns in our data, suggesting that other aspects of the ecosystem contribute importantly to the regulation of population dynamics. Prey abundance can obviously affect bear condition and survival independently, to an extent, of sea ice conditions. Numerous factors such as warming-induced increases in primary productivity (Zhang et al. 2010), phenology-based trophic mismatches (Post et al. 2013), changing disease vectors (Jensen et al. 2010), increased contaminant transport (Sonne 2010), and expanding human activity in the Arctic (Smith and Stephenson 2013) may interact with the primary effects of sea ice conditions and prey accessibility. As the Arctic continues to warm, ecosystem structure and function can be expected to respond (e.g., Lasternas and Agustí 2010, Hezel et al. 2012, Carroll et al. 2013, Hinzman et al. 2013, Ji et al. 2013, Iverson et al. 2014, Nahrgang et al. 2014), perhaps in ways that are difficult to foresee. Although sea ice availability is expected to be the dominant driver of population dynamics over the long term (Amstrup et al. 2008, Stirling and Derocher 2012), other aspects of the ecosystem can be expected to either mitigate or exacerbate the effects of sea ice loss in the short term. The changing Arctic ecosystem may induce increased short-term variation in vital rates and elevate the risk of abrupt population decline (Derocher et al. 2013).

### Conclusions

Our results collectively suggest that polar bears in the SBS experienced a significant reduction in survival and abundance from 2004 through 2007. However, suspected biases in the abundance estimates for the earliest years of the investigation, potential biases in the USCA estimates in the latter years, and statistical variation associated with estimates necessitate cautious expression of the magnitude of population decline. Conservatively, the decline seems unlikely to have been <25%, but may have approached 50%. Improved survival and stability in abundance at the end of the investigation are cause for cautious optimism. However, given projections for continued climate warming (IPCC 2013), polar bear ecology in the SBS and elsewhere in the Arctic is expected to become increasingly forced by sea ice loss (Amstrup et al. 2008, Stirling and Derocher 2012). Behavioral plasticity and ecosystem productivity may enable some populations to temporarily maintain recruitment and abundance, despite deteriorating hab-

itat conditions (e.g., Rode et al. 2014), but seem unlikely to counterbalance the extensive habitat degradation projected to occur over the long term (IPCC 2013). Continued research into the ecological mechanisms underlying polar bear population dynamics is necessary to refine projections of their future status and develop appropriate strategies for their management.

#### ACKNOWLEDGMENTS

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# SUPPLEMENTAL MATERIAL

## Ecological Archives

Appendices A–F are available online: <http://dx.doi.org/10.1890/14-1129.1.sm>

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APPENDIX A (TABLE A1). Definitions of covariates and covariate combinations (groups) used to model survival and recapture probabilities of southern Beaufort Sea polar bears.

| Covariate group | Covariate   | Definition  |
|-----------------|-------------|---|
| Age0            | Age0        | Matrix of indicator variables where a 1 indicates an individual (row) was a cub in a particular year (column) and a 0 otherwise.  |
| Age01.23Fem     | Age01.23Fem | Matrix of indicator variables where a 1 indicates an individual (row) was a cub (age 0) or yearling (age 1) of either gender, a subadult female (age 2–4), or an adult female (age >4) in a particular year (column) and a 0 otherwise. |
| Age01.3Fem      | Age01.3Fem  | Matrix of indicator variables where a 1 indicates an individual (row) was a cub (age 0) or yearling (age 1) of either gender or an adult female (age > 4) in a particular year (column) and a 0 otherwise.                              |



|         |         |  |
|---------|---------|--|
| Age1    | Age1    | Matrix of indicator variables where a 1 indicates an individual (row) was a yearling (age 1) in a particular year (column) and a 0 otherwise.          |
| Age2    | Age2    | Matrix of indicator variables where a 1 indicates an individual (row) was a subadult (age 2–4) in a particular year (column) and a 0 otherwise.        |
| Age2Fem | Age2Fem | Matrix of indicator variables where a 1 indicates an individual (row) was a subadult (age 2–4) female in a particular year (column) and a 0 otherwise. |
| Age3    | Age3    | Matrix of indicator variables where a 1 indicates an individual (row) was an adult (age > 4) in a particular year (column) and a 0 otherwise.          |
| Age3Fem | Age3Fem | Matrix of indicator variables where a 1 indicates an individual (row) was an adult (age > 4) female in a particular year (column) and a 0 otherwise.   |

|             |             |  |
|-------------|-------------|--|
| BI2006      | BI2006      | Matrix of indicator variables where a 1 indicates an individual (row) had a home stratum (Home) of Barter Island in the year (column) 2006 and a 0 otherwise.  |
| CA          | Home.CA     | Matrix of indicator variables where a 1 indicates an individual (row) had a home stratum of Canada (invariant across years/columns) and a 0 otherwise.   |
| Cap-procliv | Cap-procliv | Matrix of time-varying proportions reflecting an individual's (row) tendency to be captured in the years from its initial capture through the preceding year, used to model recapture heterogeneity. See Appendix F. |
| Eff-CA      | Eff-CA.l    | Matrix of indicator variables where a 1 indicates capture effort was low in Canada (invariant across bears/rows) and a 0 otherwise. Effort was classified as low in Canada in 2001–2002.                             |
| Eff-CA      | Eff-CA.m    | Matrix of indicator variables where a 1 indicates capture effort was medium in Canada (invariant across bears/rows) and a 0  |

|        |          |  |
|--------|----------|--|
|        |          | otherwise. Effort was classified as medium in Canada in 2007–2010.   |
| Eff-CA | Eff-CA.h | Matrix of indicator variables where a 1 indicates capture effort was high in Canada (invariant across bears/rows) and a 0 otherwise. Effort was classified as high in Canada in 2003–2006.                       |
| Eff-US | Eff-US.l | Matrix of indicator variables where a 1 indicates capture effort was low in the U.S. (invariant across bears/rows) and a 0 otherwise. Effort was classified as low in the U.S. in 2010.                          |
| Eff-US | Eff-US.m | Matrix of indicator variables where a 1 indicates capture effort was medium in the U.S. (invariant across bears/rows) and a 0 otherwise. Effort was classified as medium in the U.S. in 2001–2003 and 2006–2009. |
| Eff-US | Eff-US.h | Matrix of indicator variables where a 1 indicates capture effort was high in the U.S. (invariant across bears/rows) and a 0 otherwise. Effort was  |

|             |             |  |
|-------------|-------------|--|
|             |             | classified as high in the U.S. in 2004–2005.   |
| Home        | Home.BAR    | Matrix of indicator variables where a 1 indicates an individual (row) had a home stratum of Barrow, Alaska (invariant across years/columns) and a 0 otherwise.                             |
| Home        | Home.DEHBTI | Matrix of indicator variables where a 1 indicates an individual (row) had a home stratum of Deadhorse, Alaska or Barter Island, Alaska (invariant across years/columns) and a 0 otherwise. |
| Home        | Home.CA     | Matrix of indicator variables where a 1 indicates an individual (row) had a home stratum of Canada (invariant across years/columns) and a 0 otherwise.                                     |
| Melt-season | Melt-season | Matrix of covariate values with each row containing normalized values of the length of the melt season each year (columns). See Fig. 2.  |
| Radio       | Radio       | Matrix of indicator variables with a 1 indicating an individual (row) had an active radio  |



|                |                |   |
|----------------|----------------|---|
|                |                | collar in a particular year (column) and a 0 otherwise.   |
| Search         | Search         | Matrix of covariate values with each row containing normalized values of the approximate number of hours spent actively searching for bears in the U.S. and Canada each year (columns). |
| Search-US      | Search-US      | Matrix of covariate values with each row containing normalized values of the number of hours spent actively searching for bears in the U. S. each year (columns).                       |
| Summer-habitat | Summer-habitat | Matrix of covariate values with each row containing normalized values of the area of optimal summer habitat each year (columns). See Fig. 2.  |
| Time           | Time.a         | Matrix of indicator variables where a 1 indicates the year 2002 (column) and a 0 otherwise (invariant across bears/rows).   |
| Time           | Time.b         | Matrix of indicator variables where a 1 indicates the year 2003 (column) and a 0 otherwise (invariant across bears/rows).   |

|      |        |   |
|------|--------|---|
| Time | Time.c | Matrix of indicator variables where a 1 indicates the year 2004 (column) and a 0 otherwise (invariant across bears/rows). |
| Time | Time.d | Matrix of indicator variables where a 1 indicates the year 2005 (column) and a 0 otherwise (invariant across bears/rows). |
| Time | Time.e | Matrix of indicator variables where a 1 indicates the year 2006 (column) and a 0 otherwise (invariant across bears/rows). |
| Time | Time.f | Matrix of indicator variables where a 1 indicates the year 2007 (column) and a 0 otherwise (invariant across bears/rows). |
| Time | Time.g | Matrix of indicator variables where a 1 indicates the year 2008 (column) and a 0 otherwise (invariant across bears/rows). |
| Time | Time.h | Matrix of indicator variables where a 1 indicates the year 2009 (column) and a 0 otherwise (invariant across              |

|            |                 |  |
|------------|-----------------|--|
|            |                 | bears/rows).   |
| Time       | Time.i          | Matrix of indicator variables where a 1 indicates the year 2010 (column) and a 0 otherwise (invariant across bears/rows).      |
| Time-cubic | Time-cubic.lin  | Linear component of annual time (year), with 2001 being defined as 1.  |
| Time-cubic | Time-cubic.quad | Quadratic component of annual time (year <sup>2</sup> ), with 2001 being defined as 1.   |
| Time-cubic | Time-cubic.cube | Cubic component of annual time (year <sup>3</sup> ), with 2001 being defined as 1.   |
| TS-sur     | TS-sur.a        | Matrix of indicator variables where a 1 indicates an early period, 2001–2003, and a 0 otherwise (invariant across bears/rows). |
| TS-sur     | TS-sur.b        | Matrix of indicator variables where a 1 indicates a middle period, 2004–2006, and a 0 otherwise (invariant across bears/rows). |
| TS-sur     | TS-sur.c        | Matrix of indicator variables where a 1 indicates a late period, 2007–2009, and a 0  |

|    |               |   |
|----|---------------|---|
|    |               | otherwise (invariant across bears/rows).  |
| UA | UA.Age01.3Fem | Matrix of indicator variables where a 1 indicates an individual (row) with a home stratum of Canada was a cub (age 0) or yearling (age 1) of either gender or an adult female (age > 4) during any of the years 2007–2010 (column) and a 0 otherwise. |
| UA | UA.Age2       | Matrix of indicator variables where a 1 indicates an individual (row) with a home stratum of Canada was a subadult (age 2–4) during any of the years 2007–2010 (column) and a 0 otherwise.  |
| UA | UA.Age3Male   | Matrix of indicator variables where a 1 indicates an individual (row) with a home stratum of Canada was an adult male (age > 4) during any of the years 2007–2010 (column) and a 0 otherwise.   |
| US | US            | Matrix of indicator variables where a 1 indicates an individual (row) had one of the three home strata in the U.S. (Home.BAR or Home.DEH or HOME.BTI) (invariant  |



|  |  |   |
|--|--|---|
|  |  | across years/columns) and<br>a 0 otherwise. |
|--|--|---|

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APPENDIX B. Southern Beaufort Sea polar bear capture statistics.

TABLE B1. The number of southern Beaufort Sea polar bears captured (N), and the number (M) and percentage (%) that were previously captured, by sex (♀ = Female, ♂ = Male), year, and age-class in the USGS data set.

|     |      | Cub | Yearling |   |      | Subadult |   |      | Adult |    |      |
|-----|------|-----|----------|---|------|----------|---|------|-------|----|------|
| Sex | Year | N   | N        | M | %    | N        | M | %    | N     | M  | %    |
| ♀   | 2001 | 11  | 15       | - | -    | 9        | - | -    | 56    | -  | -    |
| ♀   | 2002 | 11  | 2        | 0 | 0.0  | 11       | 5 | 45.5 | 48    | 24 | 50.0 |
| ♀   | 2003 | 5   | 1        | 0 | 0.0  | 8        | 4 | 50.0 | 33    | 15 | 45.5 |
| ♀   | 2004 | 11  | 2        | 0 | 0.0  | 18       | 2 | 11.1 | 47    | 17 | 36.2 |
| ♀   | 2005 | 7   | 1        | 0 | 0.0  | 8        | 1 | 12.5 | 32    | 17 | 53.1 |
| ♀   | 2006 | 4   | 7        | 1 | 14.3 | 8        | 1 | 12.5 | 31    | 15 | 48.4 |
| ♀   | 2007 | 5   | 4        | 0 | 0.0  | 3        | 1 | 33.3 | 26    | 13 | 50.0 |
| ♀   | 2008 | 6   | 0        | 0 | -    | 10       | 1 | 10.0 | 33    | 19 | 57.6 |

|   |      |    |  |    |   |      |  |    |   |      |  |    |    |      |
|---|------|----|--|----|---|------|--|----|---|------|--|----|----|------|
| ♀ | 2009 | 10 |  | 6  | 3 | 50.0 |  | 2  | 1 | 50.0 |  | 36 | 24 | 66.7 |
| ♀ | 2010 | 5  |  | 3  | 1 | 33.3 |  | 2  | 1 | 50.0 |  | 27 | 16 | 59.3 |
|   |      |    |  |    |   |      |  |    |   |      |  |    |    |      |
| ♂ | 2001 | 9  |  | 11 | - | -    |  | 3  | - | -    |  | 21 | -  | -    |
| ♂ | 2002 | 10 |  | 4  | 1 | 25.0 |  | 13 | 4 | 30.8 |  | 19 | 2  | 10.5 |
| ♂ | 2003 | 11 |  | 4  | 1 | 25.0 |  | 8  | 4 | 50.0 |  | 37 | 4  | 10.8 |
| ♂ | 2004 | 13 |  | 6  | 1 | 16.7 |  | 19 | 9 | 47.4 |  | 32 | 10 | 31.3 |
| ♂ | 2005 | 14 |  | 1  | 0 | 0.0  |  | 6  | 4 | 66.7 |  | 27 | 15 | 55.6 |
| ♂ | 2006 | 4  |  | 0  | 0 | -    |  | 5  | 3 | 60.0 |  | 31 | 20 | 64.5 |
| ♂ | 2007 | 6  |  | 2  | 0 | 0.0  |  | 3  | 0 | 0.0  |  | 31 | 15 | 48.4 |
| ♂ | 2008 | 7  |  | 1  | 0 | 0.0  |  | 4  | 0 | 0.0  |  | 27 | 15 | 55.6 |
| ♂ | 2009 | 11 |  | 7  | 2 | 28.6 |  | 0  | 0 | -    |  | 40 | 22 | 55.0 |
| ♂ | 2010 | 8  |  | 7  | 2 | 28.6 |  | 3  | 2 | 66.7 |  | 20 | 16 | 80.0 |

TABLE B2. The number of southern Beaufort Sea polar bears captured (N), and the number (M) and percentage (%) that were previously captured, by sex (♀ = Female, ♂ = Male), year, and age-class in the USCA data set.

|  |  |  |  |  |  |  |  |
|--|--|--|--|--|--|--|--|
|  |  |  |  |  |  |  |  |
|--|--|--|--|--|--|--|--|

|     |      | Cub |  | Yearling |   |      |  | Subadult |   |      |  | Adult |    |      |
|-----|------|-----|--|----------|---|------|--|----------|---|------|--|-------|----|------|
| Sex | Year | N   |  | N        | M | %    |  | N        | M | %    |  | N     | M  | %    |
| ♀   | 2001 | 11  |  | 15       | - | -    |  | 9        | - | -    |  | 56    | -  | -    |
| ♀   | 2002 | 11  |  | 2        | 0 | 0.0  |  | 11       | 5 | 45.5 |  | 48    | 24 | 50.0 |
| ♀   | 2003 | 10  |  | 3        | 0 | 0.0  |  | 15       | 5 | 33.3 |  | 49    | 17 | 34.7 |
| ♀   | 2004 | 17  |  | 9        | 1 | 11.1 |  | 39       | 6 | 15.4 |  | 91    | 25 | 27.5 |
| ♀   | 2005 | 14  |  | 9        | 0 | 0.0  |  | 29       | 9 | 31.0 |  | 87    | 34 | 39.1 |
| ♀   | 2006 | 8   |  | 11       | 2 | 18.2 |  | 10       | 4 | 40.0 |  | 54    | 25 | 46.3 |
| ♀   | 2007 | 5   |  | 8        | 0 | 0.0  |  | 7        | 6 | 85.7 |  | 44    | 22 | 50.0 |
| ♀   | 2008 | 7   |  | 2        | 0 | 0.0  |  | 10       | 1 | 10.0 |  | 43    | 27 | 62.8 |
| ♀   | 2009 | 12  |  | 10       | 4 | 40.0 |  | 5        | 4 | 80.0 |  | 54    | 34 | 63.0 |
| ♀   | 2010 | 5   |  | 6        | 1 | 16.7 |  | 3        | 1 | 33.3 |  | 40    | 22 | 55.0 |
|     |      |     |  |          |   |      |  |          |   |      |  |       |    |      |
| ♂   | 2001 | 9   |  | 11       | - | -    |  | 3        | - | -    |  | 21    | -  | -    |
| ♂   | 2002 | 10  |  | 4        | 1 | 25.0 |  | 13       | 4 | 30.8 |  | 19    | 2  | 10.5 |

|   |      |    |  |    |   |      |  |    |    |      |  |    |    |      |
|---|------|----|--|----|---|------|--|----|----|------|--|----|----|------|
| ♂ | 2003 | 13 |  | 5  | 1 | 20.0 |  | 19 | 4  | 21.1 |  | 53 | 5  | 9.4  |
| ♂ | 2004 | 21 |  | 9  | 1 | 11.1 |  | 32 | 15 | 46.9 |  | 73 | 16 | 21.9 |
| ♂ | 2005 | 17 |  | 7  | 0 | 0.0  |  | 19 | 7  | 36.8 |  | 69 | 31 | 44.9 |
| ♂ | 2006 | 8  |  | 2  | 0 | 0.0  |  | 9  | 4  | 44.4 |  | 48 | 29 | 60.4 |
| ♂ | 2007 | 6  |  | 5  | 2 | 40.0 |  | 5  | 4  | 80.0 |  | 36 | 19 | 52.8 |
| ♂ | 2008 | 8  |  | 1  | 0 | 0.0  |  | 6  | 2  | 33.3 |  | 31 | 19 | 61.3 |
| ♂ | 2009 | 13 |  | 11 | 2 | 18.2 |  | 3  | 1  | 33.3 |  | 49 | 35 | 71.4 |
| ♂ | 2010 | 8  |  | 11 | 2 | 18.2 |  | 3  | 2  | 66.7 |  | 21 | 17 | 81.0 |

TABLE B3. The number of times individual polar bears were captured during the study period. Initial captures of new bears in 2010 are included.

| No. times captured | USGS data | USCA data |
|--------------------|-----------|-----------|
| 1                  | 516       | 767       |
| 2                  | 115       | 200       |
| 3                  | 47        | 72        |
| 4                  | 26        | 32        |



|       |     |       |
|-------|-----|-------|
| 5     | 9   | 12    |
| 6     | 1   | 2     |
| 7     | 1   | 1     |
| Total | 715 | 1,086 |

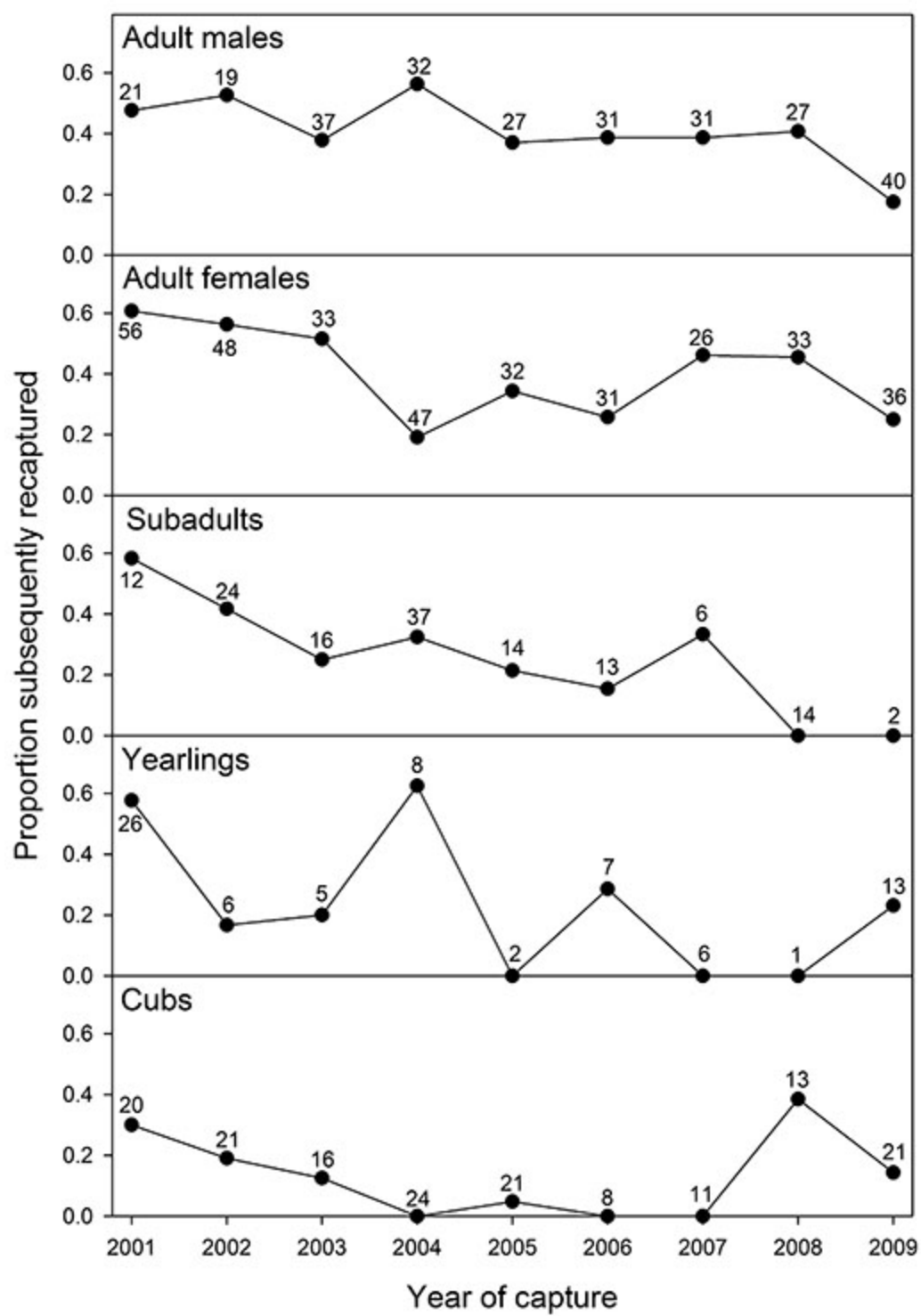


FIG. B1. The proportion of individuals subsequently recaptured by capture year and age class for the USGS data set. Numbers co-located with data points indicate the number of bears captured each year.

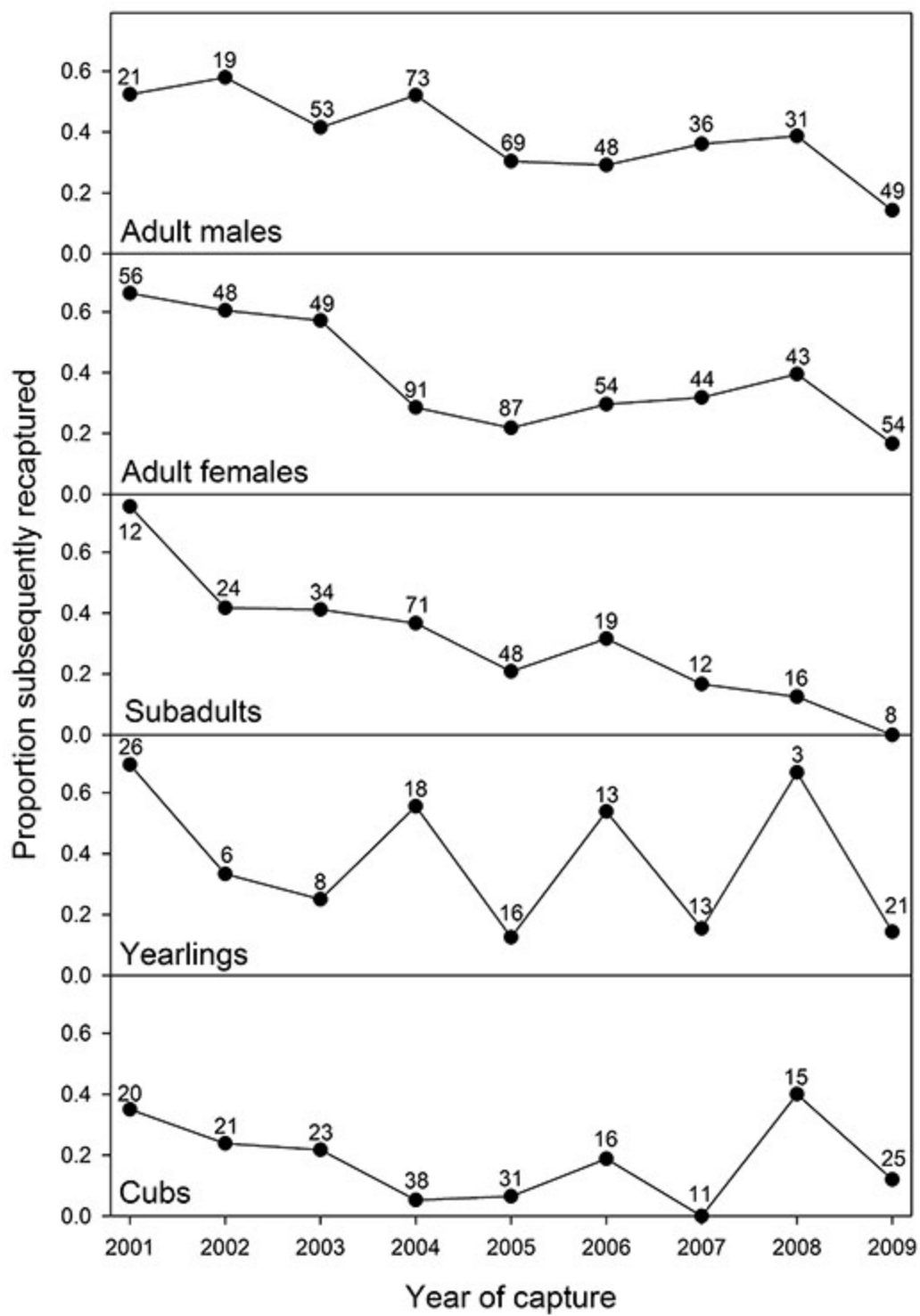


FIG. B2. The proportion of individuals subsequently recaptured by capture year and age class for the USCA data set. Numbers co-located with data points indicate the number of bears captured each year.

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APPENDIX C. Model-averaged estimates of recapture probabilities for southern Beaufort Sea polar bears and total model weights associated with recapture probability covariate structures.

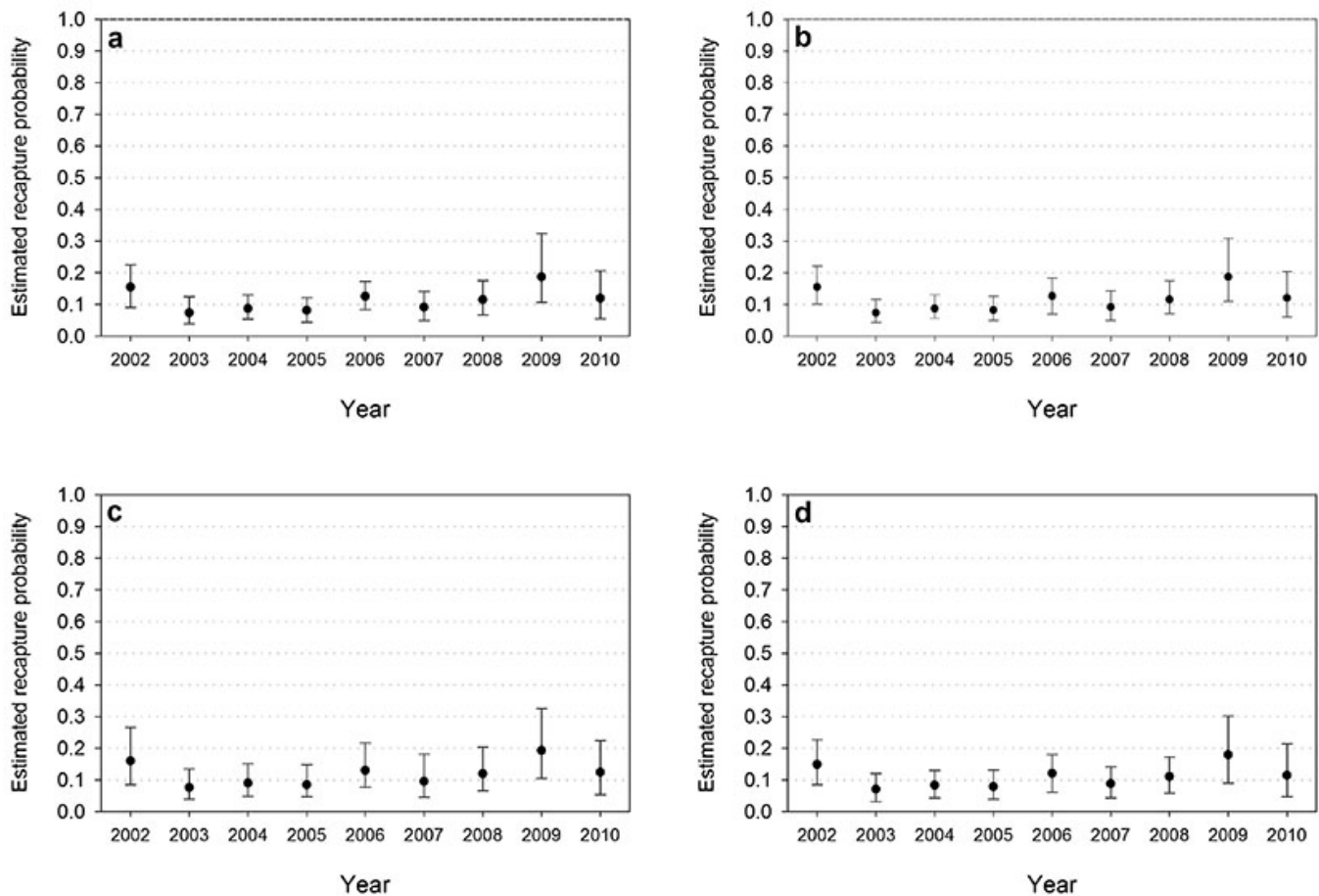


FIG. C1. Model-averaged estimates of recapture probabilities, by age class and sex, for polar bears with a home stratum of Barrow, Alaska, based on the USGS data set; (a) adult males, (b) adult females and dependent young, (c) subadult males, and (d) subadult females. Estimates do not incorporate the influence of the covariates *Radio* or *Cap-procliv*. Error bars represent 90% bias-corrected confidence intervals based on 100 bootstrap samples.

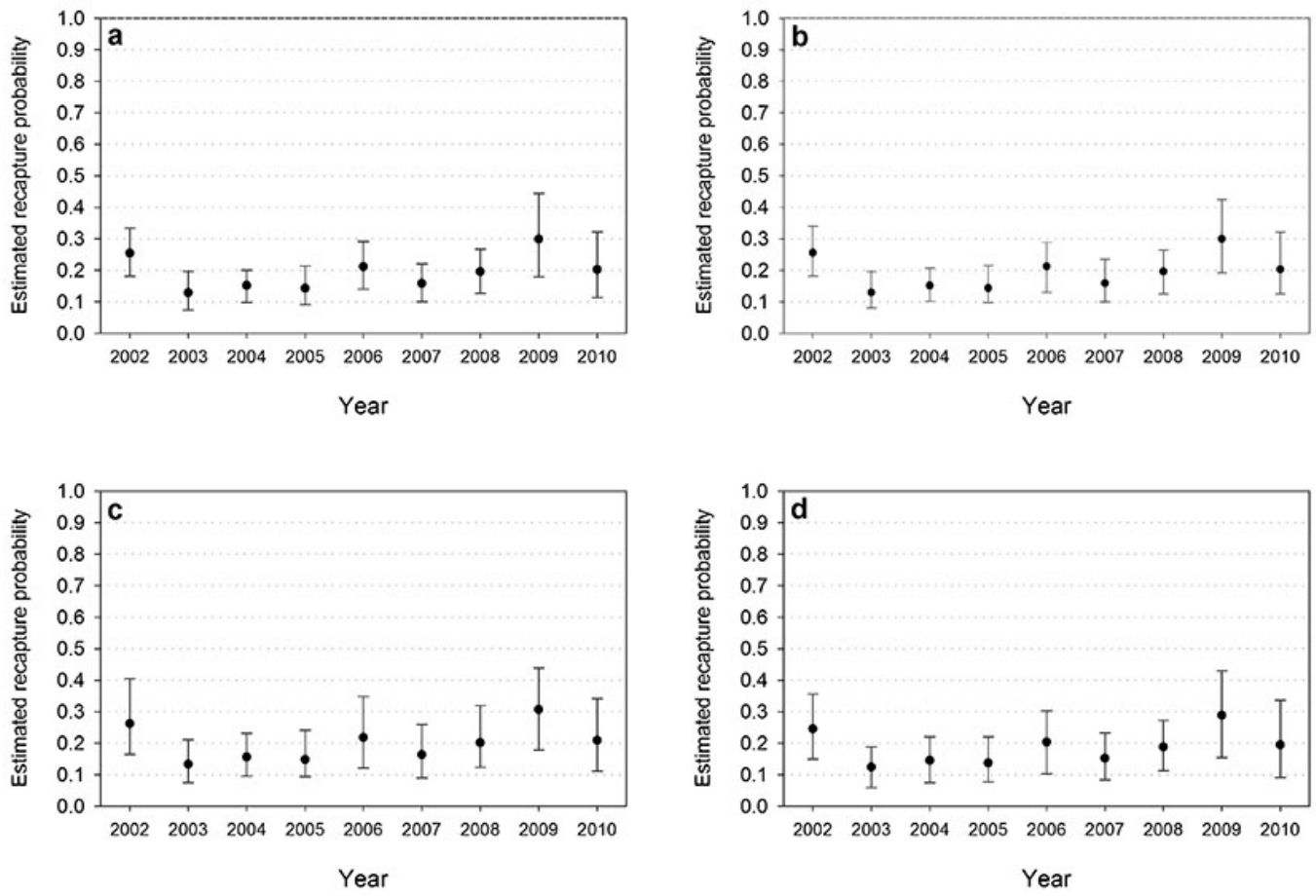


FIG. C2. Model-averaged estimates of recapture probabilities, by age class and sex, for polar bears with a home stratum of Deadhorse, Alaska, based on the USGS data set; (a) adult males, (b) adult females and dependent young, (c) subadult males, and (d) subadult females. Estimates do not incorporate the influence of the covariates *Radio* or *Cap-procliv*. Error bars represent 90% bias-corrected confidence intervals based on 100 bootstrap samples.



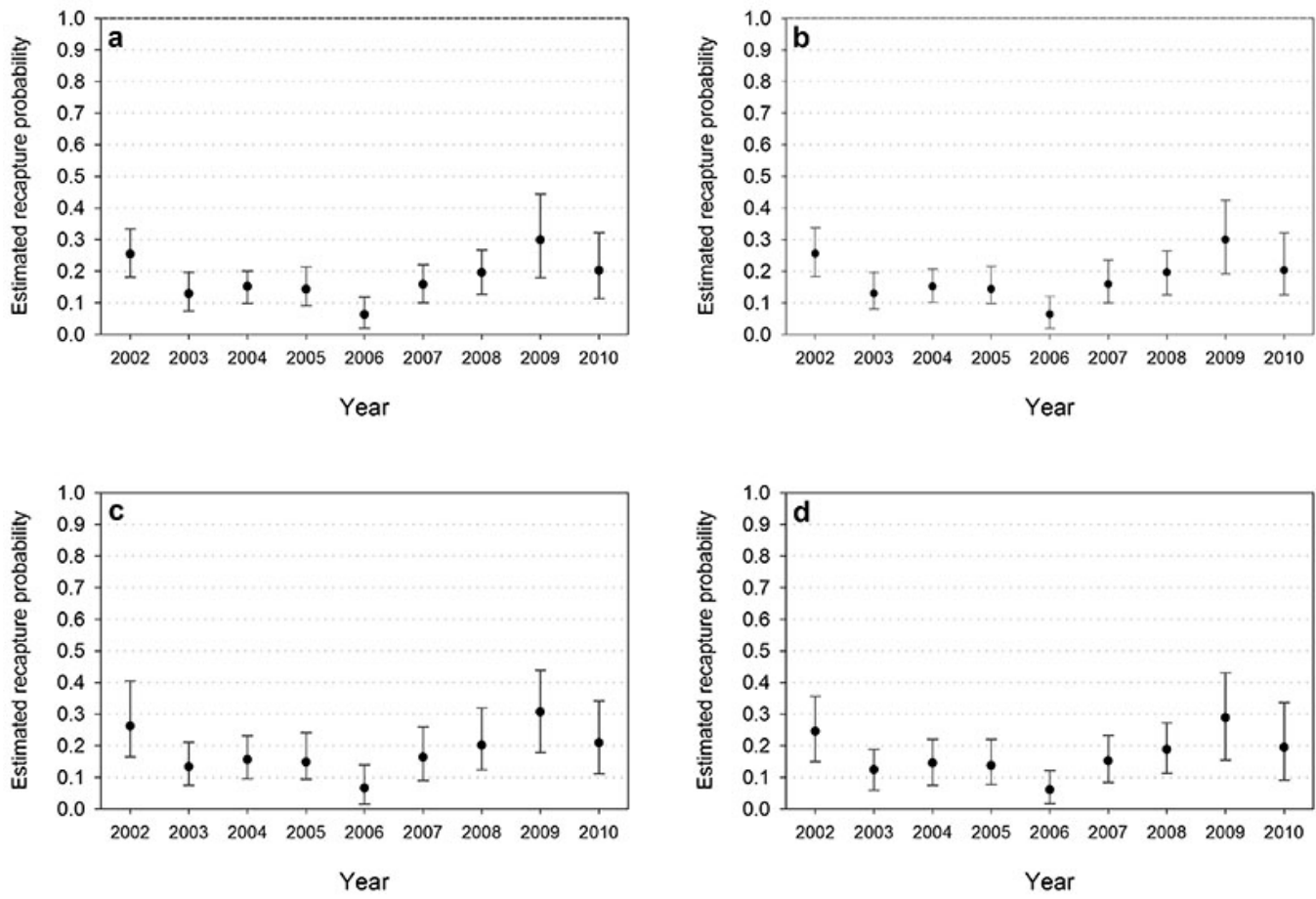


FIG. C3. Model-averaged estimates of recapture probabilities, by age class and sex, for polar bears with a home stratum of Barter Island, Alaska, based on the USGS data set; (a) adult males, (b) adult females and dependent young, (c) subadult males, and (d) subadult females. Estimates do not incorporate the influence of the covariates *Radio* or *Cap-procliv*. Error bars represent 90% bias-corrected confidence intervals based on 100 bootstrap samples.

TABLE C1. Total AICC model weight associated with age-sex and abiotic (temporal and geographic) covariate structures of recapture probability models based on the USGS data set. Covariate structures with a weight of less than 0.01 are excluded. A "+" denotes an additive term and "\*" denotes a covariate interaction. Some covariates consisted of multiple related covariates that were always used jointly; details are provided in Appendix A.

| Source  | Covariate structure | Weight |
|---------|---------------------|--------|
| Age-sex | -                   | 0.443  |
| Age-sex | Age01.23Fem         | 0.186  |
| Age-sex | Age2                | 0.177  |

|         |  |       |  |
|---------|--|-------|--|
| Age-sex | Age01.3Fem + Age2 + Age2Fem                        | 0.122 |  |
| Abiotic | Time + Home*US + BI2006 + Radio + Cap-procliv      | 0.869 |  |
| Abiotic | Eff-US + Home*US + BI2006 + Radio + Cap-procliv    | 0.079 |  |
| Abiotic | Home*US + BI2006 + Radio + Cap-procliv             | 0.028 |  |
| Abiotic | Search-US + Home*US + BI2006 + Radio + Cap-procliv | 0.021 |  |

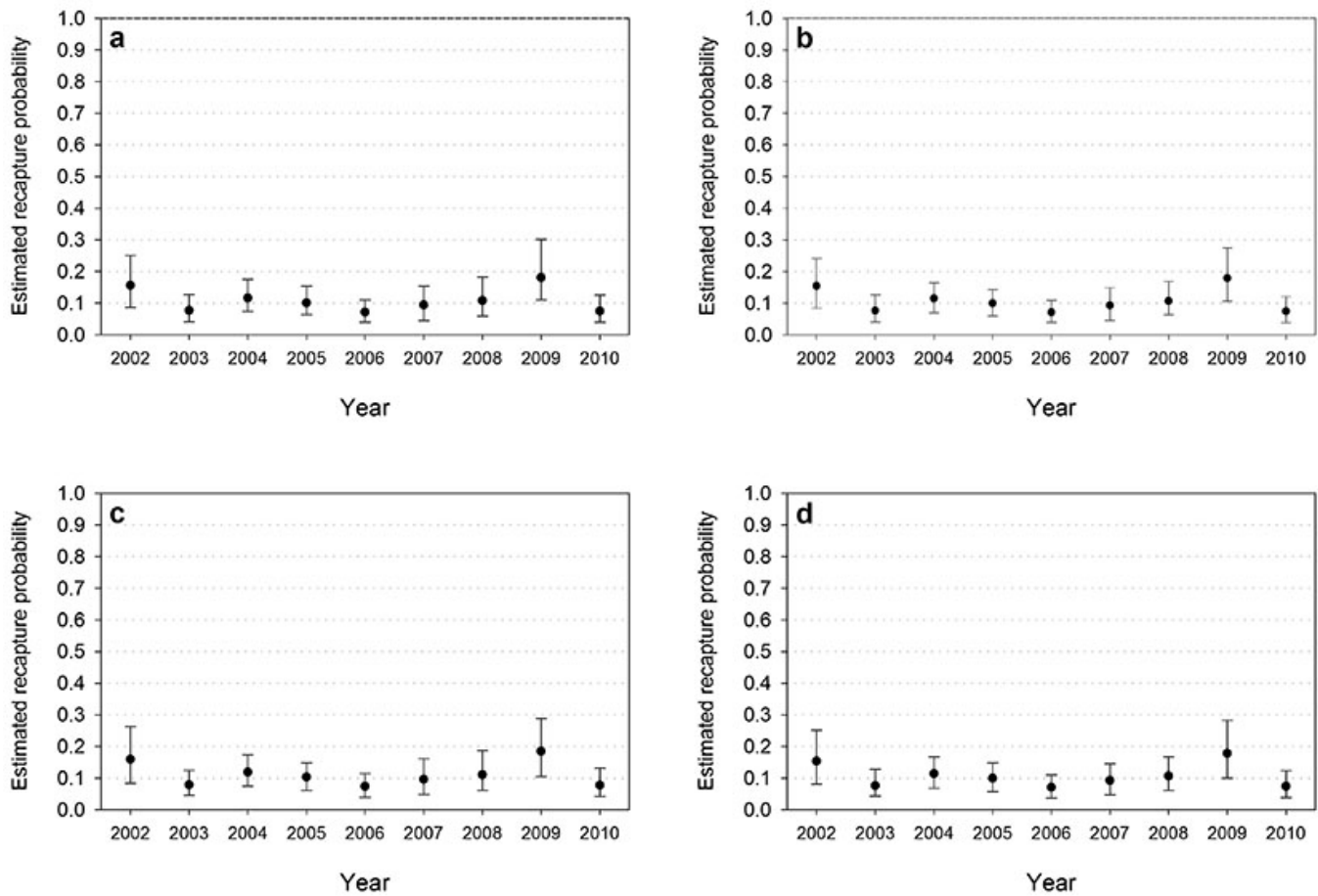


FIG. C4. Model-averaged estimates of recapture probabilities, by age class and sex, for polar bears with a home stratum of Barrow, Alaska, based on the USCA data set; (a) adult males, (b) adult females and dependent young, (c) subadult males, and (d) subadult females. Estimates do not incorporate the influence of the covariates *Radio* or *Cap-procliv*. Error bars represent 90% bias-corrected confidence intervals based on 100 bootstrap samples.

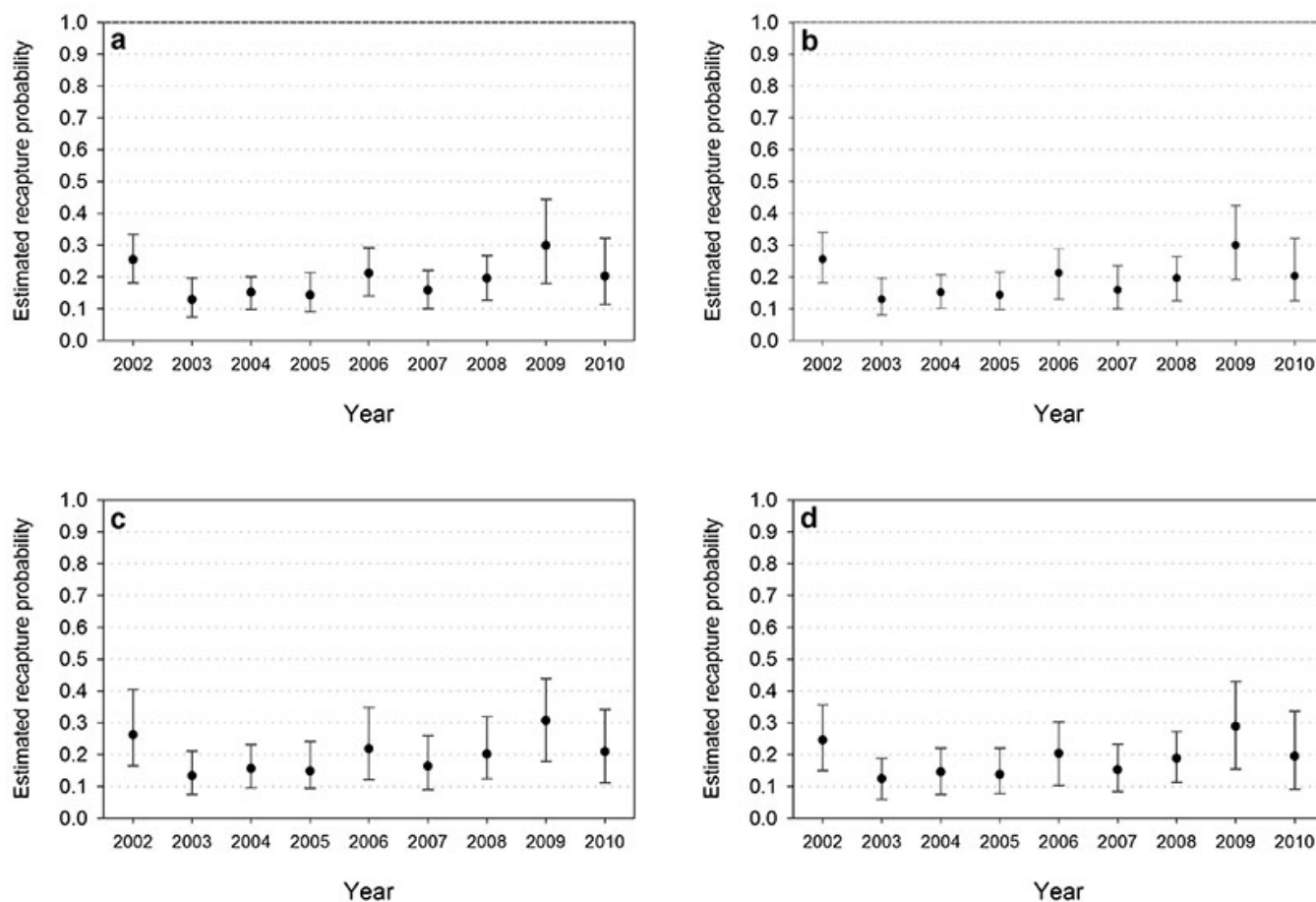


FIG. C5. Model-averaged estimates of recapture probabilities, by age class and sex, for polar bears with a home stratum of Deadhorse, Alaska, based on the USCA data set; (a) adult males, (b) adult females and dependent young, (c) subadult males, and (d) subadult females. Estimates do not incorporate the influence of the covariates *Radio* or *Cap-procliv*. Error bars represent 90% bias-corrected confidence intervals based on 100 bootstrap samples.

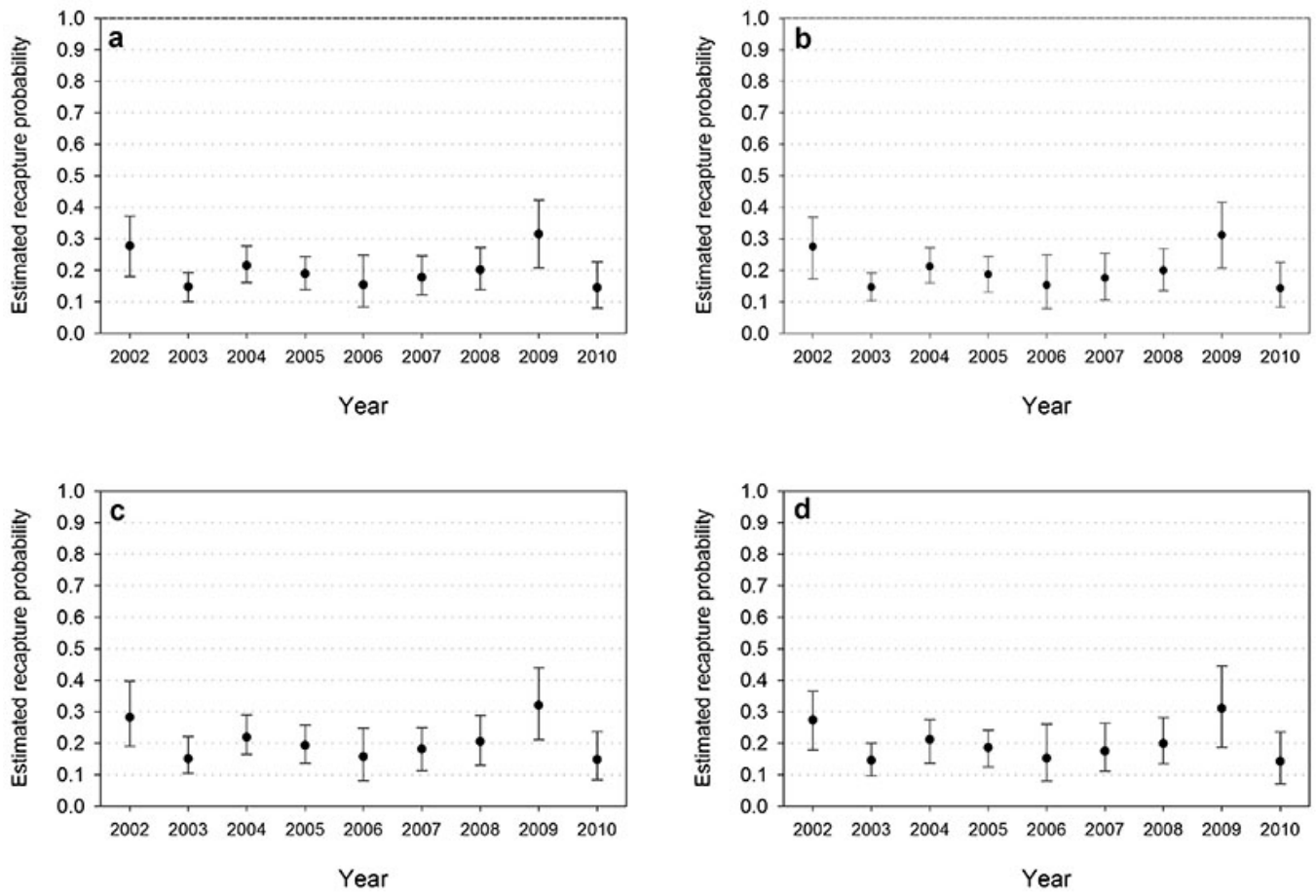


FIG. C6. Model-averaged estimates of recapture probabilities, by age class and sex, for polar bears with a home stratum of Barter Island, Alaska, based on the USCA data set; (a) adult males, (b) adult females and dependent young, (c) subadult males, and (d) subadult females. Estimates do not incorporate the influence of the covariates *Radio* or *Cap-procliv*. Error bars represent 90% bias-corrected confidence intervals based on 100 bootstrap samples.

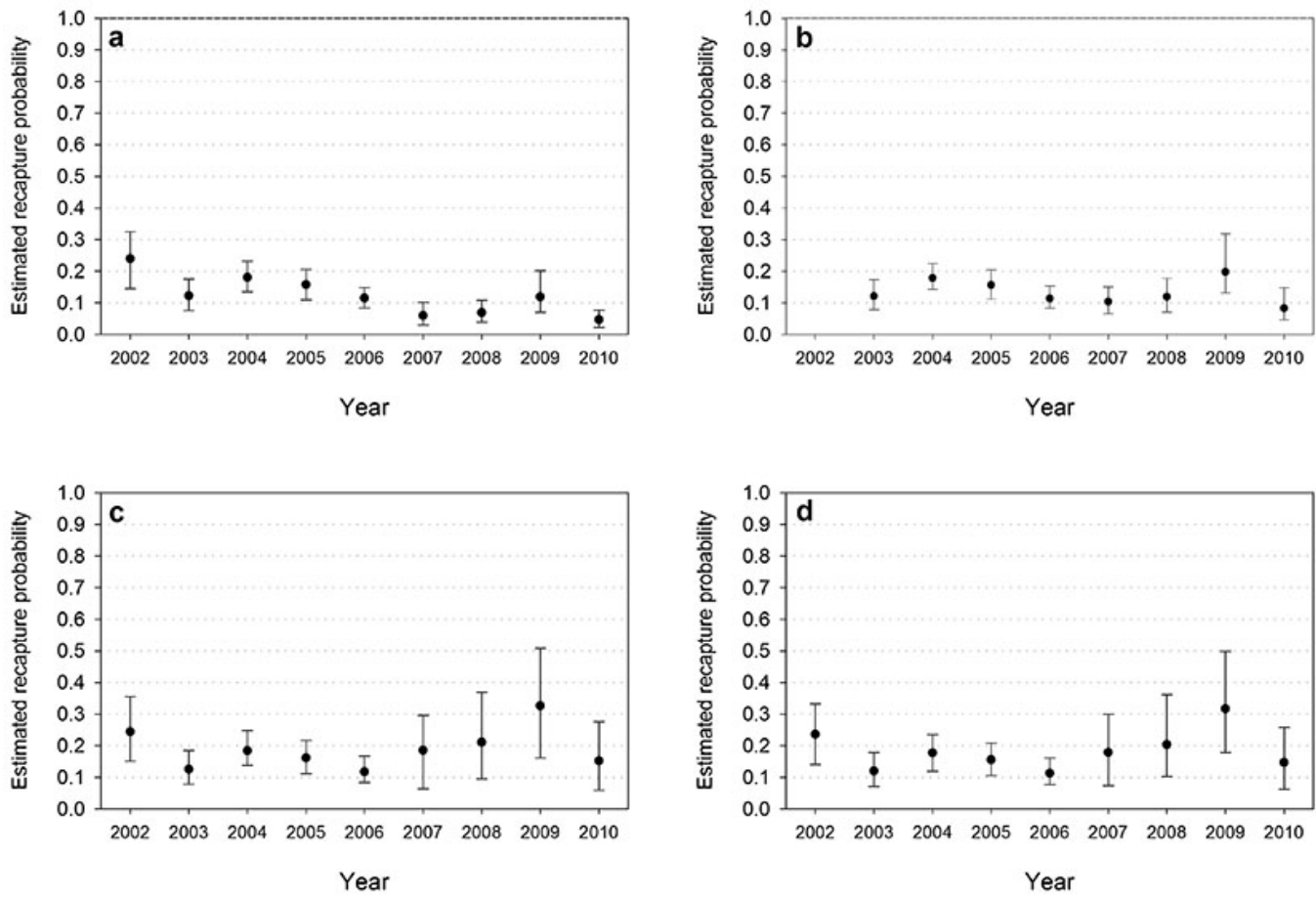


FIG. C7. Model-averaged estimates of recapture probabilities, by age class and sex, for polar bears with a home stratum of Canada, based on the USCA data set; (a) adult males, (b) adult females and dependent young, (c) subadult males, and (d) subadult females. Estimates do not incorporate the influence of the covariates *Radio* or *Cap-procliv*. Error bars represent 90% bias-corrected confidence intervals based on 100 bootstrap samples.

TABLE C2. Total AICC model weight associated with age-sex and abiotic (temporal and geographic) covariate structures of recapture probability models based on the USCA data set. Covariate structures with a weight of less than 0.01 are excluded. A "+" denotes an additive covariate term. Some covariates consisted of multiple related covariates that were always used jointly; details are provided in [Appendix A](#).

| Source  | Covariate structure              | Weight |
|---------|----------------------------------|--------|
| Age-sex | UA                               | 0.521  |
| Age-sex | Age01.23Fem + UA                 | 0.219  |
| Age-sex | Age2 + UA                        | 0.184  |
| Age-sex | Age01.3Fem + Age2 + Age2Fem + UA | 0.075  |



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APPENDIX D. An analysis of movement data from southern Beaufort Sea polar bears instrumented with radio-collars.

## INTRODUCTION

Movements of marked and unmarked individuals between capture occasions can be an important aspect of mark-recapture investigations because some types of movement have the potential to bias parameter estimates. For mobile species, emigration (movement to exit the study area) has received considerable attention in the mark–recapture literature. Emigration that is temporary and random, in the sense that each individual has a common probability of being within the study area, is not problematic. Under these conditions, recapture probability parameters can be thought of as the product of two probabilities, the probability of being within the study area and the conditional probability of capture given presence (Burnham 1993, Kendall et al. 1997, Schwarz and Stobo 1997). Estimates of survival remain unbiased and estimates of abundance include members of the population that have temporarily emigrated. Conversely, permanent emigration is more troublesome because it is indistinguishable from death (e.g., Nichols 2005). Permanent emigration reduces survival rate estimates because survival parameters incorporate both the probability of remaining in the study area and true survival of individuals that remain part of the population. For this reason, survival in Cormack-Jolly-Seber models is often termed "apparent survival". Estimates of recapture probabilities, from which abundance estimates are derived, apply to individuals that remain in the study area. A pulse of permanent emigration, perhaps in response to deteriorating ecological conditions, can appear as a temporary decline in survival and a permanent decline in abundance. Temporary emigration near the end of a mark-recapture investigation is difficult to distinguish from permanent emigration.

Movement patterns also can be problematic if individuals are only captured within a portion of the geographic range of a population. If the movement of individuals within the entire population range is random, the net effect is equivalent to random temporary emigration and parameter estimation is not adversely affected. However, patterns of individual movement could create non-random structure in recapture probabilities within the population. For example, some individuals may tend to prefer habitats within the capture region and other individuals may prefer habitats outside that region. Such a movement pattern is effectively equivalent to heterogeneity in recapture probabilities. The presence of un-modeled heterogeneity in recapture probabilities can bias estimates of recapture probabilities and abundance (Carothers 1973), though estimates of survival probabilities are more robust to heterogeneity (Carothers 1979, Abadi et al. 2013), but also see Fletcher et al. (2012). However, some patterns of Markovian movement between consecutive capture events can bias survival rate estimates (Kendall et al. 1997, Schaub et al. 2004).

## METHODS

The potential influence of both emigration and availability within a restricted capture region are of interest in the mark-recapture investigation of southern Beaufort Sea polar bears. Deteriorating sea ice conditions (Fig. 2) may have altered the distribution of bears during the course of this investigation and are projected to do so in the future (Durner et al. 2009). In addition, polar bears can only be captured within the near-shore habitats within the range (~160 km) of capture helicopters (Fig. 1), and bears are known to roam further offshore (Amstrup et al. 2004). To detect potential changes in movement patterns that might have biased estimates, we analyzed movement data from radio collars deployed by the U. S. Geological Survey on female polar bears in the southern Beaufort Sea.

We analyzed location data from individual polar bears with radio collars between 1999 and 2010. Data were examined for evidence that bears had successfully removed their collars and locations subsequent to a suspected early removal were excised from the data. We restricted analyses to those animals for which location data were available within a  $365 \pm 30$

day window from the date they were collared. Our primary interest was the location of bears during the spring capture season in the years of this investigation, so individuals with location data during the months of March to May each year from 2001 to 2010 were identified. These screening filters resulted in a data set containing 116 time series of spring locations from 71 unique bears.

Each bear in each year was classified as being either available or unavailable for capture based on its location data. We tested several classification criteria to ensure that results were not sensitive to the criteria used. Results are only reported for the analysis in which a bear was deemed available for capture if it had at least one location within 100km of the coast between  $-160^{\circ}$  W and  $-141^{\circ}$  W from 1 March to 31 May. Restricting the 100km distance criterion to 50km, or requiring an individual to have at least two locations within the study area separated by at least 14 days, had no influence on the results.

## RESULTS

The proportions of radio-collared bears available for capture each year did not display a temporal trend (Fig. D1). The null hypothesis that the proportions were equal was tested using an exact binomial test (Agresti 2002), using 10,000 replications to estimate significance (Patefield 1981), and the proportions were not found to differ ( $p$ -value = 0.990). In addition, a generalized additive model (Wood 2006) with potential nonlinearity through time was used to approximate the proportion data. The estimated parameter for year was not significantly different than zero ( $p$ -value = 0.934), suggesting a straight line provided the best model fit to the data, which is consistent with the results of the exact binomial test.

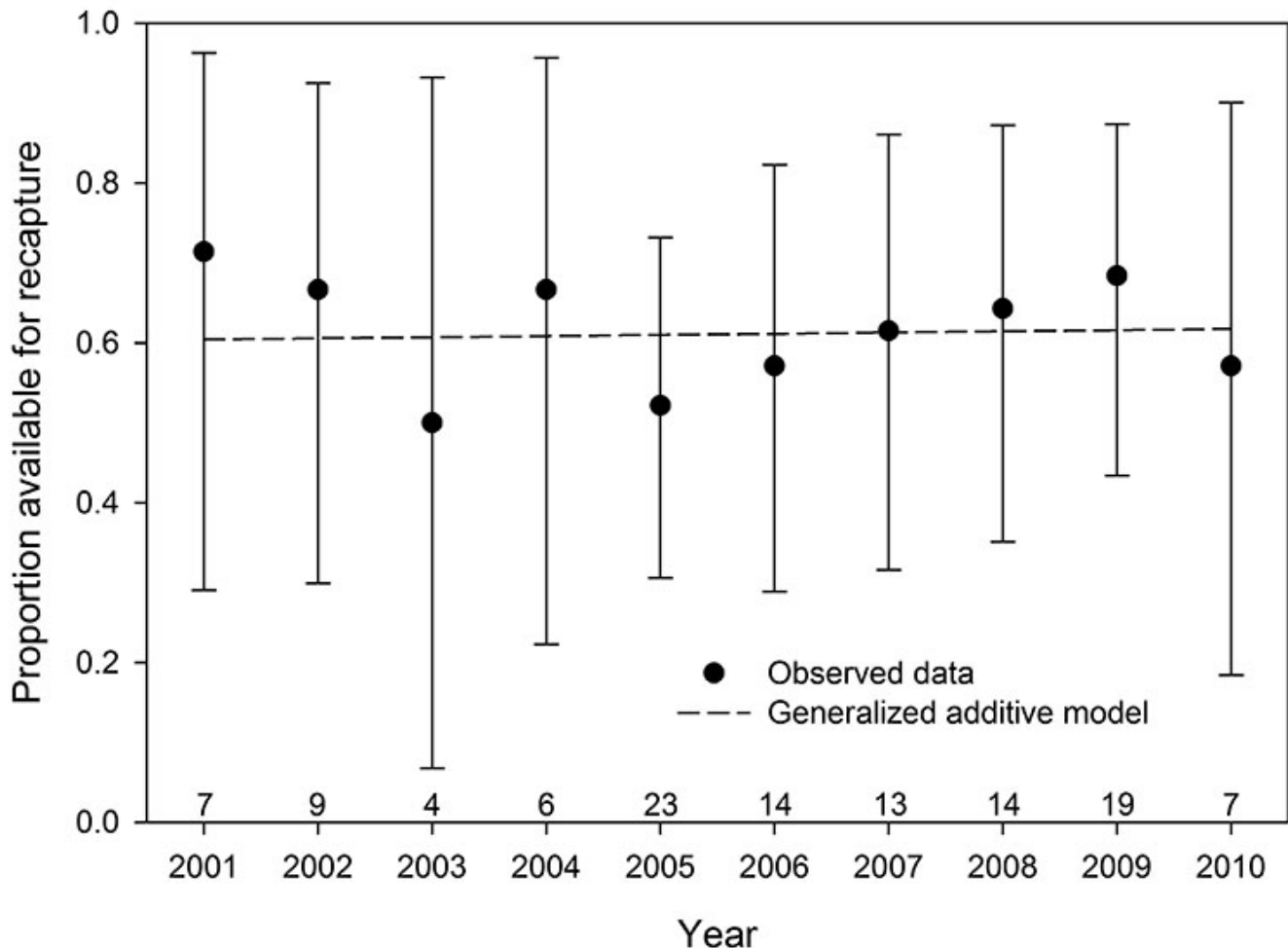


FIG. D1. The proportion of radio-collared polar bears from the southern Beaufort Sea available for recapture in the study area, by year, with exact 95% confidence intervals and an estimated generalized additive model. The number of bears

with location data each year is shown immediately above the horizontal axis.

The location data included 42 cases for which the availability of an individual within the Alaskan portion of the southern Beaufort Sea capture region in consecutive years could be determined (Fig. D2). The hypothesis of conditional independence between availability in consecutive years was tested using an exact Cochran-Mantel-Haenszel test (Agresti 2002). The test was significant ( $p$  value = 0.002), suggesting that availability within the capture region is not purely random between consecutive years.

|        |   |          |  |    |      |      |   |   |   |      |   |   |  |   |
|--------|---|----------|--|----|------|------|---|---|---|------|---|---|--|---|
|        |   | 2002     |  |    |      | 2003 |   |   |   | 2004 |   |   |  |   |
| 2001   |   | 0        |  | 1  |      | 0    |   | 1 |   | 0    |   | 1 |  |   |
|        | 0 | 0        |  | 0  | 2002 | 0    | 2 |   | 0 | 2003 | 0 | 1 |  | 0 |
|        | 1 | 0        |  | 4  |      | 1    | 0 |   | 2 |      | 1 | 0 |  | 1 |
|        |   | 2005     |  |    |      | 2006 |   |   |   | 2007 |   |   |  |   |
| 2004   |   | 0        |  | 1  |      | 0    |   | 1 |   | 0    |   | 1 |  |   |
|        | 0 | 2        |  | 0  | 2005 | 0    | 2 |   | 3 | 2006 | 0 | 1 |  | 0 |
|        | 1 | 1        |  | 1  |      | 1    | 1 |   | 2 |      | 1 | 0 |  | 2 |
|        |   | 2008     |  |    |      | 2009 |   |   |   | 2010 |   |   |  |   |
| 2007   |   | 0        |  | 1  |      | 0    |   | 1 |   | 0    |   | 1 |  |   |
|        | 0 | 1        |  | 0  | 2008 | 0    | 1 |   | 2 | 2009 | 0 | 2 |  | 0 |
|        | 1 | 1        |  | 4  |      | 1    | 0 |   | 4 |      | 1 | 0 |  | 2 |
|        |   | Year i+1 |  |    |      |      |   |   |   |      |   |   |  |   |
| Year i |   | 0        |  | 1  |      |      |   |   |   |      |   |   |  |   |
|        | 0 | 12       |  | 5  |      |      |   |   |   |      |   |   |  |   |
|        | 1 | 3        |  | 22 |      |      |   |   |   |      |   |   |  |   |

FIG. D2. Contingency tables cross-classifying the number of radio-collared polar bears available (1) or unavailable (0) for capture within the southern Beaufort Sea study area of Alaska in consecutive pairs of years from 2001 to 2010.

## CONCLUSIONS

We found no evidence to suggest that the proportion of bears available within the capture region during the spring capture season has trended or otherwise changed during the study period (Fig. D1). Consequently, the reduced survival rates estimated for the middle portion of the study period (Fig. 3, 4) are unlikely to have been caused by a pulse in permanent emigration in response to unfavorable summer ice conditions (Fig. 2). The temporal consistency in the annual proportions reinforces the finding that a period of reduced survival during the middle portion of the study period led to a decline in abundance.

Although we found no reason to suspect animal movements within the study area could explain the temporal patterns in survival rate and abundance estimates, apparent non-randomness in movements of individuals between consecutive years was detected. Such Markovian temporary emigration has the potential to bias estimates of survival (Kendall et al. 1997, Schaub et al. 2004), as well as recapture probability estimates and therefore abundance estimates (Carothers 1973, Kendall et al. 1997, Schwarz and Stobo 1997). However, the observed pattern in movements between consecutive years

(Fig. D2) is consistent with conditions under which the bias in survival probability estimates was low (Schaub et al. 2004). Consequently, although our tests corroborate a conclusion that the estimated decline in survival and abundance during the middle portion of the study period reflects actual population dynamics, the absolute magnitude of the estimates could incorporate some negative bias. We have no reason to suspect that such bias would differ substantially among years and potentially influence temporal trends in parameter estimates. In addition, the covariate *Cap-procliv* was designed to account for sources of heterogeneity in recapture probabilities and may partially abate the influence of any such bias (Appendix F).

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APPENDIX E. Projected trends in the abundance of southern Beaufort Sea polar bears based on estimated survival rates.

Capture probabilities of southern Beaufort Sea polar bears are thought to vary primarily in response to environmental and ecological conditions that influence their movements and spatial distribution. Unfortunately, our ability to identify and measure pertinent variables and incorporate them into models as covariates is limited. Because abundance estimates in Cormack-Jolly-Seber (CJS) models are derived from estimated recapture probabilities using the Horvitz-Thompson (HT) estimator (McDonald and Amstrup 2001), un-modeled structure in recapture probabilities has the potential to introduce bias. As noted in the summary of USGS modeling results, estimates in the first two years, particularly 2002, are suspected of being negatively biased by the absence of capture effort from Barrow in 2001, the incomplete accumulation of marked individuals in the population (Appendix B, Table B1), and perhaps non-random movement between consecutive years (Appendix D, Fig. D2). In addition, the unusually large number of bears captured in 2004 (Table 5) may be responsible for the seemingly large point estimate of abundance in that year (Fig. 5). With respect to the USCA estimates, a lack of Canadian capture effort before 2003, as well as reduced effort and lack of capture effort in the easternmost portion of the study area after 2006, may have introduced bias into those abundance estimates, despite our attempts to model known factors potentially influencing recapture probabilities.

To investigate whether potential biases in abundance estimates might have influenced the assessment of abundance status and trend, we conducted simulations to project abundance from 2001 to 2010 based only on estimated survival probabilities, which are more robust to un-modeled heterogeneity in recapture probabilities that can bias abundance estimates (Carothers 1979, Abadi et al. 2013). USGS capture data from 1989 to 2003 were pooled and used to develop an initial probability distribution  $f$  of bears among sex, age, and family categories. Captured individuals were jointly classified by sex and age, and family groups were classified by the number and age of dependent young. The maximum age observed from 1989 to 2003 was 29, which was utilized as the maximum possible age in the simulations. The number of observations in each of the resulting 206 combinations of sex, age, and family categories was counted, and each count was increased by one so that all categories had a nonzero probability of occurring. The counts were additionally adjusted to account for the 2002–2010 mean model-averaged estimate of recapture probability for each category (Appendix C), and the resulting values were scaled to sum to 1.0 to constitute a probability distribution  $f$  for the demographic composition of the population in the initial year of 2001. The 1989–2003 USGS capture data were similarly used to construct a probability distribution  $g$  for the number of cubs in a family group (1, 2, or 3).

Initial populations of USGS and USCA bears were randomly established in 2001. Because the USGS abundance estimate from 2002, and possibly the estimates from 2003 and 2004, was suspected of being biased, as noted above, the mean initial population size was established at 1,000 individuals, the approximate mean of the 2003 and 2004 estimates. A mean initial abundance of 1,500 bears was used for the USCA population, which was approximately equal to the mean abundance estimate of 1,526 for the period 2004–2006 reported by Regehr et al. (2006). Note that these starting points are not consequential, as the trend in relative abundance through time is of primary interest. In each case, the initial population size was divided by the mean number of individuals per category in the probability distribution  $f$  to derive a sample size, accounting for multiple individuals in family groups which were sampled as a unit, and a multinomial sample of the resulting size was drawn from  $f$  to establish initial populations in 2001.

The initial populations randomly established in 2001 were projected forward in time to 2010 using survival rates. The estimated survival probabilities obtained by bootstrapping were first bias-corrected so that their means equaled the point estimates of survival (Figs. 3 and 4). In each year, a mean annual survival probability for each sex and age class was randomly drawn from the bias-corrected bootstrap estimates. Given the resulting survival probability for each sex and age class, survival was established by drawing a random Bernoulli deviate for each individual in the population. All individuals that survived to the maximum age of 29 died prior to the following year. If an adult female with dependent young died, the young also died. If a female survived but all her dependent young died, she was available to reproduce the following year.



A measure of production (B) related to the litter production rate (Ramsay and Stirling 1988) and breeding success (Wiig 1998)

$$B = \frac{\# \text{ females with cubs}}{\# \text{ females with cubs} + \# \text{ lone females}}$$

was computed from the spring capture data each year from 2002 to 2010 and used to establish new litters for a portion of the females without dependent young. Although B does not incorporate mortality over the interval from birth to the capture of a female with cubs, that is consistent with CJS estimates of cub survival. Given the value of B in any one year, a random Bernoulli deviate was drawn to determine if each adult female without dependent young acquired a new litter of cubs. Litter sizes for reproductive females were randomly established using the probability distribution  $g$ . Consistent with the structure of the mark-recapture models used in the analysis, the sex of yearlings that survived to age 2, the youngest sub-adult age, was established with a random Bernoulli deviate having a mean of 0.5.

The sequence of randomly establishing an initial population in 2001 and projecting abundance forward in time to 2010 by simulating survival and births was replicated 1,000 times; simulations for the USGS and USCA data sets were independent. The mean abundance across replications in each year was plotted along with the 5th and 95th quantiles as error bars (Figs. E1 and E2). Mean projected abundance across replications in each year was scaled to minimize the squared difference between the mean projection and estimated abundance, weighted by the inverse width of abundance confidence intervals, and plotted with point estimates of abundance and their 90% confidence intervals to facilitate a comparison of their trends (Fig. E3, E4).

Trends in abundance from the projections were similar to the trends in the abundance estimates, excepting the earliest years in which the estimates are suspected of being biased. The projected abundance trends with both data sets increased through 2004 and declined through 2007 (Figs. E1 and E2). The rate of decline in USGS projections moderated from 2009 to 2010 and the USCA projections were stable from 2008 to 2010. The correlation between the estimated and projected USGS abundance trends from 2002 to 2010 was 0.85, and 0.90 from 2003 to 2010 (Fig. E3). The corresponding correlations for the USCA trends were 0.89 from 2002 to 2010 and 0.95 from 2003 to 2010 (Fig. E4).

Given that the abundance projections are partially independent of the abundance estimates, their concordance increases confidence in our finding that a period of low survival from 2004 to 2006 led to a substantial decline in the abundance of polar bears in the southern Beaufort Sea.

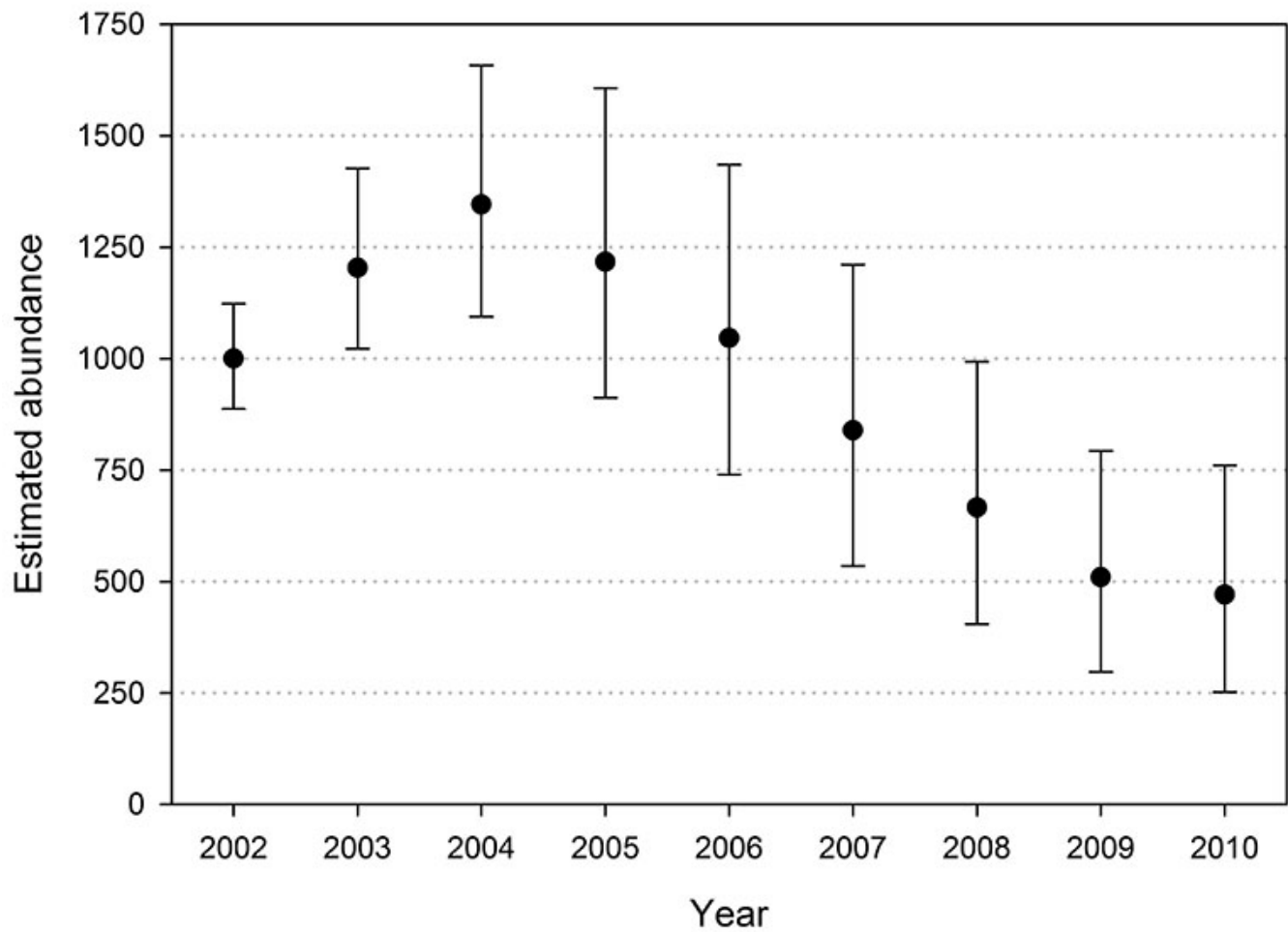


FIG. E1. Abundance trends of southern Beaufort Sea polar bears observed across replications of the population projection based on survival rates estimated with the USGS data set. Error bars denote the 5th and 95th quantiles observed across the 1,000 replications.

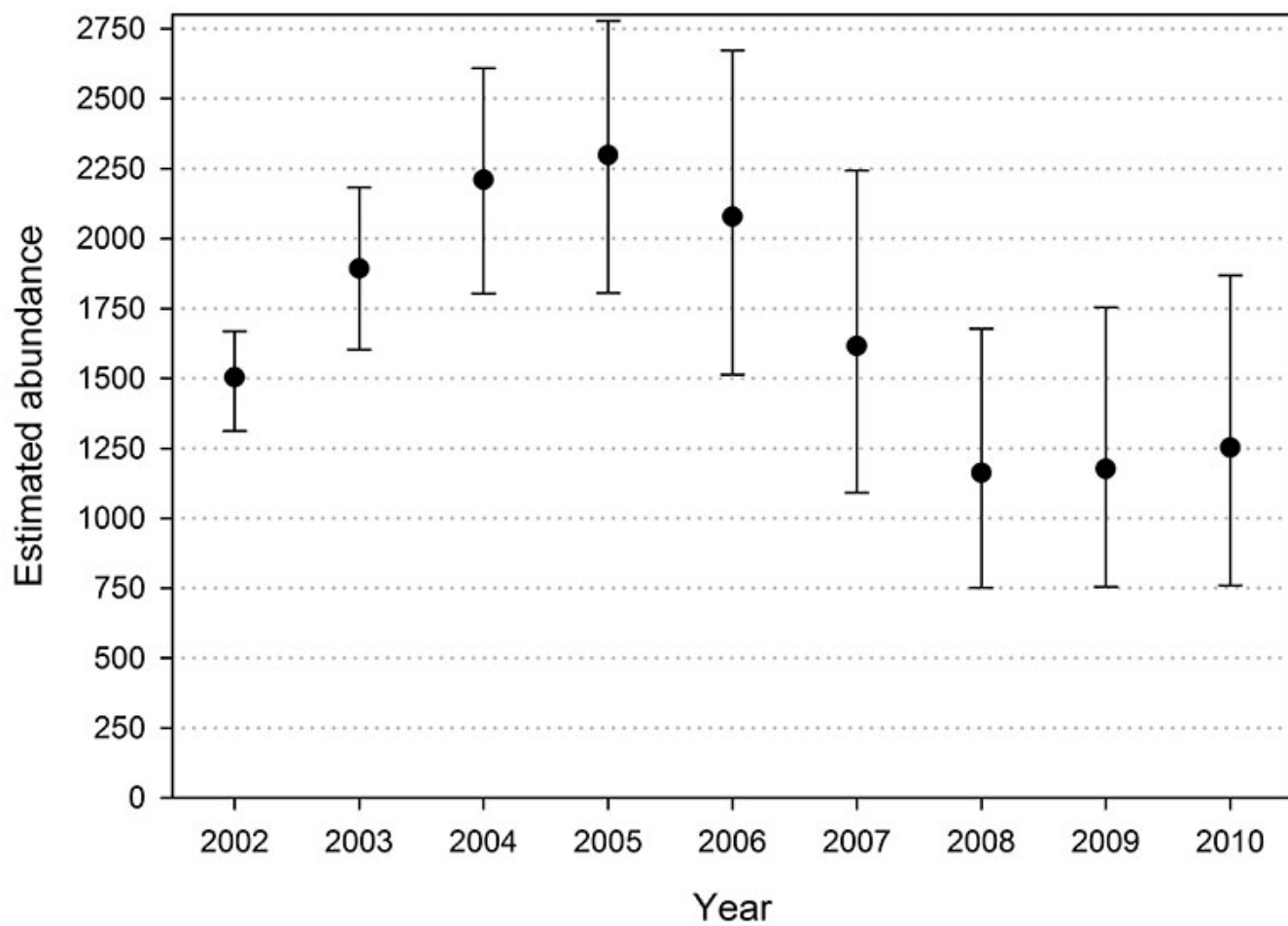


FIG. E2. Abundance trends of southern Beaufort Sea polar bears observed across replications of the population projection based on survival rates estimated with the USCA data set. Error bars denote the 5th and 95th quantiles observed across the 1,000 replications.

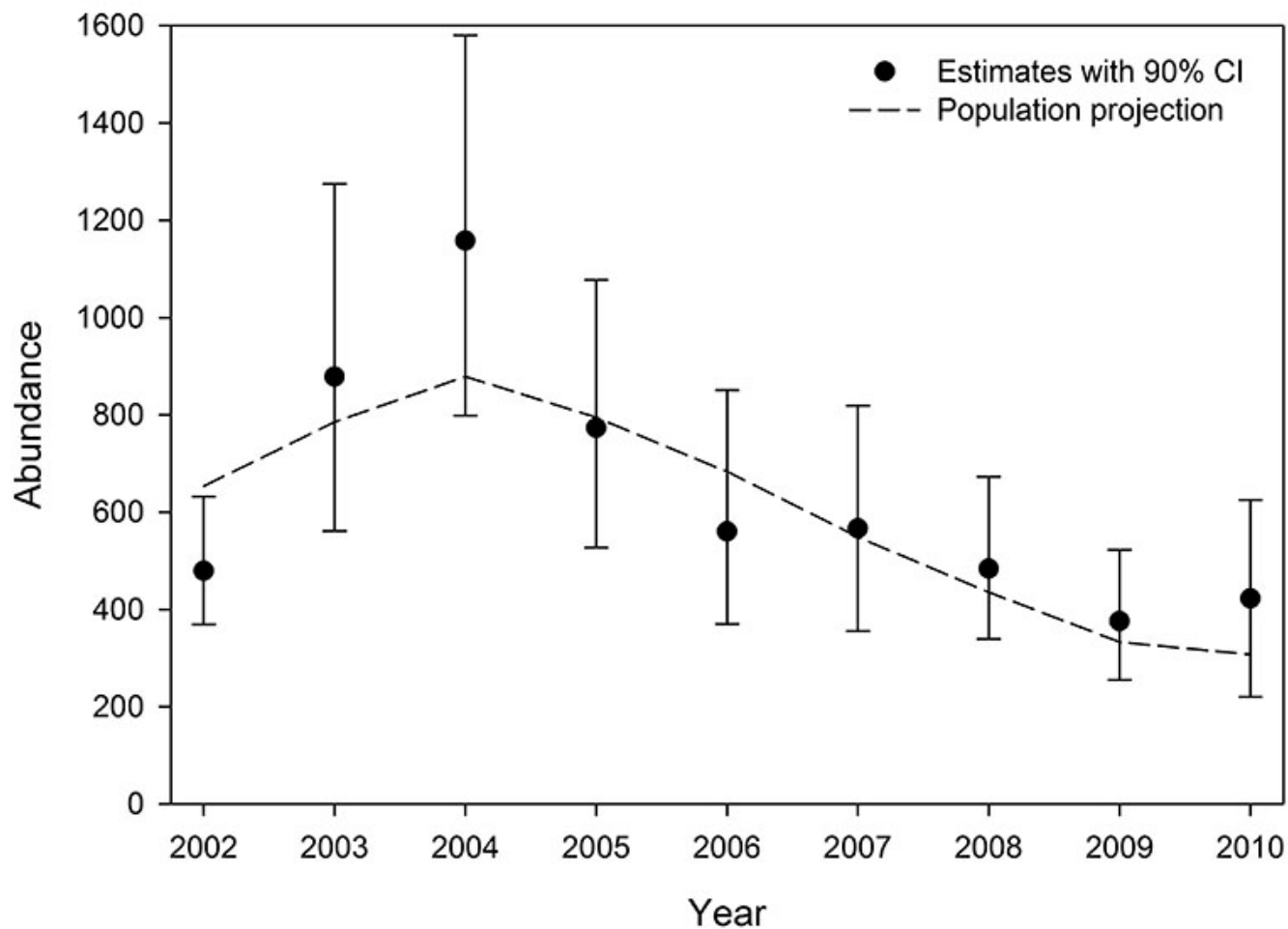


FIG. E3. Annual abundance estimates with 90% bias-corrected bootstrap confidence intervals for southern Beaufort Sea polar bears based on the USGS data set, and the re-scaled mean annual abundance observed during the 1,000 replications of the USGS population projection.

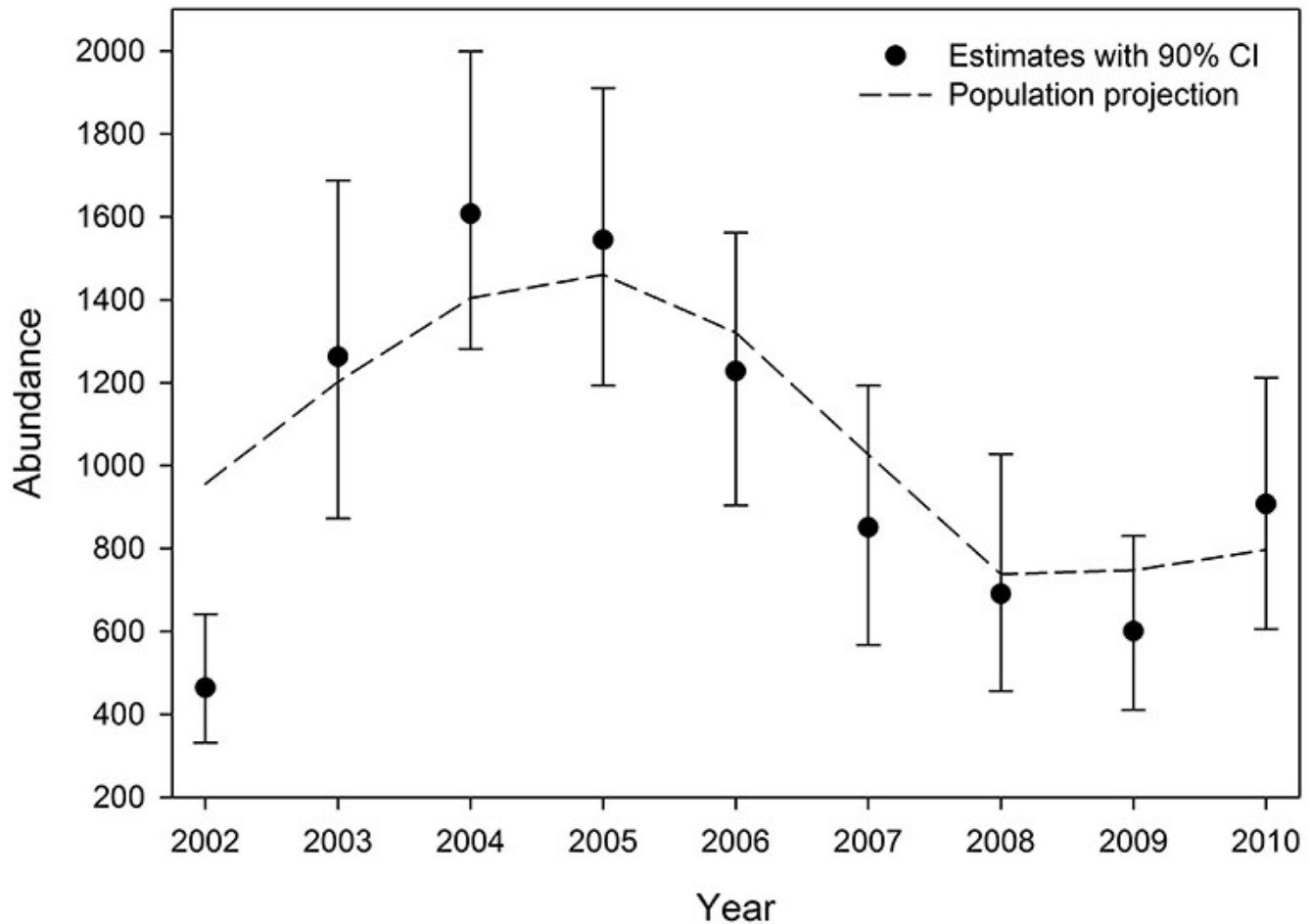


FIG. E4. Annual abundance estimates with 90% bias-corrected bootstrap confidence intervals for southern Beaufort Sea polar bears based on the USCA data set, and the re-scaled mean annual abundance observed during the 1,000 replications of the USCA population projection.

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APPENDIX F. The covariate *Cap-procliv* used to model heterogeneous recapture probabilities of southern Beaufort Sea polar bears.

Heterogeneity in capture or recapture probabilities is one of the most prevalent violations of mark-recapture model assumptions. The presence of un-modeled heterogeneity in Cormack-Jolly-Seber models causes bias in the estimation of recapture probabilities (Pledger et al. 2003), and therefore in estimates of abundance derived from them using the Horvitz-Thompson estimator (McDonald and Amstrup 2001). Covariates such as indicators of sex and age class, measures of capture effort, and various forms of temporal structure can be used to model capture probabilities and reduce the influence of heterogeneity attributable to known or suspected factors (Lebreton et al. 1992), and we attempted to do so. However, the sufficiency of such covariates for long-lived mammals such as polar bears is uncertain, as their recapture probabilities may depend on individual characteristics such as behavioral tendencies, experiential history, and preferences in habitat or prey.

We developed the recapture heterogeneity covariate *Cap-procliv* to use an individual's prior capture history as one potential measure of its proclivity to be recaptured in the future, given continued survival. Such an approach could indirectly account for individual characteristics that influence recapture probability, such as behavior, for which it would be impossible to directly obtain quantitative covariates. If  $f_i$  and  $r_i$  denote the capture occasions during which individual  $i$  was initially captured and first recaptured, respectively, the value of the *Cap-procliv* covariate for individual  $i$  during capture occasion  $j$  ( $c_{ij}$ ) was defined as

$$c_{ij} = \begin{cases} 0 & j \leq r_i \\ \frac{1}{j - f_i} \sum_{m=f_i}^{j-1} h_{im} & j > r_i \end{cases} \quad (\text{F.1})$$

where  $h_{im} \in \{0,1\}$  was the indicator of capture during occasion  $m$  for individual  $i$ . The covariate effectively separates individuals into two categories for each capture occasion, those that have and have not been previously recaptured. In that sense, the covariate is a generalization of the "transient" concept that has become common in mark-recapture models (e.g., Pradel et al. 1997, Conn et al. 2011, Smout et al. 2011). Beginning with an individual's first recapture, the covariate incrementally accumulates knowledge of an individual's tendency to be captured as a mark-recapture investigation proceeds through time. Note that the value of *Cap-procliv* for occasion  $j$  utilizes capture information from occasions prior to  $j$  only, and is therefore independent of the capture event at occasion  $j$ . The capture history of an adult male polar bear from the southern Beaufort Sea and the resulting *Cap-procliv* covariate are provided as an example (Table F1).

TABLE F1. An example of the recapture heterogeneity covariate *Cap-procliv* for an adult male polar bear captured five times from 2001 to 2010.

| Occasion | Capture indicator | <i>Cap-procliv</i> |
|----------|-------------------|--------------------|
|          |                   |                    |



|      |   |     |
|------|---|-----|
| 2001 | 0 | 0   |
| 2002 | 0 | 0   |
| 2003 | 0 | 0   |
| 2004 | 1 | 0   |
| 2005 | 1 | 0   |
| 2006 | 0 | 2/2 |
| 2007 | 0 | 2/3 |
| 2008 | 1 | 2/4 |
| 2009 | 1 | 3/5 |
| 2010 | 1 | 4/6 |

The influence of the *Cap-procliv* covariate on recapture probability estimates was illustrated by comparing the parameter estimates of two nearly identical models based on the USGS data set. The first model, which included *Cap-procliv*, had the minimum value of AIC among the suite of models considered, and the second model contained the same parameters excepting *Cap-procliv*. Estimates of the parameters of the model including *Cap-procliv* are consistently smaller (Fig. F1) than the estimated parameters of the model excluding the covariate (Fig. F2). This was expected, as the structure of the covariate allows the estimated recapture probabilities of individuals caught frequently to increase (reducing their negative bias), and the estimates for individuals caught less frequently to decrease (reducing their positive bias). In addition, the AICC values in the two models differed by 16, which reflects the improved model fit the covariate provided. As an additional example, the estimated recapture probabilities for an adult male with the capture history in Table F1 obtained from the two models are presented in Fig. F3. In the model including *Cap-procliv*, recapture probabilities for this individual are reduced from 2002 to 2005, compared to the model excluding the covariate. It was first recaptured in 2005, after which its recapture probability is elevated from 2006 to 2010 relative to the model without *Cap-procliv*. The additional flexibility to model heterogeneity in recapture probabilities is expected to reduce negative bias for individuals captured frequently and positive bias for individuals captured infrequently.

| Capture var                   | Est      | SE      |
|-------------------------------|----------|---------|
| (Intercept)                   | -1.66658 | 0.50330 |
| tvar(time, drop = c(1, 3)):10 | -0.30413 | 0.72181 |
| tvar(time, drop = c(1, 3)):3  | -1.01524 | 0.55419 |
| tvar(time, drop = c(1, 3)):4  | -0.83823 | 0.51981 |
| tvar(time, drop = c(1, 3)):5  | -0.74555 | 0.51938 |
| tvar(time, drop = c(1, 3)):6  | -0.13571 | 0.54665 |
| tvar(time, drop = c(1, 3)):7  | -0.60366 | 0.56822 |
| tvar(time, drop = c(1, 3)):8  | -0.42821 | 0.55019 |
| tvar(time, drop = c(1, 3)):9  | 0.25114  | 0.64604 |
| home2.DEHBTI                  | 0.58421  | 0.33417 |
| BTI.2006                      | -1.40099 | 0.99461 |
| radio                         | 0.70858  | 0.40898 |
| cap.procliv                   | 1.01963  | 0.39319 |

Message = SUCCESS: Convergence criterion met  
 Link = logit  
 Model df = 27  
 Log likelihood = -972.660161468715  
 Deviance = 1945.32032293743  
 AIC = 1999.32032293743  
 AICc = 2001.52119629987

FIG. F1. Partial output of the function `F.cjs.estim` from the R package `mra` for the example model including the covariate *Cap-procliv*.

| Capture var                   | Est      | SE      |
|-------------------------------|----------|---------|
| (Intercept)                   | -1.78164 | 0.53114 |
| tvar(time, drop = c(1, 3)):10 | 0.1814   | 0.69257 |
| tvar(time, drop = c(1, 3)):3  | -0.64429 | 0.53554 |
| tvar(time, drop = c(1, 3)):4  | -0.45187 | 0.52043 |
| tvar(time, drop = c(1, 3)):5  | -0.43179 | 0.52114 |
| tvar(time, drop = c(1, 3)):6  | 0.2096   | 0.55925 |
| tvar(time, drop = c(1, 3)):7  | -0.30286 | 0.59654 |
| tvar(time, drop = c(1, 3)):8  | -0.07795 | 0.56254 |
| tvar(time, drop = c(1, 3)):9  | 0.73151  | 0.63327 |
| home2.DEHBTI                  | 0.72003  | 0.34285 |
| BTI.2006                      | -1.49103 | 0.94443 |
| radio                         | 0.90472  | 0.42260 |

```

Message = SUCCESS: Convergence criterion met
Link = logit
Model df = 26
Log likelihood = -981.779123233998
Deviance = 1963.558246468
AIC = 2015.558246468
AICc = 2017.59894414241

```

FIG. F2. Partial output of the function `F.cjs.estim` from the R package `mra` for the example model excluding the covariate *Cap-procliv*.

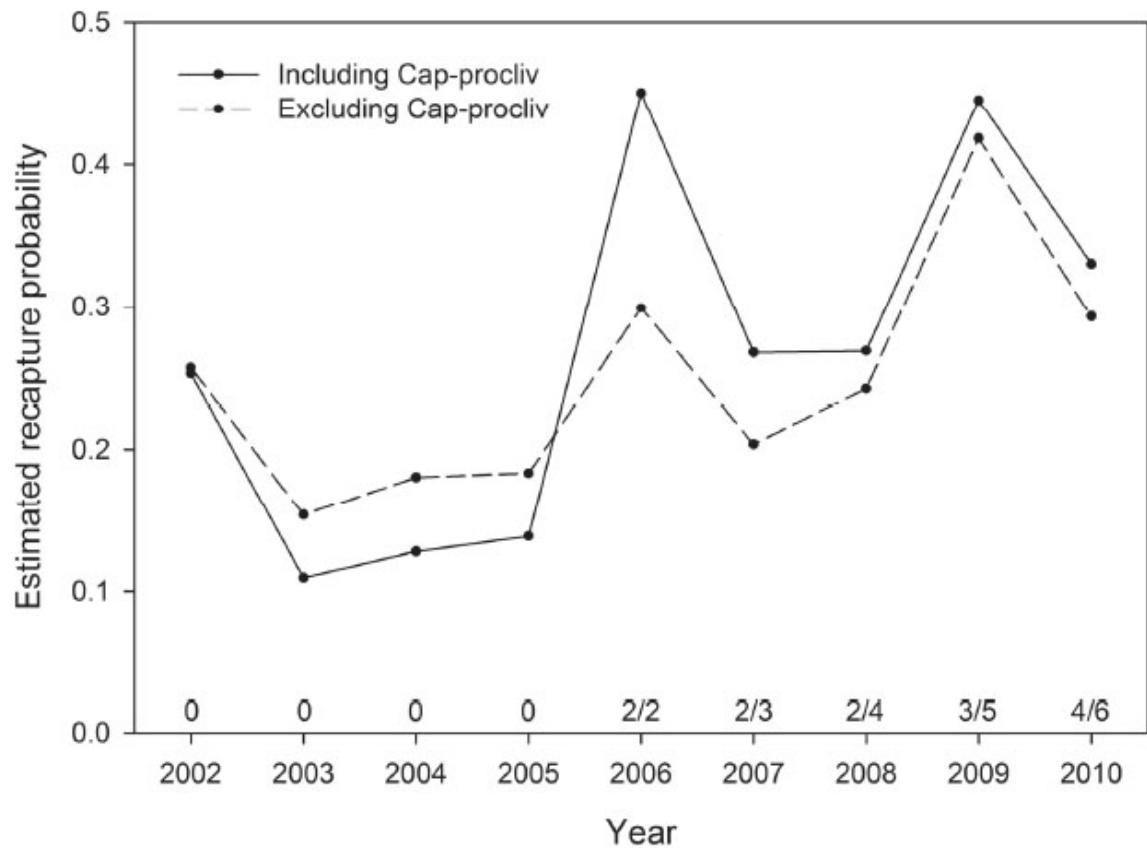


FIG. F3. Estimated recapture probabilities for an adult male bear in the USGS data set with the capture history in Table F1 and a home stratum of Deadhorse, Alaska, based on models that were identical except for their inclusion of the recapture heterogeneity covariate *Cap-procliv*. The value of the *Cap-procliv* covariate for this individual in each year (Table F1) is shown as a fraction immediately above the horizontal axis.

The influence of the *Cap-procliv* covariate on estimates of abundance was assessed by comparing model-averaged estimates of abundance obtained from the USGS data set with and without use of the covariate. Estimates of abundance obtained using the *Cap-procliv* were obtained from the original analysis of the USGS data set. The covariate was eliminated from each model, the parameters of each model were re-estimated, and the resulting estimates of abundance were averaged over the model set. The difference between the two time series of abundance estimates (Fig. F4) was consistent with expectations (Carothers 1973, Pledger et al. 2010). The increased flexibility to indirectly model unknown sources of heterogeneity in recapture probabilities appears to have reduced bias in abundance estimates. The covariate allowed the smaller subset of individuals captured frequently to have increased recapture probabilities and decreased their contribution to the Horvitz-Thompson abundance estimates (McDonald and Amstrup 2001). Coincidentally, estimated recapture probabilities for the larger subset of individuals captured less frequently decreased, which increased their contribution to the abundance estimates. The net effect was a reasonably consistent increase in the annual abundance estimates, averaging 17% across all 9 years (Fig F4).

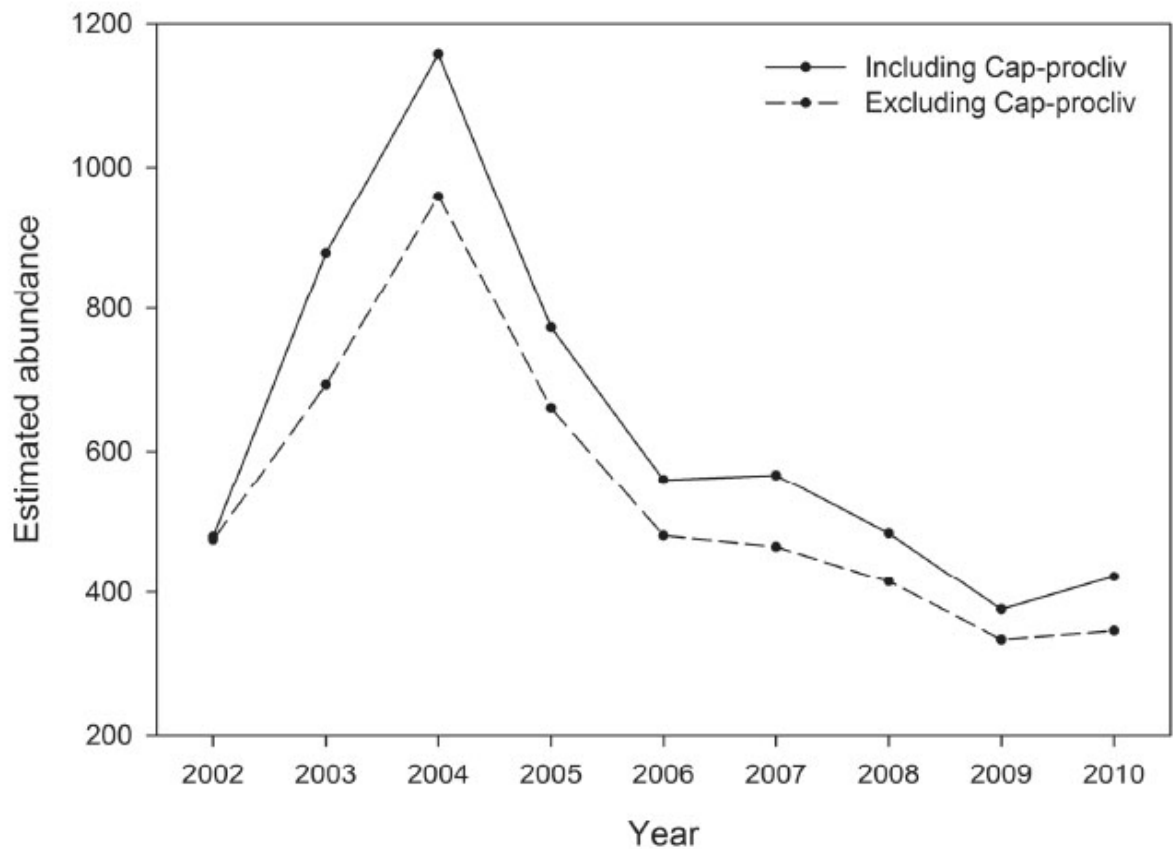


FIG. F4. Model-averaged estimates of annual abundance, with and without use of the recapture heterogeneity covariate *Cap-procliv*, based on the USGS data set.

Methods of modeling individual heterogeneity in probabilities of capture and survival remains an area of active interest in mark-recapture applications because of the estimation bias unexplained heterogeneity can cause (e.g., Abadi et al. 2013). Random effect (Royle 2008) and mixture (Pledger et al. 2010) models are two approaches that have gained widespread utilization. The covariate *Cap-procliv* we introduced provides an additional option that directly utilizes information in the capture histories of individual animals, which record the ultimate effects of heterogeneity, and is easy to implement in Cormack-Jolly-Seber models using the standard covariate approach (Lebreton et al. 1992). The covariate performed as expected in this application, appearing to appropriately counteract bias of known direction in both recapture probabilities and abundance estimates. The comparative merits of alternative methods of accounting for heterogeneity in recapture probabilities are difficult to assess with a data set resulting from a single realization of a mark-recapture experiment. For that reason, a simulation to investigate the performance of this approach under known conditions is planned.

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