
From: Hayes, Miriam (Nicole) <mnhayes@blm.gov>
Sent: Friday, March 22, 2019 11:13 AM
To: coastalplainAR; Sean Cottle
Cc: Amy Lewis; Chad Ricklefs; Craig Perham
Subject: Fwd: [EXTERNAL] Correction to Comments on Draft Coastal Plain Oil and Gas Leasing Program EIS
Attachments: 2019 03 22 Sierra Club Amstrup Errata Letter.pdf

Follow Up Flag: Follow up
Flag Status: Completed

Nicole Hayes

Project Coordinator
Bureau of Land Management
222 W. 7th Avenue #13
Anchorage, Alaska 99513
Desk: (907) 271-4354
Cell: (907) 290-0179

----- Forwarded message -----

From: **Karimah Schoenhut** <karimah.schoenhut@sierraclub.org>
Date: Fri, Mar 22, 2019 at 10:10 AM
Subject: [EXTERNAL] Correction to Comments on Draft Coastal Plain Oil and Gas Leasing Program EIS
To: <mnhayes@blm.gov>, <blm_ak_coastalplain_EIS@blm.gov>
Cc: Steven Amstrup <Samstrup@pbears.org>, Barbara Nielsen <bnielsen@pbears.org>, Bridget Psarianos <bpsarianos@trustees.org>, Brook Brisson <bbrisson@trustees.org>

Dear Project Coordinator Hayes,

Please find attached an errata letter pertaining to the March 8, 2019 report by Dr. Steven Amstrup that Sierra Club submitted to BLM during the public comment period for the draft Coastal Plain Oil and Gas Leasing Program EIS. Sierra Club is submitting the attached letter, and associated letter from Dr. Amstrup, to correct errata in the March 8, 2019 report, and accordingly correct Sierra Club's comments on the DEIS citing to the report.

Sincerely,
Karimah Schoenhut

--



Karimah Schoenhut
Staff Attorney
Sierra Club Environmental Law Program

50 F Street NW, 8th Floor
Washington DC 20001
Phone: 202-548-4584
karimah.schoenhut@sierraclub.org

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March 22, 2019

Coastal Plain Oil and Gas Leasing Program EIS
222 West 7th Avenue, Stop #13
Anchorage, Alaska 99513 -7504
Attn: BLM Project Coordinator Nicole Hayes
blm_ak_coastalplain_EIS@blm.gov
mnhayes@blm.gov

RE: Correction to Comments on Draft Coastal Plain Oil and Gas Leasing Program EIS

SUBMITTED VIA EMAIL

Dear Project Coordinator Hayes,

On behalf of the Sierra Club, I am writing to submit a correction to the expert analysis of BLM's Draft Environmental Impact Statement (DEIS) for the Coastal Plain Oil and Gas Leasing Program, prepared by Dr. Steven Amstrup, Chief Scientist for Polar Bears International, and dated March 8, 2019. Sierra Club retained Dr. Amstrup's expert services through Polar Bears International to provide an assessment of the impact of the proposed oil and gas activities on polar bears, and an evaluation of the DEIS. During the public comment period for the DEIS, Sierra Club submitted Dr. Amstrup's March 8, 2019 report along with a comment letter emphasizing legal issues and deficiencies in the DEIS associated with the impacts to polar bears that Dr. Amstrup's analysis illuminates. Sierra Club also commented on these deficiencies, and presented Dr. Amstrup's report, in a comment letter filed jointly with numerous other organizations on March 13, 2019.

As described in the attached letter from Dr. Amstrup, his report stated an estimated range for the number of polar bears denning annually in the Coastal Plain as 20 to 29 bears. As Dr. Amstrup explains in the attached letter, the range should have been stated as 19 to 29 bears instead. Dr. Amstrup's attached letter explains that this correction does not change the other calculations or conclusions presented in his report. His letter reiterates that other than the specific text edits described in the letter, he makes no other changes to the text or statements in his March 8, 2019 analysis.

Accordingly, where Sierra Club's joint and separate comment letters to BLM, in reliance on Dr. Amstrup's report, stated the range for the number of polar bears denning annually in the Coastal Plain as 20 to 29 bears, we amend our comments to reflect his correction of that range to 19 to 29 bears. No other statement in our comments is altered by this amendment.

If you have any questions about this submission, please contact me at the phone number or e-mail address below.

Sincerely,

A handwritten signature in purple ink, appearing to be 'KS' or 'K.S.', enclosed in a thin black rectangular border.

Karimah Schoenhut
Staff Attorney
Sierra Club
Environmental Law Program
50 F St NW, Eighth Floor
Washington, DC 20001
202-548-4584
karimah.schoenhut@sierraclub.org



Polar Bears International
P.O. Box 3008
Bozeman, MT 59772

March 22, 2019

Bureau of Land Management
Coastal Plain Oil and Gas Leasing Program EIS
222 West 7th Avenue, Stop #13
Anchorage, Alaska 99513 -7504

Attention: Nicole Hayes, Project Coordinator

I am writing to notify you of corrections and additions that are required in my review of the DEIS for Oil and Gas development of the Arctic Refuge Coastal Plain, which was submitted to your office during the public comment period ending March 13, 2019, as an attachment to comments filed by the Sierra Club and other organizations.

First, due to a tabulation error, the 4th and 5th lines on page 11, which now read:

"...dens 15 (15%) were on the Arctic Refuge Coastal Plain, suggesting we could expect 20 dens (15% of 131 dens) each year on the Arctic Refuge Coastal Plain."

should be changed to read:

"...dens 14 (14%) were on the Arctic Refuge Coastal Plain, suggesting we could expect 19 dens (14% of 131 dens) each year on the Arctic Refuge Coastal Plain."

Second, changing "20 dens" to "19 dens" is required on the middle of page 11:

"...estimated range (19-29) of dens occurring each year on the Arctic Refuge Coastal Plain,"

Also, at the top of page 13: "With between 19 and 29 pregnant females denning on the much more..."

At the bottom of page 16: "Therefore, whether as few as 19 females enter maternal dens on the Arctic..."

And, at the bottom of page 40: "....between 19 and 29 bears are currently denning on the Arctic Refuge Coastal Plain"

Note that replacing 20 with 19 does not affect other numbers in the review or conclusions derived from those numbers.

Third, several places in the text of my report I mistyped the citation for the paper by Bromaghin and others as "*Bromaghin et al. 2016*". The correct

citation is "*Bromaghin et al. 2015*". This paper is correctly referenced in the Literature Cited section.

Finally, I noticed that 4 papers cited in the body text of my review were not included in the Literature Cited section. These 4 papers are:

Atwood TC, Peacock E, McKinney MA, Lillie K, Wilson R, Douglas DC, et al.
(2016) Rapid Environmental Change Drives Increased Land Use by an Arctic Marine Predator. PLoS ONE 11(6):e0155932.
doi:10.1371/journal.pone.0155932.

Regehr, E.V., **Amstrup, S.C.**, and Stirling, Ian, 2006, Polar bear population status in the southern Beaufort Sea: U.S. Geological Survey Open-File Report 2006-1337, 20 p.

Regehr, E. V., Hunter, C. M., Caswell, H., **Amstrup, S. C.**, Stirling, I. Survival and breeding of polar bears in the southern Beaufort Sea in relation to sea ice. J. Anim. Ecol. 79, 117-127 (2010)

Rode, K. D., **Amstrup, S. C.**, Regehr, E.V. Reduced body size and cub recruitment in polar bears associated with sea ice decline. Ecol. Appl. 20, 768-782 (2010).

I apologize for these errors and omissions and thank you in advance for adding this letter of correction to my review file. I reiterate that other than the specific text edits described above, I am making no changes to any other statement or portion of the text of the report.

Sincerely,



Steven C. Amstrup, PhD
Chief Scientist
Polar Bears International



From: Amy Lewis
Sent: Friday, March 29, 2019 3:11 PM
To: Sean Cottle
Cc: Chad Ricklefs
Subject: FW: [EXTERNAL] Correction to Comments on Draft Coastal Plain Oil and Gas Leasing Program EIS
Attachments: Regehr_et_al-2010-Journal_of_Animal_Ecology.pdf; Regehr_2006_ofr20061337.pdf; Rode_etal_2010_reduced body size and cub recruitment in polar bears associated with sea ice decline.pdf; Atwood 2016.PDF
Follow Up Flag: Follow up
Flag Status: Completed

Amy Lewis
EMPSi Environmental Management and Planning Solutions, Inc.
121 SW Salmon St., Suite 1100
Portland, OR 97204
tel: 503-308-4667
www.EMPSi.com Twitter: EMPSiInc Facebook: EMPSi

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From: Hayes, Miriam (Nicole) <mnhayes@blm.gov>
Sent: Friday, March 29, 2019 3:06 PM
To: Chad Ricklefs <chad.ricklefs@emp.si.com>; Amy Lewis <amy.lewis@emp.si.com>; coastalplainAR <coastalplainAR@emp.si.com>; Craig Perham <craig.perham@boem.gov>
Subject: Fwd: [EXTERNAL] Correction to Comments on Draft Coastal Plain Oil and Gas Leasing Program EIS

Nicole Hayes
Project Coordinator
Bureau of Land Management
222 W. 7th Avenue #13
Anchorage, Alaska 99513
Desk: (907) 271-4354
Cell: (907) 290-0179

----- Forwarded message -----

From: Karimah Schoenhut <karimah.schoenhut@sierraclub.org>
Date: Fri, Mar 29, 2019 at 11:52 AM
Subject: Re: [EXTERNAL] Correction to Comments on Draft Coastal Plain Oil and Gas Leasing Program EIS

To: Hayes, Miriam (Nicole) <mnhayes@blm.gov>

Cc: BLM_AK CoastalPlain_EIS <blm_ak_coastalplain_EIS@blm.gov>, Bridget Psarianos <bpsarianos@trustees.org>

Dear Ms. Hayes,

Please find attached four additional scientific papers that should have accompanied the report submitted by Dr. Steven Amstrup, which Sierra Club attached to our comments on the Coastal Plain DEIS.

I apologize for any inconvenience.

With thanks,

Karimah Schoenhut

On Fri, Mar 22, 2019 at 2:14 PM Hayes, Miriam (Nicole) <mnhayes@blm.gov> wrote:

Received - thank you!

Nicole

Nicole Hayes

Project Coordinator

Bureau of Land Management

222 W. 7th Avenue #13

Anchorage, Alaska 99513

Desk: (907) 271-4354

Cell: (907) 290-0179

On Fri, Mar 22, 2019 at 10:10 AM Karimah Schoenhut <karimah.schoenhut@sierraclub.org> wrote:

Dear Project Coordinator Hayes,

Please find attached an errata letter pertaining to the March 8, 2019 report by Dr. Steven Amstrup that Sierra Club submitted to BLM during the public comment period for the draft Coastal Plain Oil and Gas Leasing Program EIS. Sierra Club is submitting the attached letter, and associated letter from Dr. Amstrup, to correct errata in the March 8, 2019 report, and accordingly correct Sierra Club's comments on the DEIS citing to the report.

Sincerely,

Karimah Schoenhut

--



Karimah Schoenhut

Staff Attorney

Sierra Club Environmental Law Program

50 F Street NW, 8th Floor

Washington DC 20001

Phone: 202-548-4584

karimah.schoenhut@sierraclub.org

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Karimah Schoenhut

Staff Attorney
Sierra Club Environmental Law Program
50 F Street NW, 8th Floor
Washington DC 20001
Phone: 202-548-4584
karimah.schoenhut@sierraclub.org

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Survival and breeding of polar bears in the southern Beaufort Sea in relation to sea ice

Eric V. Regehr^{1*}, Christine M. Hunter², Hal Caswell³, Steven C. Amstrup⁴ and Ian Stirling⁵

¹US Geological Survey, Alaska Science Center, 4210 University Dr., Anchorage, AK 99508, USA; ²Institute of Arctic Biology, University of Alaska Fairbanks, PO Box 757000, Fairbanks, AK 99775, USA; ³Biology Department, MS-34, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA; ⁴US Geological Survey, Alaska Science Center, 4210 University Dr., Anchorage, AK 99508, USA; and ⁵Canadian Wildlife Service, 5320 122 St. NW, Edmonton, AB, Canada T6H 3S5

Summary

1. Observed and predicted declines in Arctic sea ice have raised concerns about marine mammals. In May 2008, the US Fish and Wildlife Service listed polar bears (*Ursus maritimus*) – one of the most ice-dependent marine mammals – as threatened under the US Endangered Species Act.

2. We evaluated the effects of sea ice conditions on vital rates (survival and breeding probabilities) for polar bears in the southern Beaufort Sea. Although sea ice declines in this and other regions of the polar basin have been among the greatest in the Arctic, to date population-level effects of sea ice loss on polar bears have only been identified in western Hudson Bay, near the southern limit of the species' range.

3. We estimated vital rates using multistate capture–recapture models that classified individuals by sex, age and reproductive category. We used multimodel inference to evaluate a range of statistical models, all of which were structurally based on the polar bear life cycle. We estimated parameters by model averaging, and developed a parametric bootstrap procedure to quantify parameter uncertainty.

4. In the most supported models, polar bear survival declined with an increasing number of days per year that waters over the continental shelf were ice free. In 2001–2003, the ice-free period was relatively short (mean 101 days) and adult female survival was high (0.96–0.99, depending on reproductive state). In 2004 and 2005, the ice-free period was longer (mean 135 days) and adult female survival was low (0.73–0.79, depending on reproductive state). Breeding rates and cub litter survival also declined with increasing duration of the ice-free period. Confidence intervals on vital rate estimates were wide.

5. The effects of sea ice loss on polar bears in the southern Beaufort Sea may apply to polar bear populations in other portions of the polar basin that have similar sea ice dynamics and have experienced similar, or more severe, sea ice declines. Our findings therefore are relevant to the extinction risk facing approximately one-third of the world's polar bears.

Key-words: climate change, habitat loss, life-cycle graph, stage-specific vital rates

Introduction

Changes in habitat due to climatic warming have been associated with changes in distribution, phenology and demography for a wide range of species (Walther *et al.* 2002; Parmesan & Yohe 2003). Some of the most pronounced habitat changes are expected to occur at high latitudes (Arctic Climate Impact Assessment 2005), where both observed and forecasted warming are the greatest (Serreze & Francis 2006). In Arctic marine regions, a major effect of warming has been

a decline of 8–9.5% per decade in minimum (i.e. summer) sea ice extent since 1979. Loss of sea ice has been associated with a major ecosystem shift (Grebmeier *et al.* 2006) and has raised concerns about species with obligate relationships to sea ice (Tynan & Demaster 1997; Hunt *et al.* 2002; Gaston, Woo & Hipfner 2003; Moore & Huntington 2008).

Polar bears (*Ursus maritimus*; Kurtén 1964) are among the most ice-dependent Arctic marine mammals (Amstrup 2003; Laidre *et al.* 2008). They require sea ice as a substrate for long-distance movements, mating, some maternal denning, and for access to their primary prey, ringed seals (*Phoca hispida*) and bearded seals (*Erignathus barbatus*). In western

*Correspondence author. E-mail: eric_regehr@fws.gov

Hudson Bay, Canada, where the sea ice melts completely each year and forces polar bears to spend several months on shore, earlier sea ice breakup has been associated with declines in body condition, reproduction, survival of all age classes except prime-adults and population size (Stirling, Lunn & Iacozza 1999; Regehr *et al.* 2007b). In the southern Beaufort Sea, declines in sea ice extent have been associated with changes in habitat use (Fischbach, Amstrup & Douglas 2007; Durner *et al.* 2009) and indicators of nutritional stress (Regehr, Amstrup & Stirling 2006; Cherry *et al.* 2008; Rode, Amstrup & Regehr 2009). Until now, sea ice loss in the southern Beaufort Sea and other regions of the polar basin has not been linked directly to polar bear population dynamics.

Polar bears in the southern Beaufort Sea strongly prefer sea ice situated over shallow waters of the continental shelf (Durner *et al.* 2009), where biological productivity (Pomeroy 1997; Wang, Cota & Comiso 2005) and seal densities are high (Stirling, Kingsley & Calvert 1982). As sea ice melts each summer, most polar bears in this region remain on the pack ice as it retreats from the coast towards the centre of the polar basin, although at least 4–8% of the population has remained on land in recent years (Schliebe *et al.* 2008). Polar bears on land are largely food deprived, although some may take advantage of beach-cast marine mammals or the carcasses of subsistence-harvested bowhead whales (Bentzen *et al.* 2007). Whether polar bears are on sea ice beyond the continental shelf or on land, they cannot hunt in their preferred habitat. Longer ice-free periods over the continental shelf could thus lead to reduced foraging success, nutritional stress, reproductive failure and starvation.

We used multistate models (e.g. Nichols *et al.* 1992; Fujiwara & Caswell 2002) to estimate stage-specific vital rates, and the relationships between vital rates and sea ice, from capture–recapture data collected on polar bears in the southern Beaufort Sea from 2001 to 2006. The parameters and relationships from this study were used in analyses published elsewhere to evaluate the demography of southern Beaufort

Sea polar bears, and to project future population growth in relation to forecasted sea ice conditions (Hunter *et al.* 2007).

Materials and methods

STUDY AREA AND CAPTURE DATA

The data consisted of 818 captures of 627 individual polar bears in the southern Beaufort Sea population (Fig. 1; Aars, Lunn & Derocher 2006). Details of the study area, field methods and capture sample are provided in Appendix S1.

SEA ICE

The dependence of polar bears on sea ice, particularly for access to seals, suggests their survival and breeding probabilities are linked to sea ice conditions. The southern Beaufort Sea is typically ice covered from October to June and partially or completely ice free from July to September. In recent years, the distance of sea ice retreat from the coast in summer has increased (Comiso 2006a, b; Richter-Menge *et al.* 2006). We developed an environmental covariate, which we denote as $ice(t)$, for use in multistate analyses to evaluate the relationships between polar bear vital rates and sea ice.

We defined $ice(t)$ as the number of days during the calendar year t on which the ice cover in waters over the continental shelf was less than a threshold value. Continental shelf waters were defined as waters within the study area < 300 m deep. We quantified sea ice cover in only this relatively near-shore area because of the strong preference of polar bears (Durner *et al.* 2004, 2009) and ringed seals (Stirling *et al.* 1982) for shallow waters. Ice concentration was derived from passive microwave satellite imagery from the National Snow and Ice Data Center, Boulder, CO, USA (<ftp://sidacs.colorado.edu/pub/>). A day was considered to be below the threshold (we call such days 'ice free') if the mean ice concentration of the 139 imagery grid cells (25 × 25 km) over the continental shelf was < 50%, based on previous studies suggesting that polar bears abandon the sea ice below this concentration (Stirling *et al.* 1999; Durner *et al.* 2006).

The number of ice-free days per year in waters over the continental shelf increased during the study: $ice(t) = \{90, 94, 119, 135, 134\}$, for $t = 2001, \dots, 2005$. For analyses, we standardized the values of $ice(t)$

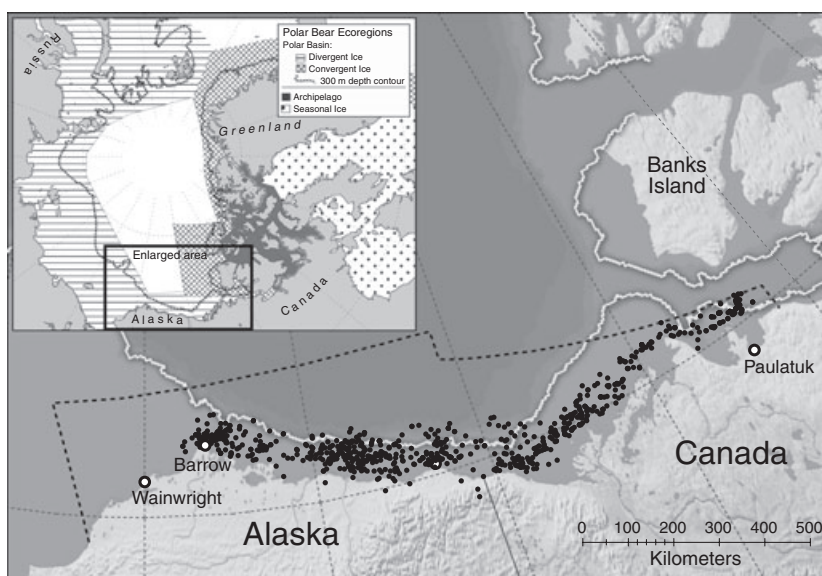


Fig. 1. Locations of polar bears captured in the southern Beaufort Sea, from 2001–2006 (black dots). The dashed line is the population boundary, established by the International Union for the Conservation of Nature and Natural Resources (IUCN) Polar Bear Specialist Group. The white line is the 300 m bathymetry contour. Inset shows the four circumpolar 'ecoregions' for polar bears per Amstrup *et al.* (2008).

by subtracting the mean and dividing by the standard deviation. Longer-term trends in $ice(t)$ and a comparison of this covariate with a more detailed habitat metric are provided in Appendix S2.

MODEL STRUCTURE

Polar bear life-cycle graph

We used multistate capture–recapture models to account for differences in survival, breeding and recapture probabilities between sex, age and reproductive states. These states, hereafter referred to as stages, are defined by the life-cycle graph for polar bears in the southern Beaufort Sea (Fig. 2). Female polar bears in this region are generally first available to mate in April–June of their fifth year (Stirling, Pearson & Bunnell 1976; Lentfer & Hensel 1980). Pregnant females enter dens in autumn, give birth in December–January, and nurse their cubs until they are large enough to leave the den in March–April. Young remain with their mothers for *c.* 2.3 years and are weaned in the spring of their third year (Amstrup 2003).

We modelled the polar bear life cycle with six female and four male stages (Fig. 2). Stages 1, 2 and 3 are subadult females age 2, 3 and 4 years respectively. We included three adult female stages: females available to breed (solitary or accompanied by 2-year-olds; stage 4), females accompanied by cubs (stage 5) and females accompanied by yearlings (stage 6). This structure considered mothers and dependent young (cubs or yearlings) as units rather than individuals, to account for the dependent fates of family groups. Young polar bears were not explicitly included in the life-cycle graph, or the multistate model, until capable of independent survival as 2-year-olds. Stages 7, 8 and 9 were subadult males age 2, 3 and 4 years respectively. Stage 10 included males ≥ 5 years of age.

Transitions among stages, represented by arcs in the life-cycle graph, depend on three types of parameters: survival, cub litter survival and breeding probabilities. Apparent survival (hereafter referred to as survival), $\sigma_i(t)$, is the probability that an individual in stage i ($i = 1, 2, \dots, 10$) in the spring of year t survives to the spring of year $t + 1$ and remains in the study area. Losses include natural mortality, harvest and permanent emigration. The probability that at

least one member of a litter of cubs survives from the spring of year t to the spring of year $t + 1$ is $\sigma_{L0}(t)$.

Breeding probability, $\beta_i(t)$ (for $i = 4, 5$), is the probability that a female in stage i produces a litter of cubs in year t , conditional on survival. Because sampling occurred in the spring, $\beta_i(t)$ represents the probability that a female gives birth and that at least one member of the litter survives until den emergence. The breeding probability for a female that already has cubs, $\beta_5(t)$, is conditional on both loss of the litter and survival of the mother. Thus, $\beta_5(t)$ implicitly accounts for the probability that a female with cubs loses her litter early enough in the spring to end lactational anestrus and breed before the end of the mating season. The transition from stages 6 to 5 is biologically possible but did not occur in the data, most likely because yearling survival was high (Amstrup & Durner 1995) and this transition is conditional on the loss of a yearling litter. Thus, the transition from stages 6 to 4 occurs with probability 1 if the female survives, because females with yearlings were available to breed the following year whether their yearlings died or were successfully weaned.

The life-cycle graph defines the structure of the multistate model. Within that structure, many statistical models can be specified by constraining various survival, breeding and recapture probabilities to be equal, or by allowing parameters to vary as functions of time or external covariates. We created a candidate set of multistate models based on biology and study design, and used model selection and model averaging to obtain parameter estimates.

Recapture models

Each stage has a recapture probability, $p_i(t)$, the probability that an animal in stage i is recaptured at time t given that it is alive. We considered three constraint models for recapture probability, based on study design and a previous analysis of the southern Beaufort Sea data (Regehr *et al.* 2006). The first model constrained recapture probabilities to be equal for all stages. The second model included separate recapture probabilities for females (stages 1–6) and males (stages 7–10). This allowed for the possibility that long movements of male polar bears in search of mates (Ramsay & Stirling 1986) might increase our probability of encountering their tracks in the snow. The third model included separate recapture probabilities for adult females with cubs (stage 5), all other females (stages 1–4 and 6) and all males (stages 7–10). This allowed for a different encounter rate for females with cubs, which could occur if family groups avoided areas of active sea ice preferred by other polar bears (Stirling, Andriashek & Calvert 1993).

We considered both time-invariant models and models with additive time variation in recapture probability. Additionally, all recapture models included an individual covariate and a group covariate. The time-varying, individual covariate *radio* indicated whether a polar bear wore a functional radiocollar at each sampling occasion. Because most radiocollared polar bears were located by telemetry, we expected recapture probabilities for these individuals to be high. The group covariate *agency* indicated whether a polar bear was first captured in the USA or Canada. Polar bears in the southern Beaufort Sea exhibit geographic fidelity (Amstrup, McDonald & Durner 2004). Thus, regional differences in weather, polar bear distribution and other variables could lead to different recapture probabilities for bears with fidelity to the USA and Canadian portions of the study area. Finally, all models included a separate recapture probability for Canadian agency bears in 2006, irrespective of time dependence in other recapture probabilities, because of apparently lower densities of polar bears in the Canadian region in 2006.

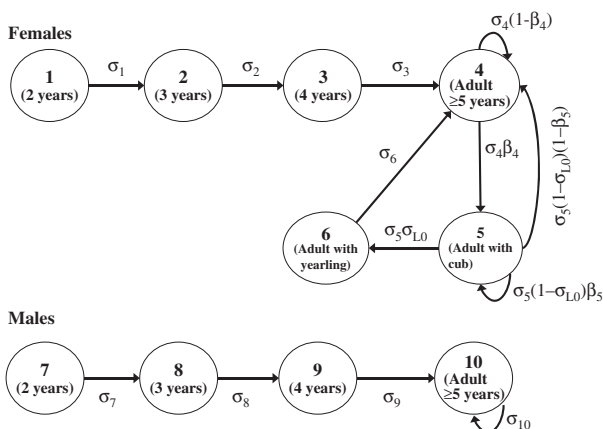


Fig. 2. Ten-stage life-cycle graph for polar bears in the southern Beaufort Sea. Stages 1–6 are females and stages 7–10 are males. $\sigma_i(t)$ is the probability of an individual in stage i surviving from the spring of year t to the spring of year $t + 1$; $\sigma_{L0}(t)$ is the probability of at least one member of a cub litter surviving to the following spring; $\beta_i(t)$ is the probability of an individual in stage i breeding, thus producing a litter of cubs, conditional on survival.

Survival and breeding models

We defined three constraint models for female survival and three constraint models for male survival, for a total of nine combinations of survival constraint models (Table 1). The simplest female model, F1, constrained survival to be equal for all females (stages 1–6). Model F2 assumed equal survival among subadult females (stages 1–3) and equal survival among adult females (stages 4–6). Model F3 assumed equal survival among subadult females and allowed survival of females with cubs (stage 5) to differ from other adult females (stages 4 and 6). This allowed for potential effects of the physiological stress of cub production and fasting experienced by reproducing females (Ramsay & Stirling 1986).

Model M1 constrained subadult male (stages 7–9) survival to be equal to subadult female survival, and adult male (stage 10) survival to be equal to adult female survival. Model M2 assumed equal survival for all males (stages 7–10), but allowed male and female survival to differ. Model M3 assumed equal survival among subadult males and a separate survival for adult males, with no equality constraints between males and females. Models M1 and M3 permitted different survival for adults than subadults. Models M2 and M3 allowed female and male survival to differ due to potential effects of sex-selective harvest (Brower *et al.* 2002), stresses associated with the competition for mates among males (Ramsay & Stirling 1986; Cherry *et al.* 2008) and the physiological stress of reproduction for females.

No equality constraints were imposed on the breeding probabilities β_4 and β_5 . We evaluated four types of time dependence in survival and breeding probabilities:

- 1 Time-invariant models, denoted by (.), where each parameter of a given type was equal for all sampling occasions (for p) or intervals (for σ and β).
- 2 Additive time variation (+ t), which allowed the value of one parameter of a given type (e.g. survival of adult

males) to vary freely from year to year and constrained other parameters of the same type (e.g. survival of subadult males) to vary in parallel on the logit scale.

- 3 Additive covariate time variation (+ ice), which allowed one parameter of a given type to vary as a logistic function of the environmental covariate $ice(t)$ and constrained other parameters of the same type to vary in parallel on the logit scale.
- 4 Covariate time variation (ice), which allowed each parameter of a given type to vary as independent logistic functions of the environmental covariate $ice(t)$.

To limit the size of the candidate model set (Burnham & Anderson 2002), we considered only models that imposed the same type of time dependence on all parameters of a given type (p , σ or β). For example, we did not consider a model with time-invariant female survival and time-varying male survival. This acknowledged that previous analyses did not support differences in time dependence among sex and age classes (Regehr *et al.* 2006).

We treated cub litter survival (σ_{L0}) in two ways: (i) as an independent parameter, in which case σ_{L0} could be time-invariant (.), a function of time (t), or a function of the environmental covariate (ice), irrespective of the type of time dependence in the stage-dependent survival parameters (σ_i); and (ii) as a survival parameter, in which case σ_{L0} assumed the same type of time dependence as stage-dependent survival. Thus, if time dependence in σ_i was (+ t) or (+ ice), σ_{L0} was additive to the σ_i and was denoted (+ σ).

We used model notation similar to previous capture–recapture analyses (e.g. Lebreton *et al.* 1992). For each parameter type, subscripts denote stages or stage constraint models, and parentheses denote time dependence. For example, the model $\sigma_{F1,M2}(+t) \sigma_{L0}(+\sigma) \beta_{4,5}(ice)$ has additive time variation in σ for the two aggregate stages of the survival constraint models F1,M2; cub litter

Table 1. (a) Constraint models for female (F1, F2, F3) and male (M1, M2, M3) stage-dependent survival probabilities (σ_i for $i = 1, \dots, 10$) implemented in multistate modelling. (b) Equalities among survival probabilities for combinations of female and male constraint models

Constraint model	Survival equalities	
(a)		
F1	$\sigma_1 = \sigma_2 = \sigma_3 = \sigma_4 = \sigma_5 = \sigma_6$	
F2	$\sigma_1 = \sigma_2 = \sigma_3, \sigma_4 = \sigma_5 = \sigma_6$	
F3	$\sigma_1 = \sigma_2 = \sigma_3, \sigma_4 = \sigma_6, \sigma_5$	
M1	$\sigma_1 = \sigma_2 = \sigma_3 = \sigma_7 = \sigma_8 = \sigma_9, \sigma_4 = \sigma_{10}$	
M2	$\sigma_7 = \sigma_8 = \sigma_9 = \sigma_{10}$	
M3	$\sigma_7 = \sigma_8 = \sigma_9, \sigma_{10}$	
Constraint model	Survival equalities	k
(b)		
F1,M1	$\sigma_1 = \sigma_2 = \sigma_3 = \sigma_4 = \sigma_5 = \sigma_6 = \sigma_7 = \sigma_8 = \sigma_9 = \sigma_{10}$	1
F1,M2	$\sigma_1 = \sigma_2 = \sigma_3 = \sigma_4 = \sigma_5 = \sigma_6, \sigma_7 = \sigma_8 = \sigma_9 = \sigma_{10}$	2
F1,M3	$\sigma_1 = \sigma_2 = \sigma_3 = \sigma_4 = \sigma_5 = \sigma_6, \sigma_7 = \sigma_8 = \sigma_9, \sigma_{10}$	3
F2,M1	$\sigma_1 = \sigma_2 = \sigma_3 = \sigma_7 = \sigma_8 = \sigma_9, \sigma_4 = \sigma_5 = \sigma_6 = \sigma_{10}$	2
F2,M2	$\sigma_1 = \sigma_2 = \sigma_3, \sigma_4 = \sigma_5 = \sigma_6, \sigma_7 = \sigma_8 = \sigma_9 = \sigma_{10}$	3
F2,M3	$\sigma_1 = \sigma_2 = \sigma_3, \sigma_4 = \sigma_5 = \sigma_6, \sigma_7 = \sigma_8 = \sigma_9, \sigma_{10}$	4
F3,M1	$\sigma_1 = \sigma_2 = \sigma_3 = \sigma_7 = \sigma_8 = \sigma_9, \sigma_5, \sigma_4 = \sigma_6 = \sigma_{10}$	3
F3,M2	$\sigma_1 = \sigma_2 = \sigma_3, \sigma_4 = \sigma_6, \sigma_5, \sigma_7 = \sigma_8 = \sigma_9 = \sigma_{10}$	4
F3,M3	$\sigma_1 = \sigma_2 = \sigma_3, \sigma_4 = \sigma_6, \sigma_5, \sigma_7 = \sigma_8 = \sigma_9, \sigma_{10}$	5

k is the number of parameters. Stages are subadult females (1–3), solitary adult females or adult females with 2-year-olds (4), adult females with a cub litter (5), adult females with a yearling litter (6), subadult males (7–9) and adult males (10).

survival (σ_{L0}) varies additively with stage-dependent survival; and breeding probabilities (β_i) vary independently as functions of the covariate $ice(t)$. Data limitations precluded a fully time- and stage-dependent model. Thus, our most general model was $\sigma_{F3,M3}(+t)$ $\sigma_{L0}(t) \beta_{4,5}(+t)$.

MODEL SELECTION AND MODEL AVERAGING

Before model selection, we analysed the goodness-of-fit of the data to multistate models (Appendix S3). We then used Akaike's information criterion (AIC) to evaluate support for the various statistical models and to calculate model-averaged parameter estimates (Burnham & Anderson 2002). To explore the large potential model space created by multiple equality constraints and types of time dependence, we used a three-step model-selection procedure (Appendix S3). First, we selected the most supported constraint model and type of time dependence for p . Second, we fixed the model for p and selected the most supported type of time dependence for β . Finally, we fixed models for p and β , and jointly evaluated all combinations of constraints and time dependence for σ_i and σ_{L0} .

We derived model-averaged parameter estimates based on AIC weights (Burnham & Anderson 2002, Section 4.2) from two sets of time-varying models. First, the overall best model set containing all models with $\Delta AIC < 4$ (i.e. AIC_i for model i minus the minimum AIC value for the model set). Second, the best non-covariate model set containing models with $\Delta AIC < 4$ that did not include the covariate $ice(t)$. The non-covariate model set provided an evaluation of temporal variation in vital rates that was not influenced by the use of the logistic function to link $ice(t)$ to the life-cycle parameters. We also derived model-averaged results for the best time-invariant models (nine total), which provide the best single estimates of each parameter.

PARAMETER ESTIMATION

We estimated parameters by constructing the likelihood function from individual capture histories (Caswell & Fujiwara 2004) and maximizing the log of the likelihood with respect to the parameters (Appendix S4). We fit models using customized programmes in MATLAB (MathWorks Inc., Natick, MA, USA) with the Tomlab Knitro optimization routine (Forth & Edvall 2006). Before fitting models, we checked parameter estimability by computing the rank of the Jacobian matrix for each candidate model (Hunter & Caswell 2009). All models were full rank, implying that all parameters could be estimated (Appendix S4).

Bootstrap confidence intervals

We developed a parametric bootstrap procedure to evaluate uncertainty in model-averaged parameter estimates (Appendix S5). The procedure generated bootstrap sampling distributions for each parameter, which included sampling uncertainty (as reflected in the covariance matrix for each model), model uncertainty (as reflected in differences in parameter estimates among models) and the relative support for different models (as reflected in the AIC weights). The 90% confidence limits on each parameter were obtained as the 5th and 95th percentiles of the bootstrap sample (Efron & Tibshirani 1993). We used 90% rather than 95% confidence limits because some bootstrap sampling distributions were left-skewed and bimodal, which made more extreme confidence limits unreliable as a description of uncertainty. Standard errors were obtained as the standard deviations of the bootstrap sample for each parameter.

Temporary emigration

Each year, some members of the southern Beaufort Sea population were outside of the relatively near-shore area accessible by helicopter, and therefore temporarily unavailable for capture (Amstrup *et al.* 2004). If such temporary emigration is not random it can bias survival estimates (Kendall, Nichols & Hines 1997; Schaub *et al.* 2004). We used radiotelemetry data collected from 1985 to 2006 in the US portion of the study area to investigate whether, in general, movements with respect to the sampling area were random, or Markovian, in which case the probability of being outside the sampling area depended on an individual's location on the previous occasion. Radiotelemetry data collected during the period of this study alone were too few for a similar investigation. Whether Markovian or random, disproportionate movement outside the sampling area in the last years of a short study could affect parameter estimates. We tested for such a change in movements by comparing the proportion of radio-collared bears that were within the sampling area during capture efforts each year from 2001 to 2006.

Results

VITAL RATES IN RELATION TO SEA ICE

The overall best model set included models in which survival and, in some cases, cub litter survival varied as functions of the sea ice covariate $ice(t)$. This model set contained 29 models with $\Delta AIC < 4$ (Table 2). The weight of evidence in support of a specific model, based on AIC weights, was relatively evenly spread among these models, emphasizing the importance of model averaging to estimate parameters.

Survival

Model-averaged survival estimates from the overall best model set were high for all stages in 2001–2003 and markedly lower in 2004 and 2005 (Fig. 3; Appendix S6). For example, estimated survival of adult females available to breed (stage 4) declined from 0.99 to 0.79 between 2001 and 2005. The decline was less pronounced for adult males than for other stages. Bootstrap confidence intervals showed a large amount of overlap among years. However, the wide confidence intervals in 2001–2003 were the result of left-skewed probability distributions, and most of the probability was centred on the maximum likelihood estimate (note the narrow boxes and long tails in Fig. 3).

There was clear support for the hypothesis that survival is a function of sea ice conditions. Twenty-five of the top 29 models included the covariate $ice(t)$, supporting a link between geophysical aspects of climatic variation and polar bear biology. The sum of the AIC weights was 0.62 for models with additive covariate time variation ($+ice$), and 0.90 for models with additive or independent covariate time variation ($+ice$ or ice ; Table 2). Within the observed range in the number of ice-free days over the continental shelf, survival varied little up to about 127 ice-free days (Fig. 4). Beyond that threshold, survival declined as the number of ice-free days increased. This pattern was evident for all stages, with only a slight shifting of the threshold value among stages.

Table 2. Overall best model set (i.e. all models with $\Delta\text{AIC} < 4$) for multistate modelling

Survival model	Litter survival model	np	AIC	AAIC	w
$\sigma_{F1,M3}(+ice)$	$\sigma_{L0}(\cdot)$	16	1187.8	0.0	0.12
$\sigma_{F1,M2}(+ice)$	$\sigma_{L0}(\cdot)$	15	1189.4	1.6	0.05
$\sigma_{F2,M1}(+ice)$	$\sigma_{L0}(\cdot)$	15	1189.4	1.6	0.05
$\sigma_{F2,M3}(+ice)$	$\sigma_{L0}(\cdot)$	17	1189.5	1.6	0.05
$\sigma_{F1,M3}(ice)$	$\sigma_{L0}(\cdot)$	18	1189.6	1.8	0.05
$\sigma_{F2,M1}(+ice)$	$\sigma_{L0}(+\sigma)$	15	1189.7	1.9	0.05
$\sigma_{F1,M2}(ice)$	$\sigma_{L0}(\cdot)$	16	1189.7	1.9	0.05
$\sigma_{F3,M1}(+ice)$	$\sigma_{L0}(\cdot)$	16	1189.8	2.0	0.04
$\sigma_{F2,M1}(+ice)$	$\sigma_{L0}(ice)$	16	1190.2	2.4	0.04
$\sigma_{F1,M3}(ice)$	$\sigma_{L0}(ice)$	19	1190.4	2.5	0.03
$\sigma_{F1,M1}(+ice)$	$\sigma_{L0}(+\sigma)$	14	1190.4	2.6	0.03
$\sigma_{F1,M3}(+ice)$	$\sigma_{L0}(+\sigma)$	16	1190.5	2.7	0.03
$\sigma_{F1,M2}(ice)$	$\sigma_{L0}(ice)$	17	1190.5	2.7	0.03
$\sigma_{F2,M1}(+ice)$	$\sigma_{L0}(+t)$	19	1190.6	2.8	0.03
$\sigma_{F1,M2}(+t)$	$\sigma_{L0}(+\sigma)$	18	1190.7	2.8	0.03
$\sigma_{F1,M3}(ice)$	$\sigma_{L0}(+t)$	22	1190.8	2.9	0.03
$\sigma_{F1,M1}(ice)$	$\sigma_{L0}(\cdot)$	14	1190.8	2.9	0.03
$\sigma_{F2,M1}(+t)$	$\sigma_{L0}(+\sigma)$	18	1190.8	2.9	0.03
$\sigma_{F1,M2}(ice)$	$\sigma_{L0}(+t)$	20	1190.9	3.1	0.03
$\sigma_{F3,M1}(+ice)$	$\sigma_{L0}(ice)$	17	1191.0	3.1	0.02
$\sigma_{F1,M1}(+t)$	$\sigma_{L0}(+\sigma)$	17	1191.0	3.1	0.02
$\sigma_{F2,M2}(+ice)$	$\sigma_{L0}(\cdot)$	16	1191.0	3.2	0.02
$\sigma_{F2,M1}(ice)$	$\sigma_{L0}(\cdot)$	16	1191.1	3.3	0.02
$\sigma_{F3,M3}(+ice)$	$\sigma_{L0}(\cdot)$	18	1191.4	3.5	0.02
$\sigma_{F3,M1}(+ice)$	$\sigma_{L0}(+t)$	20	1191.5	3.7	0.02
$\sigma_{F3,M1}(+ice)$	$\sigma_{L0}(+\sigma)$	16	1191.5	3.7	0.02
$\sigma_{F1,M1}(ice)$	$\sigma_{L0}(ice)$	15	1191.6	3.7	0.02
$\sigma_{F3,M1}(+t)$	$\sigma_{L0}(+\sigma)$	19	1191.6	3.7	0.02
$\sigma_{F2,M2}(+ice)$	$\sigma_{L0}(ice)$	17	1191.8	4.0	0.02

All models included the most supported model for capture probabilities and additive time variation for breeding probabilities. Survival (σ) constraint models are defined in Table 2. The covariate *ice* is the number of ice-free days per year in waters over the continental shelf. np, total number of estimated parameters in the model; AIC, Akaike's information criterion; ΔAIC , difference in AIC from the minimum AIC value; w, AIC weight.

Survival estimates varied slightly among stages, generally with lower values for subadults than adults. Survival estimates were similar for the three adult female reproductive stages (stages 4–6). Nearly 80% of support for the survival constraint models was shared among 4 models: F1,M3; F2,M1; F1,M2 and F3,M1 with 26%, 21%, 19% and 13% of the total support respectively.

Breeding probabilities and cub litter survival

Model-averaged estimates for breeding and cub litter survival probabilities showed a similar pattern to survival, with high values in 2001–2003 and lower values in 2004 and 2005 (Fig. 5). For example, estimated breeding probability of adult females in stage 4 (β_4) declined from 0.49 to 0.09 between 2001 and 2005.

Additive time variation was the most supported type of time dependence in breeding probabilities (Appendix S6). In step 2 of the model-selection procedure, the sum of the AIC

weights for models with $\beta_i(t)$ was 0.68. Although breeding probabilities declined in 2004 and 2005, when annual ice-free periods were long, the relationship between β_i and *ice*(*t*) was not logistic, probably because of the high values of β_i in 2003.

For cub litter survival, support for a time-invariant model (summed AIC weights = 0.50) was equivalent to the combined support for time-varying models. The sum of the AIC weights was 0.23 for models with additive time variation, 0.16 for models with covariate time variation and 0.11 for models with independent time variation (Table 2).

Recapture probabilities

Recapture probabilities for polar bears without radiocollars ranged from 0.06 to 0.24 (Appendix S6). The most supported model for *p* was time invariant and allowed *p* to differ for females (stages 1–6) and males (stages 7–10). This model included the individual covariate *radio*, the group covariate *agency* and a separate parameter for Canadian agency bears in 2006.

Temporary emigration

We did not find evidence for Markovian dependence in temporary emigration. From 1985 to 2006, the mean proportion of radiocollared polar bears outside the sampling area during the spring capture period was 0.40 (SE = 0.05). The probability of being located outside the sampling area at *t* + 1 was 0.11 (SE = 0.04) for polar bears inside the sampling area at *t*, and 0.18 (SE = 0.05) for polar bears outside the sampling area at *t*. The null hypothesis that being in or out of the sampling area at *t* did not affect the probability of being in or out at *t* + 1 could not be rejected (*P* = 0.30).

Ten of 19 (53%) and 9 of 14 (64%) radiocollared polar bears were within the sampling area during spring capture operations in 2005 and 2006 respectively. The mean proportion of radiocollared polar bears within the sampling area in 2005 and 2006 (0.59, *n* = 33) was lower than in 2002–2004 (0.76, *n* = 32), although this difference was not statistically significant (*P* = 0.14).

NON-COVARIATE AND TIME-INVARIANT MODELS

Model-averaged parameter estimates from the non-covariate model set were similar to estimates from the overall best model set. Importantly, they exhibited a similar transition from high to low survival and breeding probabilities in years with longer ice-free periods. Survival estimates from the non-covariate model set were slightly lower than estimates from the overall best model set in 2001–2003, and slightly higher in 2004 and 2005 (Regehr *et al.* 2007a). The mean per cent difference for all stages and years was 2.9 (SD = 6.9%). In general, confidence intervals on survival estimates were narrower for the non-covariate model set in 2001–2003. Estimates and confidence intervals for breeding and cub litter survival probabilities were similar between the two models sets.

Fig. 3. Survival probabilities (σ_i for $i = 1, \dots, 10$) from the overall best model set for polar bears in the southern Beaufort Sea, 2001–2005. Boxplots show the median, lower and upper quartiles of the bootstrap sampling distribution. Whiskers are 5th and 95th percentiles. Survival probabilities are plotted for the five stages or combinations of stages with unique estimates: subadult females (1–3), adult females available to breed or with a yearling litter (4 and 6), adult females with a cub litter (5), subadult males (7–9) and adult males (10).

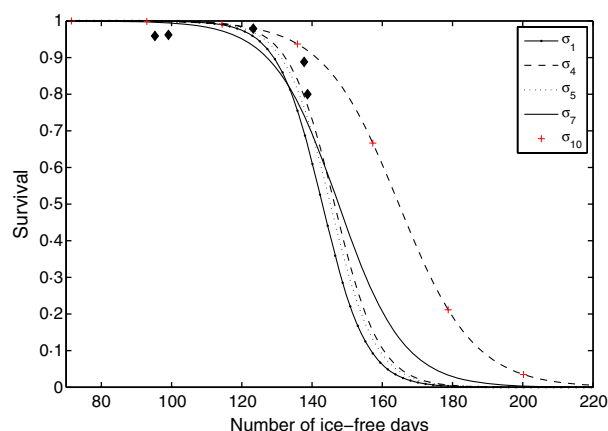
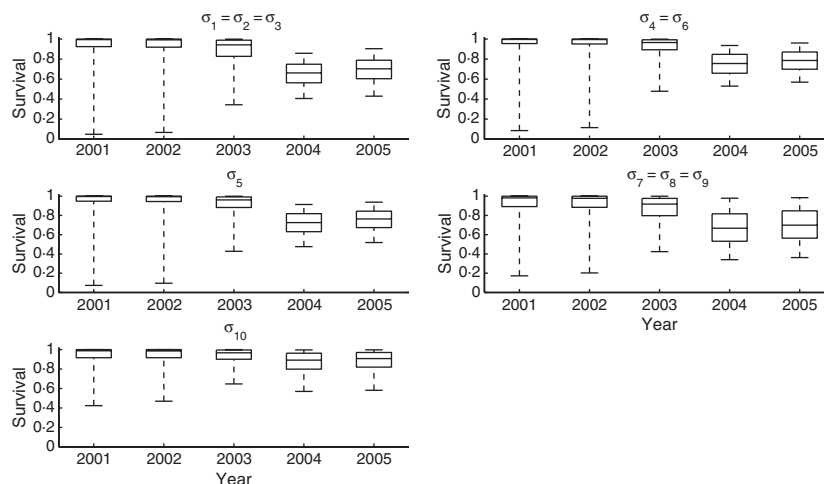


Fig. 4. Survival probability (σ_i for $i = 1, \dots, 10$) as a logistic function of the number of ice-free days per year in waters over the continental shelf from 2001 to 2005 [i.e. the covariate $ice(t)$], averaged over the overall best model set. Survival curves are plotted for the five stages or combinations of stages with unique estimates: subadult females (1–3), adult females available to breed or with a yearling litter (4 and 6), adult females with a cub litter (5), subadult males (7–9), and adult males (10). Solid diamonds are model-averaged survival estimates for adult females available to breed (σ_4) for non-covariate models, plotted for comparison with the covariate-based values from the overall best model set.

The time-invariant survival, breeding and cub litter survival probabilities were between the high values for 2001–2003 and the low values for 2004 and 2005 from the time-varying models (Table 3).

Discussion

POLAR BEARS AND SEA ICE

Declines in polar bear survival during the period 2001–2005 were associated with longer annual ice-free periods over the continental shelf. Breeding probabilities also declined, but did not exhibit the same relationship to sea ice conditions as survival. We hypothesize that declining sea ice affects polar bear vital rates primarily via increased nutritional stress. In

years with longer ice-free periods, polar bears have less time in summer and autumn to hunt over the continental shelf. Instead, they spend more time on multiyear ice over less-productive Arctic basin waters (Pomeroy 1997), or on land (Schliebe *et al.* 2008). Reduced foraging opportunities associated with longer ice-free periods, whether spent on land or over deep waters, likely cause polar bears to enter the winter in poorer nutritional condition.

Additional evidence suggests that polar bears in the southern Beaufort Sea are under increasing nutritional stress. From 1982 to 2006, body size and body condition for most sex and age classes were positively correlated with the availability of sea ice habitat, and exhibited a statistically significant decline during this period. Cub litter mass and the number of yearlings per female also declined following years with lower availability of sea ice habitat (Rode *et al.* 2009). Using serum biomarkers, Cherry *et al.* (2008) found that a higher proportion of polar bears were fasting in the springs of 2005–2006 (21.4% and 29.3%), compared to 1985–1986 (9.6% and 10.5%). The year 1985 had one of the lowest numbers of ice-free days on record, and 1986 was similar to 2001–2002, so this comparison is particularly relevant to our findings. Finally, the longer ice-free periods in 2004 and 2005 were associated with an unusual number of reports of inefficient foraging behaviours by polar bears (Stirling *et al.* 2008), observations of cannibalism (Amstrup *et al.* 2006) and observations of polar bears that had apparently starved to death (Regehr *et al.* 2006). Historically, such observations were rare or non-existent.

Polar bears depend on sea ice for movement and reproduction, as well as for hunting. In 2004, abrupt retreat of sea ice from the coast, combined with stormy weather, resulted in drownings in the southern Beaufort Sea (Monnett & Gleason 2006). Extensive open water and increased ice roughness, caused by the action of winter storms on thinner ice, may reduce foraging success (Stirling *et al.* 2008), increase the energetic costs of locomotion (Derocher, Lunn & Stirling 2004) and increase the risk of injury or death for cubs. Less stable sea ice also has apparently led to more females denning on land (Fischbach *et al.* 2007). Finally, the increasing seasonal retreat

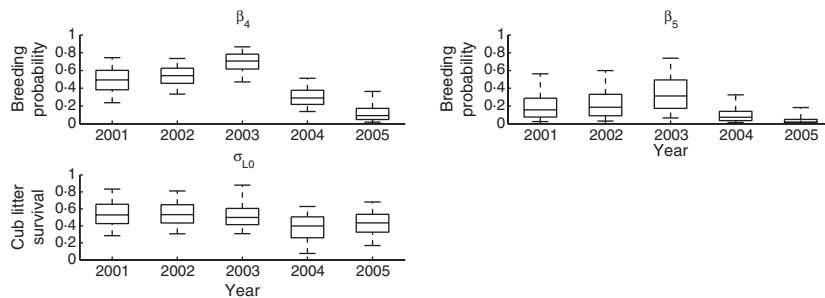


Fig. 5. Cub litter survival (σ_{L0}), breeding probability for adult females available to breed (β_4), and breeding probability for adult females with a cub litter (β_5) from the overall best model set for polar bears in the southern Beaufort Sea, 2001–2005. Boxplots show the median, lower and upper quartiles of the bootstrap sampling distribution. Whiskers are 5th and 95th percentiles.

Table 3. Time-invariant estimates and 90% confidence intervals for survival (σ_i , for $i = 1, \dots, 10$), cub litter survival (σ_{L0}), and breeding probabilities (β_i , for $i = 4, 5$) for multistate capture–recapture modelling for polar bears in the southern Beaufort Sea, 2001–2006

Parameter	Stage	Estimate	90% CI
σ	1–3	0.916	0.605–0.995
σ	4,6	0.947	0.750–0.992
σ	5	0.950	0.679–0.995
σ	7–9	0.870	0.622–0.976
σ	10	0.933	0.753–0.985
σ_{L0}	NA	0.496	0.326–0.668
β	4	0.437	0.325–0.558
β	5	0.104	0.021–0.384

Stages are subadult females (1–3), solitary adult females or adult females with two-year-olds (4), adult females with a cub litter (5), adult females with a yearling litter (6), subadult males (7–9) and adult males (10).

of sea ice may require polar bears to travel farther between multiyear pack ice, where most animals spend the summer, and the onshore denning areas or coastal hunting areas that they use at other times of the year (Bergen *et al.* 2007).

Climatic warming is likely also to have indirect ecological effects on Arctic marine mammals (Tynan & Demaster 1997; Derocher *et al.* 2004; Laidre *et al.* 2008). Polar bears are susceptible to changes in the abundance and age structure of seal populations (Stirling 2002). In particular, mortality rates of ringed seal pups, the most important component of the polar bear's diet, may increase in years when the sea ice breaks up early. Pup mortality also may increase when warmer temperatures lead to rains early in the breeding season, which can melt the under-snow lairs that pups need for shelter (Smith & Harwood 2001; Stirling & Smith 2004). In some regions, climatic warming may temporarily increase the availability of alternate prey species for polar bears, such as recent increases in harp seals on the sea ice in Davis Strait (Iverson, Stirling & Lang 2006) and walrus in coastal haul-outs in the Chukchi Sea (N. Ovsyanikov, unpublished data). As top predators, polar bears can be expected to integrate ecological changes at lower trophic levels, which have been documented in northern Hudson Bay (Gaston *et al.* 2003) and may be occurring in other parts of the Arctic. Simultaneous with ecological changes, polar bears face increasing potential for conflicts with humans in a warming Arctic, as industrial activity expands (Arctic Climate Impact Assessment 2005), longer ice-free periods force polar bears to spend more time on land

(Schliebe *et al.* 2008) and nutritional stress encourages polar bears to seek anthropogenic food sources (Regehr *et al.* 2007b).

Our time-varying survival estimates for 2001–2003 were similar to estimates for adult females in the southern Beaufort Sea from 1981 to 1992 (0.969; Amstrup & Durner 1995) and similar to, or higher than, estimates for adult females in other populations (0.940–0.997; Table 2 in Aars *et al.* 2006). Our survival estimates for 2004 and 2005 were lower than have been previously reported for polar bears. In an earlier, single-state analysis of capture–recapture data from the southern Beaufort Sea, Regehr *et al.* (2006) also found that survival may have declined from 2001 to 2005. Although Regehr *et al.* (2006) found weak support for a relationship between survival and the covariate *ice(t)*, comparison of the two analyses is complicated by different model structures and data sets. We may have been more successful in detecting sea ice effects because the multistate models included different reproductive stages for adult females and because, unlike Regehr *et al.* (2006), we evaluated models with different recapture probabilities for females and males.

Our conclusions are strengthened by the use of multimodel inference and model averaging, and by agreement between models with parametric dependence on the environmental covariate *ice(t)* and models that allowed parameters to vary freely over time. Multimodel inference is particularly important for estimating statistical relationships from short time series of data in a variable environment. By permitting recapture probabilities to vary by sex, reproductive stage, tagging method and region of capture, we accounted for sources of heterogeneity often present in capture–recapture studies. Nonetheless, some individual heterogeneity may have resulted from the movement of polar bears with respect to the sampling area. For example, polar bears with small home ranges centred in the core of the sampling area may have been more likely to be captured than those with home ranges that were either large or centred near the edge of the sampling area. Our analysis of radiotelemetry data collected from 1985 to 2006 suggests emigration patterns in the southern Beaufort Sea are random, making it unlikely that survival estimates in the current study were biased due to Markovian dependence in temporary emigration (Kendall *et al.* 1997; Kendall & Nichols 2002; Schaub *et al.* 2004). Nonetheless, sea ice loss and increased variability in annual sea ice extent have the potential to affect polar bear distribution and movements, including the possible breakdown of historic population

boundaries (Derocher *et al.* 2004). Although statistical tests for within-study changes in emigration were not significant, our ability to evaluate the type of emigration that occurred 2001–2006, and its potential effects on parameter estimates, was limited by the small sample size of radiotelemetry data. The lower-point estimate of the proportion of radiocollared polar bears inside the sampling area in 2005 and 2006, compared to 2002–2004, suggests caution in interpreting the magnitude of estimated declines in apparent survival.

IMPLICATIONS FOR CONSERVATION

The apparent dependence of polar bear vital rates on sea ice is relevant to evaluations of conservation status for this and other species. Moore & Huntington (2008) classify Arctic marine mammals into ice-obligate species (polar bear, walrus, bearded and ringed seals) and ice-associated species (beluga and bowhead whales; narwhal; harp, hooded, ribbon and spotted seals). Our results generalize most readily to ice-obligate marine mammals and to subarctic ice seals (see the analysis of sensitivity to climate change in Laidre *et al.* 2008). However, even species that depend directly on sea ice as a platform for foraging and other aspects of their life history may exhibit different responses to sea ice loss. Walrus, for example, are generally limited to foraging in waters < 100 m deep. Their demography will be most affected by the distribution of sea ice over these shallow waters, although some walrus may be buffered from the effects of sea ice loss by their ability to use terrestrial haul-outs between feeding excursions (Sheffield & Grebmeier 2009). Additional demographic studies are needed to understand the impacts of climate change on Arctic marine mammals.

We believe that the analyses reported here and in a companion manuscript (Hunter *et al.* 2007) provide a template for assessments of extinction risk for other species with similar types of data. The first step is to estimate vital rates, which determine the potential for population growth, and to evaluate the relationships between vital rates and environmental conditions. If environmental conditions are expected to change, both the environment-dependent vital rates and the forecasted range of environmental conditions can be incorporated into a demographic model to project future population status. For polar bears in the southern Beaufort Sea, Hunter *et al.* (2007) used matrix-based projection models (e.g. Caswell 2001) to combine the vital rates estimated here with sea ice forecasts. That analysis indicated that the southern Beaufort Sea population faces a high risk of extirpation within the 21st century if sea ice loss continues as projected.

Sea ice declines and the associated impacts on marine mammals are expected to vary across the Arctic (Laidre *et al.* 2008; Moore & Huntington 2008; Thiemann, Derocher & Stirling 2008). Units based on taxonomy, genetic distinction, ecology and distribution are common in evaluations of conservation status (Green 2005), and can be used to extrapolate from well-studied populations to larger portions of a species' range. Amstrup, Marcot & Douglas (2008) used regional differences in sea ice dynamics and ecology to identify four 'eco-

regions' for polar bears. The Divergent Ice Ecoregion, characterized by the formation and subsequent melting or advection of annual sea ice, includes the southern Beaufort, Chukchi, Laptev, Kara and Barents seas (Fig. 1). It is reasonable to expect that the relationships between sea ice loss and polar bears in the southern Beaufort Sea also apply to other portions of the Divergent Ice Ecoregion, where sea ice loss has been greater (Meier, Stroeve & Fetterer 2007) but data on polar bears are not available. Sea ice declines throughout the Divergent Ice Ecoregion are projected to be long term and severe (Amstrup *et al.* 2008). Because this region includes c. 7500 polar bears, one-third of the current world population (Aars *et al.* 2006), our findings in the southern Beaufort Sea were considered relevant to the extinction risk facing a large portion of the world's polar bears. This contributed to the listing, in May 2008, of polar bears as a threatened species under the US Endangered Species Act.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1. Study area, field methods and capture data.

Appendix S2. Sea ice covariate details.

Appendix S3. Goodness-of-fit and model-selection details.

Appendix S4. Multistate modelling and parameter estimation details.

Appendix S5. Bootstrap confidence interval details.

Appendix S6. Model-selection results and parameter estimates for the overall best model set.

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Polar Bear Population Status in the Southern Beaufort Sea

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U.S. Department of the Interior
U.S. Geological Survey

Polar Bear Population Status in the Southern Beaufort Sea

By Eric V. Regehr and Steven C. Amstrup, U.S. Geological Survey; and Ian Stirling, Canadian Wildlife Service

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Conversion Factors, and Abbreviations, Acronyms, and Symbols

Conversion Factors

Multiply	By	To obtain
kilometer (km)	0.6214	mile (mi)
meter (m)	3.281	foot (ft)
meter (m)	1.094	yard (yd)

Abbreviations, Acronyms, and Symbols

Abbreviations, Acronyms, and Symbols	Meaning
AIC	Akaike's information criterion
CI	confidence interval
CJS	Cormack-Jolly-Seber
COYs	cubs of the year
CWS	Canadian Wildlife Service
GOF	goodness-of-fit
PRB	percent relative bias
QAIC	quasi-likelihood adjustment of AIC
SE	standard error
SBS	southern Beaufort Sea
USGS	U.S. Geological Survey

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Polar Bear Population Status in the Southern Beaufort Sea

By Eric V. Regehr¹, Steven C. Amstrup¹, and Ian Stirling²

Abstract

Polar bears depend entirely on sea ice for survival. In recent years, a warming climate has caused major changes in the Arctic sea ice environment, leading to concerns regarding the status of polar bear populations. Here we present findings from long-term studies of polar bears in the southern Beaufort Sea (SBS) region of the U.S. and Canada, which are relevant to these concerns. We applied open population capture-recapture models to data collected from 2001 to 2006, and estimated there were 1,526 (95% CI = 1,211; 1,841) polar bears in the SBS region in 2006. The number of polar bears in this region was previously estimated to be approximately 1,800. Because precision of earlier estimates was low, our current estimate of population size and the earlier ones cannot be statistically differentiated. For the 2001–06 period, the best fitting capture-recapture model provided estimates of total apparent survival of 0.43 for cubs of the year (COYs), and 0.92 for all polar bears older than COYs. Because the survival rates for older polar bears included multiple sex and age strata, they could not be compared to previous estimates. Survival rates for COYs, however, were significantly lower than estimates derived in earlier studies ($P = 0.03$). The lower survival of COYs was corroborated by a comparison of the number of COYs per adult female for periods before (1967–89) and after (1990–2006) the winter of 1989–90, when warming temperatures and altered atmospheric circulation caused an abrupt change in sea ice conditions in the Arctic basin. In the latter period, there were significantly more COYs per adult female in the spring ($P = 0.02$), and significantly fewer COYs per adult female in the autumn ($P < 0.001$). Apparently, cub production was higher in the latter period, but fewer cubs survived beyond the first 6 months of life. Parallel with declining survival, skull measurements suggested that COYs captured from 1990 to 2006 were smaller than those captured before 1990. Similarly, both skull measurements and body weights suggested that adult males captured from 1990 to 2006 were smaller than those captured before 1990. The smaller stature of males was especially notable because it corresponded with a higher mean age of adult males. Male polar bears continue to grow into their teens, and if adequately

nourished, the older males captured in the latter period should have been larger than those captured earlier. In western Hudson Bay, Canada, a significant decline in population size was preceded by observed declines in cub survival and physical stature. The evidence of declining recruitment and body size reported here, therefore, suggests vigilance regarding the future of polar bears in the SBS region.

Introduction

Polar bears are entirely dependent on sea ice as a platform to access the marine mammals that provide their nutritional needs (Amstrup, 2003). In recent years, a warming climate and changing atmospheric circulation patterns have resulted in major changes in the Arctic sea ice environment (Comiso, 2002; Rigor and others, 2002; Comiso and Parkinson, 2004; Rigor and Wallace, 2004; Stroeve and others, 2005). Polar bears residing in the southern Beaufort Sea (SBS) region of the U.S. and Canada have been studied since 1967. Results of these studies provide insights into how changes in the environment may affect the status of polar bears in this region.

Radiotelemetry data collected from female polar bears during the mid-1980s suggested that the SBS region contained a single population of polar bears, extending from west of Barrow, Alaska, to east of Paulatuk, Northwest Territories, Canada (Amstrup and others, 1986; Amstrup and DeMaster, 1988). In response to that finding, an agreement was established between U.S. and Canadian user groups to cooperatively manage the hunting of polar bears throughout the entire SBS region (Brower and others, 2002).

To determine sustainable harvest levels, early polar bear research in the SBS region was focused on estimating population size and developing indices of recruitment and survival which could be used to evaluate trends in population status. The size of the SBS polar bear population was first estimated to be approximately 1,800 animals in 1986 (Amstrup and others, 1986). Survival rates of adult females and dependent young were estimated from radiotelemetry data collected from the early 1980s to the mid-1990s (Amstrup

¹U.S. Geological Survey

²Canadian Wildlife Service

and Durner, 1995). Throughout the 1980s and early 1990s, empirical observations such as the frequency of encounters of polar bears during research flights over the sea ice, increased sightings of polar bears near onshore human settlements, and increasing numbers of maternal dens observed on land, suggested that the population of the SBS region was increasing. Because of interest among user groups in a larger harvest, population size and trend were re-assessed in the late 1990s (Amstrup and others, 2001a; McDonald and Amstrup, 2001). That analysis was limited to female polar bears because research objectives resulted in the under-sampling of males in some years. The estimate of 1,180 females (95% CI = 635; 1,725) for the late 1980s was consistent with the previous estimate of at least 1,800 total polar bears (i.e., females and males) in the SBS region at that time (Amstrup and others, 1986). For the late 1990s, the estimated number of females developed by Amstrup and others (2001a) suggested that the total population may have increased to as many as 2,500 polar bears. However, because of interannual variation in sample size and other sources of heterogeneity within the data for the late 1990s, the estimate of 2,500 polar bears was not considered reliable. Therefore, managers took a conservative approach and harvest decisions continued to be based on a total population size of 1,800 polar bears in the SBS region.

We initiated a new study in 2001, to re-assess the status of the SBS polar bear population and to address the potential effects, on polar bear status, of changing sea ice conditions in the Arctic basin. Here we present estimates of survival and population size derived from capture-recapture data collected from 2001 to 2006, and compare these estimates to those developed earlier. We also document changes in the productivity and physical stature of polar bears using data collected from the late 1960s through the present.

Methods

Polar bear research began in the SBS region in 1967, and has continued through 2006. We captured polar bears by injecting the drugs tiletamine hydrochloride plus zolazepam hydrochloride (Telazol®, Warner-Lambert Co.), using projectile syringes fired from helicopters (Stirling and others, 1989). All captured polar bears were ear-tagged with a unique identification number, and tattooed on both sides of the inner surface of the upper lip. We determined body weight of captured bears with a spring or dynamometer scale and recorded various body measurements, including the condylobasal length and zygomatic width of the skull. Age was determined for all captured bears. Cubs-of-the-year (COYs; approximately 3 months old in spring) were always with their mothers and could be visually aged without error (Ramsay and Stirling, 1988). A vestigial premolar was extracted from other captured polar bears and age was

estimated by counting cementum annuli (Calvert and Ramsay, 1998). Beginning in 1981, selected adult females were fitted with radio-tracking collars that allowed us to relocate them from aircraft. All capture and marking protocols were approved by independent animal care and welfare committees.

Capture-Recapture Analysis

For the purpose of estimating population size and survival rates in this study, we captured polar bears in coastal areas of the SBS region, from Point Barrow, Alaska (about 157°W) to Cape Parry, Northwest Territories, Canada (about 125°W). Capture-recapture data were collected by the U.S. Geological Survey (USGS) in the U.S. portion of the SBS region, from late March through early May of 2001–06, and in October and November of 2001. Additional capture-recapture data were collected by the Canadian Wildlife Service (CWS) in the Canadian portion of the SBS region in April and May of 2003–06 (fig. 1). In each year from 2001 to 2006, our objectives were to maximize sample size, maximize the geographic distribution of capture effort throughout the SBS region, and ensure that all polar bears in the study area were equally exposed to capture efforts. Sample sizes in many years before 2001 were approximately equivalent to those of 2001–06, but sampling strategies and time-frames of capture varied among many early years of study. Therefore, all animals were not subjected to equal capture effort in many of those early years. Previous studies have shown the difficulties of estimating demographic parameters from data collected under a non-random sampling protocol that varied among years, and did not include the entire study area (Amstrup, 1995; Amstrup and others, 2001a; McDonald and Amstrup, 2001). Therefore, we limited the current capture-recapture analyses to data collected from 2001 to 2006.

In our analysis of survival and population size for the 2001–06 period, we included data for polar bears encountered by standard search methods (polar bears encountered randomly, while flying in polar bear habitat), and data for polar bears encountered by radiotelemetry. We use the term “capture” to refer to the physical capture of a polar bear, or the visual sighting of a polar bear for which the individual identity was known via radiotelemetry. Although some polar bears were captured multiple times per year, we used a maximum of one capture per bear per year in our analyses.

The data for each polar bear were summarized as an individual capture history and covariates. For example, bear 20579 had the capture history {101100}, where 0 indicates not captured at sampling occasion j , and 1 indicates captured and released alive at sampling occasion j ($j = 1, 2, \dots, k$). Individual covariates for this polar bear included *sex* = female, *age* (at-first-capture) = 0 yr, and *agency* = U.S., based on which agency originally captured bear 20579. The time-dependent covariate *radio* indicated when adult female polar bears were

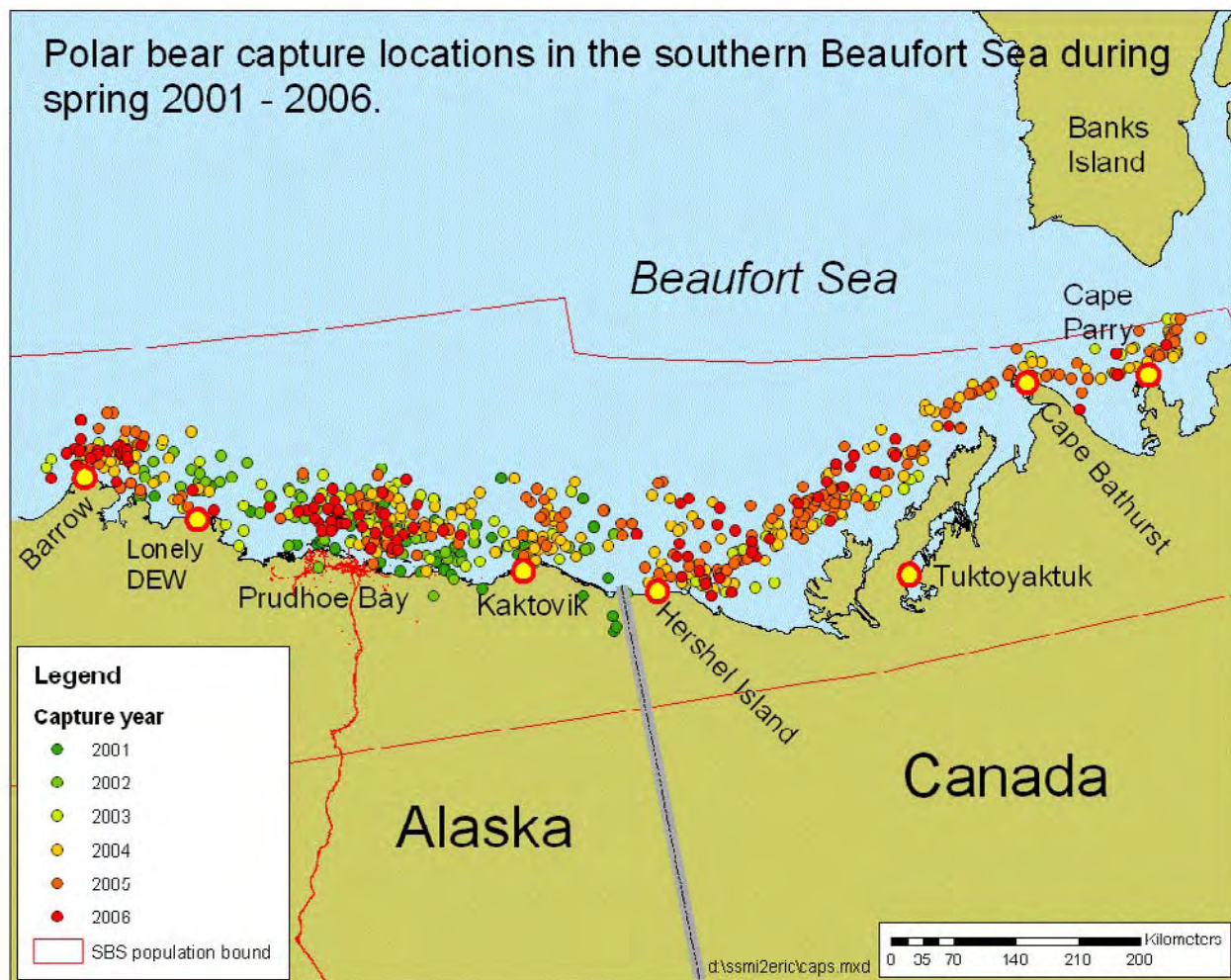


Figure 1. Distribution of polar bear captures from 2001 to 2006 that were included in capture-recapture estimates of survival and population size.

available for recapture by radiotelemetry, based on radiocollar deployment information and real-time satellite telemetry data (Harris and others, 1990). Dependent young that accompanied radiocollared females also were considered to be available for recapture by radiotelemetry.

To investigate the potential relationship between sea ice and polar bear survival, we quantified spatiotemporal trends in sea ice coverage from 2001 to 2006 using sea ice concentration data for 25×25 km grid cells, derived from passive microwave imagery using the NASA Team algorithm (National Snow and Ice Data Center, Boulder, Co., <ftp://sidacs.colorado.edu/pub/>). First, we defined an area of preferred polar bear habitat as all grid cells in the SBS population boundary with an ocean depth of less than 300 m (International Bathymetric Chart of the Arctic Ocean, <http://www.ngdc.noaa.gov/mgg/bathymetry/arctic/arctic.html>). We then averaged daily ice concentrations in the area of preferred habitat, and calculated the number of days during each calendar year j that the mean ice concentration was

less than 50% (x_j). We derived the covariate ice_j for use in capture-recapture models, by standardizing x_j via the formula: $ice_j = (x_j - \bar{x}) / SD(x)$, where \bar{x} is the mean and $SD(x)$ is the standard deviation of x_j for $j = 2000-05$ (Franklin, 2001).

Goodness-of-Fit

The valid estimation of demographic parameters from capture-recapture data requires an analysis of goodness-of-fit (GOF), to determine how well the data meet the assumptions of the model being used (Lebreton and others, 1992; Cooch and White, 2005, Chapter 5; McDonald and others, 2005). Because no single method is sufficient in practice, we used multiple methods to obtain a thorough consideration of GOF. First, we partitioned the data into sex- and age-based strata and used program RELEASE (Burnham and others, 1987) to investigate patterns in the data. Second, we used the parametric bootstrap procedure in program MARK (White and Burnham, 1999) to evaluate the fit of a general model,

and to estimate a bootstrapped value of the variance inflation factor \hat{c} (White and others, 2001). We also used MARK to estimate a value of median \hat{c} (Cooch and White, 2005: Chapter 5). Third, we estimated a “biological” \hat{c} based on the lack of independence among the fates of adult female polar bears and their dependent young, via the formula: $\hat{c} = n/(n - n_c)$, where n is the total number of captures, and n_c is the number of captures of dependent young (Taylor and others, 2002). Finally, we note that radiotelemetry captures present methodological difficulties for program RELEASE and the parametric bootstrap, and were excluded from the GOF analysis. However, it is unlikely that this lead to an underestimation of \hat{c} , because all reasonable capture-recapture models explicitly allowed for telemetry-based variation in recapture probabilities by incorporating the individual covariate *radio*.

Estimating Survival Rate and Population Size

We estimated survival using Cormack-Jolly-Seber (CJS) models (Lebreton and others, 1992) fitted to the data with R-language software for the “general regression” approach to capture-recapture (McDonald and others, 2005, <http://www.west-inc.com>). The CJS model conditions on first capture, and estimates the probabilities of survival (ϕ) and recapture (p) most likely to produce the observed capture histories. Estimates of ϕ_j represent total apparent survival, which is the cumulative probability of remaining alive and in the study area between sampling occasions j and $j+1$.

We considered models that allowed ϕ to vary by time, sex, and four age classes: COYs, yearlings, subadults (2–4 yr), and adults (5+ yr). We modeled ϕ_j as a function of ice_j and ice_{j-1} , to investigate the hypothesis that reduced sea ice coverage would affect polar bear survival by limiting access to the biologically productive waters over the continental shelf. We also fitted models with a generic linear trend that allowed for a monotonic change in survival. Finally, we considered an additive effect in ϕ following the occasion of first capture for male subadults and adults, based on the indication of “transient” males within the population from program RELEASE (Pradel and others, 1997). Transients are defined as individuals that entered the study population, were captured once, and subsequently emigrated. In theory, the influence of these individuals on estimates of apparent survival can be mitigated using a parameterization for ϕ that allows the transients to “die” (i.e., leave the study area) following first capture.

For recapture probability (p), we considered models that included the individual covariate *agency*, and the covariate *effort*, which was based on the annual number of helicopter hours flown in capture operations. For example, an interaction between *agency* and *effort* produced estimates of p_j for “U.S.” bears as a function of USGS capture effort, and separate estimates of p_j for “Canadian” bears as a function of CWS capture effort. This approach was based on evidence

that individual polar bears exhibit geographic fidelity in the SBS region (Amstrup and others, 2004, 2005), which we hypothesized would lead to a correlation between where an individual was originally captured, and where it was available for recapture. We considered models with time-dependence in p , and with interactions between time-dependence and *agency*. This reflected the hypothesis that p_j varied as a cumulative function of sampling effort, general fidelity patterns, and unknown ecological phenomena (e.g., interannual variation in the spatial distribution of polar bears, as influenced by sea ice conditions). We also considered models with an intermediate form of time-dependence in p , based on observations by the CWS that polar bear densities in the eastern portion of the SBS region were dramatically lower in 2006 than in other years. Finally, in nearly all models the covariate *radio* allowed for an additive effect in p for polar bears that were available for recapture by radiotelemetry.

Model selection was based on Akaike’s information criterion (AIC) (Burnham and Anderson, 2002), as well as considerations of biological plausibility and other statistical issues (e.g., the number of parameters in the model that could be estimated). We adjusted AIC for overdispersion (i.e., QAIC) based on the GOF analysis, and evaluated 152 CJS models representing all combinations of the hypothesized parameterizations for ϕ and p . We derived final parameter estimates by averaging across models in the candidate set with $\Delta QAIC \leq 7.0$. We used this cutoff because $\Delta QAIC = 7.0$ corresponds to a normalized Akaike weight (w_i) of approximately 0.01, below which the impact on model-averaged estimates is negligible. This approach ensured that model selection uncertainty was reflected in all real parameter estimates, and their associated variances (Burnham and Anderson, 2002).

We estimated population size (N) from the model-averaged estimates of recapture probability (p) derived from the CJS models, via a Horvitz-Thompson estimator (McDonald and Amstrup, 2001). This approach has several advantages over traditional Jolly-Seber methods (McDonald and others, 2005). First, it retains the flexibility of the CJS modeling framework. Second, it is straightforward to estimate N from models in which p is a function of individual covariates. Third, it is straightforward to estimate N from model-averaged estimates of p . We estimated the variance of N by bootstrapping (Manly, 1997), because conventional variance estimators for the HT approach (e.g., the Laake estimator in Taylor and others, 2002) require estimates of the covariance among p for all strata, which were not available for the model-averaged estimates. The bootstrap procedure involved re-sampling the individual capture histories (and covariates) to generate 1,000 new datasets, fitting each dataset with all models in the original candidate set with $\Delta QAIC \leq 7.0$, and deriving model-averaged parameter estimates for each iteration. We then estimated the variance of N by assuming that the distribution of bootstrapped, model-averaged \hat{N}_j represented the sampling distribution of true population size.

Cub Production and Physical Stature

We analyzed numbers of young accompanying adult female polar bears captured each spring in 1967–79, 1982–92 (except 1990) and 1998–2006, and each autumn in 1981–86, 1988, 1989, 1994, 1997, and 1998–2001. We analyzed physical stature using skull size and body weight data for polar bears captured in the spring only. For both analyses, we compared data from two periods: 1967–89 and 1990–2006. This comparison was motivated by dramatic changes in the polar basin sea ice beginning in 1989–90 (Rigor and others, 2002). We hypothesized that these changes would affect the nutritional condition of polar bears, resulting in altered production and survival of cubs, and altered physical stature for all polar bears (Stirling and others, 1999).

We compared data between the two periods using logistic regression, the Kruskal-Wallis rank sum test, and contingency tables. Cub production and survival were assessed using the proportion of adult females accompanied by litters, and the number of dependent young (COYs, yearlings, and 2-year-olds) per female. Because the comparison of indices requires the assumption of equal detectability among years, we limited our analysis of spring cub production rates to data collected in April and May. In early years of the study, COYs were under-sampled because much of the field work occurred in March before new family groups emerged from their dens (Amstrup and DeMaster, 1988; Amstrup, 1995). Almost all females with COYs, however, had emerged from dens by the first week in April (Amstrup and Gardner, 1994).

Results

The combined 2001–06 USGS data, and 2003–06 CWS data, consisted of 1,099 captures of 843 individual polar bears (table 1, fig. 1). Approximately 90 percent of captures were for polar bears encountered by standard search, and 10 percent of captures were for polar bears encountered by radiotelemetry. Approximately 87 percent of captures occurred during the annual spring capture seasons (mean date of capture April 14), and 7 percent of captures occurred during the autumn capture season by the USGS in 2001 (mean date of capture October 30). The remaining 6 percent of captures occurred as visual sightings during winter aerial radiotelemetry surveys. Appendix A includes a statistical description of the sex and age composition of the capture sample, information regarding marked polar bears that were harvested, and other summary statistics.

A total of 45 individual polar bears occurred in both the USGS and CWS samples: 38 “U.S.” bears (i.e., bears originally captured by the USGS) appeared in the Canadian sample, while 7 “Canadian” bears appeared in the U.S. sample. Although the larger number of U.S. bears in the

Canadian sample may reflect the deployment of more marks into the U.S. portion of the SBS region, it also may reflect a distributional phenomenon. Annual encounter rates with polar bears were higher in Canada than in the U.S., except in 2006.

The covariate ice_j was based on sea ice concentration data for 2000–05, because we hypothesized that ice conditions in year j could predict polar bear survival in year $j+1$, and because CJS models cannot estimate survival following the final sampling occasion (i.e., 2006). For $j = 2000, 2001 \dots 2005$: $ice_j = \{-1.03, -0.89, -0.71, 0.41, 1.13, 1.09\}$, where larger values indicate a longer ice-free period. A simple linear regression on the covariate (prior to standardization) indicated that the mean number of days with less than 50 percent ice concentration in the SBS region of preferred habitat increased from approximately 82 days in 2000, to 138 days in 2005 ($\hat{\beta} = 11.29$ d/yr, $SE(\hat{\beta}) = 1.84$, $P = 0.004$).

Goodness of Fit

Program RELEASE investigates whether capture-recapture data meet the assumptions of the standard CJS model $\phi(t) p(t)$, which allows ϕ and p to vary independently with time for a single stratum (see appendix B for a detailed description of model notation). We found no evidence for lack of fit in the female data (overall $\chi^2 = 14.23$, $df = 12$, $P = 0.29$). In contrast, the male data did not fit model $\phi(t) p(t)$ due entirely to a lack of fit in the program RELEASE component TEST3.SR ($\chi^2 = 25.45$, $df = 4$, $P < 0.001$). The directionality of TEST3.SR indicated a lower future recovery rate of newly marked male animals, which is often caused by age-specificity in ϕ (Choquet and others, 2002). However, the lack of fit in the male data persisted despite progressive subsetting on age (i.e., from polar bears of all ages, to adults only), and despite the complete removal of harvested polar bears, which could exacerbate lack of fit due to a male bias in the harvest. Therefore, it is possible that the lack of fit in the male data represented a biological phenomenon, such as the presence of “transient” individuals (Cooch and White, 2005, Chapter 8).

In theory, program RELEASE can be used to estimate \hat{c} for a global model that is equivalent to independently fitting model $\phi(t) p(t)$ to multiple strata in the data (Sendor and Simon, 2003). In this study, small sample size resulted in estimation problems for highly parameterized models that incorporated sex \times time and age \times time interactions in both ϕ and p . Therefore, we estimated \hat{c} using an 11-parameter model that was sufficiently general to allow for major hypothesized sources of variation, but did not suffer from estimation problems, and thus was a reasonable starting point for model selection. The 11-parameter general model estimated time-constant ϕ for three strata: COYs of both sexes, female polar bears older than COYs, and male polar bears older than COYs. Recapture probabilities were time-dependent

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Table 1. Total number and proportion each sex and age class of polar bears captured by standard search and radiotelemetry in the Southern Beaufort Sea by the U.S. Geological Survey, 2001–06, and by the Canadian Wildlife Service, 2003–06.

		Females captured		Males captured	
		Number	Proportion	Number	Proportion
2001	Adult ¹ without dependent young	21	0.15	21	0.15
	Adult with dependent young	36	0.26	NA	0.00
	Subadult ¹	5	0.04	2	0.01
	Two-year-old	4	0.03	1	0.01
	Yearling	16	0.12	11	0.08
	Cub-of-the-year	11	0.08	9	0.07
2002	Adult without dependent young	21	0.19	20	0.18
	Adult with dependent young	24	0.21	NA	0.00
	Subadult	5	0.04	3	0.03
	Two-year-old	4	0.04	7	0.06
	Yearling	2	0.02	6	0.05
	Cub-of-the-year	11	0.10	10	0.09
2003	Adult without dependent young	14	0.08	55	0.32
	Adult with dependent young	33	0.19	NA	0.00
	Subadult	9	0.05	11	0.06
	Two-year-old	7	0.04	8	0.05
	Yearling	3	0.02	7	0.04
	Cub-of-the-year	10	0.06	13	0.08
2004	Adult without dependent young	39	0.14	70	0.25
	Adult with dependent young	48	0.17	NA	0.00
	Subadult	27	0.09	20	0.07
	Two-year-old	15	0.05	10	0.04
	Yearling	9	0.03	9	0.03
	Cub-of-the-year	17	0.06	21	0.07
2005	Adult without dependent young	47	0.19	67	0.27
	Adult with dependent young	39	0.16	NA	0.00
	Subadult	17	0.07	13	0.05
	Two-year-old	12	0.05	7	0.03
	Yearling	9	0.04	7	0.03
	Cub-of-the-year	14	0.06	17	0.07
2006	Adult without dependent young	28	0.19	49	0.34
	Adult with dependent young	22	0.15	NA	0.00
	Subadult	6	0.04	6	0.04
	Two-year-old	7	0.05	0	0.00
	Yearling	10	0.07	1	0.01
	Cub-of-the-year	8	0.06	8	0.06

¹Adult (≥5 yr); Subadult (3–4 yr).

with an interactive *agency* effect, which allowed independent estimates of p_j for U.S. versus Canadian polar bears. Program MARK gave a bootstrap $\hat{c} = 1.45$ and a median $\hat{c} = 1.21$ (SE = 0.01) for this model, which indicated a moderate amount of overdispersion. The “biological” \hat{c} based on the number of dependent young in the capture sample was 1.34, which was similar to the statistically based estimates. Because there was no clear theoretical basis for deciding which value of \hat{c} to select, we used the arithmetic mean of the three values, which gave $\hat{c} = 1.33$.

As noted above, the simulation-based estimates of \hat{c} were derived for a model that was a compromise between an ideal (i.e., very general) global model, and limitations in the data. The parameterization for ϕ in that model also was influenced by the practical difficulty of bootstrapping in MARK with complex group structure. In the actual CJS analysis, we considered several models with more general parameterizations for ϕ . It is therefore possible that the simulation-based estimate of \hat{c} was larger than necessary.

Estimating Survival Rate and Population Size

The low-QAIC model included a simple parameterization for ϕ that estimated time-constant survival for two groups: COYs versus all polar bears older than COYs (model No. 1, [table B1](#), [appendix B](#)). This model provided estimates of “average” ϕ for 2001–05, which could be compared to time-constant estimates of ϕ published for other polar bear populations. Estimates of total apparent survival probability (ϕ) from the low-QAIC model were 0.43 (SE = 0.11) for COYs, and 0.92 (SE = 0.04) for all polar bears older than COYs.

Although the low-QAIC model estimated time-constant ϕ for two groups, there also was support in the data for models that included other sex- and age-based groups, and allowed for temporal variation in ϕ ([table B1](#), [appendix B](#)). Because all these models represented valid biological hypotheses, we derived estimates of ϕ by averaging across models in the candidate set with $\Delta\text{QAIC} \leq 7.0$, with two exceptions. First, we excluded model No. 13 ($\Delta\text{QAIC} = 4.0$) because of difficulty in interpreting the transient effect for male subadults and adults (see [appendix C](#)). Second, we excluded model No. 14 ($\Delta\text{QAIC} = 6.0$), which was the only model with a time-dependent parameterization for ϕ , because it resulted in confounded estimates of p_{2006} for some individuals.

We report model-averaged estimates of survival probability for three groups: COYs, female polar bears older than COYs, and male polar bears older than COYs ([table 2](#)). Although some models considered for model-averaging included additional groupings (e.g., subadult females separated

from adult females), the resulting differences in parameter estimates were limited to the third or fourth significant digit, and therefore are not reported. The unconditional standard errors in [table 2](#) reflect both the sampling variance of each model, and the additional variance associated with model selection uncertainty (Buckland and others, 1997). The percent variation due to model selection uncertainty was approximately 14 percent for COYs, 20 percent for females older than COYs, and 32 percent for males older than COYs.

All CJS models with $\Delta\text{QAIC} \leq 7.0$ included a single parameterization for p , with the exception of model No. 15 ([table B1](#), [appendix B](#)). Recapture probabilities differed between U.S. and Canadian polar bears, and were time-constant with the exception of p_{2006} for Canadian bears. Also, an additive effect was allowed for polar bears that were available for recapture by radiotelemetry. We derived final estimates of p by model-averaging over the same candidate model set as considered for survival. We used this approach because the point estimates of p varied slightly among models, due to interdependence with ϕ . The model-averaged estimates of p were 0.14 (SE = 0.02) for U.S. bears, 0.20 (SE = 0.04) for Canadian bears in 2004 and 2005, 0.06 (SE = 0.02) for Canadian bears in 2006, and 0.49 (SE = 0.07) for all polar bears available for recapture by radiotelemetry. Overall, approximately 4 percent of the variation in recapture probability was due to model selection uncertainty.

We estimated N by applying the HT estimator to model-averaged estimates of p ([fig. 2](#)). Valid estimates of population size were available for 2004–06 only, because of interactions between sampling design, the parameterization for p , and properties of the CJS model. The explanation is as follows. First, the CJS model cannot produce estimates of N in the first year of the study (i.e., 2001). Second, \hat{N}_{2002} was biased low because it only represented polar bears in the portion of the SBS region that was sampled by the USGS. Third, \hat{N}_{2003} also was biased, because 2003 was the first year of sampling by the CWS, and therefore the estimate of p_{2003} for Canadian bears

Table 2. Model-averaged estimates of total apparent survival probability for polar bears in the southern Beaufort Sea.

Year	COYs of both sexes		Females older than COYs		Males older than COYs	
	ϕ	SE(ϕ)	ϕ	SE(ϕ)	ϕ	SE(ϕ)
2001	0.47	0.14	0.92	0.05	0.94	0.05
2002	0.45	0.13	0.92	0.05	0.94	0.05
2003	0.43	0.12	0.92	0.05	0.93	0.05
2004	0.39	0.14	0.90	0.05	0.92	0.06
2005	0.37	0.16	0.90	0.07	0.91	0.07

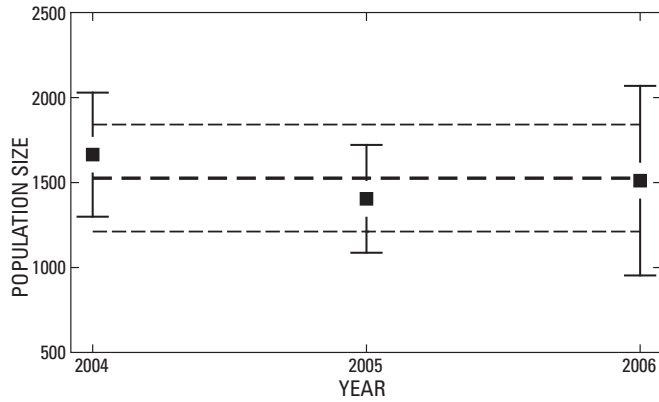


Figure 2. Total size of the southern Beaufort Sea polar bear population. Squares are annual, model-averaged estimates of population size with bootstrapped 95% confidence intervals. Heavy dashed line is the mean population size from 2004 to 2006 with bootstrapped 95% confidence intervals.

was not valid. Finally, we note that N_{2006} represents a valid estimate, because all models considered for model-averaging had time-constant parameterizations for ϕ , which allowed for the estimation of non-confounded p_{2006} .

The best estimate of the total size of the SBS polar bear population in 2006 (denoted \hat{N}_{2006}^*) was 1,526 (95% CI = 1,211; 1,841). We estimated \hat{N}_{2006}^* by taking the arithmetic mean of the model-averaged point estimates of N from 2004 to 2006. This approach was based on the observation that interannual variability in \hat{N} from 2004 to 2006 was within the limits of sampling variation, and most likely not a reflection of real changes in population size (fig. 2). We estimated $SE(\hat{N}_{2006}^*)$ using the standard deviation of the mean, model-averaged population size estimates from 2004 to 2006, for the 1,000 bootstrap iterations. [Appendix D](#) provides additional results from the bootstrap procedure regarding the statistical properties of the parameter estimates and model selection process.

Cub Production and Physical Stature

We compared numbers of young accompanying adult female polar bears captured between 1967 and 1989, to those accompanying females captured between 1990 and 2006. The spring data consisted of 788 captures of adult females (age ≥ 5 yr) located by standard search during April and May (table 3). The proportion of adult females accompanied by COYs increased from 0.15 for the earlier period, to 0.22

for the later period (logistic regression; period model versus intercept-only model, $G = 5.8$, $df = 1$, $P = 0.016$). The number of COYs per adult female also increased, from 0.25 to 0.39 (Kruskal-Wallis test; $\chi^2 = 6.35$, $df = 1$, $P = 0.012$). In contrast to the pattern observed for COYs, indices of yearling production declined between the two periods, although the changes were not statistically significant. The proportion of adult females accompanied by yearlings decreased from 0.22 to 0.19 ($G = 1.28$, $df = 1$, $P = 0.258$), while the number of yearlings per adult female decreased from 0.34 to 0.26 ($\chi^2 = 1.90$, $df = 1$, $P = 0.168$).

The autumn data, which consisted of 190 captures of adult females during October and November, showed a different pattern than the spring data (table 4). The proportion of adult females accompanied by COYs in autumn decreased from 0.40 to 0.16 ($G = 14.53$, $df = 1$, $P < 0.001$), while the number of COYs per adult female decreased from 0.61 to 0.25 ($\chi^2 = 12.70$, $df = 1$, $P < 0.001$). Similarly, although the differences were not significant, the proportion of adult females accompanied by yearlings decreased from 0.33 to 0.23 ($G = 2.39$, $df = 1$, $P = 0.122$) and the number of yearlings per adult female decreased from 0.47 to 0.34 ($\chi^2 = 2.13$, $df = 1$, $P = 0.144$).

Litter sizes in the two periods were not statistically different (table 5). For the spring data, COY litters were slightly larger in the later period (2×3 contingency table of litter sizes versus period; $\chi^2 = 2.49$, $df = 2$, $P = 0.288$), while yearling litters were somewhat smaller ($\chi^2 = 5.60$, $df = 2$, $P = 0.061$). For the autumn data, litter size was similar between periods for both COYs ($\chi^2 = 0.43$, $df = 1$, $P = 0.511$) and yearlings ($\chi^2 = 0.10$, $df = 1$, $P = 0.750$).

We compared the physical stature of polar bears between the two periods using data for COYs, yearlings of both sexes, and adults (age ≥ 5 yr) of both sexes that were captured by standard search and radiotelemetry, from March-May. Statistically significant decreases in skull measurements were observed for COYs and adult males (table 6). Body weight decreased significantly for adult males (table 7). Because male polar bears continue to grow into their teen years (Derocher and others, 2005), it was possible that changes in skull measurements and body weight were related to changes in age structure. However, the mean age of adult male polar bears in the 1990–2006 capture sample—10.9 (SE = 0.30) years—was greater than the mean age—9.4 (SE = 0.23) years—in the 1967–89 capture sample (Kruskal-Wallis test; $\chi^2 = 15.62$, $df = 1$, $P < 0.001$). Given equal nutrition, the older male bears captured in more recent years should have been larger. Therefore, it is likely that the observed changes in physical stature reflected a real shift towards smaller adult male polar bears in the SBS region.

Table 3 Cub production rates for polar bears in the southern Beaufort Sea, 1967–89 and 1990–2006.

[Data are included for polar bears captured by standard search in the spring (April–May)]

Adult female age (yr)	1967–89						1990–2006					
	Number of adult females	Prop. with COYs	COYs per adult female	Prop. with yearlings	Yearlings per adult female	Prop. with 2-year-olds	2-year-olds per adult female	Number of adult females	Prop. with COYs	COYs per adult female	Prop. with yearlings	Yearlings per adult female
5	68	0.09	0.15	0.02	0.03	0.00	0.00	38	0.18	0.26	0.00	0.00
6	58	0.16	0.21	0.16	0.21	0.02	0.03	28	0.29	0.43	0.04	0.04
7	50	0.12	0.14	0.30	0.46	0.12	0.14	34	0.15	0.27	0.27	0.29
8	48	0.19	0.27	0.33	0.44	0.13	0.23	18	0.11	0.22	0.33	0.44
9	38	0.16	0.29	0.24	0.42	0.26	0.32	25	0.16	0.32	0.24	0.32
10	33	0.09	0.18	0.33	0.52	0.18	0.27	16	0.25	0.50	0.44	0.50
11	26	0.27	0.54	0.15	0.23	0.12	0.12	17	0.41	0.77	0.18	0.18
12	17	0.35	0.59	0.24	0.35	0.12	0.12	23	0.30	0.35	0.17	0.22
13	19	0.05	0.11	0.42	0.68	0.21	0.32	20	0.20	0.35	0.20	0.25
14	13	0.23	0.39	0.23	0.39	0.08	0.15	14	0.14	0.36	0.29	0.43
15	15	0.33	0.60	0.33	0.67	0.13	0.20	11	0.18	0.36	0.18	0.27
16	20	0.20	0.40	0.20	0.25	0.25	0.35	18	0.39	0.72	0.28	0.50
17	9	0.11	0.22	0.22	0.33	0.22	0.33	9	0.11	0.22	0.33	0.44
18	5	0.00	0.00	0.40	0.80	0.20	0.40	10	0.40	0.80	0.20	0.30
19	3	0.00	0.00	0.33	0.33	0.00	0.00	5	0.40	0.80	0.00	0.00
20+	13	0.08	0.15	0.15	0.31	0.08	0.15	32	0.13	0.25	0.19	0.28
Overall¹	437	0.15	0.25	0.22	0.34	0.11	0.16	351	0.22	0.39	0.19	0.26
												0.07
												0.11

¹Overall counts include data for 2 (1967–89) and 33 (1990–2006) females that were field-aged as adults, but did not have cementum-derived ages.**Table 4.** Cub production rates for polar bears in the southern Beaufort Sea, 1967–89 and 1990–2006.

[Data are included for polar bears captured by standard search in the autumn (October–November)]

Adult female age (yr)	1967–89						1990–2006					
	Number of adult females	Proportion with COYs	COYs per adult female	Proportion with yearlings	Yearlings per adult female	Number of adult females	Proportion with COYs	COYs per adult female	Proportion with yearlings	Yearlings per adult female	Number of adult females	Proportion with yearlings
5-9	54	0.35	0.48	0.30	0.37	36	0.06	0.08	0.19	0.31		
10-14	30	0.40	0.60	0.33	0.53	26	0.35	0.58	0.19	0.27		
15-19	17	0.47	0.88	0.47	0.71	8	0.00	0.00	0.38	0.63		
20+	6	0.67	1.00	0.17	0.33	10	0.20	0.30	0.40	0.50		
Overall¹	107	0.40	0.61	0.33	0.47	83	0.16	0.25	0.23	0.34		

¹Overall counts include data for 3 (1990–2006) females that were field-aged as adults, but did not have cementum-derived ages.

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Table 5. Litter sizes of dependent young polar bears in the southern Beaufort Sea, 1967–89 and 1990–2006.

[Data are included for polar bears captured by standard search in the spring (April-May) and autumn (October-November)]

	Season	COY litter size			Yearling litter size			Two-year-old litter size		
		1	2	3	1	2	3	1	2	3
1967–89	Spring	23	44	0	47	48	2	29	21	0
	Autumn	22	22	0	19	15	2	1	0	0
	Both	45	66	0	66	63	4	30	21	0
1990–2006	Spring	21	55	2	44	23	0	11	14	0
	Autumn	5	8	0	10	8	3	1	1	0
	Both	26	63	2	54	31	3	12	15	0
	Overall	71	129	2	120	94	7	42	36	0

Table 6. Sum of skull length and skull width measurements (cm) for polar bears in the southern Beaufort Sea, 1967–89 and 1990–2006.

[Data are included for all polar bears captured in the spring (March-May)]

	1967–89			1990–2006			ANOVA		
	n	Mean	SD	n	Mean	SD	F	df	<i>P</i> versus equal means
COY males and females	70	27.8	1.8	191	26.8	1.8	16.2	1	0.000
Yearling males	34	44.6	2.4	43	44.5	2.2	0.1	1	0.771
Yearling females	26	42.2	1.9	57	41.5	2.1	2.5	1	0.121
Adult males	137	65.3	4.2	315	64.3	4.7	4.9	1	0.028
Adult females	234	55.4	1.9	425	55.3	2.6	0.6	1	0.431

Table 7. Scale weights (kg) for polar bears in the southern Beaufort Sea, 1967–89 and 1990–2006.

[Data are included for all polar bears captured in the spring (March-May)]

	1967–89			1990–2006			ANOVA		
	n	Mean	SD	n	Mean	SD	F	df	<i>P</i> versus equal means
COY males and females	66	14.1	4.0	164	13.2	3.9	2.4	1	0.124
Yearling males	13	85.8	16.2	16	94.5	25.2	1.2	1	0.286
Yearling females	11	74.9	17.6	29	74.8	15.1	0.0	1	0.988
Adult males	38	367.6	80.6	83	329.0	89.0	5.2	1	0.024
Adult females	92	185.3	28.3	180	184.1	27.6	0.1	1	0.731

Discussion

Capture-Recapture Analyses

The survival estimates derived from the 2001 to 2006 capture-recapture data appear lower than previously published estimates for this population. Amstrup and Durner (1995) derived precise estimates of survival for COYs (0.65, 95% CI = 0.610–0.675), yearlings (0.86, 95% CI = 0.751–0.903), and adult females (0.97, 95% CI = 0.952–0.983) in the SBS region by following radiocollared females. Comparison of the earlier estimates with those from the current study, however, is complicated by strata-related issues. The comparison also is complicated by the fact that estimates of apparent survival from capture-recapture studies reflect both biological survival and the probability of remaining in the study area, whereas estimates of survival from radiotelemetry data reflect biological survival only. In the current study, estimates of apparent survival from the best fitting model were 0.43 (95% CI = 0.21–0.65) for COYs and 0.92 (95% CI = 0.84–1.00) for all polar bears older than COYs. Identifying a stratum that includes all bears older than COYs represented a compromise between actual sex- and age-based variation in survival, and the ability to detect this variation in the data using capture-recapture models. For example, we know from the life history of polar bears that recently weaned subadults generally have lower survival than prime age adults. Hence, a single estimate of survival for all polar bears older than COYs represents an average over biologically distinct strata. This issue, and the distinction between apparent survival and biological survival, precluded a meaningful comparison of current survival estimates for adult females with those derived previously.

Differences in COY survival between the two studies, however, can be meaningfully compared. Adult females with COYs are less mobile than other polar bears (Amstrup and others, 2000), and therefore more likely to remain in the study area. Estimates of apparent survival for COYs, therefore, should be similar to biological survival. Also, assuming that survival rates for adult females have not changed dramatically since the early 1990s, the difference between the radiotelemetry-based survival estimate for adult females (0.97, Amstrup and Durner, 1995) and the current estimate of apparent survival for all polar bears older than COYs (0.92) sets an upper limit on the emigration component of apparent survival for COYs. Because COYs are completely dependent on their mothers and cannot leave the study area on their own, the maximum emigration component of apparent survival for COYs cannot exceed 0.05. Finally, the actual emigration component has to be less than 0.05, because the current estimate of 0.92 was an average survival rate, derived for both adult females and other polar bears with lower biological survival (e.g., subadults, senescent adults).

In contrast to the maximum possible emigration component of <0.05 , the difference between the radiotelemetry-based survival estimate for COYs (Amstrup and Durner, 1995) and the current estimate of apparent survival for COYs was 0.22 (i.e., 0.65–0.43). This difference was statistically significant (P versus the null hypothesis of equal or increasing survival = 0.03), and clearly represents a decline in biological survival since the early 1990s. The decline in COY survival is consistent with the statistically significant changes in COY and yearling production that we report here.

In our capture-recapture analysis, we used a weight of evidence approach (Burnham and Anderson, 2002) that allowed us to derive estimates of survival by averaging over multiple, well supported models. Model-averaged estimates of apparent survival were different for three sex and age groups. All three exhibited declining survival for the years 2001–05 (table 2). Because the best fitting (i.e., low-QAIC) model estimated time-constant survival, these declines in model-averaged survival are not “statistically significant” in the classical sense of testing versus the null hypothesis of no trend. However, the declines do reflect the existence of a similar degree of support in the data for several models, some of which estimated survival probabilities that changed over the course of the study. The evidence ratio between two models can be calculated as the ratio of normalized Akaike weights (w_i) (Burnham and Anderson, 2002). For example, the evidence ratio for the low-QAIC model versus model No. 3, which estimated survival as a function of sea ice conditions, was $0.18/0.12 = 1.5$ (table B1, appendix B). In other words, the low-QAIC model was approximately 1.5 times as well supported as model No. 3. This low evidence ratio indicates considerable ambiguity as to which model was actually a better representation of the data (Burnham and Anderson, 2002). Therefore, we cannot simply overlook the suggestion of a declining trend in survival.

Estimates of survival are generally robust to model assumption violations (Williams and others, 2002, Chapter 17). Because estimates of survival derived from CJS models represent “total apparent survival,” however, changes in survival can arise from interactions between study design and animal movement patterns, as well as from changes in biological survival. In the SBS region, radiotelemetry data confirm that polar bears do not restrict their movements to the areas that we can access during helicopter supported capture efforts (Amstrup and others, 2000, 2004). Over periods of multiple years, every bear in the population spends considerable time in the sampling region. However, the shorter the time-frame considered for sampling, the greater the probability that previously marked polar bears will be located outside of the effective study area, and not available for recapture prior to the end of the study. Thus, the declines we observed in model-averaged survival rates may reflect an increase in the number of “emigrants” toward the end of the study, and not an actual decrease in biological survival.

Our model selection process did not support a transient effect in survival for male subadults and adults. We were, however, curious whether there might be sex or age specific differences in recapture probability. Therefore, we performed a limited amount of secondary modeling to investigate this and other *a posteriori* hypotheses ([appendix C](#)). Although inference regarding transience remained equivocal, the secondary modeling provided some evidence for differential movement patterns between males and females, and emphasized that this is a topic worthy of further investigation.

In our analysis of the 2001–06 data, we did not find clear evidence for a relationship between sea ice coverage in the SBS region (i.e., the covariate *ice*) and survival. However, this should be interpreted in light of the short duration of the study and the limitations of the data. Polar bears are long-lived mammals that are well adapted to periods of resource shortage. Our study may not have been long enough, and may not have included enough interannual variation in sea ice, to detect a significant relationship between changing sea ice and survival. This also may be due to our inability to resolve survival patterns for subadult and senescent polar bears, which may be most affected by annual changes in sea ice conditions (Regehr and others, unpub. data, 2006). Because polar bears are entirely dependent on sea ice for foraging, reduced access to sea ice translates directly into reduced feeding opportunity. In other parts of the polar bear range, reductions in the spatiotemporal availability of sea ice have been shown to negatively impact polar bear stature, productivity, and survival of juvenile, subadult and senescent animals (Stirling and others, 1999; Stirling, 2002).

Our best estimate of the population size for the SBS region was 1,526 polar bears (95% CI = 1,211; 1,841). We believe that this estimate—the mean for the period 2004–06—is relatively unbiased for several reasons. First, it was derived from capture-recapture data that were, for the first time, collected throughout the entire SBS region under a well-defined and consistent sampling protocol. Second, a thorough GOF analysis suggested that the data met the most important capture-recapture assumptions. The CJS models fitted to the data included covariates for all major sources of variation of which we were aware, and the resulting coefficient estimates were biologically plausible. Third, estimates of population size were insensitive to model selection, as evidenced by the low percent variation in recapture probability associated with model selection uncertainty ([appendixes C and D](#)). Finally, the point estimates of population size were relatively stable for 2004–06 (i.e., the years for which valid estimates could be derived).

Stability in point estimates for 2004–06 is further evidence that they reflect the total number of polar bears in the SBS region. In each year of the study, some individuals probably were located outside of the effective sampling area. However, the estimates of population size derived from CJS models represent the total number of individuals that had a finite probability of being exposed to sampling (i.e.,

the “superpopulation”), whether or not they were actually accessible to the USGS or CWS in every year (Kendall and others, 1997). The stability of estimated population sizes for the latter years of the study, when both agencies were performing field work, indicates that new individuals were not continuing to be “recruited” into the superpopulation as they cycled through the area exposed to sampling efforts.

Amstrup and others (2001a) estimated that there were 1,180 (95% CI = 635; 1,725) female polar bears in the SBS region in the late 1980s. Sample sizes during this period were similar to those in the 2001–06 study, which allows for a reasonable comparison of estimated population sizes. If the sex ratio of the population in the late 1980s was similar to what (54 percent female) we estimated for the 2001–06 period, the Amstrup and others (2001a) female-only estimate corresponded to a total population size in the late 1980s of approximately 2,185 polar bears. Because the estimate and confidence interval were calculated for females only, however, we do not know the statistical variance associated with this estimate of the total population size. We do know, however, that the variance associated with the estimate of the total population was necessarily greater than the variance for the female-only estimate (SE = 278). Therefore, the confidence interval around the total population size estimate of 2,185 must have exhibited considerable overlap with the confidence interval around the current estimate of 1,526 (95% CI = 1,211; 1,841). This overlap, in conjunction with the similarity between the current estimate and the original Amstrup and others (1986) estimate of 1,800 (95% CI not available), precludes a statistical determination that the total number of polar bears in the SBS region has changed in recent years.

Estimating the size of wildlife populations is inherently difficult (e.g., Pollock and others, 1990; Pledger and Efford, 1998). This is especially true for animals that occur at low densities in remote regions, because of the potential for bias introduced by heterogeneity in recapture probability (e.g., due to differences in distribution, behavior, sightability). We believe that the estimated population sizes for 2004–06 are accurate. However, evaluation of long-term trends in population size via *post hoc* comparison with previous analyses is clearly a challenge. To address this issue more thoroughly, we are preparing an integrated analysis of historic and current data for polar bears in the SBS region, including both capture-recapture and radiotelemetry data.

Cub Production and Physical Stature

The changes we observed in cub production between the early (1967–89) and latter (1990–2006) time periods appear to reflect a decrease in the survival of polar bear cubs during their first 6 months of life. Polar bears have a multi-year reproductive cycle (Amstrup, 2003). Females give birth in January and emerge from the maternal den with new cubs in March or early April. Young typically accompany their mother for 2.3 years while they learn the methods of survival

in the Arctic (Amstrup, 2003). For polar bears captured during the autumn, the number of COYs per adult female declined significantly ($P < 0.001$) from a mean of 0.61 in the early period to a mean of 0.25 in the latter period. This decline can only be explained by lower survival of cubs after den emergence. In contrast to the autumn data, the numbers of COYs per adult female captured in the spring increased between the two periods. This reflects a shortened inter-birth interval for the recent period. Apparently, more females are losing their cubs shortly after den emergence, breeding again shortly after losing their cubs, denning again the following autumn, and emerging with another litter the following spring. In short, numerous cubs are currently being born in the SBS region, but many of them are not being recruited into the population.

The evaluation of changes in cub production requires the recognition of possible sampling differences between the early and latter study periods. Amstrup and DeMaster (1988) and Amstrup (1995) suggested that COYs were often under-sampled in spring captures. In the early period, this under-sampling was reflected by a higher proportion of yearlings than COYs in spring captures, and by a higher proportion of COYs captured in the autumn than in the spring. Because it is not possible for actual cub production to increase between the spring and autumn of a single year, a higher proportion of females with cubs in the autumn must represent a bias in the index. Two sampling issues may contribute to the bias against the spring capture of COYs. First, polar bear families often do not emerge from the maternal den until early April (Amstrup and Gardner, 1994). Because family groups located in dens are not available for capture, capture efforts conducted in March are likely to under-sample females with COYs. Second, Amstrup and Gardner (1994) showed that many female polar bears in the Beaufort Sea denned on the far offshore pack ice. Females emerging from dens far offshore may be less available to capture by research crews operating from logistical bases onshore.

In our analysis of cub production data, we controlled for the first source of bias by excluding capture data from March. For the 1967–89 period, however, spring samples still included a higher proportion of yearlings than of COYs. This suggests that the under-representation of COYs in the spring sample for the early period was due to bears that denned far offshore. Indeed, new analyses of the distribution of denning in the U.S. portion of the SBS region confirm that more bears denned in far offshore regions in early years of polar bears studies than in the recent decade (Fischbach and others, unpub. data, 2006). We attribute this shift in denning distribution to sea ice conditions that have become less suitable as a substrate for denning.

The suspected shift over time towards more onshore denning cannot account for the profound decline in the number of COYs per adult female captured in the autumn (0.61 versus 0.25). During the freeze-up period of our autumn

sampling, polar bears in the SBS region are concentrated in the nearshore areas (Durner and others, 2004) where they are highly vulnerable to capture by shore-based research crews. Therefore, the observed decline in the number of COYs per adult female captured in the autumn must reflect an actual decline in the survival of cubs between den emergence and the autumn sampling period, and not a sampling artifact. This decline in turn appears to be the principal cause of the increase in COYs and decrease in yearlings that we observed in the spring capture data after 1989.

Observed changes in the physical stature of polar bears in the SBS region appear to parallel declines in recruitment. Declines in skull size for both COYs and adult males were significant. The decline in body weight for adult males was significant. Such changes in physical stature may suggest different impacts of reduced summer sea ice on adult male and female polar bears. In the spring, adult males often forgo foraging opportunities and focus their efforts on locating females for mating. Therefore, adult males enter the summer period in relatively poorer nutritional condition. They may then be more vulnerable to summer sea ice retreats, which can separate polar bears from foraging habitats thought to be the most productive (Amstrup and others, 2006). Conversely, reduced foraging opportunity for adult females usually is first reflected in poorer survival of young. Although the average body weight of COYs did not decline significantly between the two periods, their weights were slightly lower in the latter period. Evidence from other portions of the polar bear's range suggest lower weights, combined with significantly smaller skull sizes, may be related to the poorer survival we observed for COYs in recent years. In western Hudson Bay, Canada, which is near the southern extreme of the species range, declines in cub survival and physical stature were recorded for years (Stirling and others, 1999; Derocher and others, 2004) before a statistically significant decline in population size was confirmed. In western Hudson Bay, we associated the decline in population size with reduced survival of juvenile polar bears and adults that were beyond prime ages. Poorer survival of animals in those age classes was directly related to the reduced availability of sea ice (Regehr and others, unpub. data, 2006). The situation in western Hudson Bay offers insight into the future status of polar bears in more northern regions such as the SBS, because recently observed declines in the area and extent of sea ice are predicted to continue throughout the polar basin (Overpeck and others, 2005; Stroeve and others, 2005).

Evidence of declining physical stature and poorer survival of COYs in the SBS region is consistent with other observations, which suggest that changes in the sea ice may be adversely affecting polar bears. Previously, human harvest accounted for most documented polar bear mortalities in the SBS region (Amstrup and Durner, 1995). In contrast, several recently observed mortalities were directly related to sea ice retreat, or appeared related to changes in food availability that may be associated with sea ice retreat. In autumn of

2004, four polar bears were observed to have drowned while attempting to swim between shore and the distant pack ice. Despite offshore surveys extending back to 1987, similar observations had not previously been recorded (Monnett and Gleason, 2006). During winter and early spring of 2004, three observations were recorded of polar bears hunting, killing, and consuming other polar bears in the Beaufort Sea (Amstrup and others, 2006). Similar observations had not been recorded in that region despite studies extending back for decades. In spring of 2006, three adult female polar bears and one yearling were found dead. Two of these females and the yearling had depleted their lipid stores and apparently starved to death. Although the third adult female was too heavily scavenged to determine a cause of death, her death appeared unusual because prime age females have had very high survival rates in the past (Amstrup and Durner, 1995). Similarly, the yearling that was found starved was the offspring of another radiocollared prime age female that had recently disappeared from the airwaves. Annual survival of yearlings, given survival of their mother, was previously estimated to be 0.86 (Amstrup and Durner, 1995). Therefore, the probability that this yearling died while its mother was still alive was only approximately 14 percent. These anecdotal observations, in combination with both the changes in survival of young and in physical stature reported here, suggest mechanisms by which a changing sea ice environment can affect polar bear demographics and the status of populations.

Conclusions

Information on changes in survival and physical stature, reported here, indicate that the status of polar bears in the SBS region is changing. Annual survival rates of COYs estimated from the 2001 to 2006 capture-recapture study were lower than survival rates estimated in previous studies. The increased loss of cubs during the first 6 months of life may be associated with the smaller physical stature of COYs observed in recent years. The smaller physical stature of COYs was paralleled by a smaller physical stature of adult males, even though the average age of adult males has increased. Despite these indicators of a declining status for the SBS polar bear population, our best estimate of the current size of the population does not show a statistically significant decline. This may mean there has been no change in numbers in recent years, or it could reflect insufficient precision in current and past estimates to resolve such a change.

Although our 2001–06 capture-recapture study did not provide evidence for a change in the size of the SBS polar bear population, significant changes in cub survival and physical stature must ultimately have population level effects. Lowered body weight has been implicated in declining survival of polar bear cubs in western Hudson Bay, Canada. There, reduced cub survival, associated with declines in physical stature caused by reduced foraging opportunity, was recorded long

before a statistically significant decline in population size was confirmed. The relationship between decreased availability of sea ice and declining population size in western Hudson Bay, which is near the southern extreme of polar bear range, is cause for concern regarding the future status of polar bears in more northern regions such as the SBS. Because more profound declines in sea ice area and extent are predicted for these northern regions, continued monitoring and conservative management of the SBS polar bear population is warranted.

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Appendix A. Description of Sex Composition, Age Composition, and Other Summary Statistics for Polar Bears Captured in the Southern Beaufort Sea, 2001–06.

We summarized the sex composition, age composition, and proportion of marked versus unmarked bears using captures of polar bears encountered by standard search only, because polar bears encountered by radiotelemetry consisted mostly of adult females and dependent young. Trends were described using standard regression techniques (e.g., Boyce, 1984; Comiso, 1986). For example, we assessed temporal variation in the sex ratio by computing a likelihood ratio test for a logistic model with an intercept only (H_0), versus a logistic model with an intercept and five design variables, which allowed the proportion of females to differ among years (H_A).

[Table A1](#) summarizes the proportion of adult polar bears in the capture sample that were previously marked. The proportion of females in the capture sample was variable among years (logistic regression; time-dependent model versus time-constant model, $G = 19.22$, $df = 5$, $P = 0.002$), due to the difference between a high proportion of females in 2001 and a low proportion of females in 2003 (Tukey-type multiple comparison test for proportions; $q_{2001-2003} = 1.07$, $SE(q_{2001-2003}) = 0.25$). The high in 2001 reflects the fact that autumn sampling occurred in that year of the study. Historically, autumn samples have included high proportions of females and young. The overall proportion of females in the capture sample was 0.54 ($SE = 0.02$).

Table A1. Proportion of adult (age ≥ 5 yr) polar bears with a previous capture in the current study.

[Data are for polar bears captured by standard search in the southern Beaufort Sea by the U.S. Geological Survey, 2001–06, and the Canadian Wildlife Service, 2003–06]

Year	Total captures	Recaptures	Proportion recaptures
2001	73	0	0.00
2002	50	10	0.20
2003	93	12	0.13
2004	157	29	0.18
2005	146	45	0.31
2006	100	39	0.39

The overall age class composition of the capture sample was 0.12 ($SE = 0.03$) COYs, 0.09 ($SE = 0.03$) yearlings, 0.07 ($SE = 0.03$) 2-year-olds, 0.12 ($SE = 0.03$) subadults, and 0.60 ($SE = 0.02$) adults. The proportion of females in each age class was 0.47 for COYs, 0.55 for yearlings, 0.62 for 2-year-olds, 0.56 for subadults, and 0.55 for adults. The proportion of adult polar bears in the capture sample was stable among years (logistic regression; time-dependent model versus time-constant model, $G = 6.62$, $df = 5$, $P = 0.251$), with an overall value of 0.60 ($SE = 0.02$). The age of adult (i.e., age ≥ 5 yr) females was stable among years (Kruskal-Wallis test; $\chi^2 = 4.16$, $df = 5$, $P = 0.527$), with a mean value of 11.8 yr ($SE = 0.33$). The age of adult males was stable among years (Kruskal-Wallis test; $\chi^2 = 6.18$, $df = 5$, $P = 0.289$), with a mean value of 10.8 yr ($SE = 0.33$).

From 2001 to 2006, 37 previously marked polar bears were killed as part of a legal, regulated harvest by Inuit hunters in the SBS region ([table A2](#)). Because CJS models are appropriate for live-recapture data only, we excluded these deaths and 15 natural deaths (i.e., polar bears that we found dead on the sea ice, or cubs that were presumed dead because their mothers were later observed alone) from the data. We included death records for two research-related mortalities that occurred from 2001 to 2006, which the CJS model effectively handles by right-censoring the individual capture histories of animals not released back into the population following capture.

Table A2. Previously marked polar bears harvested in the southern Beaufort Sea, 2001–06.

	Female	Male
Adult ¹	7	13
Subadult	1	10
Two-year-old	5	1
Yearling	0	0
Cub-of-the-year	0	0

¹Adult (≥ 5 yr); Subadult (3–4 yr)

Appendix B. Description of Model Notation, and the Model Selection Table for Cormack-Jolly-Seber (CJS) Models Fitted to Capture-Recapture Data for Polar Bears in the Southern Beaufort Sea, 2001–06.

The model notation used in [table B1](#) is an extension of the standard CJS notation developed by Lebreton and others (1992). We fitted models that allowed survival (ϕ) and recapture (p) probability to vary as functions of individual, group, and environmental covariates. Time-constant and time-dependent parameterizations were denoted $(.)$ and (t) , respectively. In the parameterization for ϕ , we considered four age classes: cubs-of-the-year (i.e., COYs, 0 yr; denoted $a1$), yearlings (1 yr; $a2$), subadults (2–4 yr, $a3$), and adults (5+ yr; $a4$). We denoted combinations of age classes using the letter “ a ” followed by several integers. For example, an aggregate age class comprising COYs ($a1$) and yearlings ($a2$) was written $a12$. Age structure was written in square brackets. For example, the model $\phi([a12, a3, a4])$ estimated time-constant survival probabilities for three age classes: $a12$, $a3$, and $a4$. We denoted models that included both additive (“+”) and interactive (“ \times ”) effects using nested brackets. For example, model $\phi(a1 + \{[a2, a3, a4] \times \text{sex}\})$ estimated a single survival

probability for COYs, but included age \times sex interactions for yearlings, subadults, and adults. The environmental covariates ice^{i, ϕ_j} and $\text{ice}^{i, \phi_{j+1}}$ were used to relate the sea ice conditions in the year j to survival probabilities in the year j and $j+1$, respectively. The covariate *linear* represented a generic linear trend in ϕ . The covariate *trans* represented transience, which was parameterized as an additive effect in ϕ following the occasion of first capture for subadult and adult male polar bears.

In the parameterization for p , the covariate *effort* represented the number of helicopter hours flown in capture operations each year. The individual covariate *agency* indicated whether each polar bear was first captured by the USGS or CWS. We used the notation *agency** to indicate a parameterization for p that estimated time-constant p for U.S. and Canadian bears, but allowed p_{2006} to differ for Canadian bears. The time-dependent individual covariate *radio* indicated whether each polar bear was available for recapture by radiotelemetry.

Table B1. Model selection table for CJS models fitted to capture-recapture data for polar bears in the southern Beaufort Sea, 2001–06.

[QAIC = Akaike’s information criterion adjusted for on a variance inflation factor (\hat{c}) of 1.33; dev = model deviance, np = number of estimated parameters, and w_i = normalized Akaike weight. Of the 152 total CJS models fitted in the analysis, only models with $\Delta\text{QAIC} \leq 7.0$ (which corresponds to approximately $w_i \geq 0.01$) were considered for model averaging, and are shown here]

No.	Survival	Recapture	np	dev	QAIC	w_i
1	$\phi([a1, a234])$	$p(\text{agency}^* + \text{radio})$	6	1416.10	1076.73	0.18
2	$\phi([a1 + \{[a234] \times \text{sex}\}])$	$p(\text{agency}^* + \text{radio})$	7	1414.06	1077.20	0.14
3	$\phi([a1, a234] + \text{ice}^{i, \phi_{j+1}})$	$p(\text{agency}^* + \text{radio})$	7	1414.51	1077.54	0.12
4	$\phi([a1, a234] + \text{linear})$	$p(\text{agency}^* + \text{radio})$	7	1414.75	1077.73	0.11
5	$\phi([a1, a234] + \text{ice}^{i, \phi_{j+1}})$	$p(\text{agency}^* + \text{radio})$	7	1414.94	1077.86	0.10
6	$\phi(\{a1 \times \text{ice}^{i, \phi_{j+1}}\} + [a234])$	$p(\text{agency}^* + \text{radio})$	7	1415.82	1078.53	0.08
7	$\phi(\{a1 \times \text{linear}\} + [a234])$	$p(\text{agency}^* + \text{radio})$	7	1415.96	1078.64	0.07
8	$\phi(\{a1 \times \text{ice}^{i, \phi_j}\} + [a234])$	$p(\text{agency}^* + \text{radio})$	7	1415.98	1078.65	0.07
9	$\phi([a1, a234])$	$p(\text{agency}^* + \text{radio})$	7	1416.03	1078.68	0.07
10	$\phi([a1 + \{[a2a3a4] \times \text{sex}\}])$	$p(\text{agency}^* + \text{radio})$	9	1413.20	1080.56	0.03
11	$\phi[a1a2a3a4]$	$p(\text{agency}^* + \text{radio})$	8	1415.99	1080.65	0.03
12	$\phi([a12, a34])$	$p(\text{agency}^* + \text{radio})$	6	1423.30	1082.15	0.01
13	$\phi([a1, a2, a34] + \text{trans})$	$p(\text{agency}^* + \text{radio})$	8	1416.02	1080.68	NA ¹
14	$\phi([a1, a2, a3, a4] + t)$	$p(\text{agency}^* + \text{radio})$	10	1413.45	1082.74	NA ¹
15	$\phi([a1, a234] + \text{ice}^{i, \phi_{j+1}})$	$p(\text{radio})$	5	1428.00	1083.68	0.01

¹Models No. 13 and 14 were excluded from model averaging; see Results: Estimating survival rate and population size.

Appendix C. Secondary Capture-Recapture Analysis to Investigate *a posteriori* Hypotheses.

After completing the main analysis, we performed a secondary analysis to investigate sex-specificity in recapture probability. This was motivated by the *a posteriori* hypothesis that females with dependent young may avoid male polar bears by limiting their use of preferred habitats (Stirling and others, 1981), which also were the habitats that we searched most intensively in our capture efforts. We began by modifying the most general model from the main analysis, to include an additive sex effect in p for subadult and adult males. After including this more general parameterization for p , we found that the data supported a “transient” effect in ϕ for subadult and adult males. Transience had been considered in the main analysis, but was poorly supported at that time (table B1, appendix B). Because differential capture probabilities between males and females and transience among males were both reasonable biological hypotheses, we evaluated their impact by continuing with a complete secondary model selection process.

The low-QAIC model from the secondary analysis was identical to the low-QAIC model from the main analysis, except that for subadult and adult males it included both the additive effect in p ($\hat{\beta} = 0.78$, $\text{SE}(\hat{\beta}) = 0.23$; likelihood ratio test versus null model without β : $\chi^2 = 13.37$, $\text{df} = 1$, $P < 0.001$), and the additive transient effect in ϕ ($\hat{\beta} = -2.23$, $\text{SE}(\hat{\beta}) = 0.83$; likelihood ratio test versus null model without β : $\chi^2 = 7.06$, $\text{df} = 1$, $P = 0.008$). The magnitude of the sex effect in p was such that subadult and adult males had nearly twice the recapture probability of other polar bears (e.g., 0.21 versus 0.11 for “U.S.” polar bears). Although a higher p for males was consistent with our hypothesis of sex-based habitat segregation, the magnitude of this effect was not realistic. Apparently, the estimated p for males was exaggerated by interaction with the transient effect (see below).

Evidence for transience was consistent with the GOF analysis, which indicated that the data contained an unusually large number of subadult and adult males that were captured once, and never recaptured. These polar bears were considered “transients” based on the assumption that they were present in the study area for a relatively short period (during which they were exposed to sampling efforts), after which they emigrated permanently. The transient parameterization of the CJS model handles this by estimating a different survival probability following first capture. From a modeling perspective, this allows transient individuals to “die” (i.e., to leave the study population), and therefore minimizes their impact on the estimates of apparent survival for non-transient individuals. We considered that this approach might be reasonable,

because the annual use areas of highly mobile polar bears were potentially large with respect to the study area (Amstrup and others, 2000).

Both the GOF analysis and the secondary modeling indicated that transience was limited to male polar bears, which suggests differential movement patterns between males and females. This finding may be significant, because although there are few movement data for male polar bears, the limited information that is available suggests that movements of male and female polar bears are similar (Amstrup and others, 2001b). The low-QAIC model from the secondary analysis estimated that ϕ was 0.63 ($\text{SE} = 0.10$) for newly marked subadult and adult males. The estimated value of ϕ for all other polar bears older than COYs (i.e., females, and males subsequent to their first capture) was 0.94 ($\text{SE} = 0.04$). This “transient-corrected” value of ϕ was higher than the estimate of 0.92 ($\text{SE} = 0.04$) from the main analysis, and likely represents an intermediate value between apparent survival and biological survival. We used the ratio of the two survival probabilities from the low-QAIC model to derive a rough estimate of the proportion of transients among newly-captured subadult and adult males: $1 - 0.63 / 0.94 = 0.33$ (Cooch and White, 2005, Chapter 8).

Aside from the inclusion of the two effects discussed above, model selection was similar for the main and secondary analyses. Also, the mean of the 2004–06 model-averaged estimates of population size from the secondary analysis was 1,523, which is nearly identical to the estimate of 1,526 from the main analysis. However, the inclusion of a sex effect in p in the secondary analysis resulted in a strongly skewed sex ratio in the subadult and adult components of the population (approximately 0.70 female). This was unrealistic, and largely an artifact of model structure. The CJS model that allowed for both sex-specificity in p and transience in ϕ for males, effectively estimated values of p (and consequently N) that applied only to the males in the population that were considered “residents.” However, the delineation of “transients” versus “residents” was somewhat arbitrary, because it was a cumulative function of study duration, movement patterns, and other unknown phenomena. Furthermore, valid estimation of population size requires the assumption that estimated recapture probabilities apply to all animals in the population, which is clearly not the case here. In conclusion, the 2001–06 capture-recapture data suggested the potential for differences in movement patterns for males and females. Ultimately, these differences were beyond the ability of the data to resolve.

Appendix D. Statistical Properties of Parameter Estimates and the Model Selection Process

The bootstrap procedure that we used to estimate the variance in \hat{N}_j also allowed us to investigate some statistical properties of the real parameter estimates, and of the model selection procedure. For survival, mean percent relative bias (PRB) was less than 1% between the model-averaged point estimates, and the mean values of the bootstrapped estimates. For population size, mean PRB was -1% between the model-averaged point estimates, and the mean values of the bootstrapped estimates. Mean PRB was 17% between $SE(\hat{N}_j)$ derived from the Laake estimator (Taylor and others, 2002) for the low-QAIC model, and $SE(\hat{N}_j)$ estimated from the distribution of the model-averaged bootstrapped estimates. This suggests reasonable agreement between theoretical and simulation-based variance estimators. Finally, we found that model selection frequencies from the bootstrap procedure were similar to the QAIC weights for models with $\Delta QAIC \leq 7.0$ (Burnham and Anderson, 2002) ([table D1](#)).

Table D1. Comparison between QAIC weights and bootstrapped model selection frequencies for the CJS models as defined in [table B1](#).

No.	QAIC weight	Frequency
1	0.18	0.25
2	0.14	0.29
3	0.12	0.14
4	0.11	0.06
5	0.10	0.07
6	0.08	0.04
7	0.07	0.02
8	0.07	0.02
9	0.07	0.00
10	0.03	0.05
11	0.03	0.01
12	0.01	0.03
13	NA	NA
14	NA	NA
15	0.01	0.04

For more information concerning the research in this report, contact
Director, Alaska Science Center
U.S. Geological Survey
1011 East Tudor Road
Anchorage, Alaska 99503
<http://alaska.usgs.gov/>

Reduced body size and cub recruitment in polar bears associated with sea ice decline

KARYN D. RODE,^{1,3} STEVEN C. AMSTRUP,² AND ERIC V. REGEHR^{1,2}

¹U.S. Fish and Wildlife Service, Marine Mammals Management, 1011 East Tudor Road, Anchorage, Alaska 99503 USA

²U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska 99508 USA

Abstract. Rates of reproduction and survival are dependent upon adequate body size and condition of individuals. Declines in size and condition have provided early indicators of population decline in polar bears (*Ursus maritimus*) near the southern extreme of their range. We tested whether patterns in body size, condition, and cub recruitment of polar bears in the southern Beaufort Sea of Alaska were related to the availability of preferred sea ice habitats and whether these measures and habitat availability exhibited trends over time, between 1982 and 2006. The mean skull size and body length of all polar bears over three years of age declined over time, corresponding with long-term declines in the spatial and temporal availability of sea ice habitat. Body size of young, growing bears declined over time and was smaller after years when sea ice availability was reduced. Reduced litter mass and numbers of yearlings per female following years with lower availability of optimal sea ice habitat, suggest reduced reproductive output and juvenile survival. These results, based on analysis of a long-term data set, suggest that declining sea ice is associated with nutritional limitations that reduced body size and reproduction in this population.

Key words: body size; climate; condition; habitat; morphometrics; polar bears; sea ice; southern Beaufort Sea, Alaska, USA; *Ursus maritimus*.

INTRODUCTION

The global climate is undergoing rapid change (Hansen et al. 2005, Lemke et al. 2007, Meehl et al. 2007, Overland and Wang 2007). Biologists have the difficult task of determining the best way to monitor potential responses of wildlife populations to these changes. Population level effects of environmental change are difficult to detect, particularly for large, long-lived species (Ginzburg et al. 1990, Parmesan and Yohe 2003). In many cases, collection of the individual-based data necessary to monitor population status is precluded by logistical constraints, expense, coordination across international boundaries, and other obstacles. Even when population size and vital rates can be estimated, historical data are often insufficient to allow a meaningful assessment of trends over time (Regehr et al. 2006).

Morphometric data may provide a useful alternative for monitoring long-term trends and future changes because these data are often available from harvested or captured animals and can be indicative of current or future vital rates (Testa and Adams 1998, Karels et al. 2000, Hall et al. 2001, Regehr et al. 2007). Growth rates in mammals are largely influenced by nutrient availability (Mahoney et al. 2001, Eifler et al. 2003), which may

be mediated by changes in ecosystem productivity or changes in relative animal density. Sustained increases or decreases in availability of nutrients to growing animals can, therefore, affect the size of fully grown adults within a population (Geist 1987). Measurements of body mass and skeletal size have been shown to reflect changes in environmental conditions over time and space (Kingsley 1979, Post et al. 1997, Derocher and Stirling 1998b, Lopez-Fuster et al. 2000, Kojola and Laitala 2001, Herfindal et al. 2006, Mysterud and Ostbye 2006, Cardini et al. 2007) and have been linked to reproduction and population density (Atkinson and Ramsay 1995, Post et al. 1997, Laundre et al. 2007, Wauters et al. 2007). Morphometric measurements, therefore, can provide insights into demographic processes as well as indicators of the mechanisms that may be driving those processes.

Morphometric data are commonly collected for ursids and have been linked to diet (Hilderbrand et al. 1999a, b, Mowat and Heard 2006), reproduction (Derocher and Stirling 1994, 1998a, Noyce and Garshelis 1994, Atkinson and Ramsay 1995, Stirling et al. 1999), cub survival (Derocher and Stirling 1996), and population density (Hilderbrand et al. 1999b, Ferguson and McLoughlin 2000). Heavier females have been shown to have larger litters and heavier cubs (Derocher and Stirling 1994), suggesting that body mass is a good indicator of female condition (Noyce and Garshelis 1994). Size of cubs-of-the-year (COY, bears <1 year old) and yearlings (bears >1 and <2 years of age) has

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³ E-mail: karyn_rode@fws.gov

been related to cub survival (Derocher and Stirling 1996) and age of first reproduction (Kingsley et al. 1988, Garshelis 1994, Derocher and Stirling 1998a). Measurements of bear size, including mass, skull size, and length, have been associated with temporal and spatial variation in environmental conditions (Ferguson and McLoughlin 2000, Derocher and Wiig 2002, Mowat and Heard 2006).

The extent and thickness of Arctic sea ice have been in decline for decades (Richter-Menge et al. 2006, Lemke et al. 2007, Meehl et al. 2007), and climate models project greater sea ice changes in the foreseeable future (Overland and Wang 2007, Serreze et al. 2007, Stroeve et al. 2007). Polar bears (*Ursus maritimus*) depend upon sea ice as a platform for accessing seals (Amstrup 2003), their primary prey throughout their circumpolar range (Iverson et al. 2006). As a result, the nutritional status and growth of polar bears are closely tied to the availability of sea ice habitat. Spatial and temporal reductions in sea ice cover in southern portions of the species' range have corresponded with declines in body condition, survival, and population size (Stirling et al. 1999, Regehr et al. 2007). However, of the 19 polar bear populations recognized throughout the circumpolar Arctic, data on long-term trends in polar bear condition and vital rates in response to changing sea ice conditions are rare and to date have only been evaluated for a single population in western Hudson Bay (Stirling et al. 1999, Regehr et al. 2007).

Several studies suggest that the southern Beaufort Sea (SB) population may be responding to changing ice conditions. There, denning distribution shifted between 1985 and 2004 to include fewer sites on the pack ice and more sites on land, a change that corresponded with a reduction in the availability and quality of pack ice denning habitat (Fischbach et al. 2007). Regehr et al. (2006) estimated that the size of the SB polar bear population (1526) was lower than the previous estimate of 1800 in 1986 (Amstrup et al. 1986). Although low precision of the earlier estimate prevented a determination that this represented a statistically meaningful decline, Regehr et al. (2009) subsequently reported that survival and reproduction of polar bears in the southern Beaufort Sea of northern Alaska and adjacent Canada declined in years of reduced sea ice availability. Impacts of continuing declines in the spatiotemporal extent of sea ice on polar bear population size and trend will depend on the sum of the effects sea ice changes have on breeding success, denning success, and survival. Currently, however, the mechanisms by which sea ice loss affects these variables are poorly understood.

One of the primary mechanisms by which sea ice loss may affect polar bears is via poorer body condition and growth patterns resulting from reduced access to prey. Polar bears can only hunt ice seals, their primary prey, effectively from the sea ice and are rarely successful at capturing seals in open water. Reduced food intake associated with sea ice loss could cause changes in body

size (e.g., skull size and body length) that are indicators of nutritional limitations. Similarly, nutritionally driven declines in body condition (e.g., body mass or condition indices) can lead to reductions in reproduction and juvenile survival (Noyce and Garshelis 1994). In this study we examined relationships between interannual variation in sea ice availability and several potential indicators of bear condition (skull size, body mass, and condition indices that account for differences in body length) and reproduction (litter mass and cubs/female) collected on polar bears in the Alaskan portion of the SB region from 1982 to 2006. To evaluate potential cumulative effects of changing sea ice conditions on polar bears we also examined long-term trends in these metrics. While changes in body size (e.g., skull size and body length) may provide indications of nutritional limitations, changes in body condition (e.g., body mass or condition indices) can have consequences for survival and reproduction. A variety of condition indices have been suggested for ursids. One of our first objectives was to determine which of several proposed condition measures (body mass, skull size, Quetelet's index, and body condition index [BCI]) exhibited the closest relationships with reproductive output.

Specifically, we addressed the following four questions: (1) Is reproductive output, quantified as litter mass, associated with maternal condition? If so, what measures of female stature/condition (condition indices, body mass, skull size) are most closely related to reproductive output? (2) Did body mass, skull size, or condition relate to interannual variation in available ice habitat? (3) Did body mass, skull size, or condition of polar bears exhibit a trend between 1982 and 2006? (4) Did reproductive output (litter mass and cubs per female) exhibit a trend between 1982 and 2006? Was it related to interannual variation in available ice habitat?

MATERIALS AND METHODS

Capture, handling, and measurement of bears

Polar bears were captured in coastal areas of the SB region, from Point Barrow, Alaska (~157° W) to the U.S.–Canadian border (at 141° W) (Fig. 1, Plate 1). Captures occurred from March through early May in 1982–1989, 1991–1992, and 1998–2006, with additional autumn captures occurring between October and November in 1982–1983, 1985–1989, 1994, 1997, and 1999–2001. Polar bears were located using a helicopter. Most bears were located by following their tracks across the snow and ice, though some bears were located without tracking. Searching occurred over the continental shelf, which has been identified as the area where bears concentrate in the spring (Durner et al. 2004). Search paths followed areas of likely polar bears habitat, such as leads, seal haul-outs, and pressure ridges. Before pack ice reformed in autumn, bears were captured on land, barrier islands, or newly formed land-fast ice in lagoons. Adults and subadults were captured by administration of immobilizing drugs with projectile

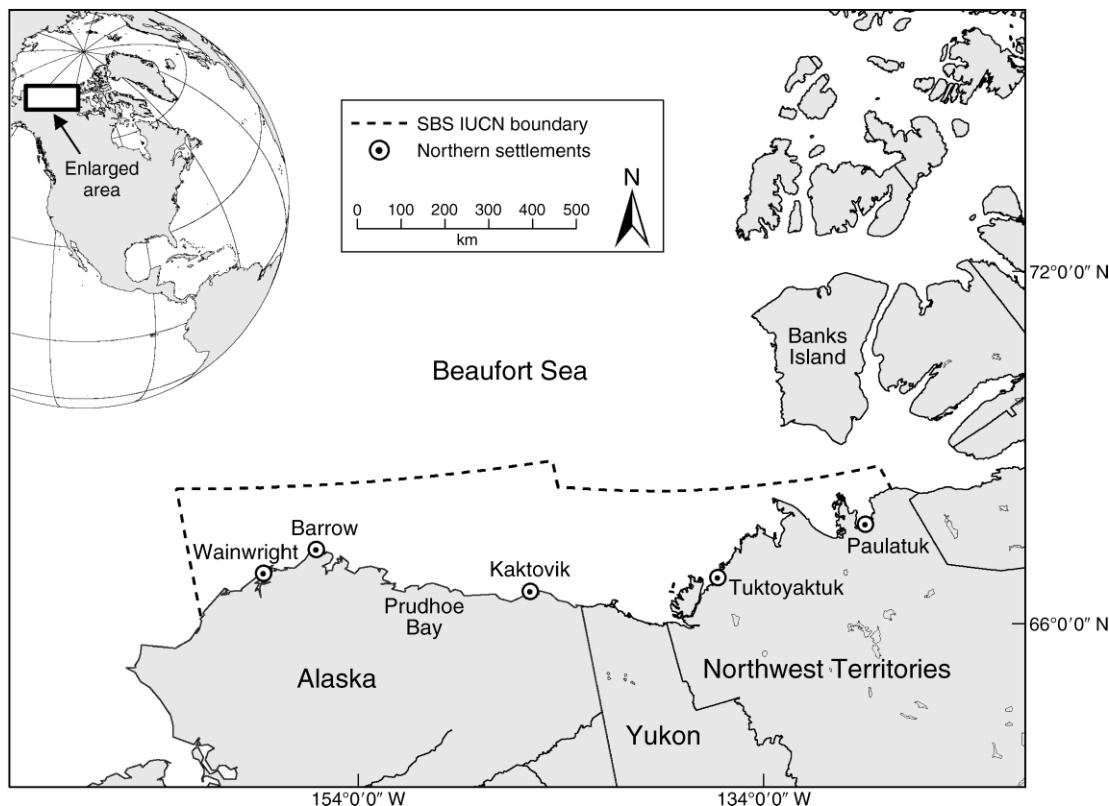


FIG. 1. The southern Beaufort Sea (SB) management unit for polar bears (*Ursus maritimus*), established by the World Conservation Union (IUCN) Species Survival Commission.

syringes fired from helicopters. Yearlings and cubs-of-the-year accompanying adult females were captured by darting from the ground or hand injection. After 1986, all bears were immobilized with Telazol (Fort Dodge Animal Health, Fort Dodge, Texas, USA). In earlier years of the project, polar bears were immobilized with either Sernylan or M-99. The timing of spring captures overlapped with timing of den emergence, but lasted beyond the time period when all females would have emerged from dens (i.e., early May).

Calipers were used to measure the zygomatic width of bear skulls. Though a variety of measurements have been used to quantify the skull size of ursids (Noyce and Garshelis 1994, Chestin and Mikeshina 1998, Derocher and Stirling 1998b), zygomatic width, or head circumference, has been shown to vary between populations that experience different environmental conditions (Derocher and Stirling 1998b, Zedrosser et al. 2006). Because skull measurements of live bears can include a fat layer, this measure could be responsive to annual variation in environmental conditions even for bears that have stopped growing. Body length (length) was measured because it is required to calculate several types of condition indices. Length was measured as the straight line distance from the tip of the nose to either the end of the last tail vertebrae (for bears caught after 2001) or to the base of the tail (for bears caught prior to

2002) using a measuring tape extended several centimeters above the bear, avoiding variation with the body contour, in ventral (sternal) recumbency. Tail length was measured from the base to the last tail vertebrae. Mean tail lengths were determined for each sex and age class and used to standardize body length measurements by subtracting mean tail length as needed. This correction was unbiased because tail length was not correlated with body lengths for any of these classes (Pearson's correlation: $P > 0.3$ for all classes).

Bears were weighed to the nearest kilogram using a spring or dynamometer scale. Observers taking measurements varied throughout the study, but all were trained by S. Amstrup and attention was paid to ensuring consistency in measurements between observers. A vestigial premolar was extracted for age determination upon first capture, except for dependent young, which could be visually aged based on size and dentition. Age from teeth was estimated by counting cementum annuli (Calvert and Ramsay 1998).

Condition indices that relate body mass to body length have frequently been used to assess the status of polar bear populations and relationships with reproduction (Derocher and Stirling 1998a, Stirling et al. 1999, Cattet et al. 2002, Obbard et al. 2006). We used body mass and length to calculate two indices of condition for reproductive females: Quetelet's (W/L^2) and BCI (Cattet

et al. 2002). We used these measures to identify which condition measure (BCI, Quetelet's, or body mass) most closely related to litter mass and therefore, might be best used to infer how changes in female condition might affect reproduction. In addition, we included skull width as a possible condition measure for adult females that could relate to litter mass. Skull width measured on live bears likely may include a fat layer and be indicative of female condition. For all sex and age classes, we calculated only Quetelet's index because values have been found to relate directly to the lipid content of adipose tissue and subjective fat index ratings applied to polar bears (Stirling et al. 2007). While BCI may be a similarly meaningful measure of condition, for simplicity we chose to use one index only.

Quantifying annual availability of ice habitat

We quantified the availability of sea ice habitat using resource selection function (RSF) models (Manly et al. 2002). We defined the SB population range according to Amstrup et al. (2004) as the area lying within the 95% contour of the utilization distribution of the SB population. Location data from satellite radio-collared polar bears collected from 1985 to 1995 were used to build RSFs during each of four seasons based on bathymetry, proximity to land, ice concentration, and distance to ice edges. These models, when applied to independent data collected from 1996 to 2006 consistently identified habitats most frequently used by polar bears (Durner et al. 2009). Because 70% of polar bear locations consistently occurred within the upper 20% of the RSF-valued area, optimal habitat was defined as the mean RSF value that separated the upper 20% from the lower 80% of the RSF-valued area for each season. All mapped pixels with raw RSF values greater than the upper 20% threshold, were included in optimal habitat. We summed the area (km^2) of optimal habitat for each month to generate an annual value of available optimal sea ice habitat, which we called "ice." We used ice to assess change in habitat availability ($\text{km}^2 \times \text{month}$) among years of the study. For a more detailed description of the methods used to generate RSFs and the optimal habitat metric, see Durner et al. (2009).

Use of growth curves to define age classes

Five classes of bears were defined for analyses: slow-growing (SG) males and females, fast-growing (FG) males and females, and dependent cubs. "Cubs" included both cubs-of-the-year and yearlings. Two-year-olds were excluded due to a small sample size in this age group. These classes were chosen because they face different nutritional constraints, and changing environmental conditions were expected to affect them differently. For example, young, fast-growing bears have different nutritional requirements resulting from the need to acquire muscle mass in addition to the seasonal accumulation of body fat acquired by adult (slow-growing or fully-grown) bears. These categories

were also chosen because covariates that may affect morphometric measures differ among these classes. For example, the reproductive status of SG females can affect body mass and litter size can affect the size of individual cubs.

FG and SG classes were determined based on growth rates (e.g., Fig. 2). Body mass, skull width, and body length do not increase linearly with age. Rather, they increase rapidly in the early years of an animal's life, approach an asymptote, and then continue growing at a much slower rate for the rest of the animal's life (Kingsley 1979). FG bears were defined as those that had not yet reached 97% of their maximum growth (Derocher and Stirling 1998b, Derocher and Wiig 2002), and SG bears were defined as those that had reached 97% of growth. The age at which bears reached 97% of their maximum growth was determined by fitting modified von Bertalanffy curves to relationships between age and the skull size, body length, and body mass of spring-caught bears (von Bertalanffy 1938, Kingsley 1979, Kingsley et al. 1988, Derocher and Wiig 2002). We chose 97% as a cutoff because this value previously has been used to compare growth between polar bear populations (Derocher and Stirling 1998b). Also, because polar bears continue to grow in most measures throughout their lifetime, it is not possible to use 100% as a cutoff. Furthermore, sexual maturity in females tends to coincide with the time in which they reach 97% of maximum growth (Derocher and Stirling 1998b); thus, this cutoff therefore allows differentiation of classes with and without nutritional demands associated with reproduction.

Data analysis

We used body mass, skull width, and body condition as indicators of interannual variation in nutritional status. Because skull measurements of live bears can include a fat layer, this measure could be responsive to annual variation in environmental conditions even for slow-growing bears. Therefore, all of these measures were examined for relationships with interannual variation in sea ice availability. We also examined whether changes in available sea ice habitat may be associated with long-term trends in these measures between 1982 and 2006 by examining trends in available sea ice habitat and each morphometric measure.

We conducted separate analyses for bears of different sex and age classes because some explanatory variables were only appropriate for certain classes (e.g., sizes of litters associated with adult females), and we conducted separate analyses for data collected in the spring and the autumn.

Question 1: Is reproductive output associated with maternal condition?—We used general linear models to compare the relationships between maternal measures of condition (skull width, body mass, Quetelet's index, and BCI) and litter mass. Litter size (litsize) and capture date

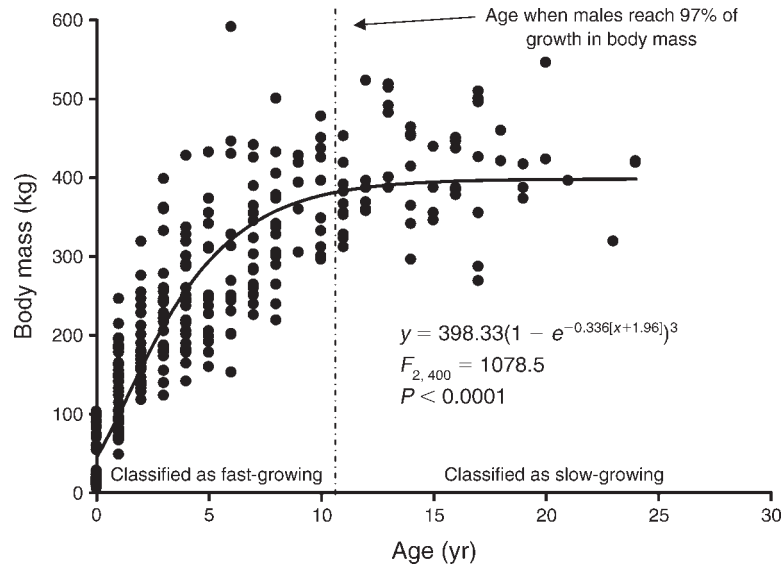


FIG. 2. Relationship between body mass and age of male polar bears in the southern Beaufort Sea fit with a von Bertalanffy growth curve. The age when males reached 97% of maximal growth was used to distinguish fast-growing males from slow-growing males in body mass analyses.

(cdate) were initially included in candidate models due to their potential effects on litter mass.

Questions 2 and 3: Did body mass, skull size, or condition of polar bears relate to interannual variation in available sea ice habitat or exhibit a trend between 1982 and 2006?—As in Question 1, we used general linear models to identify relationships between body size, mass, and condition and ice availability (ice) or year (Table 1). Year or ice were included in models as continuous independent variables (covariates). We did not include both year and ice in the same model because the two measurements reflect different temporal scales: a relationship between bear size, mass, or condition and ice could illustrate an annual response to changing ice conditions, whereas a trend with year could illustrate the cumulative effects of changing environmental conditions or other unmeasured factors over time. Ice conditions during the previous year ($t - 1$) were related to

measurements of bears captured in the spring, and ice conditions during the current year (t) were related to measurements of bears captured in the autumn. Due to low and inconsistent sampling in the autumn, sample sizes were sufficient to only evaluate body size, mass, and condition for SG females and cubs.

We controlled for factors such as age and capture date, which can affect skull size, length, and mass (Table 1). These factors differed between sex and age classes (Table 2). Age was included as a covariate in all models. Because this relationship is not linear for measures of skull width, body length, and body mass, we conducted a log-transformation to allow for the nonlinear relationship between age and bear size. Linearity was confirmed by examining the relationship between predicted values and residuals. Because data were log-transformed, coefficients of models do not provide a direct indication of the degree to which year or ice may have affected each

TABLE 1. Abbreviated name and description of factors included in linear models for polar bears (*Ursus maritimus*).

Abbreviated factor name	Description
Year	year a bear was captured, from 0 to 24
Age	bear age estimated by counting cementum annuli in teeth or as a result of a bear being captured as a dependent young
Cdate	Julian capture date (0–365 days)
Cubs	categorical variable used for slow-growing (SG) females where “0” indicates she was not accompanied by dependent young, and “1,” “2,” and “3” indicate she was accompanied by cubs-of-the-year, yearlings, and two-year-olds, respectively
Ice	annual availability of optimal ice habitat
Litsize	litter size: categorical variable where “1” indicates a litter size of 1 and “2” indicates a litter size of 2 or more
Sex	categorical variable used in models of yearling mass and skull size with a “1” for females and a “2” for males
Mmass	maternal body mass
Mquetelets	maternal body condition based on Quetelet’s index
Mbci	maternal body condition using a body condition index (BCI) established by Cattet et al. (2002)
Mskull	maternal skull width

TABLE 2. Independent variables initially included in linear models for each condition and size metric and sex/age class.

Dependent variable	Independent variables
Slow-growing (SG) males and females	
Length (for both sexes)	age, year, age \times year
SG male mass, skull size, and condition	age, cdate, year (or ice), age \times year (or ice)
SG female mass, skull size, and condition	age, cdate, year or ice, cubs, cubs \times year (or ice), age \times year (or ice), cubs \times cdate, cdate \times year
Fast-growing (FG) males and females	
Skull size, length, mass and condition (for both sexes)	age, cdate, ice or year, age \times year (or ice)
Cubs	
Skull size and mass	cddate, ice or year, sex, litsize, litsize \times cdate, cdate \times year (or ice), age,† age \times year

† Age for cubs was either 0 for cubs-of-the-year or 1 for yearlings.

morphometric measure. To obtain a biologically meaningful estimate of the degree to which any observed changes occurred, models were applied to various combinations of parameters to estimate annual change.

Measures of condition combine body length and mass and are meant to be independent of age effects (Billewicz et al. 1962, Cattet et al. 2002). However, age has been shown to be an important covariate when applying Quetelet's index in humans (Gallagher et al. 1996), and we similarly expected inherent differences in condition between younger growing animals and fully grown adults. Therefore, we included age in models of condition based on Quetelet's index. Because the relationship between age and condition based on Quetelet's index is linear, a transformation was not required. Age/sex categories of SG and FG bears for analysis of condition were based on body mass because this measure takes the longest to approach an asymptotic value.

The number of cubs in a litter (litsize) can affect cub size (Ramsay and Stirling 1988, Derocher and Stirling 1998a) and was therefore included in models for cubs. Furthermore, due to the potential for cub production to affect female body mass and condition, females were categorized as accompanied by cubs (1), accompanied by yearlings (2), accompanied by two-year-olds (3), or not accompanied by dependent young (0). This category (cubs) was included as a fixed effect. Although cub size does not appear to differ between males and females until sometime after the first year (Derocher and Stirling 1998a), we included sex in all models of cub size to control for potential differences. Unlike adults, all measurements of cub size were expected to respond to interannual variation in ice conditions. Additionally, while condition indices are commonly used for independent bears, condition of cubs has primarily been quantified using skull size and body mass (Derocher and Stirling 1994, 1996, 1998a, Noyce et al. 2002). Therefore, we chose to examine trends in only these two measures for dependent young.

Question 4: Did reproductive output exhibit a trend between 1982 and 2006? Was it related to interannual

variation in available ice habitat?—General linear models were used to identify trends over time and relationships with ice for litter mass and the number of cubs-of-the-year or yearlings per female. Females without yearlings or two-year-olds were included in the sample examining trends and relationships in cubs-of-the-year per female. Females with no cubs-of-the-year or two-year-olds were included in the sample to examine yearlings per female. Cubs-of-the-year per female was used as an indicator of annual reproduction. The number of yearlings per female was used as an indicator of recruitment and/or cub survival with the assumption that the number of yearlings per female should remain relatively static over time if levels of cub survival during the first year are maintained. While trends in litter size may also document trends in mortality, it does not account for the possibility of whole litter loss that could occur by the end of the first year. Our measure is, however, complicated by these two values not being totally independent (i.e., if first-year cub survival declines, more lone females are present in the population influencing the estimate of the number of cubs-of-the-year per female in the population), and we have taken this into consideration in our interpretation.

Measures of cubs per females only included counts of females age five years and older because no females under the age of five years were ever observed with cubs. We did not examine trends in the ratios of two-year-olds per female because sample sizes were small and an unknown fraction of two-year-olds were weaned (i.e., independent of their mothers) by the time we sampled them in the spring.

We controlled for potential effects of variation in capture date among samples by including cdate in all models. An inverse binomial was used to model cubs per female. Timing of the capture effort was similar across years, but the mean date in which bears were encountered and captured could have varied. Because younger females may be less likely to reproduce, changes in age structure of the female population could affect our estimates of cubs per female. Therefore, we compared the percentage of all females 5–10 years of age between

the early (1981–1990) and latter (1996–2006) part of the study period using a paired *t* test.

Model selection

Main effects and interactions with fixed effects that were considered to be biologically meaningful initially were included in models (Table 2). For example, interactions between year or ice and age were included due to the potential for bears of different ages to exhibit different responses (e.g., ice could have a different effect on younger vs. older FG bears). AIC values were used to compare candidate models that included one or more explanatory variables and interactions between variables based on knowledge about bear biology. Models with the lowest AIC were considered to explain the most variation with the fewest parameters. Because models with $\Delta\text{AIC} < 2$ should receive consideration in making inferences (Burnham and Anderson 2002), only models with $\Delta\text{AIC} < 2$ are reported in the results. Models that contained interactive effects were removed from candidate models if those interactions did not appear to be biologically significant (i.e., upon graphing there was only a slight variation in slope and trends were similar across parameter values; e.g., for an age \times year interaction, if grouping data by age showed that relationships with year were similar for all age groups). All statistical analyses were conducted in SPSS (version 15.0; SPSS, Chicago, Illinois, USA).

Verification of model assumptions

Collinearity between predictor variables can confound the interpretation of observed variation in response variables (Gotelli and Ellison 2004). Because several continuous predictor variables (e.g., age, year or ice, and cdate) were included in most models, we examined collinearity between all predictor variables. Collinearity condition indices above 15 were considered to be of concern. However, if variance proportions were not similar between variables (i.e., 0.30 or higher) collinearity was deemed to have little effect on model results.

Anderson-Darling tests of normality were used to examine residual distributions to identify possible outliers. Homogeneity of variance was tested using a Levene's test for categorical variables, which includes the effects of covariates on between-category comparisons. We also examined regression residuals for evidence of heteroscedasticity. If variances were not equal, transformations were attempted. Linear models are robust to non-normality (Green 1979) and were therefore used even when data appeared to have non-normal distributions.

RESULTS

From 1982 to 2006, we captured 60.2 ± 33.9 bears/yr (mean \pm SE, range: 11–152) during the spring (March–May) and 38.2 ± 20.9 bears/yr (range: 5–70) during the autumn (October–November). Variation in the number of bears captured per year resulted from variation in

effort and weather conditions. Of all captured bears aged ≥ 3 years, 42% were recaptures. Recaptures were excluded from data analysis to eliminate potential effects of capture history and to ensure data independence. Sample sizes varied among measurements because all measurements were not taken for all bears (Appendices A–C).

Trends in bear length over time and in relation to ice conditions were not biased by the correction factor (i.e., mean tail length for the sex/age class) used to standardize all length measurements to exclude tail length. Model results were the same when using data sets in which only direct measurements of length were made and when using data sets including direct measurements and corrected values. Therefore, our results in the tables are for the larger data set, including both measured and adjusted values for length.

Growth curves

The age when bears reached 97% of their maximum growth differed between sexes and among measurements. Females reached 97% of asymptotic length by 3.9 years (including tail: $y = 195.16[1 - \exp(-0.78[x + 0.60])]$), body mass by the age of 4.8 years ($y = 208.02[1 - \exp(-0.80[x + 0.88])]$), and skull width by the age of 5.9 years ($y = 20.50[1 - \exp(-0.48[x + 1.47])]$). Males reached 97% of asymptotic length by the age of 6.0 years ($y = 226.29[1 - \exp(-0.52[x + 0.79])]$), body mass by the age of 11.7 years ($y = 398.3[1 - \exp(-0.34[x + 0.196])]$), and skull width by the age of 11.9 years ($y = 26.11[1 - \exp(-0.25[x + 2.14])]$).

Because females achieved most of their growth in length and mass by the age of 5 years, females >4 years were defined as slow-growing (SG) and younger, independent females were classified as fast-growing (FG). Because no females younger than 5 years were accompanied by cubs, mass of females in the FG category were not affected by the demands of reproduction and reproductive covariates were not considered for FG females. For analyses of skull width, SG females were defined as >5 years of age and FG females were independent 3–5 year olds. Males >6 years old were classified as SG for analyses of body length while younger, independent males were defined as FG. Though males achieved most of their growth in length by age 6, they continued relatively rapid growth in skull width and mass up to age 12 (e.g., Fig. 2). Therefore, in analyses of male skull size and body mass, SG males were defined as those >11 years old and FG males were 11 years old and younger.

Question 1: Is reproductive output associated with maternal condition?—Maternal mass was related to litter mass for cubs-of-the-year (COY) in the spring and autumn (Table 3). Maternal skull width was most closely related to litter mass of yearlings in the fall and was secondary to maternal mass in accounting for variation in litter mass of COY in the spring. Maternal mass explained five times more of the variation in litter

TABLE 3. Models examining relationships between three maternal condition measures (body mass, Quetelet's index, and BCI) and litter mass of cubs and yearlings in spring and autumn.

Model	ΔAIC	w	F (model)	P (model)	P (condition)
COY spring litter mass					
0.73cdate + 13.04litsize + 0.15mmass + 89.6	0	0.81	8.93	<0.0001	0.012
0.76cdate + 11.61litsize + 5.27mskull + 144.61	1.61	0.16	8.19	<0.0001	0.029
COY autumn litter mass					
-98.85litsize + 0.39mmass + 60.54	0	0.56	7.86	0.002	0.037
-109.4litsize + 126.5mqutelets + 80.94	1.27	0.16	6.96	0.004	0.088
Yearling spring litter mass					
-104.0litsize + 0.17cdate + 12.78	0	0.59	8.96	0.001	NA
-106.76litsize + 0.15cdate + 0.19mmass + 72.70	1.58	0.12	5.96	0.003	0.51
-106.45litsize + 0.15cdate + 54.05mqutelets + 46.6	1.74	0.10	5.88	0.003	0.61
Yearling autumn litter mass					
75.64mskull + 162.70litsize + 1130.44	0	0.85	9.96	0.001	0.009
76.27mskull + 160.59litsize + 0.22cdate + 1201.83	1.95	0.12	6.43	0.002	0.01

Notes: COY is cubs-of-the-year. Models reported are only those with $\Delta AIC < 2$.

mass of COY than either Quetelet's index or BCI. Models including Quetelet's index as a condition measure had ΔAIC values < 2 , suggesting that Quetelet's index shows some relationship with litter mass, but none of these models were significant. BCI values of mothers were not related to litter mass.

Trends in sea ice conditions

There was a chronic decline in the spatiotemporal availability of optimal ice habitat (ice) during the course of our study. Between 1982 and 2006, ice declined by $12.4 \pm 5.9 \text{ km}^2\text{-months}$ per year (Fig. 3; $P = 0.046$). In addition to this chronic decline, values of ice varied greatly among years. Ice availability varied from a low of $1021.8 \text{ km}^2\text{-months}$ in 1998 to a high of $1852.0 \text{ km}^2\text{-months}$ in 1985.

Question 2: Did body mass, skull size, or condition relate to interannual variation in available ice habitat?—Availability of sea ice habitat ("ice") was important in explaining mean skull width in the spring and body mass

and condition of SG and FG females in the spring and autumn (Table 4; Appendix A). Skull width of autumn-caught females with cubs and yearlings was lower during years with reduced ice habitat, but the opposite relationship occurred for females with no cubs. Body length of FG females was also positively related to ice.

Skull width, body length, mass, and condition of FG males were positively related to ice. Similarly, skull width, body mass, and condition of SG males exhibited positive relationships with ice ($\Delta AIC < 2$); none of these models were significant.

Spring skull width and body mass of COY and yearlings were greater following years with shorter ice free periods. There was less evidence to support similar relationships in the autumn where the top models did not include ice as a covariate and AIC weights of models that did include ice were ≤ 0.15 .

Question 3: Did body mass, skull size, or condition of polar bears exhibit a trend between 1982 and 2006?—Mean

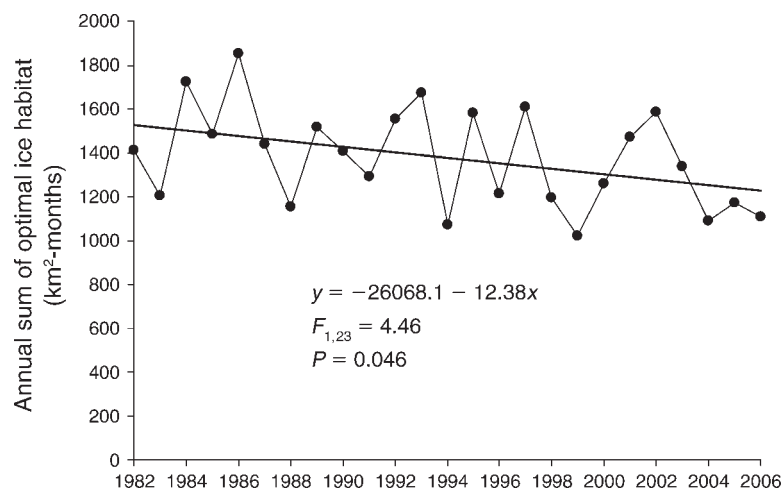


FIG. 3. Annual variation in the availability of optimal ice habitat within the known range of polar bears in the southern Beaufort Sea between 1982 and 2006.

TABLE 4. Relationships between the skull width, body length, mass, and condition of polar bears and the availability of optimal ice habitat within their range in the southern Beaufort Sea.

Bear measurement	Slow-growing		Fast-growing		Cubs
	Female	Male	Female	Male	
Skull width (spring)	+	0	+	+	+
Body length (spring)	NA†	NA	+	+	NA
Mass (spring)	+	0	0	+	+
Condition (spring)	+	0	0	+	NA
Skull width (fall)	+/-‡	NA§	NA§	NA§	0
Mass (fall)	+	NA§	NA§	NA§	0
Condition (fall)	+	NA§	NA§	NA§	NA

Note: A “+” indicates a positive relationship with ice for a model with a $\Delta AIC < 2$ and a significance of $P \leq 0.05$, “-” indicates a negative relationship, “0” indicates no relationship, and “NA” indicates not applicable.

† Relationships between ice and body length were not examined for slow-growing bears because this measure would not be responsive to interannual variation in environmental conditions.

‡ Females with cubs-of-the-year and yearlings exhibited positive relationships with the availability of sea ice, whereas females with no cubs exhibited a negative relationship.

§ Data were insufficient.

skull width and body length of SG and FG females declined by ~ 0.02 – 0.04 and 0.4 – 1.1 cm/yr, respectively (Table 5; Appendix B). The biggest declines were among younger bears. Trends in body mass and condition of females were complex, varying among age groups and reproductive classes. Mean spring body mass of 3–4 year old females declined by ~ 1 kg/yr. While spring body mass of older bears (> 8 years) also declined (0.1 – 0.6 kg/yr), females in the age range of 5–8 years exhibited increases in body mass of ~ 0.07 – 0.3 kg/yr. In the autumn, trends in body mass and skull width differed between bears depending on reproductive status. Females with no cubs or accompanied by COY, exhibited declines in mean body mass of ~ 1.6 and 0.1 kg/yr, respectively, whereas mean body mass of females accompanied by yearlings increased by up to 2 kg/yr. Skull width of autumn-caught females increased among younger bears but declined among older bears. Quetelet's index of FG females in the spring declined, whereas it increased for SG females during both the spring and autumn.

Mean skull width and body length of SG and FG males also declined between 1982 and 2006. Mean body length declined by 0.4 – 0.5 cm/yr for both SG and FG males. Declines in mean skull size were greatest among younger males (0.05 – 0.09 cm/yr for bears < 15 years) as evident by declines in FG males and an age \times year interactive effect in SG males (Fig. 4). Mean body mass and Quetelet's index also declined among younger males (< 10 years) by ~ 1.4 – 2.2 kg/yr and 0.001 – 0.007 , respectively. Mean skull width of males > 20 years of age exhibited a slight increase in skull width (0.012 cm/yr) and Quetelet's index (~ 0.002 – 0.017).

Mean spring skull size of COY and yearlings declined by 0.007 and 0.01 cm/yr, respectively. There appears to have been a decline in spring body mass, but the model with the lowest ΔAIC value for spring body mass did not include a year effect and had an AIC weight seven times that of the second best model, which included a negative year effect. In this model, mean body mass of spring COY, and yearlings declined by ~ 0.007 and 0.04 kg/yr, respectively. In contrast, mean skull width and

TABLE 5. Trends in the skull width, body length, mass, and condition (based on Quetelet's index) of polar bears in the southern Beaufort Sea between 1982 and 2006.

Bear measurement	Slow-growing		Fast-growing		Cubs
	Female	Male	Female	Male	
Skull width (spring)	–	0/–†	–	–	–
Body length (spring)	–	–	–	–	NA
Mass (spring)	+/-‡	0	–	–/0§	–
Condition (spring)	+	+/-¶	–	–	NA
Skull width (fall)	+/-#	NA	NA	NA	+
Mass (fall)	+/-	NA	NA	NA	+
Condition (fall)	+	NA	NA	NA	NA

Note: A “+” indicates an increase over time with $\Delta AIC < 2$ and significance of $P \leq 0.05$, “-” indicates a decrease, “0” indicates no change, and “NA” indicates not applicable.

† Skull width of younger males declined, while that of older males remained relatively unchanged.

‡ Mass of younger females in this category (~ 5 – 8 yr) increased, while that of older bears > 8 years declined.

§ Mass of males < 9 years of age declined, while there was no trend for males aged 9–11 years.

¶ Body condition of younger males in this category declined, while that of older males increased.

Skull width of younger females in this age group (< 8 yr) increased, while those of older females (> 14 yr) declined.

|| Mass of females with no cubs or with cubs-of-the-year declined, while mass of females with yearlings increased.

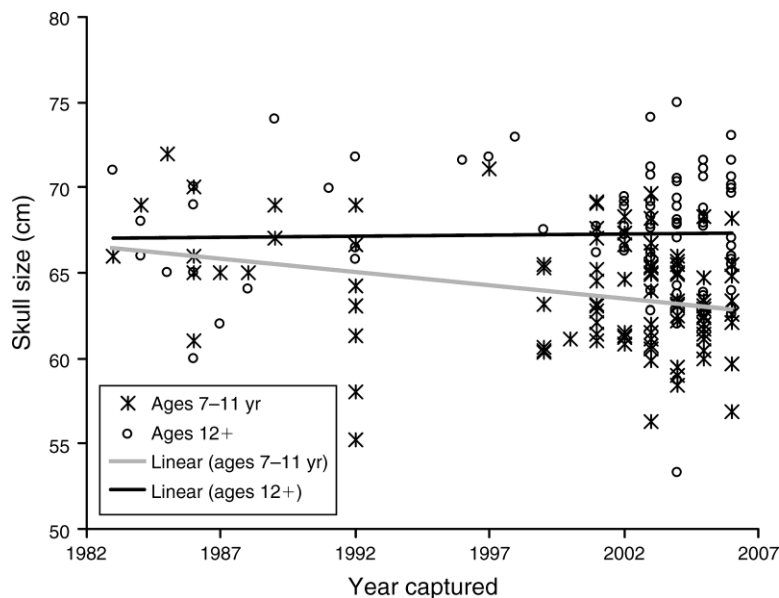


FIG. 4. Interactive effect of age and year on mean skull size of adult male polar bears in the southern Beaufort Sea.

body mass of COY and yearlings captured in the autumn increased. Skull width increased by 0.75 to 0.90 cm/yr for COY and yearlings, respectively, and body mass increased by 0.25 and 0.50 kg/yr.

Question 4: Did reproductive output exhibit a trend between 1982 and 2006? Was it related to interannual variation in available ice habitat?—Litter mass of COY and yearlings declined in both the spring and autumn between 1982 and 2006 and decreased as the availability of sea ice habitat (ice) declined (Table 6; Appendix C). The number of COY per female in the autumn and yearlings per female in the spring also declined during this time period. In the spring, the number of yearlings per female increased with an increase in ice. The percentage of females age 5, 6, 7, 8, 9, and 10 years did not differ between 1981 and 1990 and 1995 and 2006 ($t = 1.975$, $df = 5$, $P = 0.029$; 8.9%, 8.6%, 10.9%, 9.2%, 10.4%, and 5.5%, respectively).

DISCUSSION

The size and condition of most sex/age classes exhibited positive relationships with the annual availability of preferred sea ice habitats. Similarly, the decline over time in the availability of sea ice corresponded with declining trends in most measures of bear size and condition. Reduced litter mass and numbers of yearlings per female following years with lower availability of optimal sea ice habitat, suggest reduced reproductive output and juvenile survival; a result similarly documented by Regehr et al. (2007) using different methods to come to a similar conclusion. Though causation cannot be determined directly (i.e., via experimentation), these results, based on analysis of a long-term data set, are the best possible evidence that declining sea ice is the cause of reduced body size and reproduction. Declines in

the size of bears in this population have occurred during a time period when the number of bears in the region also appears to be lower than previously thought (Regehr et al. 2006), and the trend in numbers appears to be downward (Regehr et al. 2009). Though the mechanism associated with population-level change is not clear, nutritional limitations in this population are apparent as a result of the observed declines in bear skull sizes and body lengths. Nutritional limitations are further supported by a recent study that documented

TABLE 6. Trends ("Year") in litter mass and cubs per female and relationships with the availability of optimal ice habitat ("Ice") for polar bears in the southern Beaufort Sea between 1982 and 2006.

Parameter and season	Year	Ice
Litter mass†		
Spring	—	+
Fall	—	+
Cubs-of-the-year/female‡		
Spring	0	0
Fall	—	0
Yearlings/female§		
Spring	—	+
Fall	0	0

Note: A "+" indicates a positive relationship with $\Delta AIC < 2$ and a significance of $P \leq 0.05$, "—" indicates a negative relationship, and "0" indicates no relationship.

† Candidate models for litter mass included an age covariate and an age \times year or age \times ice interaction, but the best models resulted in both yearlings and cubs-of-the-year exhibiting the same trends with year and ice.

‡ Analysis of cubs-of-the-year per female included all females not accompanied by yearlings or two-year-olds in the sample.

§ Analysis of yearlings per female included all females not accompanied by cubs-of-the-year or two-year-olds in the sample.



PLATE 1. Authors Steve Amstrup and Karyn Rode measure the axillary girth of a polar bear captured in the Southern Beaufort Sea. Photo credit: Daniel Cox.

increased fasting behavior among bears in this population over the same time period as our study (Cherry et al. 2009). Thus, nutritional factors may also have played a role in the observed population-level changes.

A number of studies support that declines in body size are largely attributable to reduced nutrition, rather than other mechanisms such as disease, contaminants, or harvest effects. In Hudson Bay (Atkinson et al. 1996) and Svalbard (Derocher 2005) reductions in mean body length of polar bears have been attributed to reductions in per capita nutrition. Similarly, variation in food availability has been associated with variation in skull size of brown bears (Zedrosser et al. 2006; T.

McDonough and A. Christ, *unpublished data*). Skeletal size can only be affected during the time in which an animal is growing, and interspecific rates of growth in animals are largely the result of nutritional status (Laws 1956). Polar bears in the SB prey primarily on ringed (*Phoca hispida*) and bearded (*Erignathus barbatus*) seals, which they can only access from the sea ice. Thus, loss of sea ice habitat consequently reduces prey accessibility. Because ice seal populations are difficult to census, trends in the size of prey populations, and therefore, the contribution any trends could have on polar bear nutritional status, are currently unknown in this region (Frost et al. 2002). However, observed relationships

between available sea ice and bear size and reproduction suggest that reduced prey accessibility explains a significant part of the observed trends.

Alternative explanations for reduced body size, including increased contaminants levels, disease, or size-selective harvest are unlikely to have impacted polar bears in this population, and there is little evidence of their role in affecting bear size. Contaminant levels found in polar bears in the SB are lower than those found in other Arctic populations (Kucklick et al. 2002, Evans 2004a, b, Verreault et al. 2005). We are not aware of any study documenting a significant effect of disease on any bear population. There has been no change in mean age (Schliebe et al. 2006) or skull size of polar bears harvested in the SB between 1982 and 2006 ($F = 2.01$, $P = 0.16$; U.S. Fish and Wildlife Service, unpublished data). The majority of the 63 bears harvested on average per year from the SB population (Brower et al. 2002) are taken by Native hunters who opportunistically harvest polar bears while hunting for seals or bowhead whales.

Cub size has been documented to affect juvenile survival in polar bears (Derocher and Stirling 1996), suggesting that reduced litter mass and size of cubs-of-the-year observed in this study could be contributing to reduced first-year survival. Observed relationships between mass and skull width of mothers and litter mass in combination with observed declines in the mass and skull width of females older than nine years, suggest that reduced nutritional status of females may be driving reduced reproduction and recruitment in the population. However, male cannibalism of cubs has been documented in this population (Amstrup et al. 2006) as well as several others (Taylor et al. 1985, Derocher and Wiig 1999, Dyck and Daley 2002) and could be an additional factor contributing to reduced juvenile survival. Reduced nutritional status of adult males, as documented in this study, could potentially increase the frequency of such events.

The lack of change in body mass of younger females in the population and an apparent increase in female condition as quantified by Quetelet's index were observed in spite of an observed reduction in annual availability of sea ice. A possible explanation for this apparent paradox may be the erratic nature of the sea ice decline in the SB region and the ability of females to respond to annual variation in sea ice conditions by reducing reproductive costs during poor ice years. Downward trends in litter mass and the number of yearlings per female in the spring in our study suggest that reproductive output of females in the SB population declined during the course of this study. This may have enabled some females to maintain body mass and condition, despite declining and erratic ecological conditions. The mean body mass of females with yearlings in the autumn increased over time and was inversely related to the availability of sea ice habitat further suggesting that only those females in the best

condition are successfully rearing cubs to this stage. In particular, cessation of lactation and changes in milk composition appear to enable female polar bears to conserve energy stores to ensure their own survival (Derocher et al. 1993). Reduced first year survival, as indicated by the negative trend in yearlings per female, would significantly decrease energetic demands on females because cubs experience a fourfold increase in body mass during this time frame (Derocher et al. 1993). Kojola and Laitala (2001) reported a similar phenomenon in Finland where female brown bears more readily retained a stable body mass than males, apparently as a result of their ability to forego reproduction. Reduced survival of young along with deferred reproduction is a mechanism, common in large mammals, that maintains adult health and survival in the face of resource limitation (Eberhardt 2002).

Although most sex/age classes exhibited declines in measures of size and condition, there were two exceptions to these trends: (1) sex/age classes with sample size ≤ 40 individuals (i.e., FG females and SG males), and (2) bears captured in the autumn, which included females and cubs. The latter is likely explained by differences in bear distribution between the spring and autumn relative to areas of capture effort. Aerial surveys conducted between 2000 and 2006 (Schliebe et al. 2008) estimated that $<5\%$ of the SB population occurs near shore in the autumn. Observations of radio-collared females similarly support that the majority of this population in recent years follow the pack ice as it retreats north of the continental shelf in the autumn (S. C. Amstrup and G. M. Durner, *personal observation*). As a result, our sample of polar bears in the autumn, particularly in recent years, is likely a subset of the population and in contrast to the population-wide sample captured in the spring when the population concentrates over the continental shelf (Durner et al. 2004). These autumn-caught bears appear to have altered their distribution (Gleason and Rode 2009) and increasingly foraged on subsistence-harvested bowhead whale carcasses (*Balaena mysticetus*), which are available for a 4–6 week period in September and October (Miller et al. 2006, Bentzen et al. 2007, Schliebe et al. 2008). Bears feeding at whale carcasses appear to make substantial gains in body mass (S. Miller, *personal communication*).

It may be important to note that in our study two commonly used condition indices for polar bears, Quetelet's index and BCI, exhibited little or no relationship with litter mass. While BCI and Quetelet's index could be related to other measures of fecundity, such as age of first reproduction and cub survival, further study is needed to confirm the value of these indices as measures of female condition as it relates to reproduction.

Trends we observed in this study (e.g., reduced bear size and apparent first-year survival), are characteristic of population responses to nutritional limitations resulting from increased relative density (Eberhardt 2002, Miller et al. 2003, Schwartz et al. 2006,

Czetwertynski et al. 2007). Although the size of this population may have declined during the time period of our study (Regehr et al. 2006, 2009), habitat reduction may have occurred at such a rate as to increase relative bear density and reduce total foraging area. Negative trends in bear size were most pronounced for young, growing animals suggesting either that this group is most susceptible to environmental variation or that effects on the population have begun to occur primarily in the past decade. Declines in juvenile survival while cub production (i.e., cubs-of-the-year per female in the spring) was maintained, further suggest that the population has been impacted by environmental change in more recent years (Noyce and Garshelis 1994, Eberhardt 2002). Projections for continued sea ice loss, particularly in this region of the Arctic (Overland and Wang 2007) suggest cause for concern regarding the future nutritional status of and recruitment into this population.

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APPENDIX A

Model results examining relationships between the availability of sea ice habitat and measures of skull width, body length, mass, and condition of polar bears in the southern Beaufort Sea (*Ecological Archives* A020-024-A1).

APPENDIX B

Model results examining trends in measures of skull width, body length, mass, and condition of polar bears in the southern Beaufort Sea between 1983 and 2006 (*Ecological Archives* A020-024-A2).

APPENDIX C

Model results examining trends in litter mass and cubs per female and relationships with the availability of sea ice habitat for polar bears in the southern Beaufort Sea (*Ecological Archives* A020-024-A3).

RESEARCH ARTICLE

Rapid Environmental Change Drives Increased Land Use by an Arctic Marine Predator

Todd C. Atwood^{1*}, Elizabeth Peacock¹, Melissa A. McKinney², Kate Lillie³, Ryan Wilson⁴, David C. Douglas⁵, Susanne Miller⁴, Pat Terletzky³

1 U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK, 99508, United States of America, **2** University of Connecticut, Center for Environmental Sciences and Engineering and Department of Natural Resources and the Environment, 1376 Storrs Road, Storrs, CT, 06269, United States of America, **3** Utah State University, Department of Wildland Resources, Logan, UT, 84322–5230, United States of America, **4** U.S. Fish and Wildlife Service, Marine Mammals Management, 1011 E Tudor Road, Anchorage, AK, 99503, United States of America, **5** U.S. Geological Survey, Alaska Science Center, 250 Egan Drive, Juneau, AK, 99801, United States of America

* tatwood@usgs.gov



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Abstract

In the Arctic Ocean's southern Beaufort Sea (SB), the length of the sea ice melt season (i.e., period between the onset of sea ice break-up in summer and freeze-up in fall) has increased substantially since the late 1990s. Historically, polar bears (*Ursus maritimus*) of the SB have mostly remained on the sea ice year-round (except for those that came ashore to den), but recent changes in the extent and phenology of sea ice habitat have coincided with evidence that use of terrestrial habitat is increasing. We characterized the spatial behavior of polar bears spending summer and fall on land along Alaska's north coast to better understand the nexus between rapid environmental change and increased use of terrestrial habitat. We found that the percentage of radiocollared adult females from the SB subpopulation coming ashore has tripled over 15 years. Moreover, we detected trends of earlier arrival on shore, increased length of stay, and later departure back to sea ice, all of which were related to declines in the availability of sea ice habitat over the continental shelf and changes to sea ice phenology. Since the late 1990s, the mean duration of the open-water season in the SB increased by 36 days, and the mean length of stay on shore increased by 31 days. While on shore, the distribution of polar bears was influenced by the availability of scavenge subsidies in the form of subsistence-harvested bowhead whale (*Balaena mysticetus*) remains aggregated at sites along the coast. The declining spatio-temporal availability of sea ice habitat and increased availability of human-provisioned resources are likely to result in increased use of land. Increased residency on land is cause for concern given that, while there, bears may be exposed to a greater array of risk factors including those associated with increased human activities.

Competing Interests: The authors have declared that no competing interests exist.

Introduction

The long-term persistence of polar bears (*Ursus maritimus*) is linked to the health of the Arctic marine ecosystem, particularly the availability of sea-ice habitat [1, 2]. Polar bears are specialist carnivores that rely on sea ice to meet a number of life history needs including accessing prey, searching for mates, and establishing maternal dens [3]. However, the Arctic region is experiencing a warming trend that is driving pronounced changes in sea ice extent and structure. Since 1979, sea ice extent and volume during summer have declined at rates of $\approx 14\%$ and 28% /decade [4], respectively, with the most pronounced change occurring over the last 15 years. Arctic warming will likely continue for several decades given the current trends in global greenhouse gas emissions [5] and the lag times associated with global climate processes attaining equilibrium [6]. Hence, climate-induced effects on sea ice and polar bears will continue for several decades, or longer, if global greenhouse gas emissions are not reduced.

The ability of individuals to modify their behavior has been posited as the primary mechanism by which some animal populations have responded to climate-driven changes in their environment [7]. The best documented examples of behavioral modification in response to altered physical environments have involved changes in spatial distribution and phenological shifts (i.e., the seasonal timing of animal and plant activities, *sensu* [8]). For example, Perry et al. [9] documented northward shifts in distribution for a group of North Sea fishes in response to increased sea temperature. Parmesan and Yohe [10] examined over 800 terrestrial species and detected distributional shifts in approximately half: 80% of those shifts were poleward with most being influenced by the advancement of the spring season. However, species that occur at environmental extremes, such as Arctic endemics, have little opportunity to modulate climate-warming changes to their physical environment via shifts in distribution. Rather, they must display *in situ* plasticity in key behaviors or traits to cope with a changing climatic envelope.

For a habitat specialist with a long generation time such as the polar bear, the rapidly changing physical environment can create a situation where the species becomes “trapped” by its evolved response to cues that are suddenly occurring in a novel context (e.g., [11]). As a result, entrenched behaviors could become maladaptive and eventually manifest at the population level as declining vital rates—unless the species possesses sufficient phenotypic plasticity to assess and respond to highly dynamic conditions. For polar bears, there is uncertainty concerning their capacity to exhibit behavioral plasticity relative to changing sea ice phenology and availability, particularly in areas of the Arctic where bears have historically spent the entire year on the sea ice. In those areas, the decision to remain with ice as it retreats well past biologically-productive shallow waters may lead to prey scarcity and nutritional restriction [12]. By contrast, the decision to displace from retreating sea ice to shore could result in attraction to habitats that function as ecological traps because they contain inadequate resources or expose bears to novel risk factors. Understanding how polar bears respond to climate-driven displacement from primary habitat, and how this overlaps with exposure to known and novel threats, is critical to forecasting how they may fare in an increasingly dynamic environment.

Polar bears of the southern Beaufort Sea (SB) subpopulation have historically spent the entire year on the sea ice (with the exception of individuals that den on land), even when the pack ice retreated away from the coast to its minimal extent in September [1, 13]. However, over the last 15 years, the SB has experienced a marked decline in September sea ice extent, along with a pronounced lengthening of the melt season (i.e., period of time between sea ice break-up and freeze-up; [14]). The dramatic changes in the extent and phenology of sea ice habitat have coincided with evidence suggesting that use of terrestrial habitat has increased. For example, Schliebe et al. [15] estimated that between 3.7 and 8.0% of polar bears from the

SB were on land in a given autumn during 2000–2005, and that percentage increased when sea ice was farthest from the coast. In contrast to the SB, polar bears of the greater Hudson Bay region [16], for example, historically spent significant periods of time on land (1–5 months) when ice completely melted each year. In general, populations in the Hudson Bay region have been demographically productive [17, 18, 19], although an increase in the length of the ice-free season has resulted in a decline in the western Hudson Bay (WH) subpopulation [20, 21] followed later by apparent stabilization [22]. In the SB, measured declines in polar bear body condition, productivity, and abundance have also been linked to declining sea ice habitat [13, 23, 24, 25, 26]. It is unknown if the decline in productivity in the SB subpopulation is linked to increased use of land or to remaining on the sea ice as it retreats away from the biologically productive water of the continental shelf.

Here, we investigated polar bears from Alaska's SB subpopulation, where rapid environmental change may be driving a divergence in space use and foraging behaviors in the form of increased land use. Specifically, our objectives were to examine (i) the long-term trend in the use of terrestrial habitat, (ii) the influence of sea ice characteristics on the phenology of movement from sea ice to terrestrial habitats and back to ice, and (iii) the spatial distribution of bears while on shore. Last, we discuss potential cascading effects of behavioral divergence and how those effects may influence population dynamics in the SB through time.

Materials and Methods

Ethics Statement

This research was approved under the Marine Mammal Protection Act and Endangered Species Act with U.S. Fish and Wildlife Service (USFWS) permit number MA690038. Capture protocols were approved by the U.S. Geological Survey (USGS) Institutional Animal Care and Use Committee.

Study Area

The study area ranged from Baillie Island, Canada, (70.5°N, 128° W) in the east, to Point Barrow, USA, (71°N, 156° W) in the west (Fig 1a and 1b). The SB is characterized by a narrow, biologically-productive continental shelf with bathymetry contours typically $\leq 300\text{m}$, and with an abrupt shelf-break that quickly gives way to some of the deepest waters of the Arctic Ocean [27].

The SB coastal region is characterized by an industrial footprint associated with oil and gas exploration and extraction activities causing polar bears that frequent this area to be potentially exposed to industrial activities [28]. The Prudhoe Bay and Kuparuk oil fields are situated at the approximate midpoint along the coast, and the National Petroleum Reserve-Alaska (NPR-A) spans a significant stretch of the western portion of the coastal plain, though there is no significant industrial development within the NPR-A. There are 3 communities within the study area that harvest bowhead whales (*Balaena mysticetus*) in the fall: Barrow, Nuiqsut, and Kaktovik. Remains from the harvest have been sporadically aggregated at Point Barrow and consistently aggregated at Cross Island and Barter Island, all of which are nearly evenly spaced along the coast where they have served as focal attractors for polar bears [15].

Data Collection

Polar bear research in the SB has been ongoing for over 30 years, and we used both historical and contemporary data sets to investigate whether use of land has changed over time. Since the mid-1980s, polar bears have been captured on the sea ice (up to 160 km from the coast) nearly every spring. Polar bears were encountered opportunistically from a helicopter and

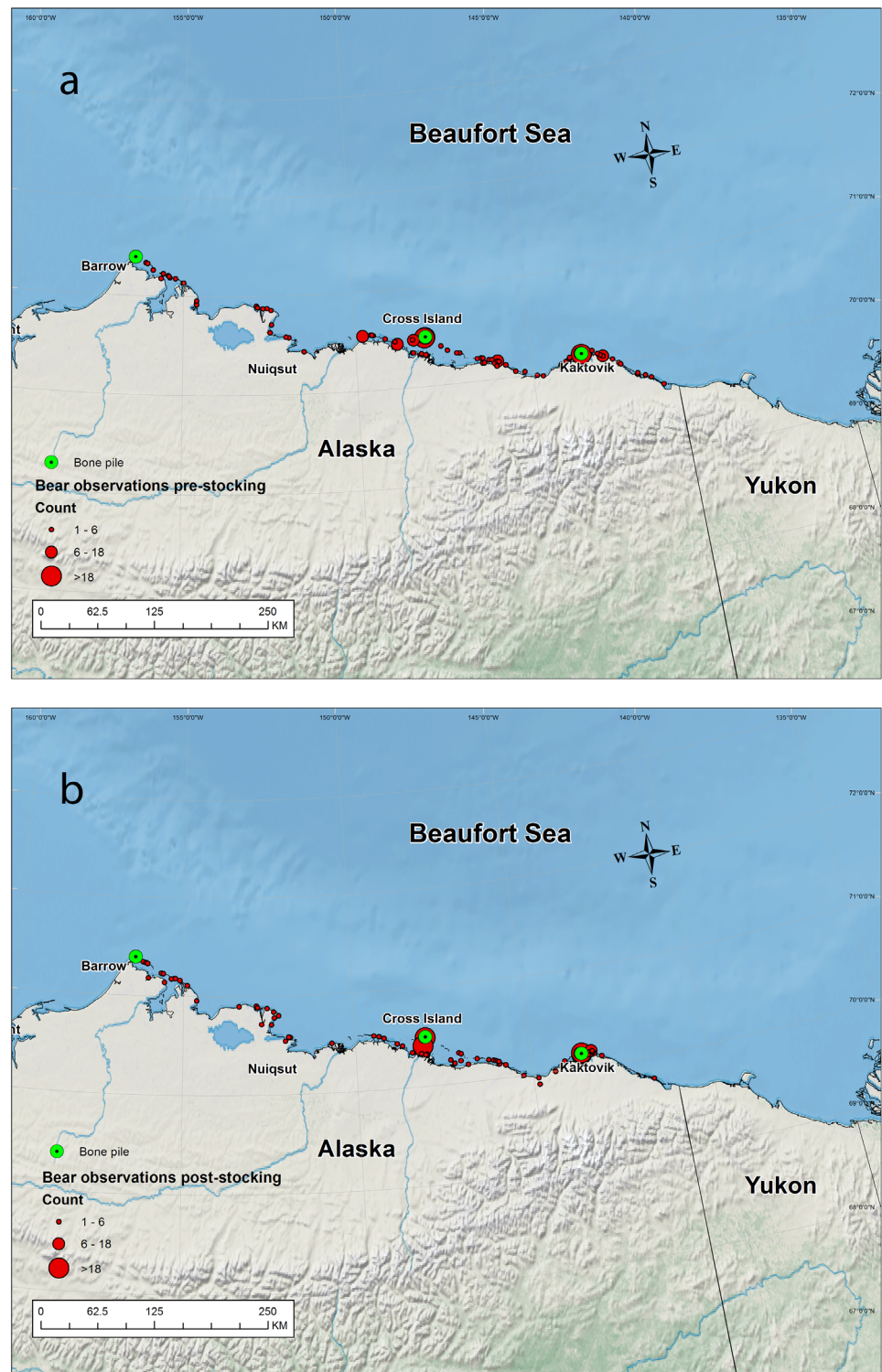


Fig 1. a-b. Spatial distribution of polar bears observed during fall aerial surveys, 2010–2013, along the coast and over barrier islands prior to the stocking of bowhead whale bone piles with remains from the subsistence harvest. Unused remains from subsistence-harvested bowhead whales are occasionally aggregated at sites on Point Barrow, and consistently at Cross Island (near Prudhoe Bay), and adjacent to Kaktovik on Barter Island following the cessation of the fall whaling season.

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immobilized with the drugs sernylan or phencyclidine (prior to 1987) and tiletamine hydrochloride plus zolazepam hydrochloride (1987–2014; Telazol[®], Fort Dodge and Warner-Lambert Co.) using a projectile syringe fired from a dart gun. A subset of adult females was fitted with either Argos or global positioning system (GPS) Platform Transmitter Terminal (PTT) satellite radio collars [13]. Age was determined by multiple methods. Cubs-of-the-year (COY) were always with their mothers and could be visually aged without error [29]. Some bears had been captured and marked in previous years, so their age was determined from their capture history. For new captures, we extracted a vestigial premolar tooth and determined age by analysis of cementum annuli [30].

Phenology of onshore behavior

We used location data from radiocollared adult females from 1986 to 2014 to determine if bears used terrestrial habitat during summer and, if so, to generate estimates of mean date of arrival on shore, duration of time spent on shore, and mean date of departure from shore back to the sea ice. The majority of locations prior to 2010 were derived with the Argos System, and have variable levels of accuracy from < 250 m to > 1500 m (see <http://www.argos-system.org/web/en/78-faq.php#faq-theme-55>). We filtered locations in an attempt to remove spurious locations by first removing all designations which had a high probability of being erroneous. We then applied the Douglas Argos-Filter algorithm [31] using a maximum redundancy function set at 10 km and minimum rate (“minrate”) of movement set at 10 km/hr.

To integrate the GPS and filtered Argos location data, which varied both in accuracy and the temporal scale of collection, we employed the continuous time correlated random walk (CRAWL) model [32] to develop predicted paths at a regularized daily time interval based on observed locations. The CRAWL model allows predicted paths to take into account variable location quality and sampling intervals. Thus, for Argos locations, we defined location accuracy based on accuracy designations for Telonics Argos collars (i.e., L3: 150 m, L2: 350 m, L1: 1000 m, L0: 1500 m; <http://www.telonics.com/technotes/argosintro.php>). Because location accuracies are not provided for locations with LA or LB designations, we provided conservative location accuracies; LA: 5,000 m, LB: 10,000 m. We assigned locations obtained from GPS collars an accuracy of 30 m.

Based on the observed location accuracy and land use, we used the R [33] package ‘crawl’ [31] to implement the CRAWL model and predict daily polar bear locations from 1 July to 31 October period. We then associated predicted locations with buffered land coverages (described below) to determine if an animal was likely to be on land at that time. Because the CRAWL model does not provide meaningful results if observed locations are too temporally dispersed [34], we excluded predicted locations that occurred between observed points separated by > 14 days. For bears that came ashore, we noted the ordinal date of arrival and departure, and calculated the total amount of time spent on shore. We then generated indices of the earliest and mean ordinal dates of arrival on shore, mean departure back to the sea ice, and length of stay on shore.

We determined if an animal’s location occurred on land by overlaying locations on one of two land coverages. The first layer was a digital elevation model (100 m resolution; <http://data.eol.ucar.edu/codiac/dss/id=106.ARCSS301>; accessed 12 Aug 2014) for the North Slope of Alaska. While this layer covered the majority of land used by bears in this study, it did not provide coverage for eastern Canada. Thus, to account for land use in that region, we used the default continent shapefile found in ArcGIS (version 10.1, ESRI, Redlands, CA). Because neither land coverage had sufficient resolution to detect small barrier islands, which are known to receive significant use by polar bears during summer [35], we buffered the land coverages by 5

km. We then determined which animal locations occurred within the 5 km land buffer and categorized those as predicted land locations. While this might have resulted in some bears not on land being classified as using land, this was unlikely to occur given that landfast ice is largely absent during this period. Thus, any animal observed within this buffer would most likely have used land at some point during that day.

Sea ice characteristics

Polar bears in the SB prefer sea ice habitat over the continental shelf because it provides greater accessibility to prey than the deeper water of the polar basin [13]. We hypothesized that the phenology of land use was influenced by sea ice characteristics, including the distance between the continental shelf break and the edge of the pack ice and the concentration of ice over the shelf. We used daily sea ice data from the National Snow and Ice Data Center (NSIDC; Boulder, Colorado, USA) to develop concentration and distance metrics. Sea ice concentrations were estimated from a 25×25 km resolution raster of passive microwave satellite imagery [36]. For the months of July through October, we estimated a number of metrics including sea ice concentrations over the continental shelf, distances from the shelf break to pack ice, the timing of break-up and freeze-up, and length of the open-water season (see Table 1 for a list of sea ice metrics). Shelf break and shelf area were delineated by the 300 m isobath for the offshore region within the boundary of the SB polar bear subpopulation [1]. We defined areas covered by sea ice with two criteria based on different ice concentration thresholds, $>15\%$ and $>50\%$. We then generated daily estimates of the proportion of the continental shelf area covered by >15 or 50% sea ice concentration, and the mean distance between the shelf break and the ice pack, where ice pack was comprised by ice concentrations >15 or 50% . We chose to use ice metrics based on both thresholds because $>50\%$ is most commonly cited as the threshold above which sea ice habitat is most suitable for polar bears [20], while break-up and freeze-up are often defined as the time when $\geq 15\%$ concentration sea ice melts or refreezes [14]. Additionally, because the SB is characterized by a narrow continental shelf, we hypothesized that bears may remain over the productive shelf even as ice concentrations drop below 50% .

Distribution

When polar bears of the SB come ashore, they mostly stay within a narrow band of the coast or on barrier islands [15]. From 2010 to 2013 we conducted transect-based aerial surveys twice (≤ 3 weeks apart) each fall along the coast between Point Barrow and the U.S.A.-Canada border to characterize distribution. In fall, polar bears are easy to detect when on land because of the contrast between the colors of bears and the snow- and ice-free substrate [37, 22]. Transects were 8-km in length and included segments oriented perpendicular to the coast line connected by alternating inland or coastal segments. We flew Bell 206B and Aerostar 305A helicopters at an altitude of ≈ 90 m and airspeed of ≈ 80 knots. In addition, total counts were conducted over every barrier island encountered, with the exception of Barter Island. The village of Kaktovik is located on Barter Island, and is adjacent to a bowhead whale carcass aggregation site which provides opportunities for commercial polar bear viewing. As such, we did not fly over Barter Island over concerns that helicopter activity would disturb commercial bear viewing ventures. We did, however, collect ground-based total counts of all bears present at the Barter Island carcass site and local vicinity on the same day as our aerial survey. We flew over carcass aggregation sites at Point Barrow and Cross Island, though no carcasses were present at Point Barrow in 2013. When we encountered a bear, we estimated age, sex, and group size, and collected a geographic location. We combined counts from transects and barrier islands to generate a total uncorrected minimum count for each of the two annual surveys and used the total counts to examine spatial distribution.

Table 1. Description of sea ice variables used in the analysis of factors influencing the timing of arrival on shore, length of stay, and timing of departure back to sea ice by polar bears from the Southern Beaufort Sea subpopulation.

Variable	Description
FD \leq 15%	The first date (day of year) when the proportion of the continental shelf covered by >15% sea ice concentration decreased to \leq 15%.
FD \leq 50%	The first date when the proportion of the continental shelf covered by >50% sea ice concentration decreased to \leq 50%.
Shelf>15%_wk	The mean proportion of the shelf covered by >15% concentration sea ice 1 week prior to arrival on shore.
Shelf>50%_wk	The mean proportion of the shelf covered by >50% concentration sea ice 1 week prior to arrival on shore.
Mdis>15%_wk	The mean distance (km) of >15% concentration sea ice from the continental shelf 1 week prior to arrival on shore.
Mdis>50%_wk	The mean distance of >50% concentration sea ice from the continental shelf 1 week prior to arrival on shore.
OW15%	The duration (number of days) of the open-water season, defined as when the proportion of the continental shelf covered by >15% sea ice concentration decreases below \leq 15%.
OW50%	The duration of the open-water season, defined as when the proportion of the continental shelf covered by >50% sea ice concentration decreases below \leq 50%.
Shelf>15%_OW	The mean proportion of the continental shelf covered by >15% concentration sea ice during the open water season.
Shelf>50%_OW	The mean proportion of the continental shelf covered by >50% concentration sea ice during the open water season.
Mdis>15%_OW	The mean distance of >15% concentration sea ice from the continental shelf during the open water season.
Mdis>50%_OW	The mean distance of >50% concentration sea ice from the continental shelf during the open water season.
LD \leq 15%	The last date when the proportion of the continental shelf covered by >15% sea ice concentration was below \leq 15%.
LD \leq 50%	The last date when the proportion of the continental shelf covered by >50% sea ice concentration was below \leq 50%.
Shelf>15%_depart	The mean proportion of the continental shelf covered by >15% concentration sea ice 1 week prior to departure from shore.
Shelf>50%_depart	The mean proportion of the continental shelf covered by >50% concentration sea ice 1 week prior to departure from shore.
Mdis>15%_depart	The mean distance of >15% concentration sea ice from the continental shelf 1 week prior to departure from shore back to sea ice.
Mdis>50%_depart	The mean distance of >50% concentration sea ice from the continental shelf 1 week prior to departure from shore back to sea ice.
Year	Calendar year in which observations were collected.

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Analyses

We used a generalized additive mixed model (GAMM) with a binomial distribution to determine whether the percentage of radiocollared polar bears using land ≥ 21 consecutive days versus remaining on the sea ice changed over time. We chose the threshold of ≥ 21 consecutive days because it has been used previously [35, 38] to describe long-term use of land and thus allows for comparison to our study. Based on the previously described analysis of CRAWL-derived locations, we coded land use or lack thereof by individuals as a binary response variable (i.e., 1 = individual used land, 0 = individual did not use land). Year was analyzed as a fixed effect, but because some individual bears were radiocollared in multiple years, we used individual as a random factor. We also calculated the mean annual percentage of radiocollared bears

with long-term land use, and used a piecewise general linear regression procedure [39] with a normal distribution to determine if and when there was a discontinuity (i.e., breakpoint) in the mean annual percentage detected on shore over the 29 years of study. Parameters estimated for the piecewise regression included the intercept, change in slope prior to the breakpoint, and change in slope after the breakpoint [39]. We did not include collar type (Argos and GPS) as a variable in subsequent analyses, though it is possible that improvements in satellite collar technology could represent a confounding factor. However, while the ability to accurately estimate the true day of arrival on land and departure back to ice should be better with GPS-era collars, the Argos-era data should not be biased toward estimating either longer or shorter land tenures.

To determine the relationship between the phenology of onshore use by radiocollared bears and sea ice dynamics, we used linear mixed models to examine the influence of sea ice conditions and characteristics on the annual mean timing of arrival on shore, length of stay on shore, and timing of departure from shore back to the sea ice. For this analysis, we included bears that came ashore for ≥ 7 consecutive days and used ordinal dates of arrival and departure, and total days spent on shore as response variables. We used the ≥ 7 consecutive days threshold to exclude bears that used land incidentally. Because we sampled some of the same individuals repeatedly, we included individual identity as a random factor in the models with first-order autocorrelation as a covariance structure. We used restricted maximum likelihood (REML) methods for model estimation. When modeling timing of departure, we censored individuals that entered maternity dens on land. Predictor variables included measures of $> 15\%$ and $> 50\%$ sea ice concentrations over the continental shelf (e.g., $Mn > 15\%$, $Mn > 50\%$), distance from the shelf of $> 15\%$ and $> 50\%$ sea ice ($Mdis > 15\%$, $Mdis > 50\%$), and length of the open water season defined as the periods of time when sea ice concentration remained ≤ 15 or $\leq 50\%$ (OW15%, OW50%).

We developed, *a priori*, sets of biologically plausible candidate models (S1 Table) and used Akaike's information criterion values [40] corrected for small sample bias (AIC_c) to aid in determining top models. We used AIC_c to rank and compare models based on ΔAIC_c and normalized Akaike weights w_i and considered models with ΔAIC_c values > 2.0 to measurably differ in information content [41]. When faced with model uncertainty, we calculated 85% confidence intervals (CI) for parameter estimates to avoid unnecessarily discarding variables in models supported by lower AIC_c values [42]. Following Arnold [42], we considered parameters whose 85% CI overlapped zero to be uninformative. We assessed multicollinearity of predictor variables using variance inflation factors (VIF) and removed a correlated variable from a given model when $VIF > 10$ [43]. We used normal probability plots and coefficients of correlation to ensure that model variables were normally distributed and assessed fit using measures of model deviance [44].

We used the paired sets of annual aerial surveys to investigate whether the availability of bowhead whale remains influenced polar bear distribution. We pooled data among years from surveys conducted before and after whale remains were placed at carcass aggregation sites (Point Barrow, Cross Island, and Barter Island). We used Moran's I statistic to test the hypothesis that polar bear sightings were spatially autocorrelated (i.e., individuals were not randomly distributed) and an ArcGIS to determine the Euclidean distance of each bear sighting to the closest carcass aggregation site. We then used a Kolmogorov-Smirnov test to determine if the distribution of distances from carcass sites differed between survey sessions—i.e., whether the spatial distribution of bears differed prior to and after the stocking of carcass sites. Statistical significance for these tests was set at $\alpha = 0.05$.

Results

During aerial surveys conducted in fall of 2010–2013 we flew a total of 9,820 ($\bar{x} = 1,226 \pm 378$ km) kilometers on transect and searched an average of 31 barrier islands to determine the

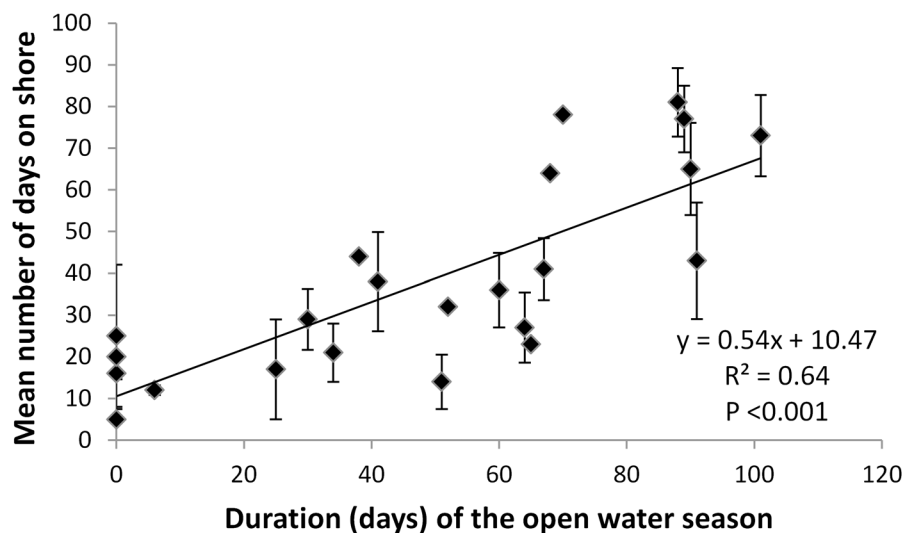


Fig 2. Proportion of radiocollared adult female polar bears that spent ≥ 21 consecutive days on shore, 1986–2014.

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spatial distribution of bears along the coast. From 1986 to 2014, a total of 389 radiocollars (satellite or GPS) were placed on 228 adult female polar bears. Results of the GAMM model indicated that the proportion of radiocollared bears coming ashore in summer and fall increased over the years ($\beta_{\text{year}} = 0.58$, $P = 0.004$). Using piecewise regression, we detected a breakpoint in the percentage of radiocollared bears on shore for ≥ 21 days at the year 2000: the average percentage of bears on shore increased from 5.8% (SE = 0.02) during 1986–1999 to 20% (SE = 0.03) during 2000–2014, reaching a high of 37% in 2013 (Fig 2).

Onshore phenology

Among all data, 68 radiocollared (39 satellite, 29 GPS) bears representing 46 individuals spent ≥ 7 days shore during the open water season, which were used to characterize onshore phenology. The piecewise regression indicated that the earliest date of arrival on shore by radiocollared bears differed between the two periods ($\bar{x}_{1986-1999} = 256$ (i.e., 13 September), SE = 3.9; $\bar{x}_{2000-2014} = 241$ (i.e., 29 August), SE = 3.1), ranging from 6 August in 1993 to 22 July in 2000. From 1986–1999, the mean length of stay on shore was 20 days (SE = 2.5 days); from 2000–2014, the mean length of stay on shore was 56 days (SE = 3.2 days). Date of departure also varied over the years, ranging from 14 August in 1993 to 7 November in 2013 ($\bar{x}_{1986-1999} = 275$ (i.e., 2 October), SE = 5.3; $\bar{x}_{2000-2013} = 294$ (i.e., 21 October), SE = 1.6).

Throughout the study, polar bear arrival on shore advanced at a rate of ~ 5 days/decade. The top model for predicting the date of arrival of bears on shore accounted for 87% of the total model set weight. Variables contained in the top model were ordinal date when sea ice concentration over the shelf dropped below 15% ($\text{FD}_{\leq 15\%}$; $\beta = 0.369$, SE = 0.06) and the proportion of the shelf covered by $> 15\%$ concentration sea ice the week prior to arrival on shore ($\text{shelf} > 15\%_{\text{wk}}$; $\beta = -0.514$, SE = 0.11) (Table 2). Examination of model coefficients indicated that earlier dates of $< 15\%$ concentration sea ice over the shelf and increased availability of $> 15\%$ concentration sea ice over the shelf resulted in earlier arrival of bears on land (Table 3). All other models for predicting the timing of arrival on shore had $\Delta\text{AIC}_c > 2$ (Table 2).

Over the course of the study, the total days spent on shore by polar bears increased by ~ 7 days/decade. The top model for predicting total days spent on shore by polar bears accounted

Table 2. Model ID, explanatory variables, AIC_c values, Akaike weights, and deviance for linear mixed models describing the timing of arrival of polar bears on shore, 1986–2014.

Model ID	Explanatory Variables	AIC _c	Akaike Wt. (w _i)	Deviance
4	FD≤15%, Shelf>15%_wk	671.4	0.87	667.3
8	FD≤15%, Shelf>15%_wk, Mdis>15%_wk, year	676.2	0.07	672.1
7	FD≤15%, Shelf>15%_wk, Mdis>15%_wk	677.5	0.04	673.4
17	Year	686.5	0.01	682.4
1	FD≤15%	686.8	<0.00	682.7
9	FD≤50%	690.5	<0.00	686.4
6	Mdis>15%_wk, FD≤15%	692.3	<0.00	688.1
12	FD≤50%, Shelf>50%_wk	692.7	<0.00	688.6
16	FD≤50%, Shelf>50%_wk, Mdis>50%_wk, year	692.6	<0.00	688.5
14	Mdis>50%_wk, FD≤50%	697.4	<0.00	693.3
10	Shelf>50%_wk	697.9	<0.00	693.8
2	Shelf>15%_wk	699.8	<0.00	695.7
15	FD≤50%, Shelf>50%_wk, Mdis>50%_wk	699.4	<0.00	695.3
11	Mdis>50%_wk	701.2	<0.00	697.0
3	Mdis>15%_wk	702.3	<0.00	698.2
5	Mdis>15%_wk, Shelf>15%_wk	703.0	<0.00	700.6
13	Mdis>50%_wk, Shelf>50%_wk	704.7	<0.00	698.9

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for 74% of the model set weight and contained the mean distance of >15% concentration sea ice from the continental shelf during the open water season (Mdis>15%_OW; $\beta = 0.022$, SE = 0.02), duration of the open water season (defined using the 15% threshold; OW15%; $\beta = 0.334$, SE = 0.11), and year ($\beta = 0.907$, SE = 0.48) (Table 4). Examination of model coefficients indicated that total number of days spent on shore increased with increasing distance of >15% sea ice from the shelf, duration of the open water season ($F_{61,14} = 8.90$, $P < 0.0001$; Fig 3), and year. However, the 85% confidence interval for Mdis>15%_OW overlapped zero, indicating the variable may be uninformative [42]. All other models for predicting the length of stay on shore had $\Delta AIC_c > 2$ (Table 4).

The top model for predicting the timing of departure of bears from shore back to the sea ice explained 77% of the model set weight and contained the proportion of the shelf covered by >15% concentration sea ice the week prior to departure (Shelf>15%_depart; $\beta = -0.158$, SE = 0.11), the mean distance of >15% sea ice concentration from the shelf (Mdis>15%_depart;

Table 3. Response and explanatory variables, model rank, AIC_c value, coefficient estimates, and 85% confidence intervals (CI) for the top general linear models describing the phenology of land use, 1986–2014.

Response	Model ID	Explanatory Variables	Mode Rank	Estimate (β)	S.E.	85% CI lower	85% CI upper	P-value
Arrival date	4	FD≤15%	1	0.369	0.06	0.27	0.45	<0.0001
		Shelf>15%_wk		-0.515	0.11	-0.68	-0.35	<0.0001
Length on shore	7	OW15%	1	0.334	0.11	0.17	-0.01	0.002
		Mdis>15%_OW		0.022	0.02	0.01	0.07	0.22
		Year		0.907	0.48	0.19	1.62	0.06
Departure date	16	Shelf>15%_depart	1	-0.158	0.11	-0.32	0.01	0.005
		Mdis>15%_depart		-0.118	0.02	-0.15	-0.09	0.21
		Year		1.059	0.36	0.52	1.59	0.03

doi:10.1371/journal.pone.0155932.t003

Table 4. Model ID, explanatory variables, AIC and AIC_c values, Akaike weights, and deviance for the linear mixed models describing the length of stay on shore, 1986–2014.

Model ID	Explanatory Variables	AIC _c	Akaike Wt. (w_i)	Deviance
7	Mdis>15%_OW, OW15%, year	658.7	0.74	656.6
1	OW15%	662.5	0.11	658.3
15	Year	663.8	0.06	659.7
4	Mdis>15%_OW, OW15%	664.6	0.04	660.4
13	Shelf>50_OW, Mdis>50%_OW, year	666.0	0.02	663.9
14	OW50%, Mdis>50_OW, year	666.2	0.01	662.0
6	Shelf>15_OW, Mdis>15_OW, year	666.8	0.01	664.8
11	Mdis>50_OW, OW50%	673.5	<0.00	669.3
8	OW50%	679.6	<0.00	675.4
12	Shelf>50_OW, Mdis>50_OW	680.6	<0.00	678.6
5	Shelf>15_OW, Mdis>15_OW	681.4	<0.00	679.3
10	Mdis>50_OW	682.1	<0.00	678.0
2	Shelf>15_OW	683.2	<0.00	679.0
3	Mdis>15_OW	686.2	<0.00	682.1
9	Shelf>50_OW	687.7	<0.00	683.6

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$\beta = -0.118$, $SE = 0.02$), and year ($\beta = 1.059$, $SE = 0.26$) (Table 5). The 85% confidence interval for the proportion of the shelf covered by >15% concentration sea ice the week prior to departure overlapped zero, suggesting it may be an uninformative variable. All other models for predicting the timing of departure from shore back to sea ice had $\Delta AIC_c > 2$ (Table 5). Inspection of model coefficients indicated that decreased availability of >15% concentration sea ice, reduced distance of >15% sea ice from the shelf, and later year resulted in later departure of bears from shore back to sea ice. Comparison of w_i for the first- and second-ranked models indicated that the first-ranked model was 4.5 times more likely to be the actual best model and deviance statistics indicated the top model best fit the data (Table 5). Over the duration of the study, departure from shore back to sea ice occurred approximately 7 days later/decade.

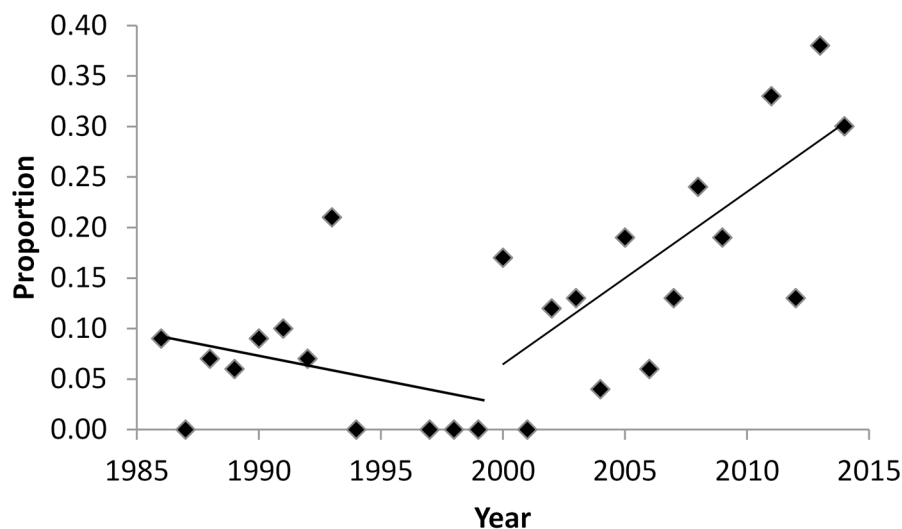


Fig 3. Mean (and standard error) length of stay on shore relative to the length of the open water season, defined as when the proportion of the continental shelf covered by >15% sea ice concentration decreases below $\leq 15\%$.

doi:10.1371/journal.pone.0155932.g003

Table 5. Model ID, explanatory variables, AIC and AIC_c values, Akaike weights, and deviance for the linear mixed models describing the timing of departure from shore back to sea ice, 1986–2014.

Model ID	Explanatory Variables	AIC _c	Akaike Wt. (w_i)	Deviance
7	Shelf>15%_depart, Mdis>15%_depart, year	527.2	0.77	525.1
16	Shelf>50%_depart, Mdis>50%_depart, year	530.2	0.17	528.1
13	LD≤50%, Mdis>50%_depart	534.4	0.02	532.3
6	Shelf>15%_depart, Mdis>15%_depart	535.1	0.01	533.0
15	LD≤50%, Shelf>50%_depart, Mdis>50%_depart	535.7	0.01	533.6
14	Shelf>50%_depart, Mdis>50%_depart	537.1	<0.00	535.0
8	LD≤15%, Shelf>15%_depart, Mdis>15%_depart	529.2	<0.00	537.1
5	LD≤15%, Mdis>15%_depart	540.6	<0.00	538.5
17	year	540.6	<0.00	538.6
2	Mdis>15%_depart	543.5	<0.00	539.4
10	Mdis>50%_depart	544.7	<0.00	540.4
9	LD≤50%	544.9	<0.00	542.8
12	LD≤50%, Shelf>50%_depart	546.4	<0.00	544.3
11	Shelf>50%_depart	547.8	<0.00	545.7
3	Shelf>15%_depart	549.0	<0.00	546.9
1	LD≤15%	550.0	<0.00	547.9
4	LD≤15%, Shelf>15%_depart	551.6	<0.00	549.5

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Distribution on land

Moran's I statistic indicated that polar bears were not randomly distributed when observed during aerial surveys conducted prior to ($z = 8.51$, $P < 0.0001$; Fig 1a) and after ($z = 15.08$, $P < 0.0001$; Fig 1b) the stocking of bowhead whale remains sites in 2010–2013. The percentage of polar bears located in close proximity to bowhead whale remains sites was greater following stocking ($D = 0.14$, $P = 0.001$). Prior to stocking, 64% of polar bear observations occurred within 16 km (i.e., mean daily distance traveled by SB polar bears; [45]) of a site. After stocking 78% of all bears observed were within 16 km of a site. During surveys conducted before and after bowhead whales were harvested, we observed the greatest percentage of bears near Barter Island (40%), followed by Cross Island (33%). Relatively few bears were observed in the vicinity of Point Barrow (<2%).

Discussion

Historical (i.e., pre-2000) use of terrestrial habitat during the open-water season by SB polar bears was relatively rare and limited to short durations [45]. Recently, land-use behavior has become more prevalent, although a majority of the SB subpopulation still remains on the sea ice during summer. We detected clear trends over time of 1) an increasing percentage of polar bears coming ashore (the percentage tripled from 2000–2014), 2) earlier dates of arrival (advancing at a rate of ~ 5 days/decade), 3) later dates of departure (~7 days later/decade), and 4) longer tenure on land (increased at a rate of ~7 days/decade). Further, increased use of terrestrial habitat was related to declines in sea ice extent and changes in sea ice phenology. Since the late 1990s, the duration of the open-water season in the SB increased by an average of 32 and 36 days based on >50% and >15% sea ice concentrations over the continental shelf, respectively, while the amount of time spent on land increased by ~3 weeks. Our results are consistent with other recent work showing increased land use by polar bears from the adjacent Chukchi Sea subpopulation over roughly the same time period [38].

The relatively infrequent historical use of land by SB polar bears was likely due to the persistent availability of sea ice over the continental shelf, even during the period of minimum sea ice extent in September. Since the late 1990s, the duration of the open-water season in the SB increased by an average of 66% or 82% (depending on sea ice concentration threshold), while the September average distance from shore to pack ice increased by 120%. Since the 2000s, the length of the open-water season has increased at a rate of ≈ 9 days/decade, which is among the largest rates of increase for the seas of the Arctic Ocean [14]. From 2006 to 2014, the distance from shore to September pack ice has increased an additional 65%, which placed the leading edge of the ice an average of 450 km from the continental shelf. Polar bears prefer to forage from sea ice over shallow, biologically productive continental shelf waters [13]. The lengthening period of sea ice absence over the shelf during summer equates to an increasing loss of preferred foraging habitat. Evidence suggests that displaced polar bears are increasingly coming ashore in response to this loss of sea ice habitat.

Previous work in the SB [15] and elsewhere (e.g., WH; [20]) has found that the timing of arrival of bears on shore was associated with sea ice dropping below a 50% concentration. More recently, Cherry et al. [46] evaluated multiple sea ice concentration thresholds in WH and determined that dates of arrival were best correlated with the timing of 30% sea ice concentration, while departure occurred after ice concentrations reached $>10\%$. Our findings, that the availability of sea ice concentrations $>15\%$ (but $<50\%$) are best correlated with the timing of arrival, length of stay, and timing of departure of SB bears, is qualitatively similar to the findings of Cherry et al. [46]. It appears that in both subpopulations, polar bears delay the transition from ice to shore until ice drops below a concentration where its use as a reliable substrate is untenable. Interestingly, our finding of an inverse relationship between timing of arrival and concentration of $>15\%$ ice over the shelf suggests that bears may come ashore before widespread disappearance of low concentration ice in order to avoid long-distance swims [47]. Collectively, our findings provide important quantitative evidence of the relationship between sea ice phenology and use of terrestrial habitat by polar bears. Monitoring the timing and rate of seasonal ice disappearance may be an effective, logistically tractable way for managers and industry to prepare for the annual arrival of bears on shore.

We found a notable increase in the proportion of radiocollared bears coming ashore in summer and fall beginning in the year 2000. From 2004 to 2007, there was a pronounced decline in the survival of SB polar bears, followed by two years (2008–2009) of apparent stability [26]. The declines and subsequent stability of survival and abundance occurred as use of terrestrial habitat was increasing. While there is no causal link between the patterns in polar bear vital rates and increased use of terrestrial habitat, there is precedence in other species for behavioral shifts ameliorating some of the adverse effects of rapid environmental change. For example, Charmentier et al. [48] found that individual adjustment of behavior allowed a population of great tits (*Parus major*) to closely track changes in prey phenology and maintain the temporal match between clutch hatch date and peak availability of prey. This suggests that behavioral adjustments that closely track key phenological shifts may lessen some impacts of rapid environmental change, at least in the short term. The decision by some polar bears from the SB to exploit terrestrial habitat, rather than remain with the retreating pack ice, appears to be a behavioral response to the loss of sea ice habitat over the continental shelf. This behavior is not necessarily surprising since other subpopulations where the sea ice completely melts every summer (e.g., WH, southern Hudson Bay, Foxe Basin, and Davis Strait) display greater use of land along with flexibility in foraging behavior [49]. In the near-term, whether bears benefit from this behavioral flexibility will likely hinge on the trade-off between the availability of food resources (and net energetic benefit), and the risks associated with accessing them, such as increased exposure to human-related activities, competition with grizzly bears (*Ursus arctos*)

[50], and increased potential for disease transmission [51]. However, for polar bears to benefit over the long term, behavioral flexibility will have to result in adaptations to environmental change on a sufficiently fast time-scale to result in evolutionary rescue [52].

Distribution data obtained from aerial surveys suggests that bowhead whale bone piles are focal attractors for bears on shore. Rogers et al. [53] found evidence of a shift in foraging behavior by some SB polar bears marked by fidelity to the nearshore region in winter and spring and consumption of bowhead whale tissue during summer and fall. It is likely that most bowhead whale tissue is consumed by bears visiting sites that have been stocked with remains following fall whaling [54], though scavenging on beach-cast whales also occurs. Nevertheless, the difference in the biomass of marine mammal food resources available to bears on shore is an important distinction between the SB and the previously mentioned five subpopulations of polar bears that have historically used land in summer. For the latter, entire subpopulations come ashore when the annual ice melts completely each summer and bears enter a hypophagic state until the ice reforms in the fall [1, 55, 56]. In WH, the open water season lasts upwards of 4 months (e.g., [57]) and model-based estimates, that assume polar bears fast while on shore, suggest that an increase beyond 5 months could trigger substantial declines in reproductive potential and survival ([58, 59, 60] but see [61]). Currently in the SB, bears are spending upwards of 2.5 months on shore and usually have access to bowhead whale remains for the latter portion of that period. If the trends of increasing use of terrestrial habitat and lengthening open water season continue in the SB, then any relative benefits of scavenging bowhead whale remains should diminish over time (assuming biomass available to bears remains consistent).

Increased use of terrestrial habitat and exploitation of human-provisioned resources by polar bears has attendant risks, including a greater potential for human-polar bear interaction and conflict. Wildlife-human conflict can have wide-ranging effects, including adversely impacting wildlife populations, causing economic losses to stakeholders, and endangering public safety [62]. The north coast of Alaska includes several villages and an industrial footprint associated with oil exploration and extraction activities, all of which are in relatively close proximity to bowhead whale remains sites (particularly at Barter and Cross Islands) where the majority of bears were detected during aerial surveys. Human-wildlife conflicts are often clustered in space and time (e.g., [63]) due to the availability and distribution of focal attractors. Given that the extent of summer sea ice is projected to decline through the 21st century [64], terrestrial habitat and human-provisioned resources are likely to become increasingly important for SB polar bears. Bears that are highly motivated to obtain food appear more willing to risk interacting with humans (e.g., [65]), and the increased frequency of bears on land, coupled with expanding human activity due to retreating sea ice, is expected to lead to greater human-polar bear interaction and conflict. Proactive management of human-polar bear interactions will be needed to reduce the future risk of conflict.

Our study suggests that SB polar bears have become more reliant on terrestrial habitat. Since the mid-2000s, the estimated proportion of the SB subpopulation coming ashore [15] has increased substantially and the behavior should no longer be considered trivial, even though the majority of the subpopulation still remains with the sea ice during the open-water season. Indeed, there is reason to hypothesize that use of terrestrial habitat may be adaptive, at least for the short-term. When summer sea ice persists in the SB, it is now relegated to the deep water of the polar basin which is less biologically productive than the continental shelf region. As a result, polar bears that remain with the ice may have fewer opportunities to encounter ringed (*Pusa hispida*) and bearded seals (*Erignathus barbatus*), which may explain reports of increased frequency of fasting, decreased kill rates [66, 67], and declining body condition [24]. By contrast, polar bears that come ashore and scavenge bowhead whales may be able to maximize

energy intake while minimizing energy expended, thereby reducing the likelihood of fasting and staving off declines in body condition.

Polar bears have evolved preferences for sea ice habitat and preying on marine mammals. In the SB, those preferences are informing two seemingly disparate strategies for coping with the loss of summer sea ice habitat: displace to shore and scavenge on predictably-available marine mammal food, or remain with the sea ice as it retracts over the polar basin and risk nutritional restriction [12]. Human-induced rapid environmental change is having profound effects on the quality and quantity of Arctic sea ice [68, 69], which will likely make it difficult for polar bears and other ice-adapted species to reliably select suitable habitats for maintaining fitness [70]. Behavioral plasticity is the initial response to dramatic environmental perturbations, followed by transmission of innovative behaviors within and across generations, eventually leading to evolution of the behavioral response over time [71] and, perhaps, evolutionary rescue [52]. However, behavioral plasticity may be an effective response by polar bears only if the rate of environmental change does not outpace transmission of behavioral innovations.

Supporting Information

S1 Table. Hypotheses and candidate linear regression models tested to predict the timing of arrival on shore, length of stay on shore, and timing of departure from shore by adult female polar bears, 1986–2014.

(DOCX)

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Author Contributions

Conceived and designed the experiments: TA EP. Performed the experiments: TA EP SM. Analyzed the data: TA KL RW DD PT. Wrote the paper: TA EP RW MM.

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