

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

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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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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

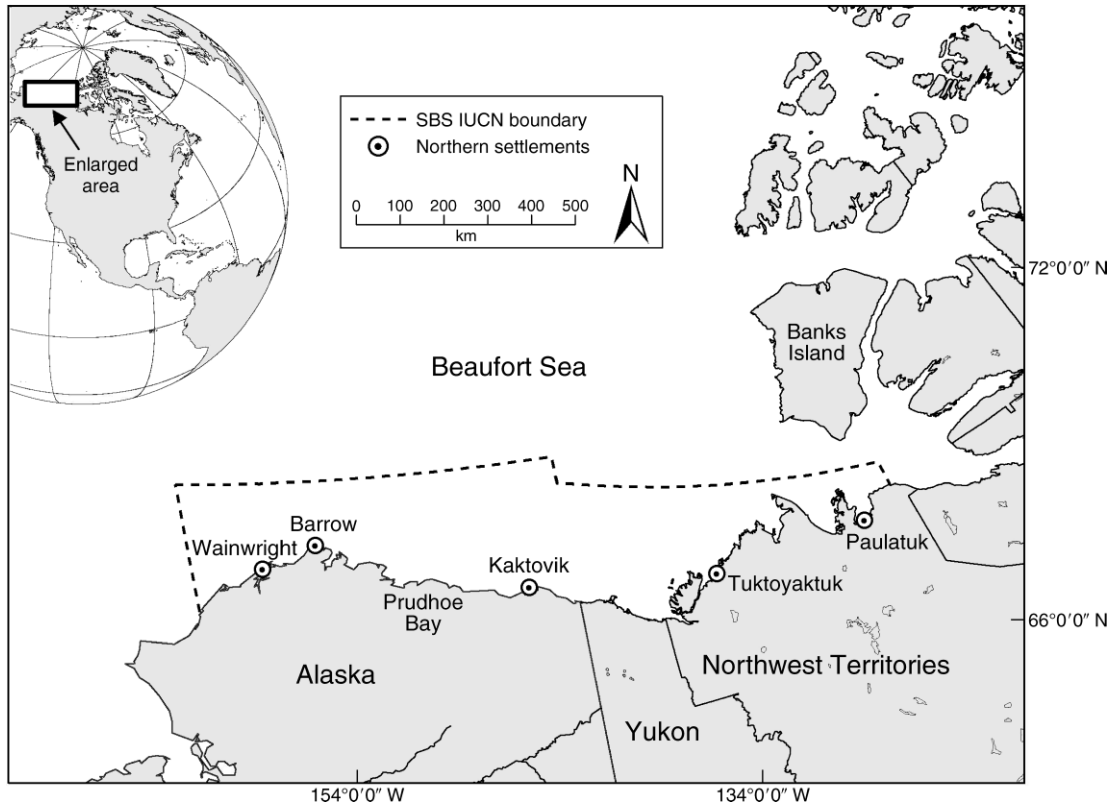


FIG. 1. The southern Beaufort Sea (SB) management unit for polar bears (*Ursus maritimus*), established by the World Conservation Union (IUCN) Species Survival Commission.

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) recumbancy. 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 ($y = 208.02[1 - \exp(-0.80[x + 0.88])]^3$), 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 ($y = 398.3[1 - \exp(-0.34[x + 0.196])]^3$), and skull width by the age of 11.9 years ($y = 26.1[1 - \exp(-0.25[x + 2.14])]$).

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 + 126.5mqquetelets – 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 + 54.05mqquetelets – 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

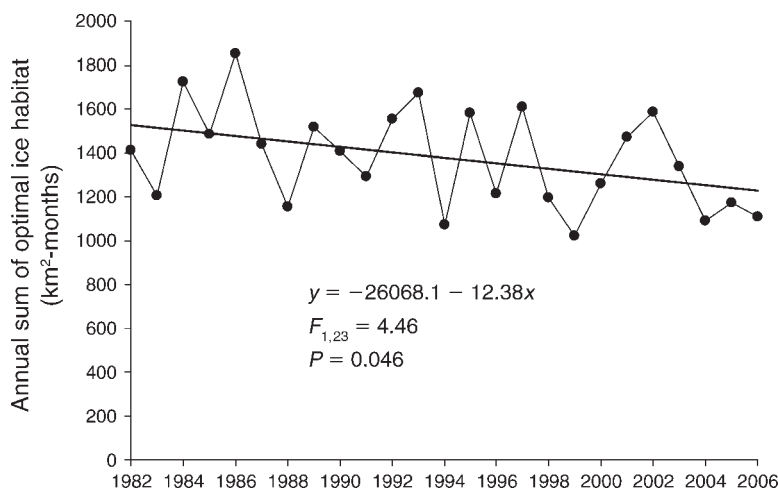


FIG. 3. Annual variation in the availability of optimal ice habitat within the known range of polar bears in the southern Beaufort Sea between 1982 and 2006.

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.

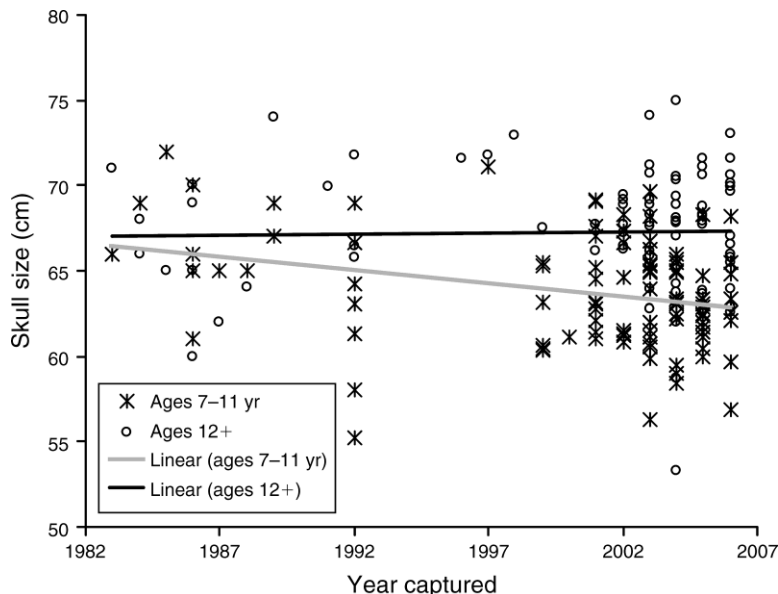


FIG. 4. Interactive effect of age and year on mean skull size of adult male polar bears in the southern Beaufort Sea.

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).