



USGS Science Strategy to Support U.S. Fish and Wildlife Service Polar Bear Listing Decision

Polar Bears in the Southern Beaufort Sea III: Stature, Mass, and Cub Recruitment in Relationship to Time and Sea Ice Extent Between 1982 and 2006

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Abbreviations, Acronyms, and Symbols

Abbreviations, Acronyms, and Symbols	Meaning
BCI	Body condition index
COY	Cub-of-the-year
SB	Southern Beaufort Sea
USFWS	U.S. Fish and Wildlife Service
USGS	U.S. Geological Survey

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Abstract

Changes in individual stature and body mass can affect reproduction and survival and have been shown to be early indicators of changes in status and trends of polar bear populations. We recorded body length, skull size, and mass of polar bears (*Ursus maritimus*) during capture/recapture studies conducted in the southern Beaufort Sea of Alaska (SB) between 1982 and 2006. We calculated a body condition index (BCI) which reflects trends in mass relative to length. We also recorded the number of dependent young accompanying females in the spring and fall as an indicator of cub recruitment. Previous work suggested stature of some sex and age classes of bears in the SB had changed between early and latter portions of this study but did not investigate trends in or causes of those changes. Here, we investigate whether these measurements changed over time or in relation to sea ice extent. Because our study required bears to be repeatedly immobilized and captured, we tested whether frequency of capture could have affected these measurements. Mass, length, skull size, and BCI of growing males (aged 3-10), mass and skull size of cubs-of-the year, and the number of yearlings per female in the spring and fall were all positively related to the percent of days in which sea ice covered the continental shelf. Skull sizes and/or lengths of adult and subadult males and females decreased over time during the study. Adult body mass was not related to sea ice cover and did not show a trend with time. BCI of adult females exhibited a positive trend over time reflecting a decline in length without a parallel trend in mass. Though

cub production increased over time, the number of cubs-of-the-year (COYs) per female in the fall and yearlings per female in the spring declined suggesting reduced cub survival. Bears with prior capture history were either larger or similar in stature and mass to bears captured for the first time, indicating that research activities did not influence trends in the data. Declines in mass and BCI of subadult males, declines in growth of males and females, and declines in cub recruitment suggest that polar bears of the Southern Beaufort Sea have experienced a declining trend in nutritional status. The significant relationship between several of these measurements and sea ice cover over the continental shelf suggests that nutritional limitations may be associated with changing sea-ice conditions.

Introduction

The U.S. Fish and Wildlife Service (USFWS) proposed listing the polar bear as a threatened species under the Endangered Species Act in January 2007. To help inform their final decision, they requested that the U.S. Geological Survey (USGS) conduct additional analyses of polar bear populations and their sea ice habitats. Between February and August 2007, USGS and collaborators developed nine reports targeting specific questions considered especially informative to the final decision. This is one of those nine reports, and one of three reports in the series that focuses on the population of polar bears residing in the southern Beaufort (SB) Sea.

During capture/recapture studies of polar bears conducted in the Alaska portion of the SB

since 1982, we collected data on skull size, length, mass and cub recruitment. Regehr et al. (2006) reported that skull sizes of cubs-of-the-year and adult males (defined as males age ≥ 5 years) were smaller and that adult males were lighter after 1990 than they were in years before 1990. Additionally, they found that the number of COY per female in the spring was higher, while the number of COY per female in the fall and number of yearlings per female in spring were lower in recent years. Regehr et al. (2006) did not evaluate trends in the data nor did they look for potential causes of the differences they reported between time periods. Here, we more thoroughly analyze these data. We specifically evaluate whether there were trends over time in skull size, length, or mass. We also test for relationships between these measurements and ice conditions in the SB.

The size (e.g., mass, length, or skull size) and growth of animals are important factors affecting their survival, behavior, and reproduction. As a result, these measures are often used as indicators of population dynamics and ecology (Stevenson and Woods 2006; Zedrosser et al. 2006). This is particularly true for brown bears (*U. arctos*) and polar bears, where body mass has been linked to reproduction (Derocher and Stirling 1994, 1998; Stirling et al. 1999), cub survival (Derocher and Stirling 1996), and population density (Hilderbrand et al. 1999). Cub survival is related to cub mass, which is affected by maternal mass and litter size (Derocher and Stirling 1994, 1998). Similarly, measures of stature, including skull size and length, are useful for identifying long-term nutritional constraints resulting from increased food competition or environmental change (McLellan 1994; Zedrosser et al. 2006). These relationships suggest that ecological factors which affect bear mass and stature can act as underlying mechanisms influencing population dynamics (Schwartz et al. 2006; Zedrosser et al. 2006). Because population trends are difficult to detect for large, long-lived species which can respond to environmental change in a variety of ways (Ginzburg et al. 1990; Parmesan and Yohe 2003), measurements such as size and weight which may be related to reproduction and

survival can provide useful information for determining and predicting population trends.

We evaluated body mass, stature (defined here as skull size and body length), and cub recruitment for temporal trends and for relationships with the availability of preferred sea ice habitats in the SB. We also calculated a condition index which standardizes body mass relative to body length. Preferred sea ice habitats are believed to represent areas with the greatest prey availability and in the SB occur primarily over the continental shelf (Durner et al. 2004). Furthermore, sea ice is required as a platform for accessing ringed seals (*Phoca hispida*) (Amstrup 2003), which are the primary prey species of the SB population (Iverson et al. 2006). Though information is available on the characteristics of ice preferentially used by polar bears, we have no information on the ice conditions required specifically for successful foraging in any polar bear population. Therefore, we used the best available current information on ice preference to develop a metric to relate to bear stature, mass, and condition. Because our metric may not have accounted for other environmental factors which could affect our measurements of polar bears, we also examined trends in bear stature, mass, and condition over time. Though current evidence suggests that capture and handling do not affect bear condition (Amstrup 1993; Derocher and Stirling 1995; Messier 2000) we controlled for potential capture history effects (Ramsay and Stirling 1986) by including them in our analyses. We focused on answering the following three questions.

1. Did bear body size and condition of different sex and age classes exhibit a trend between 1982 and 2006?
2. Were size and condition of growing bears, and mass and condition of adult bears related to annual variation in available ice habitat?
3. Did cub recruitment exhibit a trend between 1982 and 2006, and/or was it related to annual variation in available ice habitat?

Methods

Capture, handling, and measurement of bears

Polar bears were captured by the USGS in coastal areas of the SB region, from Point Barrow, Alaska (about 157°W) to the U.S.-Canadian border (at 141°W). Captures occurred from March through early May in 1982-89, 1991-92, and 1998-2006, with additional fall captures occurring between October and November in 1982-83, 1985-89, 1994, 1997, and 1999-2001. Polar bears were located using a helicopter and adults and subadults were immobilized by injecting Telazol®. Yearlings and COY were either ground-darted or injected by hand with Telazol®.

Calipers were used to measure the condylobasal length and zygomatic width of bear skulls. Straight line body length (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 above the bear in ventral (sternal) recumbancy. Axillary girth was measured by placing a nylon cord around the thoracic cavity behind the forelegs while bears were sternally recumbent (Durner and Amstrup 1996). Tail length was measured from the base to the last tail vertebrae. Bears were weighed to the nearest kg using a spring or dynamometer scale. Observers taking measurements varied throughout the study, but all were trained by S. Amstrup and careful attention was paid to ensuring consistency in measurements between observers. A vestigial premolar was extracted for age determination unless the bear could be aged as a result of previous capture as a dependent young. Age from teeth was estimated by counting cementum annuli (Calvert and Ramsay 1998).

We calculated a BCI used recently to evaluate the status of other polar bear populations (Obbard et al. 2006). BCI standardizes body mass for bear length (Cattet et al. 2002).

Measures of body mass and BCI were used as indicators of inter-annual variation in nutritional status. We used skull size and length of adult bears to evaluate long-term temporal trends because these measurements are insensitive to interannual variations in food availability or habitat quality (Zedrosser et al. 2006). This combination of measures, therefore, allowed us to evaluate physical responses to interannual variations in sea ice, as well as long term trends.

Skull size was quantified as the sum of skull length and width. BCI incorporated scale weights and body length measures which include tail length (Cattet et al. 2002). Mean tail lengths were determined for subadult females (3-4 yr olds), subadult males (3-5 yr olds), adult females, and adult males and used to correct body length measures by subtracting or adding mean tail length. This correction was unbiased since tail length was not correlated with body lengths for any of these sex/age classes ($P > 0.3$ for all classes).

Quantifying ice conditions over the continental shelf

Polar bears in the SB region select strongly for sea ice over the shallow waters of the continental shelf (Durner et al. 2004). Therefore, we defined preferred habitat as ice cover over waters within the SB subpopulation region (Aars et al. 2006) which were less than 300 m deep (International Bathymetric Chart of the Arctic Ocean; <http://www.ngdc.noaa.gov/mgg/bathymetry/arctic/arctic.html>). Mean ice concentration was calculated as the arithmetic mean of daily ice concentration values for the 139 grid cells (25×25 km) in the region (based on passive microwave satellite imagery from the National Snow and Ice Data Center, Boulder, Colorado; <ftp://sidacs.colorado.edu/pub/>). We quantified ice availability as the percent of days between April and November in which mean ice concentration was $\geq 50\%$ in continental shelf waters (*ice*). A percent was used because the number of days in which ice data were available varied between 184-365 days for the years of the

study. In all cases, however, these dates were evenly distributed throughout the year. We used 50% concentration as a cutoff because bears make little use of areas where sea ice concentration is lower (Durner et al. 2004). SB polar bears do not reach peak body weights until early winter (Durner and Amstrup 1996), and April to November is believed to be the primary foraging period for polar bears in the SB (Amstrup et al. 2000). Because the ice free period falls in this time frame, it is logical to hypothesize that a longer ice free period may affect foraging success and therefore, nutritional status. We tested for relationships between ice conditions during a given year and the mass, skull size, and length of bears during the following spring.

Use of growth curves to define sex/age classes

Separate analyses were conducted for bears of different sex/age classes because not all covariates being considered were relevant for all classes and seasons (i.e., litter size for COY, yearlings, and adult females). Body mass, skull size, and length do not increase linearly with age, but asymptotically approach a maximum size. The age at which maximize size is reached differs for each of these measures and between males and females (Derocher and Wiig 2002; Derocher et al. 2005). We therefore differentiated adults and subadults on the basis of growth rates (e.g., Figure 1) rather than the age at sexual maturity. Young bears were classified as COY or yearlings. Bears 3 years and older of both sexes were designated as either subadults or adults based on the age at which they reached 97% of asymptotic size for a specific measure. Relationships between age and the skull size, length, and body mass of spring-caught bears were fit with von Bertalanffy curves (von Bertalanffy 1938; Kingsley 1979; Kingsley et al. 1988; Derocher and Wiig 2002) and used to calculate the approximate age at which bears reached 97% of their maximum growth.

Data analysis

Objectives 1 & 2: Trends in and effects of ice conditions on bear stature, mass, and BCI

Linear models were used to identify relationships between body stature, mass, and BCI and ice conditions or year. The independent variables we used in our models are defined in Table 1. *Year* or *ice* was included in models as continuous independent variables (covariates). We did not include both *year* and *ice* in the same models because we hypothesized that these factors might be related and we were interested in examining their relationships with stature, mass, and BCI independently. Capture history (*caphis*) was included as a categorical factor in models examining both *ice* and *year* effects and was defined as either caught once (1-not captured prior to the current event), caught twice (2), or caught three times or more (3). Since adults were defined as having achieved greater than 97% of their growth, we did not expect measures of skull size and length in adults to be altered by additional captures that occurred as adults. Therefore, we excluded capture history effects from models of adult skull size and body length. Though capture history effects were included in some analyses, models did not account for possible effects associated with repeated measures of individuals that are included in the data.

Factors, such as age and capture date, can affect skull size, length, and mass. Therefore, we controlled for these factors and others in our models (Table 1), though the factors included differed between sex/age classes (Table 2). Since litter size (*litsize*) can affect cub size (Derocher and Stirling 1998), litter size also was included in models for COY and yearlings. Furthermore, due to the potential for cub production to affect female body mass and condition, a category (*cubs*) of accompanied by (1) or not accompanied by (0) COY was included as a fixed effect. While sex does not appear to affect the size of COY, it can affect yearling size

(Derocher and Stirling 1998) and therefore, was also included in models of yearling skull size and body mass. Maternal capture history was categorized as described above and was included in models of COY and yearling skull size and body mass. Skull size and body mass were the only measures used to evaluate trends in data from COY and yearlings. Unlike adults, all measures of cub size were expected to respond to variation in ice conditions, and skull size and body mass are believed to be the most accurate measures (Stevenson and Woods 2006).

All main effects and interactions with fixed effects were included initially in models (see Table 2). In addition, interactions between *year* or *ice* and *age* were included due to the potential for bears of different ages within our sex/age categories to exhibit different responses. Collinearity between predictor variables is known to affect interpretation of the amount of variation in response variables that are associated with each predictor variable (Gotelli and Ellison 2004). Because several continuous variables (e.g., *age*, *year* or *ice*, and *cdate*) were included in most models, relationships between these variables could affect our interpretation of model results. Therefore, we used correlation matrices to identify relationships between continuous variables considered for inclusion in the models.

Homogeneity of variance was tested using a Levene's test for categorical variables which includes the effects of covariates on between-category comparisons and by examining residuals for evidence of heteroscedasticity. If variances were not homogenous, transformations were attempted. If variances could not be equalized via transformations, linear models were run and considerations of the effects of unequal variances were considered. Linear models are robust to non-normality (Green 1979) and were therefore used even when data appeared to have non-normal distributions. However, we used Anderson-Darling tests of normality and examined residual distributions to identify possible outliers.

Models were reduced in a stepwise fashion. Three-way interactive terms were first removed from the model if $P \geq 0.05$. Two-way interactive

terms were then removed step-wise such that the least significant term was removed first (i.e., with the lowest F and highest P-value), the model was re-run, and subsequent non-significant terms were removed one by one. Co-variables (continuous variables) and fixed effects (categorical variables) that were not significant at the $P \leq 0.05$ level were also removed from the model in the same step-wise fashion. Though $P \leq 0.05$ was used as a statistical cut-off point for inclusion in final models, *P*-values ranging between 0.05 and 0.1 were considered in the results due to their potential biological relevance (Stephens et al. 2005). All statistical analyses were conducted in SPSS® (Version 15.0; SPSS, Inc., Chicago, IL).

Objective 3: Relationships between ice conditions and cub recruitment

Cub recruitment was indexed based on the number of COY or yearlings accompanying adult females captured in the spring and fall. If cub mortality was extensive in spring, fewer cubs would be counted at later dates in each capture season. Therefore, linear trends in capture date over time could affect estimates of cub recruitment. We controlled for this possibility by including *cdate* in models.

Results

A mean of 60.2 ± 33.9 bears (range: 11-152) were captured per year during the spring (Mar - May) and 38.2 ± 20.9 bears (range: 5-70) were captured per year during the fall (Oct-Nov) between 1982 and 2006. Sample sizes vary because all measures (i.e., skull size, body mass) were not taken for all bears captured (Tables 3, 5, and 7). Due to low and inconsistent sampling in the fall, all results examining stature, body mass, and BCI are based on spring captures only. Fall capture data were used only for evaluating trends in cub recruitment and relationships between cub recruitment and *ice*. Sample sizes of 2 year olds were too small to allow analyses and were also potentially confounded by the effects of some

being captured as independents and others being captured while they were still accompanying their mothers.

Of all adult and subadult bears captured between 1982 and 2006 that were three years old and older, 58% were captured once, 23% were captured twice, and 19% were captured three times or more. The maximum number of times any bear was captured was eleven for an adult female first captured in 1987 as a 6-year old.

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. Model results were the same when using data sets in which only direct measures of length were made and when using data sets including direct measures and corrected values. Therefore, the results presented below and in the tables are for the larger data set including both measured and adjusted values for length.

Growth curves of males and females

The age at which bears reached 97% of their maximum growth differed between sexes and among measurements. Females reached 97% of asymptotic skull size (skull length + width) by the age of 4.2 years,

$$y = 55.45(1 - e^{-0.6735(x+0.975)});$$

body mass by the age of 4.8 years,

$$y = 208.02(1 - e^{-0.803(x+0.876)})^3;$$

and length (including tail) by 3.9 years,

$$y = 195.16(1 - e^{-0.7809(x+0.6011)}).$$

Males reached 97% of asymptotic skull size by the age of 6.5 years,

$$y = 65.36(1 - e^{-0.4515(x+1.23)});$$

length by the age of 6.0 years,

$$y = 226.29(1 - e^{-0.5154(x+0.7874)});$$

and body mass by the age of 11.7 years,

$$y = 398.3(1 - e^{-0.336(x+0.196)})^3.$$

Because females achieved most of their growth in all measures by the age of 5, females 5 and older were defined as adults and younger, independent females were classified as subadults. Adult males grew rapidly in length and skull size up to approximately 6 years of age. Hence, males >6 years old were classified as adults for these measures and younger, independent males were defined as subadults. Though males achieved most of their growth in skull size and length by age 6, they continued relatively rapid growth in mass up to age 12 (Figure 1). Therefore, in analyses of male body mass, adults were defined as those >11 years old and subadults were males 11 and younger. The use of the terminology “adult” and “subadult” from this point on refer to slow-growing versus rapidly growing individuals, respectively. This terminology differs from most studies in which adults are defined as sexually reproducing individuals, which for polar bears are typically ages 5 and above.

Objective 1: Trends in bear stature, mass, and condition between 1982 and 2006

In this section we report on linear trends in the mean skull size, length, mass, and BCI of adult, subadult, yearling, and COY in the SB between 1982 and 2006. Trend results for each sex/age class are summarized in Table 3 and the linear models used to identify trends are presented in Table 4. Additionally, we report on the results of comparisons in the measurements of bears captured once and those captured twice or more in this section. Specific model results for capture history effects are also provided in Table 4.

Adult bears

There was no trend in mean skull size of adult females in the SB subpopulation ($P > 0.1$). However, mean length of adult female polar bears declined by $0.28 \pm 0.05\text{cm}$ ($\beta \pm \text{SE}$) per year. There was no trend in mass of adult females during the study, but mean BCI of females increased over time ($P < 0.0001$). Though females with COY were captured progressively earlier in latter years of the study ($r = -0.34$, $P = 0.004$), females without COY did not show this effect ($r = 0.06$, $P = 0.39$) and neither *cdate* nor *year* exhibited relationships with mean mass of females. Sample sizes differed for females with COY ($n = 70$) and females without COY ($n = 190$) which created an unbalanced design and consequently unequal variances for mass data. However, removing *cubs* effects which equalized variances and modeling females with and without COY separately had no effect on the model outcomes (i.e., *caphis* and *year* were not significant). Mean mass and BCI did not differ between adult females captured once and those captured twice or more.

Mean skull size of adult males in the population exhibited an *age* by *year* interactive effect ($F_{1,182} = 9.90$, $P = 0.002$). This effect appeared to result from skull sizes of younger males (ages 7-11) declining over time while those of older males (ages 12+) exhibited no apparent change (Figure 3). Mean length of adult males declined at a rate of $0.34 \pm 0.13\text{cm}$ per year. There was no trend in mass or BCI of adult males over time. Because few adult males were captured three times or more, only two categories of capture history were examined. Nonetheless, mean body mass and BCI did not differ between adult males captured once and those captured twice or more.

Subadult bears

Skull sizes of subadult females declined $0.7 \pm 0.3\text{mm}$ per year over the course of the study ($P = 0.039$) and mean body length declined $0.27 \pm 0.12\text{cm}$ per year ($P = 0.036$). Skull size and length were larger for females captured twice or more than those captured once only ($P < 0.04$). There was no trend in mean BCI of subadult females over time, but a decline in mean mass of $1.0 \pm 0.5\text{kg}$ per year was significant at $P = 0.06$ ($y = 2137.56 - 0.997 \text{ year}$; $F_{1,33} = 3.8$).

The mean skull size of subadult males declined $1.6 \pm 0.6\text{mm}$ per year ($P = 0.007$) and mean body length declined by $0.58 \pm 0.22\text{cm}$ per year ($P = 0.009$). Skull size and length were larger for males captured twice or more than those captured once only. Mass of subadult males in the population declined by $2.2 \pm 0.7\text{kg/year}$ over the course of the study ($P = 0.002$). BCI exhibited a similar decline over time ($\beta = 0.015 \pm 0.006$; $P = 0.01$). Subadult males captured twice were heavier than those captured once only, though this was only significant at $P = 0.08$ ($\beta = 21.28 \pm 12.14\text{kg}$; $F_{1,94} = 3.07$). There was no difference in BCI of subadult males captured once and those captured twice or more ($P = 0.97$).

Yearlings and COY

Mean body mass of yearlings did not decline over time ($P = 0.14$), but a decline in skull size was significant at $P = 0.08$ ($\beta = -0.44 \pm 0.25\text{mm}$, $F_{1,83} = 3.14$). Skull sizes and mass of male yearlings were larger than females (sex effects: skull size: $F_{1,84} = 39.3$, $P < 0.0001$, mass: $F_{1,57} = 5.77$, $P = 0.02$) and yearlings in litter sizes of one were larger than those in litters of two or more (*litsize* effects: skull size: $F_{1,84} = 6.68$, $P = 0.01$, mass: $F_{1,57} = 6.1$, $P = 0.016$). Inclusion of *litsize* resulted in unequal variances for models of COY mass, but model results for *caphis* and *year* did not differ when including or excluding litter size effects.

There was no trend over time in the skull size or mass of COY. There was a correlation between *cdate* and *year* for COY mass ($r = -0.15$, $P = 0.049$) and skull size ($r = -0.147$, $P = 0.046$). Despite the fact that capture efforts occurred in the same time frame each year (mean date of spring capture efforts related to *year*: Pearson's $r = 0.085$, $P = 0.71$), captures of females with COY occurred progressively earlier between 1982 and 2006 (Fig. 2). However, only capture date was significant in models of COY skull size and mass.

The skull size and mass of COY and yearlings of females captured once did not differ from COY of females captured twice or more ($P > 0.1$).

Objective 2: Relationships between ice availability and bear stature, mass, and BCI

This section provides results of models used to identify relationships between ice availability in the SB and measures of mass and BCI of adult bears, stature, mass, and BCI of subadults, and the mass and skull size of yearlings and COY. A summary of the relationships between *ice* and measurements for each sex/age class are provided in Table 5 and model results are provided in Table 6. Capture history effects were initially included in all models, but the specific results are presented in Table 4 and not repeated here.

There was no significant trend in the percent of days between April and November in which the continental shelf was covered by $\geq 50\%$ ice concentration (our metric) between 1982 and 2006 (Figure 4).

Adult bears

Ice was not related to the mean body mass or BCI of adult male and female polar bears in the SB population ($P > 0.1$ for all tests).

Subadult bears

Ice was not related to the length, skull size, mass or BCI of subadult females ($P > 0.1$ for all tests). In contrast, the mean mass, BCI, length, and skull size of subadult males increased with increasing *ice*.

Yearlings and COY

While there was no relationship between the mass and skull size of yearlings and *ice*, COY mass and skull size were positively related to *ice*. Similar to models including *year* effects discussed in the results under Objective 1, inclusion of litter size resulted in unequal variances for models of COY mass. However, model results for *ice* did not differ when including or excluding litter size effects.

Objective 3: Relationships between ice availability, year, and cub recruitment

The number of COY per female increased between 1982 and 2006 during the spring, but declined during the fall (Table 7). *Ice* was not related to COY per female in spring or fall. Yearlings per female decreased in the spring, but there was no apparent trend in the fall (Table 7). However, for both spring and fall, the number of yearlings per female increased with increasing *ice*.

Discussion

One of the objectives of this report was to expand on the analysis initially conducted by Regehr et al. (2006) to determine whether there was a trend in stature, mass, and/or condition of polar bears in the SB between 1982 and 2006. Our analysis differed from Regehr et al.'s (2006) in three ways. First, we specifically controlled for factors such as age and capture date which could affect measurements. Second, we examined trends over time by including year as a continuous variable rather than binning data into two time periods. Third, we used growth curves to define subadult and adult categories that represented rapidly growing and slow growing bears, respectively rather than defining classes by the age of sexual maturity.

Because of these contrasts our findings differ in the following ways from those reported by Regehr et al. (2006). Regehr et al (2006) reported that the skull sizes of adult males and COY and the mass of adult males were lower after 1989 than before 1990. In our analyses, we did not observe a declining trend in either COY mass or skull size. We found that capture dates of COY declined over the course of the study. Because cubs that are captured earlier in the season are younger and therefore smaller this may have accounted for the observed decline in COY skull size reported by Regehr et al. (2006). Though our results suggest that variation in capture date accounted for most of the negative trend in COY skull size and mass over time, data were insufficient to totally separate this effect from potential declines over time.

Our results support a decline in skull size of both adult and subadult males initially observed by Regehr et al. (2006). However, in the case of adult males, skull size declined only for younger adults up to 11 years of age (Figure 3). While we also observed a decline in the mass of males age 3-11, adult males as defined in our study did not exhibit a similar decline. The Regehr et al. (2006) observation of a decrease in body mass of adult males likely resulted because they included growing bears that we classified as subadults

among their category of adults. Lastly, by including age as a continuous covariate and examining trends over time, our results indicated declines in the length of adult and subadult females. This result was not apparent in Regehr et al. (2006). Declines between the two time periods they compared, in cub survival and recruitment (Regehr et al. 2006), were corroborated by the temporal trends we report here. In short, our results corroborate and augment the preliminary results reported by Regehr et al. (2006). Skull sizes and mass of males between 3-11 years of age and cub recruitment in the SB declined over time between 1982 and 2006. In addition, we also found declines in stature of subadult and adult females in the SB subpopulation, which Regehr et al. (2006) did not detect.

We found no evidence that bears captured twice or more were smaller or in poorer condition than bears captured once only. This negative finding was found for all sex/age classes confirming that capturing animals for our research did not influence the long-term trends observed.

Rather than finding that capture negatively affected study subjects, we made the seemingly paradoxical observation that skull sizes and body lengths of subadults captured twice or more were larger than those of subadults captured once only. This result could indicate differential survival associated with subadult size or individual heterogeneity in movement patterns which results in a higher probability of re-capturing larger subadult bears. If smaller subadults have lower survival rates, they would show up less frequently in capture/recapture records. Alternatively, differences in habitat use patterns as evident from radio-telemetry data could be responsible for the observed larger size of re-captured bears. Activity areas of individual bears in the SB vary greatly. Some individuals spend all of their time over the continental shelf waters of the SB while others occupy much larger ranges which include area beyond Alaska's continental shelf (Amstrup et al. 2000, 2004). Shelf waters are much more productive than the deeper offshore waters (Pomeroy 1997, Sakshaug

2004), and bears which spend all of their time there may have some nutritional advantage over those which occupy offshore waters for large periods of time. Our search efforts were largely limited to continental shelf regions. Therefore, bears that spend all of their time in these shallow water areas would be the most vulnerable to recapture. Consequently, these bears would be potentially larger than those that spend only part of their time over the continental shelf in the region where we focused our sampling. Either of these phenomena may explain why mean size of subadults captured once was lower in comparison to subadults captured twice or more. Importantly, we found no evidence to suggest a causal relationship in which the process of capturing a bear affected their mass, size, or condition.

The absence of capture history effects in this study could be the result of consistent use of improved drugs for immobilization (Stirling et al. 1989), and the fact that we controlled for alternative factors in our analyses. Though Ramsay and Stirling (1986) documented negative effects of drugging and handling on the size of females and their cubs, all studies of capture effects on polar bear size and condition since the use of Telazol for immobilization have found no negative impacts (Amstrup 1993; Derocher and Stirling 1995; Messier 2000). Our results further support these findings and confirm that capture efforts did not introduce bias into our models examining trends relative to *year* and *ice*.

The decline in adult and subadult skull size (of males only) and length (of both males and females) (Tables 3 & 4) suggest that some factor or combination of factors have affected physical growth of animals in this population. There is little evidence to support that factors such as size-selective harvest, contaminants levels, or disease are responsible for the trends we observed. Though some trophy hunting occurs on the Canadian side of the SB, the majority of hunting is conducted by Native hunters who opportunistically harvest polar bears while hunting for seals or bowhead whales.

Additionally, the mean age of bears harvested from the SB population does not appear to have changed since 1980 (Schliebe et al. 2006). We

are also not aware of any plausible way hunters could be selecting for size in a way that could lead to the trends observed in this study. Contaminant levels found in polar bears in the SB are lower than those found in other Arctic populations (Schliebe et al. 2006) and currently, there is no evidence of disease outbreaks that would affect bear size. In contrast, our observations of relationships between sea ice conditions and stature and mass of subadult males in the population suggests that a change related to foraging opportunity is plausible. Because the ice-free period occurs during the time when polar bears in the SB are attempting to gain weight for winter, a more protracted ice-free period could directly affect nutrition and hence, growth patterns.

The effect of sea ice conditions on the mass and size of subadult males suggest that, if sea ice conditions changed over time, this factor could be associated with the observed declines in these measures. While we hypothesized that the ice metric we used in this study was meaningful to the foraging success of polar bears, more recent habitat analyses have resulted in improvements in our understanding of preferred ice conditions of bears in the SB. Durner et al. (2007) recently identified optimal habitat based on bathymetry, proximity to land, ice concentration, and distance to ice edges using resource selection functions (RSFs). The sum of the monthly extent of this optimal habitat for each year ($\text{km}^2 \times \text{month}$) within the 95% spatial utilization distribution of the SB population (Amstrup et al. 2004) was strongly correlated with our ice metric for the 1982 to 2006 period ($r = -0.898$, $n = 25$, $P < 0.0001$). This suggests that the metric we used did effectively quantify important habitat value. While the ice metric we used did not exhibit a significantly negative trend over time, the optimal habitat available to bears in the SB, as identified by Durner et al. (2007) did significantly decline between 1982 and 2006 ($y = 26068.10 - 12.38x$; $F_{1,23} = 4.46$, $P = 0.046$). This further supports that trends in bear size and condition over time, particularly for subadult males whose mass and stature were related to sea

ice conditions, were associated with a declining trend in availability of foraging habitat.

Males in the SB population exhibited a stronger relationship with sea-ice conditions and more pronounced declines over time than females. The mean body mass of males age 3-10 (63% of all males captured over the age of 3) declined by 2.2 kg per year and were positively related to the percent of days with $\geq 50\%$ mean ice concentration over the continental shelf. Similarly, the skull size of males within this age range declined. The fact that declines were not apparent in older fully grown males, but were apparent in younger fully grown males, suggests that nutritional limitations may have occurred only in more recent years after the time when older males in the population were fully grown.

While females may exhibit responses to nutritional limitations first through reduced investment in reproduction (e.g., reduced litter size, smaller cubs, reduced lactation output), males are likely to exhibit more direct impacts on growth rates and/or body size. Because male polar bears weigh nearly twice as much as adult females, their total energy requirements are significantly higher and may make them more susceptible to changes in prey access associated with sea-ice changes. In addition, male polar bears are sexually mature by age 5 (Rosing-Asvid et al. 2002). Therefore, even bears we identified as subadults would be spending much of their time during the prime spring foraging period in pursuit of females. If males are less able to take advantage of spring foraging opportunities, they must compensate by foraging later in the season when the most significant declines in ice conditions have occurred (Lemke et al. 2007; Serreze et al. 2007). Thus, if males rely more heavily on summer and fall foraging periods than females to meet nutritional needs, this may explain the closer relationship between male size and condition and sea ice concentration. Differences in the mating behavior and total energy costs of males and females in other ursids have shown similar greater sensitivity of males than females to environmental and human-induced changes (Rode et al. 2006).

The ecological interpretation of a lack of change in body mass of adult females accompanied by an increase in BCI is not totally clear. While indices of bear condition which standardize mass relative to body length have been associated with earlier ice break-up dates and declines in cub survival for polar bears in Western Hudson Bay (Stirling et al. 1999), changes in condition there appear to have been a consequence of changes in bear mass (Derocher and Stirling 1995). Thus, changes in the condition index may have been merely reflecting changes in body mass which would have served as an equally effective indicator of future population changes. In our study, however, the observed change in mean BCI of females was associated with long-term declines in length rather than changes in body mass. This result may have a very different meaning relative to female survival and reproduction than changes in body mass. Female body mass has been linked to cub size and survival (Derocher and Stirling 1994, 1995, 1996) and may be the underlying factor responsible for observations of declining condition indices for females and associated changes in reproduction. Therefore, a change in BCI that is not associated with changes in body mass may not affect reproduction or survival, and may stem from a mechanism that allows females to make short-term adjustments to negative trends in ecological conditions.

A possible mechanism could be that the reported declines in cub survival (Regehr et al. 2006) and our observations of apparent recent declines in recruitment through the first year of life has resulted in an improvement in the mean condition of females in the population. Female polar bears normally are accompanied by dependent young for 2.3 years. Females that lose their cubs early would not incur the energetic cost of lactation and sharing of food resources with growing yearlings and/or two-year-olds. In the absence of the energetic drain of nursing and rearing young, females could more easily maintain or even regain body mass. On top of the significant declines in body stature we observed, even modest gains in mass would allow BCI to increase. Decreased cub survival and decreased

body length, therefore, could be the mechanisms by which females showed improved BCI, despite changing ecological conditions that reduce their overall nutritional plane. Poorer survival of young along with deferred reproduction are common strategies large mammals use to maintain adult health and survival in the face of resource limitation (Eberhardt 2002). If this is the case in the SB, increases in female BCI may be associated with increased cub production, but not increased recruitment of young into the population.

Though temporal trends were not evident in COY size or mass, ice conditions were positively related to skull size and mass of COY. Additionally, ice conditions were related to the numbers of yearlings per female observed in the spring and fall. These trends indicate that cub survival during their first two years of life were lower following years with less ice over the continental shelf. The lack of a relationship between maternal mass and *ice* or decline in female mass or condition over time suggests that either we failed to detect meaningful change in female condition or a mechanism other than variation in female condition is responsible for the relationship between *ice* and cub size and survival.

Polar bears are known to prefer shallow water areas over the continental shelf region (Durner et al. 2004). These regions are biologically richer than deep polar basin water (Pomeroy 1997), and polar bear foraging is thought to be more effective there. The positive relationship between the length of time ice remained over the continental shelf in summer and the size and mass of subadult males, yearlings per female, and skull size and mass of COY coincides with the perceived importance of the shelf region for foraging, and suggests that reduced access to these shallow water areas can reduce growth and recruitment in polar bears. Thus, changes in sea-ice conditions over time may indicate that declines over time observed in our study are at least partly the result of changes in ice conditions.

Conclusions

Declines in the stature of adult and subadult polar bears reported here and the relationship between sea-ice conditions and subadult male stature, mass, and condition are suggestive that bears in the SB are experiencing nutritional limitations. Principal findings were:

1. Mass of subadult male polar bears (ages 3-11) declined at a rate of 2.2 kg per year during the study. Length declined by 0.58cm per year and skull size declined by 1.6mm per year, and overall, subadult males showed the greatest declines in size and mass over time of all sex/age classes. Declines in length and skull size were also apparent for adult males, though reduced skull sizes were apparent only in younger adults suggesting that changes in stature may be a result of more recent changes in ecological conditions.
2. Skull size, length, and mass of subadult males also were also positively related to the percent of days when mean ice concentration over the continental shelf was $\geq 50\%$. In comparison to other sex/age classes, subadult males exhibited the strongest relationship to sea-ice conditions.
3. The mass of subadult females declined by approximately 1 kg per year in addition to declines in skull size and length of 0.7mm and 0.27cm per year, respectively. Adult females exhibited a decline of 0.28cm per year in length, but an increase in their body condition index (i.e., mass relative to length) over time. No measures for adult or subadult females exhibited relationships with ice conditions. Thus, the size and condition of females appear to be less closely linked to sea-ice conditions than males in this population.
4. While cub size and apparent survival during their first two years of life were negatively affected by years of poor ice coverage in near shore areas, cub mass and skull size did not decline during the study.

In conclusion, the observed decline in skull size and/or length of all adult and sub-adult classes, as well as declines in the condition and mass of subadult males in the population, supports the conclusion of Regehr et al. (2006) that the status of polar bears in the SB appears to be changing. Furthermore, changes observed in some sex/age classes and changes in sea-ice cover in recent years suggest that nutritional limitations related to changing habitat availability may be one factor causing the patterns we observed.

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Table 1. Abbreviated name and description of factors included in linear models.

<i>Abbreviated Factor Name</i>	<i>Description</i>
year	Year a bear was captured
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
cubs	Categorical variable used for adult females where “0” indicates she was not accompanied by cubs-of-the-year and “1” indicates accompanied by cubs-of-the-year
caphis	Capture history: categorical variable where “1” indicates the bear was captured once only, “2” indicates that the bear was captured more than once, and “3” indicates that the bear was captured three times or more
ice	The percentage of days in a given year between April and November when sea ice concentration over the Southern Beaufort Sea continental shelf was $\geq 50\%$
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

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

<i>Dependent Variable</i>	<i>Independent variables</i>
Adult males and females skull size & length (for both sexes)	age, year, age*year
Adult male mass & BCI	age, cdate, caphis (2 categories), ice or year, caphis*age, caphis*year (or ice)
Adult female mass & BCI	age, cdate, caphis (3 categories), year or ice, cubs, age*year (or ice), caphis*age, caphis*year (or ice), caphis*age*year (or ice)
Subadult males and females skull size, length, mass & BCI (for both sexes)	age, cdate, caphis (2 categories), ice or year, age*year (or ice), caphis*age, caphis*year (or ice), caphis*age*year (or ice)
Yearlings Skull size and mass	age, cdate, caphis (maternal: 3 categories), ice or year, sex, litsize, litsize*year (or ice), litsize*caphis, caphis*year (or ice), litsz*caphis*year (or ice)
COY Skull size and mass	age, cdate, caphis (maternal: 3 categories), ice or year, litsize, litsize*year (or ice), litsize*caphis, caphis*year (or ice), litsz*caphis*year (or ice)

Table 3. Trends in the size and condition of polar bears in the Southern Beaufort Sea between 1982 and 2006.

“+” indicates an increase over time significant at $P < 0.05$, “-” indicates a decrease, “0” indicates no change, and “NA” indicates not applicable.

<i>Bear size and condition</i>						
	Adults		Subadults		Yearlings	COY
	Male	Female	Male	Female		
Skull size	-/0 ¹	0	-	-	0	0
Length	-	-	-	-	NA	NA
Mass	0	0	-	0	0	0
BCI	0	+	-	0	NA	NA
<i>Cub Recruitment</i>						
	COY per female			Yearlings per female		
Spring	+			-		
Fall	-			0		

¹ Skull size declined for young adult males but remained the same for older adult males (see Figure 3)

Table 4. Results of linear models to assess the effects of capture history and year on polar bear body size and condition in the Southern Beaufort Sea. Sample sizes are in parentheses.

“NS” indicates that the effect was not significant. “NA” indicates not applicable. “*” indicates an interactive effect that is further discussed in the text.

	<i>Final model</i>	<i>F and p-values for caphis effects</i>	<i>F and p-values for year effects</i>	<i>Final model statistics</i>
ADULT FEMALES				
Skull size (384)	54.08 + 0.11age	NA	NS ($F_{1,381} = 0.08, P = 0.77$)	$F_{1,382} = 39.1, P < 0.0001$
Length (366)	728.88 + 0.33age - 0.29year	NA	$F_{1,363} = 26.3, P < 0.0001$	$F_{2,363} = 18.96, P < 0.0001$
Mass (260)	157.05 - 20.27cubs + 1.16age	NS ($F_{2,250} = 1.25, P = 0.292$)	NS ($F_{1,249} = 0.48, P = 0.49$)	$F_{2,253} = 22.4, P < 0.0001$
BCI (245)	-46.5 + 0.02year - 0.56cubs	NS ($F_{2,234} = 0.05, P = 0.95$)	$F_{1,242} = 13.87, P < 0.0001$	$F_{2,242} = 19.9, P < 0.0001$
ADULT MALES				
Skull size (186)	870.53 - 0.41year - 53.85age + 0.027year*age	NA	NA*	$F_{3,182} = 17.46, P < 0.0001$
Length (176)	874.42 - 0.336year + 0.68age	NA	$F_{1,170} = 9.75, P < 0.0001$	$F_{2,170} = 9.75, P < 0.0001$
Mass (43)	No factors significant	NS ($F_{1,39} = 0.016, P = 0.90$)	NS ($F_{1,42} = 1.04, P = 0.31$)	NA
BCI (31)	No factors significant	NS ($F_{1,26} = 0.59, P = 0.45$)	NS ($F_{2,28} = 2.19, P = 0.15$)	NA
SUBADULT FEMALES				
Skull size (56)	180.51 - 0.07year + 2.44age + 1.73caphis	$F_{1,52} = 8.45, P = 0.005$	$F_{1,52} = 4.51, P = 0.039$	$F_{3,52} = 11.1, P < 0.0001$
Length (57)	677.1 + 4.98caphis - 0.27year + 8.49age	$F_{1,53} = 4.63, P = 0.036$	$F_{1,53} = 4.65, P = 0.036$	$F_{3,53} = 8.49, P < 0.0001$
Mass (35)	No factors significant	NS ($F_{1,30} = 0.83, P = 0.45$)	NS ($F_{1,33} = 3.80, P = 0.060$)	NA
BCI (33)	No factors significant	NS ($F_{1,29} = 0.016, P = 0.90$)	NS ($F_{1,28} = 0.009, P = 0.92$)	NA

Table 4 (continued)

	<i>Final model</i>	<i>F and p-values for caphis</i>	<i>F and p-values for year effects</i>	<i>Final model statistics</i>
SUBADULT MALES				
Skull size (82)	373.83 + 2.16caphis + 1.83age - 0.16year	F _{1,79} = 10.4, P = 0.002	F _{1,79} = 7.79, P = 0.007	F _{3,79} = 8.2, P < 0.0001
Length (76)	1324.15 + 11.89caphis + 7.88age - 0.58year	F _{1,72} = 11.33, P = 0.001	F _{1,72} = 7.26, P = 0.009	F _{3,72} = 11.72, P < 0.0001
Mass (99)	4562.59 + 23.26age - 2.22year	NS (F _{1,94} = 3.07, P = 0.083)	F _{1,96} = 10.68, P = 0.002	F _{2,96} = 57.81, P < 0.0001
BCI (91)	599.95 + 0.15age - 0.015year	NS (F _{1,87} = 0.26, P = 0.61)	F _{1,88} = 7.0, P = 0.01	F _{2,88} = 11.85 P < 0.0001
YEARLINGS				
Skull size (88)	-1564.4 + 2.39sex + 0.04cdate - 1.0litsize	NS (F _{2,81} = 2.41, P = 0.096)	NS (F _{1,83} = 3.14, P = 0.08)	F _{3,84} = 22.01, P < 0.0001
Mass (61)	-12034.15 - 9.87litsize + 10.04sex + 0.31cdate	NS (F _{1,54} = 1.89, P = 0.16)	NS (F _{1,56} = 2.19, P = 0.14)	F _{3,57} = 6.93, P < 0.0001
CUBS-OF-THE-YEAR (COY)				
Skull size (184)	-3035.4 + 0.08cdate	NS (F _{2,179} = 0.08, P = 0.98)	NS (F _{1,171} = 0.19, P = 0.67)	F _{1,182} = 154.13, P < 0.0001
Mass (173)	-5875.3 - 2.26litsize + 0.15cdate	NS (F _{2,165} = 1.18, P = 0.31)	NS (F _{1,169} = 1.56, P = 0.21)	F _{2,170} = 27.17, P < 0.0001

Table 5. Relationship between polar bear body size and condition and the percent of days between April and November with ≥ 50 ice concentration over the continental shelf (ice) in the Southern Beaufort Sea.

“+” indicates a positive relationship with ice significant at $P < 0.05$, “-” indicates a negative relationship, “0” indicates no relationship, and “NA” indicates not applicable.

<i>Bear size and condition</i>						
	Adults		Subadults		Yearlings	COY
	Male	Female	Male	Female		
Skull size	NA	NA	+	0	0	+
Length	NA	NA	+	0	NA	NA
Mass	0	0	+	0	0	+
BCI	0	0	+	0	NA	NA
<i>Cub Recruitment</i>						
	COY per female			Yearlings per female		
Spring	0			+		
Fall	0			+		

Table 6. Results of linear models to assess the effects of capture history and ice habitat availability (ice) on polar bear body size and condition in the Southern Beaufort Sea. Sample sizes are in parentheses.

“NS” indicates that the effect was not significant. “NA” indicates not applicable. “*” indicates an interactive effect that is further discussed in the text.

<i>Final Model</i>		<i>F and p-values for ice effects</i>	<i>Final model statistics</i>
ADULT FEMALES			
Mass (260)	Same as Table 4	NS ($F_{1,249} = 0.09$, $P = 0.76$)	Same as Table 4
BCI (245)	Same as Table 4	NS ($F_{1,236} = 0.25$, $P = 0.62$)	Same as Table 4
ADULT MALES			
Mass (43)	No factors significant	NS ($F_{1,41} = 0.95$, $P = 0.34$)	NA
BCI (31)	No factors significant	NS ($F_{1,26} = 0.62$, $P = 0.44$)	NA
SUBADULT FEMALES			
Skull size (56)	$44.2 + 1.9\text{caphis} + 2.53\text{age}$	NS ($F_{1,53} = 1.98$, $P = 0.17$)	$F_{2,53} = 13.5$, $P < 0.0001$
Length (57)	$143.21 + 8.73\text{age} + 5.8\text{caphis}$	NS ($F_{1,51} = 0.03$, $P = 0.86$)	$F_{2,540} = 9.76$, $P < 0.0001$
Mass (35)	No factors significant	NS ($F_{1,32} = 1.87$, $P = 0.18$)	NA
BCI (33)	No factors significant	NS ($F_{1,31} = 1.61$, $P = 0.21$)	NA
SUBADULT MALES			
Skull size (82)	$42.88 + 2.03\text{caphis} + 1.85\text{age} + 0.15\text{ice}$	$F_{1,79} = 4.69$, $P = 0.033$	$F_{3,79} = 10.51$, $P < 0.0001$
Length (76)	$135.23 + 11.55\text{caphis} + 8.03\text{age} + 0.47\text{ice}$	$F_{1,72} = 11.12$, $P = 0.001$	$F_{3,72} = 12.7$, $P < 0.0001$
Mass (99)	$40.49 + 21.39\text{age} + 1.79\text{ice}$	$F_{1,96} = 16.64$, $P < 0.0001$	$F_{2,96} = 63.7$, $P < 0.0001$
BCI (91)	$-2.07 + 0.12\text{age} + 0.02\text{ice}$	$F_{1,88} = 14.82$, $P < 0.0001$	$F_{2,88} = 11.61$, $P < 0.0001$

Table 6 (continued)

	<i>Final Model</i>	<i>F and p-values for ice effects</i>	<i>Final model statistics</i>
YEARLINGS			
Skull size (88)	Same as Table 4	NS ($F_{1,79} = 0.27$, $P = 0.61$)	Same as Table 4
Mass (61)	Same as Table 4	NS ($F_{1,54} = 0.85$, $P = 0.36$)	Same as Table 4
CUBS-OF-THE-YEAR (COY)			
Skull size (184)	$-3196.4 + 0.08\text{cdate} + 0.04\text{ice}$	$F_{1,181} = 8.99$, $P = 0.003$	$F_{2,181} = 32.75$, $P < 0.0001$
Mass (173)	$-6574.4 + 0.17\text{cdate} + 0.12\text{ice} - 2.11\text{litsize}$	$F_{1,169} = 17.39$, $P < 0.0001$	$F_{3,169} = 25.66$, $P < 0.0001$

Table 7. Results of linear models to assess the effects of ice habitat availability (ice) and year on cubs-of-the-year (COY) and yearlings per female during spring and fall captures of polar bears in the Southern Beaufort Sea.

Sample sizes are in parentheses. “NS” indicates that the effect was not significant.

	<i>Ice Model</i>	<i>Ice Effect</i>	<i>Year Model</i>	<i>Year Effect</i>
SPRING				
COY per female (419)	NS	NS ($F_{1,418} = 0.002$, $P = 0.96$)	$-25.7 + 0.013\text{year}$	$F_{1,418} = 7.16$, $P = 0.008$
Yearlings per female (419)	$218.43 - 0.006\text{cdate} + 0.007\text{ice}$	$F_{1,418} = 6.32$, $P = 0.012$	$291.83 - 0.011\text{year} - 0.007\text{cdate}$	$F_{1,417} = 9.68$, $P = 0.002$
FALL				
COY per female (186)	NS	NS ($F_{1,185} = 1.8$, $P = 0.18$)	$46.5 - 0.023\text{year}$	$F_{1,185} = 8.67$, $P = 0.004$
Yearlings per female (186)	$-0.127 + 0.011\text{ice}$	$F_{1,185} = 5.82$, $P = 0.017$	NS	NS ($F_{1,185} = 0.47$, $P = 0.49$)

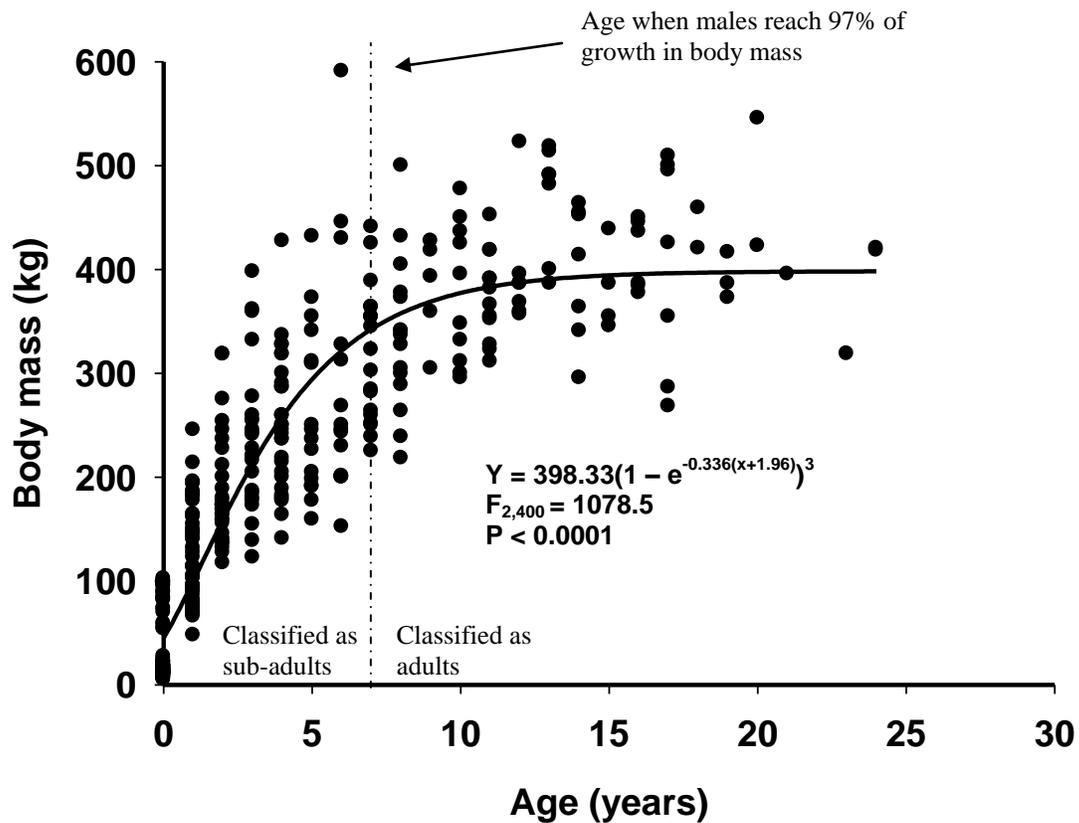


Figure 1. Relationship between age and body mass of male polar bears in the Southern Beaufort Sea fit with a von Bertalanffy growth curve.

The age when males reached 97% of maximal growth was used to distinguish subadult males from adult males in body mass analyses.

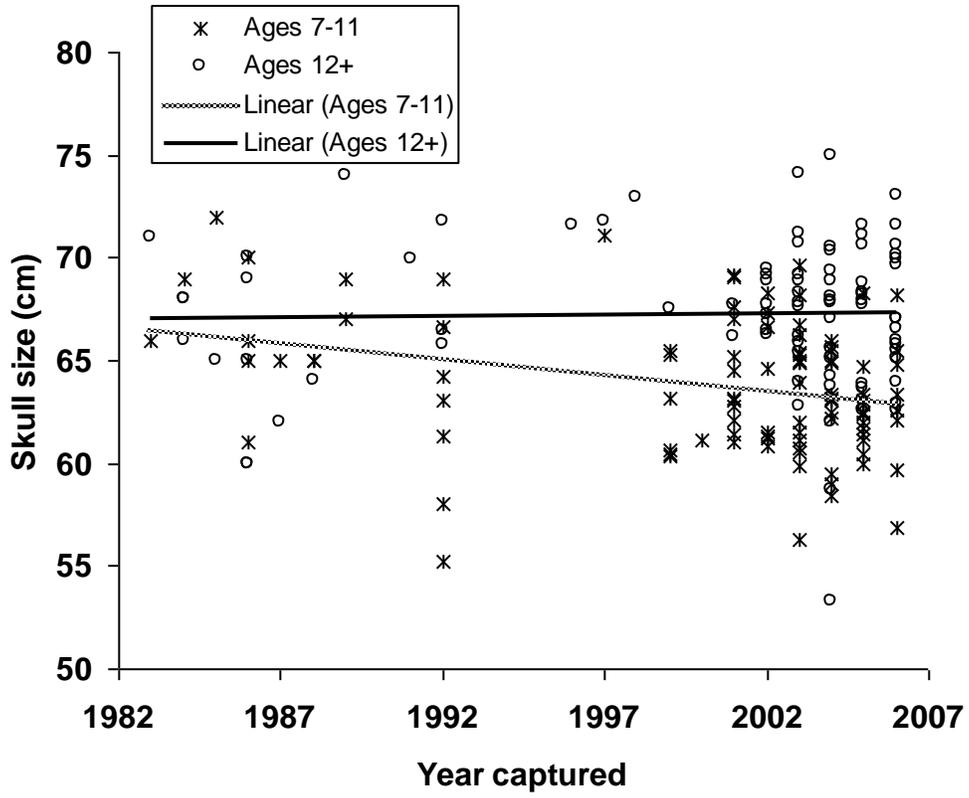


Figure 3. Interactive effect of age and year on mean skull size of adult male polar bears in the Southern Beaufort Sea.

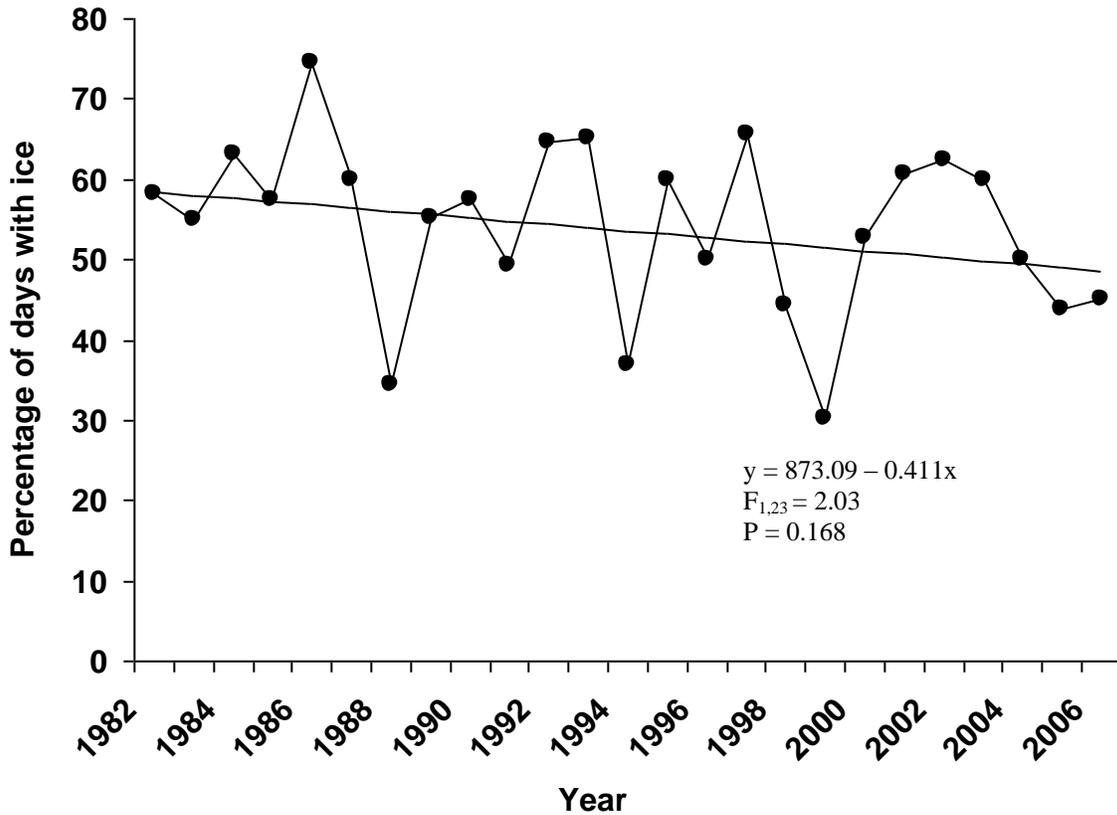


Figure 4. Annual variation in the percentage of days between April and November with ≥ 50 ice concentration over the continental shelf of the Southern Beaufort Sea.

Ice data presented are for the prior year since bear measurements in the spring were related to the prior years ice conditions.