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Variation in the response of an Arctic top predator experiencing habitat loss: feeding and reproductive ecology of two polar bear populations

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Abstract

Polar bears (*Ursus maritimus*) have experienced substantial changes in the seasonal availability of sea ice habitat in parts of their range, including the Beaufort, Chukchi, and Bering Seas. In this study, we compared the body size, condition, and recruitment of polar bears captured in the Chukchi and Bering Seas (CS) between two periods (1986–1994 and 2008–2011) when declines in sea ice habitat occurred. In addition, we compared metrics for the CS population 2008–2011 with those of the adjacent southern Beaufort Sea (SB) population where loss in sea ice habitat has been associated with declines in body condition, size, recruitment, and survival. We evaluated how variation in body condition and recruitment were related to feeding ecology. Comparing habitat conditions between populations, there were twice as many reduced ice days over continental shelf waters per year during 2008–2011 in the SB than in the CS. CS polar bears were larger and in better condition, and appeared to have higher reproduction than SB bears. Although SB and CS bears had similar diets, twice as many bears were fasting in spring in the SB than in the CS. Between 1986–1994 and 2008–2011, body size, condition, and recruitment indices in the CS were not reduced despite a 44-day increase in the number of reduced ice days. Bears in the CS exhibited large body size, good body condition, and high indices of recruitment compared to most other populations measured to date. Higher biological productivity and prey availability in the CS relative to the SB, and a shorter recent history of reduced sea ice habitat, may explain the maintenance of condition and recruitment of CS bears. Geographic differences in the response of polar bears to climate change are relevant to range-wide forecasts for this and other ice-dependent species.

Keywords: Body condition, body size, climate change, diet, feeding ecology, morphometrics, reproduction, *Ursus maritimus*

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Introduction

In the Arctic, reductions in the extent and thickness of sea ice have been observed (Maslanik *et al.*, 2011) and are projected to continue through at least 2100 based on multiple global climate models, including all models participating in the Intergovernmental Panel on Climate Change Fourth Assessment Report (Holland *et al.*, 2006; Stroeve *et al.*, 2012). Because the direct effects of climate change can be difficult to quantify, a species' projected response is often estimated by the relationship of the organism with its habitat (Parmesan, 2006). Polar bears (*Ursus maritimus*) are considered particularly vulnerable to negative effects associated with climate-induced sea ice loss because they rely on sea ice to access their primary prey, seals (Amstrup *et al.*, 2008; Laidre *et al.*, 2008).

Links between multiyear trends of declining sea ice with declining polar bear condition (Stirling *et al.*, 1999; Obbard *et al.* 2006; Rode *et al.*, 2010, 2012), reproduction (Rode *et al.*, 2010; Regehr *et al.*, 2007), and survival (Regehr *et al.*, 2007; 2009; Peacock *et al.*, 2012) have been documented for five polar bear populations (Baffin Bay, Davis Strait, Southern Hudson Bay, Southern Beaufort Sea, and Western Hudson Bay). However, declines in body condition and juvenile survival rates in Davis Strait occurred simultaneous to an increase in population density and could have been a result of density-dependent effects (Rode *et al.*, 2012; Peacock et al. 2012) and other populations have experienced sea ice loss with no apparent decline in population size or

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survival rates (i.e., Southern Hudson Bay, Gagnon and Gough 2005; Obbard *et al.,* 2007; Northern Beaufort Sea, Stirling *et al.,* 2011). These studies suggest that, among the world's 19 subpopulations, the response of polar bears to sea ice loss may vary temporally and geographically, due to variation in ecosystem function and in the life history strategies (Amstrup *et al.,* 2008). For example, bears in some populations experience several months of ice-free conditions and come onshore where they fast until sea ice returns. In other areas, the majority of bears spend the entire year on the sea ice or a small proportion of the population comes onshore during the annual sea ice minimum (Schliebe *et al*., 2008).

Reduced body size appears to be one of the proximate mechanisms by which climate change affects species (Gardner *et al.,* 2011; Sheridan and Bickford, 2011) and may be a useful indicator of organismal responses to climate change. Size and body mass of ursids respond to density-independent fluctuations in the environment and density-dependent effects (Zedrosser *et al*., 2006) and are linked to population density, reproduction, and cub survival (Noyce and Garshelis, 1994; Hilderbrand *et al.,* 1999). Studies of polar bears have documented declines in body size with increases in the duration of the ice-free period in seasonal ice habitats, and with the annual sea ice minimum extent in circumpolar regions (mass relative to length; Stirling *et al*., 1999; mass and skull size; Rode *et al.,* 2010, 2012). Although declines in body size could be an adaptive response to reduce energy requirements, observed declines in size were associated with declines in condition (i.e., measures of energy reserves relative to structural body size; Stirling *et al.,* 1999; body mass and skull width; Rode *et al.,* 2010). For polar bears, trends in body size and condition have been suggested as an indicator of potential negative effects of climate warming (Stirling and Derocher, 2012), assuming that trends in condition do not reflect population regulation (e.g., density dependence in the absence of declining habitat) or natural short-term variation (Rode *et al*., 2012). One of the most important food resources for polar bears, ringed seal (*Pusa hispida*) pups, become available in spring only (Pilfold *et al*., 2012) and continue to be an important food source until breakup in early summer (Stirling 2002). Because sea ice loss is occurring disproportionally in the summer and early autumn (Stroeve *et al*., 2012), effects of sea ice loss on bear body condition, reproduction, and survival may depend on the importance of summer foraging, vs. the contribution of foraging during other times of the year, to annual variation in condition.

Little is known about the population dynamics and ecology of the polar bear population that ranges in the Chukchi, northern Bering, and eastern Siberian seas (hereafter the Chukchi Sea "CS" population) where some of the most rapid sea ice loss in the Arctic has occurred (Rigor and Wallace, 2004; Douglas 2010). Durner *et al.,* (2009) estimated that optimal polar bear habitat in the CS declined by 8% per decade between 1979 and 2006, which is higher than declines experienced by the adjacent southern Beaufort Sea population (SB) (4.8% per decade) where reduced sea ice has been associated with declines in condition, recruitment, and survival of polar bears (Regehr *et al.,* 2009; Rode *et al.,* 2010). Observed and projected losses in sea ice habitat based on general circulation models, qualitative relationships between sea ice and population dynamics, and potential effects of other population stressors incorporated in a Bayesian Network model led Amstrup *et al.* (2008) to hypothesize that populations in the divergent ice ecoregion, which includes the CS population, may face extirpation by the mid-21st century unless climate warming is significantly mitigated.

Although the CS has experienced loss of sea ice, this region differs ecologically from the adjacent SB (Sigler *et al*., 2011) and from western Hudson Bay (WH) where polar bear populations have exhibited signs of nutritional stress and associated declines in recruitment (Stirling *et al*., 1999; Regehr *et al*., 2007, 2009; Molnár *et al*., 2010). Polar bears in WH and other eastern Canadian regions, such as Davis Strait and Baffin Bay, experience seasonally ice-free conditions and spend longer time on land as the duration of the ice-free season increases (Stirling and Parkinson, 2006). In contrast, sea ice habitat in the CS has historically persisted over part of the continental shelf even during the annual sea ice minimum (Douglas, 2010). Unlike the SB, which has a narrow continental shelf, nearly the entire CS is <300 m (Fig. 1). Productivity and polar bear prey density are much higher over the continental shelf than in deeper waters (Frost *et al*., 2002) and the CS has some of the highest marine primary productivity in the Arctic (Sakshaug, 2004). Furthermore, the CS contains a greater diversity of marine mammals as potential food resources than the SB, a factor that has been linked to increased body mass in predatory carnivores (Gittleman, 1985). In addition to the bearded seal (*Erignathus barbatus*), ringed seal, beluga whale (*Delphinapterus leucas*), and bowhead whale (*Balaena mysticetus*; primarily from subsistence harvest) that are available to polar bears in the SB, CS polar bears also overlap with spotted seal (*Phoca largha*), ribbon seal (*Histriophoca fasciata*), and Pacific walrus (*Odobenus rosmarus divergens*). However, diet composition, and its potential role in affecting body condition and reproduction have yet to be investigated for polar bears in the Chukchi Sea.

In this study, we compare body size, condition, and reproductive indices in the CS between two sampling

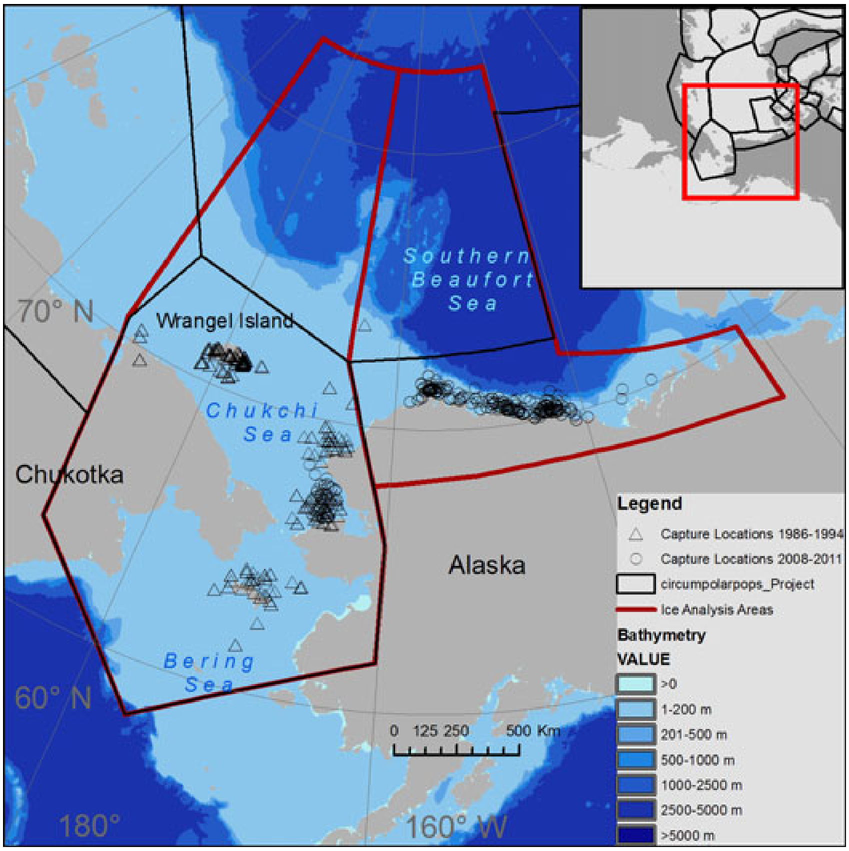

Fig. 1 Locations of captured polar bears in the Chukchi Sea (1986–1994 and 2008–2011) and in the southern Beaufort Sea (2008–2011) relative to the International Union for the Conservation of Nature Polar Bear Specialist Group's identified population boundaries (in black) for the Chukchi (also referred to as Alaska-Chukotka) and southern Beaufort Sea populations. Boundaries used for summarizing sea ice conditions for each population are outlined in red.

periods: 1986–1994 and 2008–2011 when sea ice habitat declined. We also compare body size, condition, and reproduction in the CS and SB for 2008–2011. We evaluated spatial and temporal habitat changes, using sea ice metrics based on habitat preferences of polar bears, and relationships between these metrics and body size, condition, and reproduction. We also examined how feeding ecology, including diet and fasting behavior, may affect variation in condition and reproduction.

Materials and methods

Sea ice availability

Sea ice habitat was quantified for the years before (1985–1993 and 2007–2010) collection of spring body condition and reproductive data (Rode *et al.*, 2010). SB and CS bears primarily use ice over the continental shelf (Durner *et al.*, 2004, 2009), which likely provides better access to prey and has been associated with higher body condition and reproduction than deep-water regions of the Arctic Ocean (Rode *et al.*, 2010). The study area for ice habitat analyses was bounded to the west and east by the International Union for the Conservation of Nature Polar Bear Specialist Group population boundaries for the CS and SB (Obbard *et al.*, 2010), and to the north and south by the range limits of radio-collared polar bears monitored between 1984 and 2011 (Fig. 1; US Geological Survey and US Fish and Wildlife Service, unpublished data).

We used sea ice concentration estimates derived from raster-format 25 km × 25 km resolution passive microwave satellite imagery (Cavalieri *et al.*, 1996) to calculate two habitat metrics: (i) the number of "reduced ice days" per year (*ice*), quantified as the number of days in which there was <6250 km^2 (roughly ten 25-km resolution pixels) of sea ice over the continental shelf within each population's ice analysis area (Fig. 1); and (ii) the mean daily minimum distance (hereafter referred to as "distance" or *mndist*) from each 25 km resolution pixel along the edge of the continental shelf (the 300 m isobath) to the edge of the pack ice, averaged over all days in September (the month of the annual sea ice minimum; Rigor and Wallace, 2004). When measuring the minimum distance between each shelf edge pixel and the ice edge, distances were set to zero in cases where the ice edge was south of the shelf break.

We assumed that the similar size of the two populations (CS: 2000 bears based on extrapolation of den surveys; Aars *et al.*, 2006; SB: 1526 ± 315 bears based on capture-recapture estimation; Regehr *et al.*, 2006) would allow use of a common area threshold for the "reduced ice days" metric by creating an effectively similar metric of population density. Because the area threshold representing foraging constraints is not known, we initially examined trends in ice using three thresholds: 6250, 10 000, and 20 000 km^2 (Figs. S1 and S2). Because polar bears occasionally occupy ice as low as 15% concentration (Durner *et al.* 2009), we also examined two concentration thresholds for defining the presence of ice: 15% and 50%. We found that trends, differences between populations (Figs. S1 and S2), and relationships with morphometric data were similar for the ice metric thresholds mentioned above, so we chose the most limiting area threshold of 6250 km^2 for reported analyses. We also chose to define ice habitat where concentrations were ≥50% because polar bears have exhibited strongest selection for this concentration throughout much of the year in this region (Durner *et al.*, 2004, 2006). Mann–Whitney *U* tests were used to determine if ice metrics differed between the CS during 1986–1994 and 2008–2011 and between the CS and SB during 2008–2011.

Polar bear measurement and sample collection

We analyzed data from polar bears captured and released on sea ice between mid-March and early May, during 2008–2011 in the SB and CS, and during 1986–1994 in the CS (Fig. 1; Table S1). Between 2008 and 2011, captures in both populations targeted all sex and age classes. However, females with cubs-of-the-year (COY, <12 months old) were rarely encountered in the CS during 2008–2011 because captures did not occur near key denning areas in Russia (Wrangel and Herald islands). To standardize the data sets, females with COY were excluded from all analyses. Adult males were avoided in the CS during 1986–1994 and could not be compared with the contemporary samples in the CS.

We classified adults as ≥5 years old (Regehr *et al.*, 2006); subadults as independent (i.e., without their mother) bears 2–4 years old; and dependent young as 2-year olds, yearlings, and COY. Polar bears were located from a helicopter and immobilized with a dart containing zolazepam-tiletamine (Telazol® or Zoletil®) (Stirling *et al.*, 1989). Immobilized bears were weighed to the nearest kilogram (kg) in the Alaskan portion of the SB and CS, but were not weighed in the Canadian portion of the SB. For all bears, straight-line body length, tail length, and zygomatic skull width were measured and age was determined as described in Rode *et al.* (2010). We measured straight-line body length of adults as an indicator of structural size. Body mass, skull width, and energy density (described below), which can vary annually and seasonally (Rode *et al.*, 2010), were used as measures of condition. Measures of body mass and body length were used to calculate energy density (MJ kg^{-1}) for each bear following Molnár *et al.* (2009). Energy density quantifies the 'energetic content of storage relative to the mass of tissue that requires energy for somatic maintenance' and standardizes body mass measures relative to structural size (Molnár *et al.*, 2009, 2010).

Standard methods for monitoring reproduction and offspring survival in ursids (e.g., continuous monitoring of individuals over time via resighting or radio telemetry) were not possible for the CS and SB populations because of the large and remote geographic areas. Instead, we examined indices of recruitment including yearling litter size (number of yearlings in a litter), the proportion of adult females with at least one yearling (females with yearlings/all females except those with COY), and the number of yearlings per female (number of yearlings in the sample/number of females unaccompanied by COY in the sample). We also examined relationships between maternal condition and the production and condition of COY (for the SB only) and yearlings (for the SB and CS), to investigate relationships between maternal condition and cub production.

Fat biopsies were collected from CS bears captured 2008–2011 to estimate diet. A 6-mm biopsy punch placed approximately 15 cm lateral to the base of the tail provided a full-layer core from skin to muscle (Thiemann *et al.*, 2006). Blood was collected in no-additive tubes to identify fasting behavior from bears captured in the CS during 2008–2011. Fat and blood were either not collected or unavailable for CS bears captured during 1986–1994 and for SB bears captured during 2008–2011. Information on diet composition and fasting behavior of SB bears were obtained from published studies (Thiemann *et al.*, 2008; Cherry *et al.*, 2011).

Comparisons of body size, condition, and reproduction

Comparison of body size and condition over time and among populations requires consideration of explanatory covariates, such as age. To facilitate comparisons between *samples* (e.g., between 1985–1994 and 2008–2011 in the CS and between the SB and CS samples during 2008–2011), we fit modified von Bertalanffy growth curves, relative to bear age, to measures of body mass, length, and skull size (Derocher and Wiig, 2002) and used the residuals as a dependent variable in generalized linear models (GLM; Laidre *et al.*, 2006; Rode *et al.*, 2010). Comparisons between populations and periods were made separately by including only data for the two periods in the CS and examining a *time* effect in the model or only the data for the two populations captured during 2008–2011 and examining a population (*pop*) effect in the model. We also related condition and reproduction to two potential *ice* metrics, separately, in place of either *time* or *pop* in the models. *Ice* replaced *pop* or *time* in the models to determine if ice might explain potential differences between periods or populations and because *ice* was likely to be correlated with those two factors. In addition to *pop, time,* or *ice* effects, other covariates included in candidate models included age, capture date, and litter size (for yearlings). Details about model selection are in Appendix S2.

We used asymptotic body mass, body length, and skull width from growth curves to compare the mean maximum sizes obtained by bears in different populations. Asymptotic body mass and body length were used to calculate energy density for bears in the SB and CS, as well as in the other polar bear populations that were considered for broader comparison. Body mass for other populations (Derocher, 1991; Derocher and Wiig, 2002) was calculated using girth and equations reported by Kolenosky *et al*. (1989), except for the Barents Sea population where a population-specific equation was used (Derocher and Wiig 2002).

Diet composition and fasting behavior

We examined the contribution of different prey species to the diet of independent bears captured in the CS during 2008–2011 based on quantitative fatty acid signature analysis (Iverson *et al*., 2004, Thiemann *et al*., 2008). Levels of blood urea nitrogen (BUN) and creatinine were measured in serum to identify bears that had fasted for >7 days (Derocher *et al*., 1990). Details on diet analyses are in Appendix S1. Generalized linear models were used to evaluate the contribution of a food item to dietary biomass as a function of sex, age, and body mass.

Results

Sea ice availability

The number of reduced ice days over the CS continental shelf averaged 44 days during 2007–2010 compared to 0 days during 1985–1993 (Mann–Whitney *U*-test, $df = 1$, $P = 0.003$; Fig. 2). The mean daily minimum distance in September between the CS continental shelf and pack ice increased 445 km between 1985–1993 (10 km) and 2008–2011 (455 km; Mann–Whitney *U*-test, $df = 1$, $P = 0.003$).

During 2007–2010, the reduced ice period was about twice as long in the SB (94.0 ± 3.9 days; mean ± SD) compared to the CS (44.5 ± 36.7 days; paired *t*-test: $P = 0.068$), and the mean minimum distance to the September ice edge was similar in the SB (465 ± 54 km) compared to that in the CS (455 ± 75 km; paired *t*-test: $P = 0.90$).

Comparisons of body condition and reproduction during 1986–1994 and those during 2008–2011 in the CS

During 2008–2011, CS bears were either larger and in better condition, or similar in size and condition compared to CS bears during 1986–1994. Parameters of growth curves are provided in Table S2. Comparing growth curves directly (Fig. 3a) females ≥1 year old during 2008–2011 were 27.9 kg larger in body mass (GLM including *age*: $\chi^2 = 45.1$, $P < 0.0001$) and 0.7 cm larger in skull width (GLM including *cdate*: $\chi^2 = 17.0$, $P < 0.0001$) than females during 1986–1994.

Mean body mass of CS male and female yearlings was 31.4 and 19.2 kg greater and mean skull width was 1.5 cm greater for both sexes during 2008–2011 than that during 1986–1994 (Tables 1 and S3). Differences are based on β coefficient values in Table S3 and significance of $P < 0.05$ in general linear models. Body mass and skull width of subadult females and body mass of subadult males did not differ, but skull width of subadult males was 0.9 cm larger during 2008–2011 than that found during 1986–1994. Mean body mass of adult females was 29.8 kg larger, skull width was 1.0 cm larger, and body length was 10.0 cm larger during 2008–2011 than that during 1986–1994, but energy density did not differ (Table S3). Because few adult males were captured in the CS during 1986–1994, sample sizes were insufficient for most comparisons. Mean skull width of six adult males captured during 1986–1994 did not differ from adult males captured during 2008–2011.

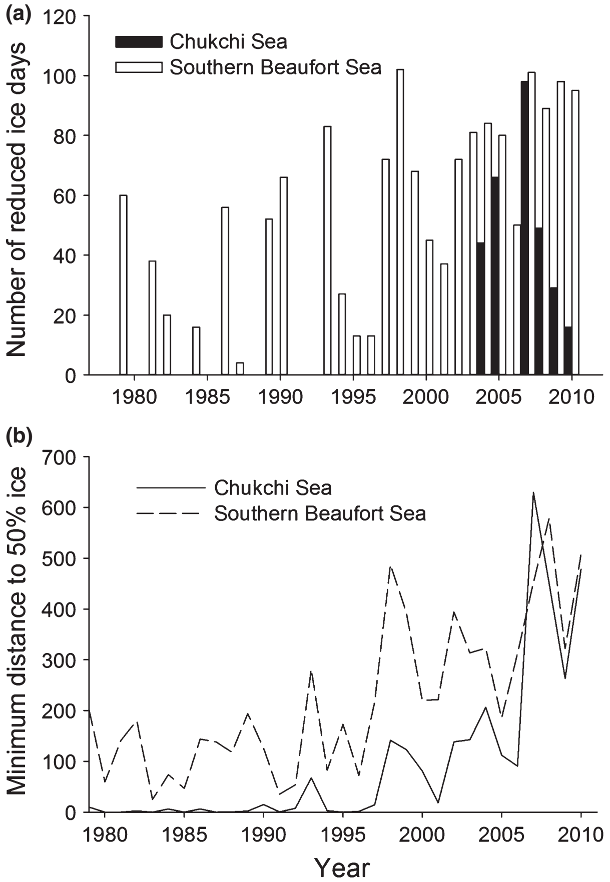

Fig. 2 Annual variation during 1979–2010 in (a) the number of days in which the extent of sea ice (≥50% concentration) was ≤6250 km^2 (absence of bars in any year indicates 0 ice-free days) and (b) September mean minimum distance between the continental shelf and sea ice of ≥50% concentration.

There was no difference in the number of yearlings per female, yearling litter size, or the annual percentage of females with yearlings between periods in the CS (Tables 2 and S3; $P > 0.50$ for all tests).

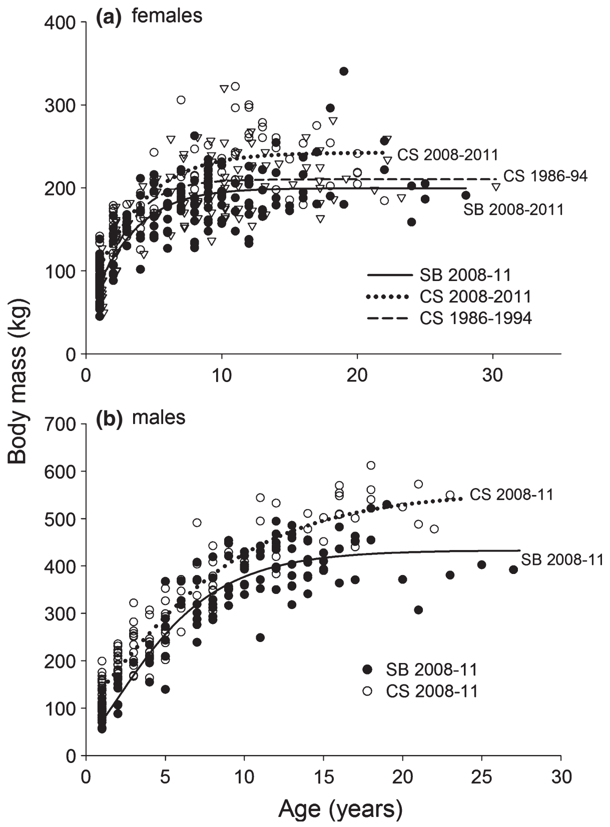

Fig. 3 Relationships between age and body mass for (a) female and (b) male polar bears in the Chukchi Sea (1986–1994 for adult females only; 2008–2010 for both sexes) and southern Beaufort Sea (2008–2011) fit with modified von Bertalanffy growth curves.

Replacing the *time* effect in general linear models with one of the two ice metrics (*ice* or *mndist*) resulted in a positive relationship between body condition and reduced ice conditions for most sex and age classes (Table 3, S3). Both ice metrics declined between 1986–1994 and 2008–2011 simultaneous to maintenance or increases in body condition. The number of yearlings per female declined as sea ice was reduced, but there was no effect of ice conditions on yearling litter size when including data over the two periods in the CS.

Comparisons between the SB and CS populations (2008–2011)

Overall, CS bears during 2008–2011 were larger and in better condition than SB bears during the same period. Comparing growth curves for body mass and skull width, females ≥ 1 year old weighed 30.2 kg more in the CS than the SB (Fig. 3a: $\chi^2 = 24.4$, $P < 0.0001$) and had skull widths 0.8 cm larger ($\chi^2 = 15.0$, $P < 0.0001$). Similarly, body mass of CS males ≥1 year old was 48.5 kg greater (Fig. 3b: $\chi^2 = 58.1$, $P < 0.0001$) and their skull width was 1.0 cm greater ($\chi^2 = 26.6$, $P < 0.0001$) than SB males.

CS female and male yearlings weighed 18.2 and 39.5 kg more and had skull widths 0.8 and 1.3 cm larger than their SB counterparts, respectively (Tables 1 and S4). CS subadult males weighed 44.3 kg more than SB subadult males, but subadult females did not exhibit a difference in mass. CS subadult females and males had skull widths that were 1.0 cm and 0.9 cm wider than SB subadult females and males, respectively. Adult females in the CS weighed 30.5 kg more, had 0.9 cm larger skull widths, and had 25% higher energy density than SB adult females, but body lengths were similar. CS adult males weighed 52.6 kg more, had 1.2 cm larger skull widths, and had 14% higher energy density than SB adult males, but body length did not differ.

The number of yearlings per female in spring was 34.8% and 43.5% higher (GLM: $\chi^2 = 8.7$, $P = 0.003$) in the CS than in the SB 2008–2011 sample (Tables 1, 2, and S4). There was no difference in yearling litter size. The percent of females with yearlings across all years was 10.9% higher in the CS than in the SB during 2008–2011, but this was not statistically different ($F_{1,6} = 0.08$, $P = 0.79$). Variation between years was large (SD = ± 20%) and annual sample sizes of females were low (20 ± 10 STD females). Yearling and COY body masses for both CS and SB were related to maternal body mass (Fig. 4).

When the *pop* effect in general linear models of the two populations was replaced with one of the two *ice* metrics, most sex and age classes had reduced body condition (body mass, skull width, and energy density) when the number of reduced ice days or the distance to sea ice in September increased (Table S4). However, subadults did not exhibit a relationship with reduced ice days; and mass of subadult males and females and skull width of subadult females was larger when there was a greater distance to ice in September. Yearlings per female and yearling litter size were lower when ice conditions were reduced.

Comparisons of body condition with other populations

Scale-measured and calculated body masses and measured skull widths of CS polar bears during 2008–2011 were among the highest reported for polar bear populations (Fig. 5). Similarly, energy density of adult males (23.0 MJ kg^{-1}) was higher than that in any population for which data were available (≤22.8 MJ kg^{-1}) and only adult females in Foxe Basin (22.1 MJ kg^{-1}) and the Central Arctic (21.7 MJ kg^{-1}) exhibited higher energy densities than CS bears during 2008–2011 (19.6 MJ kg^{-1}; Table S5).

Table 1 Comparisons between the morphometric measures of polar bears captured in the Chukchi Sea 1986–1994 ($CS_{1986–94}$) and 2008–2011($CS_{2008–11}$) and in the CS during 2008–2011 and the southern Beaufort Sea 2008–2011 ($SB_{2008–11}$) using general linear models. Comparisons of body mass, skull width, and body length (cm) for adults and subadults were made using residuals of the difference between predicted measures from a fit modified von Bertalanffy growth curve and observed measures. Energy density (MJ kg^{-1}) was determined from Molnár *et al.*, (2009). Covariates, including capture date, litter size for yearlings, and cub age for females, were included in models when $P < 0.10$. A list of models, test statistics, and *P*-values are provided in Table S3 and S4.

Sex and age class	Measure	$CS_{1986–94}$	$CS_{2008–11}$	$SB_{2008–11}$	CS *time* effects $CS_{2008–11} >$ $CS_{1986–94}$?		Population differences $CS_{2008–11} >$ $SB_{2008–11}$?	
					Time	*Ice* effect?	*Pop*	*Ice* effect?
Yearling Females	Mass	80.5 ± 20.3 (12)	99.7 ± 22.4 (12)	81.5 ± 17.1 (12)	+	0	+	–
	Skull width	14.0 ± 1.2 (19)	15.4 ± 1.0 (14)	14.6 ± 0.8 (13)	+	+	+	–
Yearling Males	Mass	101.7 ± 17.5 (17)	132.8 ± 29.7 (23)	93.3 ± 20.7 (18)	+	+	+	–
	Skull width	15.6 ± 1.0 (19)	17. 0 ± 1.1 (24)	15.7 ± 0.9 (20)	+	0	+	–
Subadult Females	Mass	156.1 ± 26.5 (9)	151.4 ± 21.2 (15)	152.6 ± 33.3 (15)	0	+	0	+
	Skull width	17.6 ± 1.2 (11)	18.2 ± 1.0 (15)	17.6 ± 1.3 (15)	0	+	+	+
Subadult Males	Mass	213.2 ± 35.2 (6)	221.4 ± 42.0 (34)	213.4 ± 43.6 (42)	0	0	+	+
	Skull width	19.4 ± 1.3 (9)	20.0 ± 1.2 (34)	19.9 ± 1.2 (41)	+	+	+	0
Adult females without coy	Mass	215.1 ± 36.5 (52)	228.2 ± 39.6 (51)	194.1 ± 31.8 (70)	+	+	+	–
	Skull width	20.6 ± 1.4 (66)	21.4 ± 1.6 (53)	20.3 ± 1.1 (82)	+	0	+	–
	Length	188.3 ± 9.5 (57)	197.3 ± 11.3 (49)	197.4 ± 8.5 (77)	+	NA	0	NA
	Energy D	20.6 ± 5.3 (47)	17.9 ± 4.1 (47)	13.9 ± 3.9 (60)	0	0	+	–
Adult Males	Mass	437.1 ± 43.5 (3)*	423.1 ± 97.9 (60)	374.4 ± 75.5 (99)	NA	NA	+	–
	Skull width	24.5 ± 2.3 (6)	25.9 ± 2.7 (65)	24.8 ± 2.0 (101)	0	+	+	–
	Length	225.4 ± 7.6 (4)*	227.5 ± 11.7 (59)	228.0 ± 13.0 (101)	NA	NA	No	NA
	Energy D	15.4 ± 1.3 (3)*	14.9 ± 2.6 (57)	12.9 ± 2.4 (97)	NA	NA	+	0

*Adult males were not targeted in CS captures 1986–1994; thus sample sizes for most *time* comparisons were insufficient

Table 2 Comparison of spring reproductive measures for bears in the Chukchi and Bering (CS; this study) and southern Beaufort Seas (SB; values reported by Regehr et al. 2006 and from this study). Sample sizes in parentheses

	CS 1986–1994†	CS 2008–2011	SB 1967–1989	SB 1990–2006	SB 2008–2011
Reproductive rate (yearlings per female)	0.62 (58)	0.66 (53)			0.46 (135)
% females with yearlings *	38.5	41.5	26	24	30.6
% females with 2-year olds	20	22.6		9	7.1
Cub-of-the-year litter size	1.85 ± 0.57 (85)	1.90, 2.17‡ (39, 24)			1.79 ± 0.52 (57)
Yearling litter size	1.64 ± 0.49 (22)	1.59 ± 0.67 (22)	1.54	1.34	1.38 ± 0.58 (45)

*Values for the southern Beaufort Sea were corrected to exclude females with COY as the Chukchi and Bering Seas sample is biased against sampling of females with COY.

†Measures exclude females captured during the spring near Wrangel Island as the Wrangel Island sample was biased toward denning females

‡Estimated by Ovsyanikov and Menyushina (2010) for 2007 and 2009 on Wrangel Island

Diet composition and fasting behavior

Ringed seal was consumed by all independent bears ($n = 182$) and contributed more than any other prey to CS bear diets during 2008–2011 (79 ± 18% of dietary biomass; Table 3). Most bears consumed some bearded seal (74 ± 12% of bears) and bowhead whale (85 ± 11% of bears), but these species contributed only 12% and 6% of dietary biomass, respectively. Walrus (41 ± 12% of bears) and beluga whale (7 ± 5% of

Table 3 Mean (± SD) contribution of prey items to diets of CS polar bears captured in the Chukchi and Bering Seas during the spring based on fatty acid composition of fat biopsies. Data represent the% contribution to polar bear fatty acid profiles and thus reflect the relative contribution to polar bear diets on a biomass basis. Subadults include bears aged 2–4 years

	Bearded Seal	Beluga Whale	Bowhead Whale	Ringed Seal	Walrus
Adult Females (55)	6.5 ± 9.2	0.5 ± 3.5	5.1 ± 6.0	87.4 ± 11.2	0.6 ± 1.4
Adult Males (61)	20.7 ± 17.3	1.4 ± 4.5	7.7 ± 7.4	65.7 ± 17.3	4.4 ± 6.0
Subadult Females (13)	2.6 ± 3.5	0.3 ± 1.0	3.9 ± 4.0	93.2 ± 3.9	0.0 ± 0.1
Subadult Males (25)	6.8 ± 7.5	1.8 ± 6.9	4.8 ± 5.7	86.4 ± 10.8	0.2 ± 0.5
MEAN	11.9 ± 14.5	1 ± 4.5	6.1 ± 6.8	78.5 ± 18.5	2.4 ± 6.7

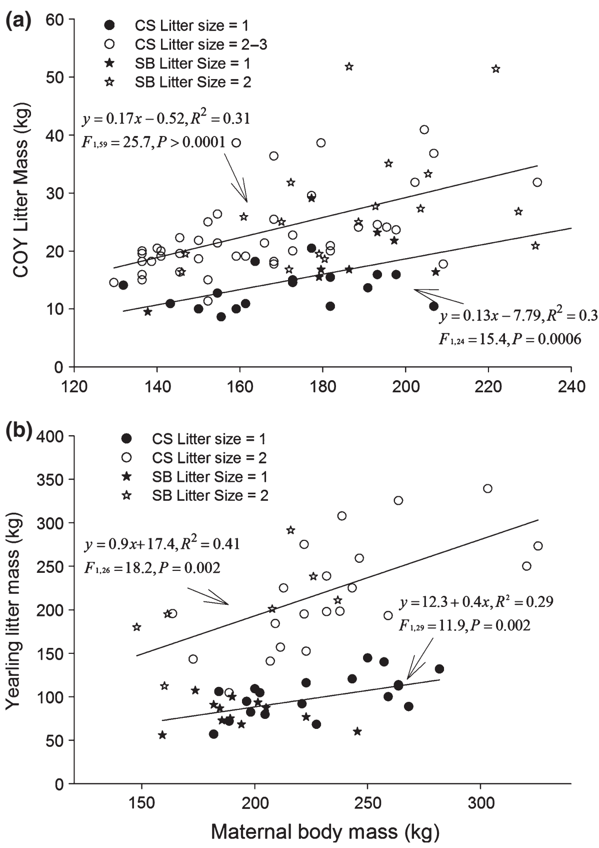

Fig. 4 Relationships between maternal body mass and litter mass of (a) COY and (b) yearlings for polar bears captured in the spring in the Chukchi Sea (1986–1994 and 2008–2011) southern Beaufort Sea (2008–2011).

bears) were consumed less frequently and contributed only 2% and 1% of dietary biomass, respectively.

The contribution of bowhead whale to dietary biomass of CS bears was 4% greater for subadults than adults (generalized linear model: $\chi^2 = 6.8$, $P = 0.009$), 3% greater for females than males ($\chi^2 = 3.7$, $P = 0.055$), and increased with body mass within age and sex classes ($\beta = 0.0003$, $\chi^2 = 11.7$, $P = 0.001$). The contribution of bearded seal to dietary biomass exhibited the opposite relationship being 12% greater in adults than subadults and 12% greater in males than females.

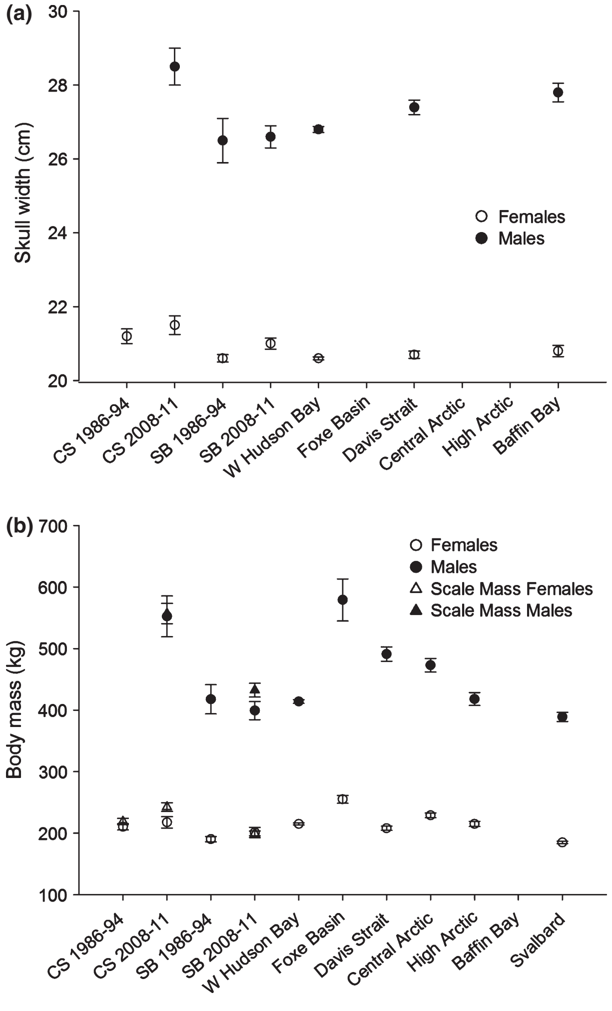

Fig. 5 Comparison of (a) asymptotic skull width and (b) body mass of male and female polar bears measured in this study (Chukchi Sea: CS 1986–1994, 2008–2011; southern Beaufort Sea: SB 2008–2011) with reported values for other populations (Derocher and Stirling 1998, Derocher and Wiig 2002; Rode et al. in press). Asymptotes were determined from fitting a modified von Bertalanffy growth curve. Calculated and scale body mass are shown for bears captured in the Chukchi and southern Beaufort Seas. Central Arctic includes portions of the Gulf of Boothia and M'Clintock Channel polar bear populations and the High Arctic includes the Lancaster Sound polar bear population.

Walrus contributed twice as much to the dietary biomass of males (3.2%) than females (1.6%; $\chi^2 = 21.2$, $P < 0.0001$). Beluga whale similarly contributed more to the dietary biomass of males (1.7%) than females (0.4%: $\chi^2 = 10.2$, $P = 0.006$). In contrast, the contribution of ringed seal to dietary biomass of CS bears did not differ between sex or age classes, but decreased with increasing body mass ($\beta = -0.001$, $\chi^2 = 65.7$, $P < 0.0001$). No bears consumed ribbon seals and only two bears consumed spotted seals.

Thirteen of the 150 CS bears (annual mean 8.0 ± 4.0%) during 2008–2011 had urea:creatinine ratios (U:C) indicative of fasting (≤10.0). Urea levels were lower (6.3 ± 1.1 mg dl^{-1}; $F_{1,148} = 16.9$, $P < 0.0001$) and creatinine levels were higher (1.8 ± 0.3 mg dl^{-1}; $F_{1,148} = 34.3$, $P < 0.0001$) for bears that had U:C ratios ≤10.0 vs. bears with U:C ratios > 10.0 (urea: 21.0 ± 12.7 mg dl^{-1}; creatinine: 1.0 ± 0.4 mg dl^{-1}), a pattern consistent with fasting. All fasting bears were adult males except one and no bears were assigned a body condition score of 1 that would suggest protein catabolism and an elevated U:C ratio while fasting.

Discussion

Our comparative analysis of ecological indicators for CS and SB polar bears, in relation to sea ice and other factors provides insights into spatial and temporal variation in the effects of diminishing ice cover. Body size, condition, and reproductive indices of CS polar bears did not decline over time between 1986–1994 and 2008–2011 despite a 44-day increase in the number of reduced ice days. Furthermore, CS bears were larger, in better condition, and appeared to have higher recruitment compared to the adjacent SB population during 2008–2011. These differences were biologically significant and could have important implications for population dynamics and resiliency to continued habitat loss: especially in the short term. For example, yearling females weighed over 18 kg more in the CS than in the SB, and adult females weighed over 30 kg more. Relationships between female body mass and yearling mass, and apparent higher recruitment in the CS, suggest that differences in body condition between populations are associated with observed differences in recruitment.

Differences in the rate and timing of sea ice loss in the CS and SB may explain the apparent variation in the response of polar bears. Although the rate of decline in sea ice habitat was twice as high in the CS (−8.0% per decade) than the SB (−4.8% per decade) (Durner *et al.*, 2009), there were twice as many reduced ice days per year in the SB (mean 90 days) than in the CS (mean 45 days) during 2007–2010. Cumulatively, there were 160 more reduced ice days in the SB than the CS during 2008–2012, although comparisons were not statistically significant due to high variability. In addition, the SB has experienced an increase in the number of reduced ice days since the mid-1990s, whereas this has only recently begun to occur in the CS (Fig. 2).

Differences between populations fit expected relationships of decreased body condition and recruitment when or where sea ice habitat is reduced. In the CS, however, body condition was maintained or improved when sea ice declined suggesting that factors other than the presence of sea ice affect temporal and geographic variation in condition and recruitment. Primary productivity in the CS (250–300 g C m^{-2} yr^{-1}; Walsh *et al.*, 1989) was 10 times higher than the Beaufort Sea (10–25 g C m^{-2} yr^{-1}; Alexander, 1974; Horner, 1984) and among the highest of any world ocean (Grebmeier *et al.*, 2006). Climate warming has not only led to sea ice loss in the CS but also resulted in warmer waters and increases in primary productivity (Zhang *et al*., 2010). Evidence of high biological productivity is apparent for polar bear prey species in the CS. Condition and reproduction of ringed seals and bearded seals, which comprise almost 80% of polar bear diets in the CS, have either increased or remained stable since the 1970s (Quakenbush *et al.*, 2011a, b). Pregnancy rates among ringed seals in the CS were the second highest recorded and females are maturing at the youngest age reported. Ringed seal pups are one of the most important food sources for polar bears (Pilfold *et al.*, 2012) and high proportions of ringed seal pups in subsistence harvest samples in the CS suggest they are abundant (Quakenbush *et al*. 2011a). Growth rates, condition, and pregnancy rates of CS bearded seals were also average or above average (Quakenbush *et al.*, 2011a). In contrast, ringed seal body condition in Amundsen Gulf in the eastern Beaufort Sea has declined in recent years (Harwood *et al.*, 2012). While continued high biological productivity in the Chukchi and northern Bering seas region may be allowing polar bears and their prey to prosper despite habitat loss, declines in the condition of SB bears may be a combination of reduced access to prey resulting from declining ice habitat (Rode *et al.*, 2010; this study), declining prey body condition (Harwood *et al*. 2012), and the much smaller area of productive, shallow continental shelf.

Our evaluation of nutritional ecology for polar bears is consistent with lower prey availability in the SB compared to the CS. Only 8% of polar bears captured in the CS appeared to be fasting in spring, compared to 21.4 and 29.3% of bears fasting in the SB in spring 2005 and 2006, respectively (Cherry *et al.*, 2009). In the CS, the majority of fasting bears were adult males (92% of fasting bears) who may forgo foraging to pursue females during the mating season (Ramsay *et al.*, 1991; Cherry *et al.*, 2009). The SB, in contrast, had 20–25% of adult females (including separate categories of females with and without dependent young) and >15% of subadults fasting.

Consumption of larger prey species or carrion or a greater diversity of prey does not appear to explain the difference in body size and condition observed between CS and SB bears. Diets consisted of 80–90% ringed and bearded seals and were relatively similar between the two populations (SB data from Thiemann *et al.*, 2008 and CS data from this study). Although CS polar bears were larger and in better condition, their diet was composed more of the smallest prey species, ringed seals (78.5%; 50–70 kg), and less of the larger bearded seal (12%; 200–430 kg), than bears in the adjacent SB (60% ringed seal, 20% bearded seal; Fig 7b. in Thiemann *et al.*, 2008). CS polar bears did consume walrus (2.4% of dietary biomass), which rarely occur in the SB and could provide large amounts of food from a single kill or carcass (800–1680 kg). An increased availability of walrus carcasses associated with summertime sea ice loss (Fischbach *et al.*, 2009) could be an important food resource for CS bears. Furthermore, summer observations on Wrangel Island suggest that walrus are frequently successfully hunted and consumed as carrion (Kochnev 2002). However, such feeding may not be reflected fully in this study because diets were based on spring-collected fat biopsies and turnover time of fatty acids in polar bears is not known.

Our spring 2008–2011 observations of CS polar bears in good condition and with high recruitment are consistent with autumn observations of bears from this population on Wrangel Island during the same period (Ovsyanikov and Menyushina, 2010) and with comparisons to other populations (Table S5). Between 100 and 400 polar bears use Wrangel Island as a summer refugia (Ovsyanikov 2012) and the majority of the CS population dens on Wrangel Island or nearby (70 km east) smaller (11.3 km^2) Herald Island (Garner *et al.* 1994; US Fish and Wildlife Service, unpublished. data). Based on a condition index (Stirling *et al.*, 2008) only 3% of the bears that came onshore on Wrangel Island in autumn of 2005–2009 appeared undernourished (condition index of 1–2), 30% were categorized as normal condition (condition index of 3), and 67% were categorized as fat (condition index of 4–5; Ovsyanikov and Menyushina, 2010). Skull width, body mass, and energy density of polar bears caught in the CS during 2008–2011 were also among the largest of any polar bear population that has been measured to date (Fig. 5).

Spring COY litter sizes reported on Wrangel Island between 2007 and 2009 were 1.90 (n = 39) and 2.17 (n = 24; Ovsyanikov and Menyushina, 2010), respectively, which is similar to litter sizes 20 years earlier (late 1980s through early 1990s, 1.81–1.85; Vaisfeld and Chestin, 1993; this study). These spring COY litter sizes are among the highest reported for 18 of 19 polar bear populations, which range from 1.50 to 2.27 for bears at the den site and 1.30–1.94 for bears that had moved away from dens in spring (Derocher, 1999). Similarly, autumn litter sizes between 2004 and 2010 were 1.59 ± 0.58 for COY (n = 170; Ovsyanikov, 2012) which are on the high end of those reported for other populations (1.49–1.58 for SB 1986–1994, Southern Hudson Bay, Western Hudson Bay, and Davis Strait; Regehr *et al.*, 2006; Peacock *et al.* 2013; Obbard *et al.*, 2010). Spring litter sizes of CS yearlings from this study (1.59) were also higher than those in other populations (SB: 1.34–1.54; Amstrup, 1995; Regehr *et al.*, 2006; Svalbard: 1.40, Wiig, 1998; 1.52, Derocher, 2005; Baffin Island: 1.57; Peacock *et al.* 2013). The larger body mass of adult females in the CS corresponded not only with larger litter sizes but also with heavier yearlings (Fig. 5), which have a greater chance of survival (Derocher and Stirling, 1996).

Our evaluation of ecological indicators for the CS population is based on 4 years of recent data in a highly variable and changing environment. Continued monitoring is needed to determine whether condition and reproduction will be maintained with projected continued loss of sea ice. The CS shelf is projected to be largely ice-free in September and October by mid-century (Douglas, 2010; Wang *et al.*, 2012), and the duration of the ice-free period is projected to reach 4 months by the end of the century (Douglas 2010). Relationships between ice availability, reproductive indices, and cub size (Stirling *et al.*, 1999; Rode *et al.*, 2010; this study) suggest that long-term continuous decline in sea ice might first affect body condition and reproduction (Stirling and Derocher, 2012) making these important metrics to be included in long-term monitoring. Continued sea ice loss could not only create challenges for bears to access prey but also to reach key denning habitats on Wrangel and Herald islands and the Chukotkan coast where the majority of CS pregnant females den. For example, changes in sea ice formation resulted in reduced use and periodic loss of a denning area in Svalbard (Derocher *et al.*, 2011). Recent observations on Wrangel Island suggest a decline in the number of denning females and low autumn yearling litter sizes of 1.31 ± 0.54 (n = 55) between 2004 and 2010, and suggests that cub survival rates have been lower in recent years (Ovsyanikov, 2012). Sea ice loss may result in other mechanisms that result in direct or indirect mortality such as drowning or increased durations spent swimming (Monnett and Gleason, 2006; Pagano *et al.*, 2012). Furthermore, the ecological indicators considered in this study do not reflect potential effects of human-caused mortality, which could affect population growth but would be unlikely to affect body condition and reproductive indices.

Our findings of geographic, temporal, and other ecological variation among polar bears experiencing sea ice loss, emphasize the challenge of developing general —yet accurate—population projections, over the short term. In our relatively short study, declines in sea ice extent alone did not completely explain variation in polar bear population productivity. This suggests that polar bears may exhibit complex and nonlinear responses to climate change, especially in the short term. The amount of available habitat, the status of prey populations, and ecosystem productivity likely all play important roles in determining the timing and magnitude of polar bear responses to sea ice loss. Parallel declines in the condition of polar bears (Regehr *et al.*, 2006; Rode *et al.*, 2010) and ringed seals (Harwood *et al.*, 2012) in the SB signal the potential for negative trophic effects that could additively affect polar bears in this region. This contrasts to maintenance of body condition and reproduction of polar bears and their primary prey (Quakenbush *et al.*, 2011a, 2011b) in the CS. Such regional covariation in the apparent response of prey and predator suggest that ecosystem-based projections (in addition to range-wide projections) may be a fruitful path of future research and conservation efforts for individual species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Detailed description of methods used to estimate diet and fasting behavior.
Appendix S2. Detailed description of statistical methods used to compare body condition and reproduction between the two polar bear populations and periods.
Table S1. Sex and age class of bears captured in the Chukchi Sea during 1985–1994 and 2008–2011 and in the southern Beaufort Sea during 2008–2011.
Table S2. Parameters of modified von Bertalanffy growth equations fit to total body length, skull width, and body mass of polar bears captured in the Chukchi and southern Beaufort Seas during 2008–2011 and in the Chukchi Sea during 1986–1994.
Table S3. Results from comparisons of body size and condition for polar bears captured in the Chukchi Sea (CS) during 1986–1994 and 2008–2011 using general linear models.
Table S4. Results from comparisons of body size and condition for polar bears captured in the Chukchi Sea (CS) and the Southern Beaufort Sea between 2008 and 2011 using general linear models.
Table S5. Estimated energy density (based on models by Molnár *et al.*, 2009) of male and female polar bears from various populations across the Arctic based on asymptotic body length and body mass from a modified von Bertalanffy growth curve.
Table S6. Contribution of prey items to diets of polar bears captured in the Chukchi and Bering Seas during the spring based on fatty acid composition of fat biopsies. Data represent the % contribution to polar bear fatty acid profiles and thus reflect the relative contribution to polar bear diets on a biomass basis. Subadults include bears aged 2–4 years.
Figure S1. Annual variation in the mean minimum distance between sea ice of 15% (a) and 50% (b) concentration and the continental shelf break (300 m isobath) between 1979 and 2010 in the Chukchi Sea and southern Beaufort Sea.
Figure S2. Annual variation in the number of reduced ice days defined as days in which there was less than 6250, 10 000, or 25 000 km^2 of either 15% (a) or 50% (b) ice concentration over the continental shelf (<300 m ocean depth) in the Southern Beaufort Sea and Chukchi Sea during 1979–2010.