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ORIGINAL PAPER

Fasting physiology of polar bears in relation to environmental change and breeding behavior in the Beaufort Sea

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Abstract We examined the use of the ratio of serum urea to serum creatinine as a physiological biomarker of fasting to monitor temporal patterns in the feeding ecology of polar bears (*Ursus maritimus*). Blood was collected from 436 polar bears in the eastern Beaufort Sea during April and May of 1985–1986 and 2005–2006. The proportions of polar bears fasting were 9.6% in 1985, 10.5% in 1986, 21.4% in 2005, and 29.3% in 2006. We used stepwise logistic regression analysis to evaluate factors that could influence the binary response variable of fasting or not fasting. Significant predictor variables of fasting were: the 2005 and 2006 capture years, solitary adult male bears, and adult male bears that were accompanying an estrous female. The increased number of polar bears in a physiological fasting state from all sex, age, and reproductive classes in 2005 and 2006 corresponded with broad scale changes in Arctic sea ice composition, which may have affected prey availability. The higher proportion of adult males fasting from all years was attributed to spring breeding behavior.

Keywords Beaufort Sea · Breeding behavior · Environmental change · Fasting physiology · Physiological biomarker · Polar bear · Sea ice · Serum urea to creatinine ratio

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Introduction

Understanding how environmental variability influences the population dynamics of a species is an integral component of conservation biology. However, measuring the effects of environmental variability on upper trophic level species is difficult due to time lags in population responses (Veit et al. 1997; Thompson and Ollason 2001; Weimerskirch et al. 2003) and the complexity involved in community structure (Hunter and Price 1992; Walther et al. 2002; Lee and Whitledge 2005). Predator management and conservation decisions are commonly based on population estimates but the underlying ecological factors influencing their population trends are often poorly understood. Nevertheless, conservation and monitoring programs focusing on apex predators are ecologically important because predator density is dependent on total ecosystem productivity (Hooker and Gerber 2004; Sergio et al. 2006). Developing methods to monitor the physiological responses of top predators to environmental change is one way to improve our understanding of factors involved in predator population fluctuations (Thompson et al. 1997; Wasser et al. 1997).

The sea ice of the Arctic has shown large-scale changes in response to climate warming. The Arctic ice-ocean system has been warming faster than global averages since the 1960s (Zhang 2005). Recent evidence from passive microwave satellite data collected between 1979 and 2006 shows significant declines in summer minimum and winter maximum Arctic sea ice extents (Comiso 2006; Stroeve et al. 2006; Serreze et al. 2007). In 2005–2006, mean surface temperatures over the Arctic ice cover were significantly higher than normal (Comiso 2006) and spring melt seasons between 2000 and 2005 began an average of 13 days earlier when compared to 1980–1989 (Stroeve et al. 2006). It has been hypothesized that such decreases in sea ice extent will affect pagophilic (ice-dependent) marine mammals throughout the Arctic (Stirling and Derocher 1993; Tynan and DeMaster 1997; Derocher et al. 2004). Continued long-term increases in global atmospheric temperatures will result in permanent habitat loss and fragmentation for several of these species (Laidre et al. 2008; Ragen et al. 2008). The polar bear (*Ursus maritimus*) is the apex predator in ice-covered Arctic seas and feeds primarily on ringed seals (*Phoca hispida*) and to a lesser extent bearded seals (*Erignathus barbatus*) (Stirling and McEwan 1975; Stirling and Archibald 1977a; Smith 1980). Earlier break-up in spring and longer ice-free periods have been linked to decreases in body condition and survival of polar bears in the southernmost part of their range, Hudson Bay (Stirling et al. 1999; Obbard et al. 2006; Regehr et al. 2007a).

The Beaufort Sea is one of several seas between the coast surrounding the Arctic Ocean and the permanent pack of the polar basin and has two populations of polar bears, the Northern Beaufort Sea and Southern Beaufort Sea (Aars et al. 2006). Although there have been many recent changes to Arctic climate and sea ice composition, direct effects of climate change on polar bears in the Beaufort Sea have not been well established. However, a number of recent observations in the Southern Beaufort Sea have been consistent with predictions regarding possible climate-induced stresses on polar bears. Unusual ice conditions and strong winds were linked to a drowning event where up to 27 polar bears were thought to have died (Monnett and Gleason 2006). Further, a report of polar bears showing unusual and energetically inefficient foraging behaviors suggests that Southern Beaufort Sea bears were food-stressed in recent years (Stirling et al. 2008a). A number of cannibalism events were also thought to be related to bears having difficulty obtaining food (Amstrup et al. 2006; Stirling et al. 2008a). Significant reductions in population size estimates have not been reported for either the Northern or Southern Beaufort Sea populations, but decreases in cub-of-the-year survival and recruitment indicate the Southern Beaufort Sea population may currently be declining (Regehr et al. 2006; Rode et al. 2007; Stirling et al. 2007). Regehr et al. (2007b) suggest that increases in the duration of ice-free periods over the continental shelf have been associated with decreases in survival and reproduction for Southern Beaufort Sea polar bears.

Even though polar bears are adept swimmers, they are dependent upon sea ice as a platform from which to hunt seals (Stirling and Derocher 1993; Ferguson et al. 2000a; Derocher et al. 2004). With the exception of pregnant females, most of which over-winter in dens on land, the majority of polar bears in the Beaufort Sea stay on the sea ice throughout the year (Amstrup et al. 2000; Stirling 2002; Fischbach et al. 2007). During winter and spring, the bears reside on sea ice over the continental shelf where seal densities are higher than farther offshore (Stirling and Archibald 1977b; Stirling et al. 1982). The Beaufort Sea continental shelf region is typically ice-free in late summer and bears are forced farther offshore onto multiyear ice that occurs over deeper and less productive waters (Pomeroy 1997; Lee and Whitledge 2005). In recent years, some Beaufort Sea polar bears have also been observed spending the late summer months on land (Schliebe et al. 2008). Regardless of where the bears go when the sea ice retreats north, they must obtain sufficient fat reserves during spring to get them through summer when prey is less available.

Despite recent anecdotal observations of nutritional stress among polar bears in the Southern Beaufort Sea (Amstrup et al. 2006; Stirling et al. 2008a), no quantitative data exist regarding the feeding frequency and hunting success of bears in the region. However, blood samples collected during routine spring mark and recapture studies can be used to assess feeding status over time by measuring serum urea to creatinine ratios (*U*/*C*) (Nelson et al. 1983, 1984; Derocher et al. 1990; Ramsay et al. 1991). Polar bear *U*/*C* values decline markedly when they are in a biochemical fasting state, which involves the recycling of nitrogenous wastes into amino acids, minimizing the loss of lean muscle tissue (Nelson 1987). This physiological fasting state is similar to winter dormancy in black bears (*U. americanus*) and grizzly bears (*U. arctos*) (Nelson et al. 1983; Nelson 1987; Derocher et al. 1990). However, polar bears are able to enter this state while active and at any time of the year, provided they have sufficient endogenous fat reserves (Derocher et al. 1990; Ramsay et al. 1991; Ferguson et al. 2000b). In rare cases when mammals completely deplete their fat stores and do not have access to food they may increase protein catabolism in skeletal and cardiac muscles resulting in elevated *U*/*C* values (Ramsay et al. 1991; Mustonen et al. 2006). However, in fasting-adapted species this only occurs when individuals are experiencing advanced stages of starvation which ultimately results in vital organ failure and death (Castellini and Rea 1992; Cattet 2000; Mustonen et al. 2006). Polar bears in this situation are rarely observed in the wild and can be identified through routine assessments of the amount of subcutaneous fat present on the body (Stirling et al. 2008b) and obvious behavioral abnormalities.

In this study we compared the serum *U*/*C* values in polar bears captured during April–May in 1985, 1986, 2005 and 2006 from the Northern and Southern Beaufort Sea populations. We tested the hypothesis that polar bear feeding success differed in response to climate-induced changes in sea ice conditions in the Beaufort Sea throughout the study period. In addition, we examined the relationship between the frequency of fasting in a given year and estimated body masses. We also tested whether the proportion of bears fasting differed between the two populations to determine if there were any broad-scale geographic differences in feeding. Finally, we compared fasting frequencies among bears differing in sex, age, and reproductive status. It has been hypothesized that adult male polar bears may enter a fasting state during the breeding season because courting behavior reduces the time available for hunting (Ramsay et al. 1991). Because our samples were collected during the breeding season it is expected that adult males may display a higher frequency of fasting than other sex, age, and reproductive classes.

Materials and methods

The study area included the offshore regions of the southeastern Beaufort Sea along the mainland coast between the Alaska/Yukon and Northwest Territories/Nunavut borders, Amundsen Gulf, and offshore of the west coast of Banks Island (Fig. 1). Polar bears were located by helicopter and anesthetized with tiletamine hydrochloride and zolazepam hydrochloride (Zoletil®) using standard immobilization techniques (Stirling et al. 1989). A vestigial premolar was extracted from each bear for age determination (Calvert and Ramsay 1998). Axillary girth (AG) measurements were taken around the chest of the bear behind the forelegs using a nylon rope tightened with approximately 1 kg of pressure. Straight-line body length (BL) was measured from the tip of the nose to the end of the last tail vertebra. Blood was drawn from a femoral vein and stored in a cooler until it was centrifuged to separate serum and cellular portions. Serum was stored frozen until analysis. Serum urea nitrogen and serum creatinine concentrations were determined for the 1985–1986 samples at the College of Medicine, University of Illinois (Chicago, IL, USA) and for the 2005–2006 samples at Central Laboratory for Veterinarians (Langley, BC, Canada). Serum urea creatinine ratios (U/C) were calculated as (urea nitrogen/0.466)/creatinine (Nelson et al. 1984). Bears with U/C values ≤ 10.0 were considered to be in a physiological fasting state based on Nelson et al. (1984). Research on polar bears in western Hudson Bay indicates that longer fasting periods result in a higher proportion of bears with U/C values in this range (Ramsay et al. 1991), and experimental fasting trials suggest that fasts >1 week are required to attain U/C values ≤ 10.0 (Derocher et al. 1990).

Statistical analyses were performed using SPSS statistical software (SPSS Inc., Chicago, IL, USA). Both forward and backward stepwise logistic regressions were used to evaluate factors identified as potentially important to the binary response variable fasting or not fasting. Entry testing for forward stepwise regression was based on the significance ($P < 0.05$) of Rao's efficient score statistics. Removal testing for forward and backward stepwise regression techniques was based on the significance ($P < 0.10$) of the Wald's statistic. All independent variables were tested for multicollinearity by placing them into an equivalent ordinary least squares regression and examining their variance inflation factor (Allison 1999). Explanatory variables considered in the model were: class (adult males, adult males accompanying an estrous female, adult females, adult

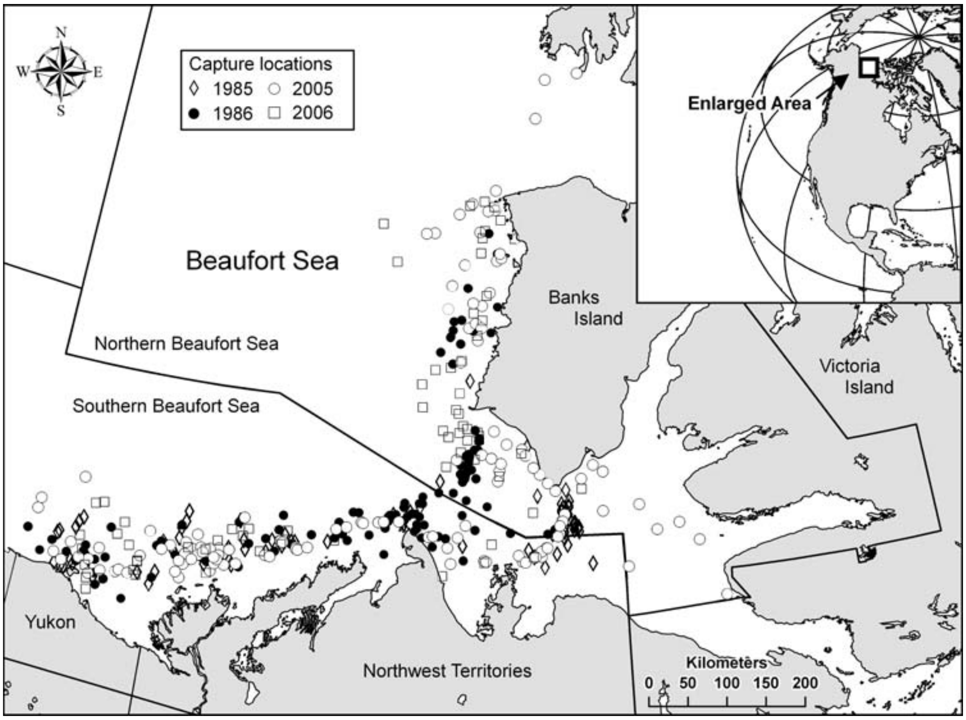

Fig. 1 Map of study site and capture locations of polar bears in the Northern Beaufort Sea and Southern Beaufort Sea populations

females with cubs, and subadults), population, and capture year. The interactions between class and capture year, and population and capture year were also tested.

Adults were defined as individuals ≥ 5 years of age. Females with cubs were defined as individuals accompanied by cubs-of-the-year, 1-, or 2-year-old cubs. Bears 3 or 4 years old were classed as subadults. Solitary 2 year olds were excluded from analyses because the timing of separation from their mother was unknown. Each individual was assigned to the population where their capture was located using boundaries defined by the IUCN/SSC Polar Bear Specialist Group (Fig. 1) (Aars et al. 2006). Polar bear captures occurred during April and May each year, but the dates of capture varied somewhat among years. Because we were concerned that differences in capture period among years might bias our fasting data, we removed 28 outliers by excluding captures occurring on days that did not overlap with capture dates from any other year.

We converted *U*/*C* values into a binary response variable of fasting or not fasting based on Nelson et al. (1984). However, Ramsay et al. (1991) found a correlation between mean *U*/*C* values and feeding opportunity, so in addition to analyzing the binary response variable we also compared mean *U*/*C* values among capture years. *U*/*C* values were log-transformed to improve normality and the log-transformed values were compared among years using an ANOVA and post-hoc Tukey-Kramer multiple comparisons of means. We also tested for yearly differences in the estimated body mass of captured polar bears to assess possible changes in body condition. Body mass (M) for each bear was estimated using AG and BL and the multiple regression equation $M = 0.00003377 \times \mathrm{AG}^{1.7515} \times \mathrm{BL}^{1.3678}$ (Derocher and Wiig 2002). The mass estimation equation developed for Beaufort Sea bears (Durner and Amstrup 1996) could not be applied because of methodological differences in measuring BL. We calculated the deviances of estimated masses from male and female specific von Bertalanffy curves fitted to age and body mass (Derocher and Wiig 2002). Each deviance measurement was calculated as a proportion of its corresponding von Bertalanffy curve value. The Kruskal–Wallis test was used to compare the proportional deviances among years for males and females separately.

Table 1 Sample sizes and mean serum urea/creatinine (*U*/*C*) values for polar bears caught in the Northern Beaufort Sea and Southern Beaufort Sea populations for 1985–1986 and 2005–2006

Year	Class	*n*	Mean *U*/*C* ± SE	*U*/*C* range
1985 *n* = 83	Solitary adult males	23	33.3 ± 2.6	5.1–109.7
	Adult males with estrous female	3		
	Solitary adult females	15		
	Females with cubs	14		
	Subadults	28		
1986 *n* = 133	Solitary adult males	36	37.0 ± 2.5	4.2–138.9
	Adult males with estrous female	10		
	Solitary adult females	34		
	Females with cubs	23		
	Subadults	30		
2005 *n* = 145	Solitary adult males	39	30.4 ± 2.2	2.0–137.4
	Adult males with estrous female	10		
	Solitary adult females	40		
	Females with cubs	28		
	Subadults	28		
2006 *n* = 75	Solitary adult males	21	26.1 ± 2.5	4.1–91.4
	Adult males with estrous female	3		
	Solitary adult females	23		
	Females with cubs	21		
	Subadults	7		

Results

Sampling effort was divided relatively evenly between the populations within each year (Fig. 1). Mean capture dates occurred on April 25 in 1985, April 29 in 1986, April 22 in 2005, and April 22 in 2006. The number of individuals resampled once or more among years was small, ranging from 0 to 13 individuals for a given year, so each sample was considered independent. We sampled 83, 133, 145, and 75 individual polar bears in 1985, 1986, 2005, and 2006, respectively (Table 1). None of the bears displayed physical or behavioral traits indicative of an animal in the advanced stages of starvation. The percentage of all polar bears captured that were in a fasting state was 9.6% in 1985, 10.5% in 1986, 21.4% in 2005, and 29.3% in 2006 (Fig. 2).

Forward and backward stepwise logistic regression techniques produced an identical significant model (Model $\chi^2 = 28.90$, $df = 7$, $P < 0.001$). The model showed that solitary adult males (Wald $\chi^2 = 4.24$, $df = 1$, $P = 0.039$), adult males accompanying an estrous female (Wald $\chi^2 = 8.06$, $df = 1$, $P = 0.005$), and the 2005 (Wald $\chi^2 = 4.27$, $df = 1$, $P = 0.039$) and 2006 (Wald $\chi^2 = 8.18$, $df = 1$, $P = 0.004$) capture years were significant predictors of polar bear fasting (Table 2; Fig. 3). When the independent variables were placed in an equivalent ordinary least squares regression their variance inflation factors were 1.02 for both population and class, and 1.03 for capture year. Allison (1999) suggests that multicollinearity is not an issue when the variance inflation factor is <10, which was the case for all of our independent variables.

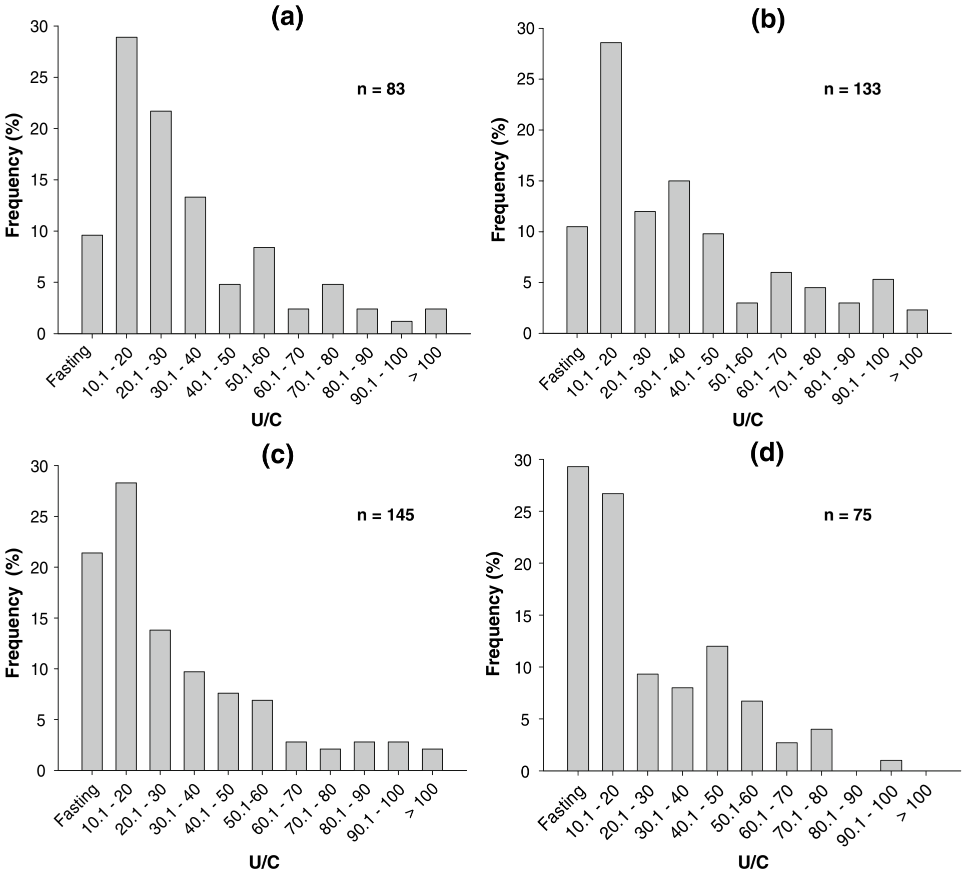

Fig. 2 Frequency distribution of serum urea/creatinine (*U*/*C*) values for polar bears captured in the Northern Beaufort Sea and Southern Beaufort Sea during spring in **a** 1985, **b** 1986, **c** 2005, and **d** 2006. Fasting individuals were defined as those with *U*/*C* values ≤10.0 following Nelson et al. (1984)

Table 2 Variables and their corresponding parameter estimates for the final logistic regression model predicting fasting in polar bears ($n = 436$) from the Beaufort Sea. Non-significant factors (population, class × capture year, and population × capture year) are not shown

Predictor variable	β	SE	Wald's statistic	P	Exp (β)
Class[a]					
Solitary adult males	0.76	0.37	4.24	0.039	2.14
Adult males with estrous female	1.47	0.52	8.06	0.005	4.35
Females with cubs	0.54	0.40	1.80	0.180	1.71
Subadults	−0.06	0.46	0.016	0.901	0.94
Capture year[a]					
1986	0.02	0.47	0.002	0.961	1.02
2005	0.89	0.43	4.27	0.039	2.44
2006	1.32	0.46	8.18	0.004	3.74

[a] References for class and capture year are solitary adult females and 1985, respectively

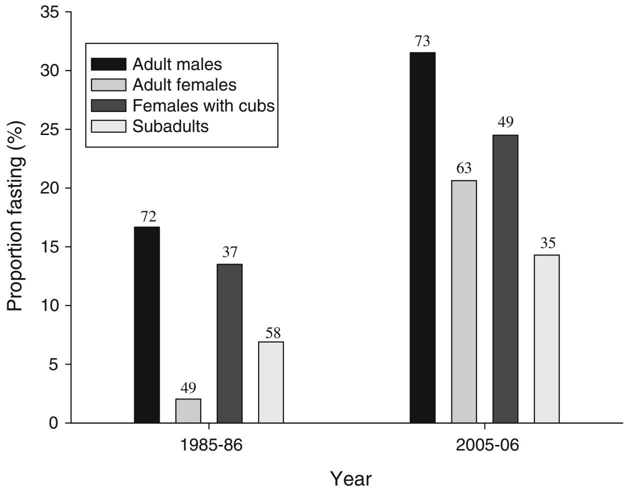

Fig. 3 Proportion of polar bears fasting in each class during April and May in the Beaufort Sea. The adult male class represents both solitary individuals and adult males which were accompanied by a female at the time of capture. *Numbers above the bars* indicate sample size. Data were pooled among years which were significant predictors in the logistic regression model (2005 and 2006) and separately for years which were not significant (1985 and 1986)

There was a significant difference in *U*/*C* means among capture years (ANOVA, log-transformed, $F_{3,432} = 4.99$, $P = 0.002$). A post-hoc Tukey–Kramer multiple comparison of means showed the log-transformed *U*/*C* values in 2006 were lower than 1985 ($P = 0.046$) and 1986 ($P = 0.007$). The 2005 log-transformed *U*/*C* values did not differ from 1985 ($P = 0.17$) but were lower than those in 1986 ($P = 0.031$). There was no difference between the log-transformed *U*/*C* values in 1985 and 1986 ($P = 0.98$) or

2005 and 2006 ($P = 0.78$). There were no yearly differences in proportional deviations from the von Bertalanffy curves fitted to age and body mass for males (Kruskal–Wallis: $\chi^2 = 0.97$, $df = 3$, $P = 0.81$) or females (Kruskal-Wallis: $\chi^2 = 1.72$, $df = 3$, $P = 0.63$).

Discussion

Physiological studies are becoming increasingly important in conservation biology and can help determine how animals respond to environmental change (Walker et al. 2005; Carey 2005; Wikelski and Cooke 2006). Numerous blood parameters have been used to monitor wildlife health and nutritional status with varying degrees of success (e.g., Seiser et al. 2000; Golet et al. 2002; Bowyer et al. 2003; Trites and Donnelly 2003; Sanchez-Guzman et al. 2004). In our study, serum *U*/*C* values were used as a specific blood biomarker to monitor fasting by polar bears in the Beaufort Sea. Our results indicate that polar bears from all sex, age, and reproductive classes in 2005–2006 were more likely to be in a physiological fasting state than in 1985–1986. Adult males from all years of the study, especially those engaged in breeding activity at the time of capture, were also more likely to be fasting than bears in other sex, age, and reproductive classes. Population was not a significant predictor variable of fasting during any year, indicating that feeding opportunity was similar in the Northern versus Southern Beaufort Sea.

The observed increase in bears fasting during 2005–2006 is consistent with other reports which provide evidence that polar bears in the Beaufort Sea may have been food-stressed in recent years (Amstrup et al. 2006; Rode et al. 2007; Stirling et al. 2008a). Beaufort Sea bears reach their lightest weights in late March and rely on a 2–3 month spring feeding period, when fat and naive ringed seal pups are available, to gain the fat reserves necessary for survival and reproduction (Stirling and Øritsland 1995; Stirling 2002). Because polar bears are typically in a hyperphagic state during the spring (Ramsay and Stirling 1988; Derocher and Taylor 1994), the recent increase in bears fasting during April and May suggests that there has been a decrease in prey availability at that time of year. Although there have been large-scale changes in sea ice extent and condition throughout the Arctic Ocean (Comiso 2006; Stroeve et al. 2006; Serreze et al. 2007), the precise means through which prey have apparently become less available to polar bears in the Beaufort Sea remains unknown. It is possible that changes to ice composition have made hunting conditions less favorable and thus diminished hunting success. Stirling et al. (2008a) propose that wide expanses of open water during the winters in 2005–2006, combined with intense wind storms, created extensive rubble fields of thick ice making it difficult for polar bears in the southern Beaufort Sea to access ringed seal lairs. Changes to sea ice composition during the spring or other times of the year could also affect ringed seal abundance. Information on seal densities in the Beaufort Sea is lacking; however, warmer spring temperatures and earlier spring breakup can affect ringed seal pup development and survival (Harwood et al. 2000; Smith and Harwood 2001; Ferguson et al. 2005). Any environmental changes affecting local ringed seal population dynamics are likely to influence the amount of food available for polar bears.

The higher proportion of adult males fasting could be attributed to spring breeding behavior which was supported by the logistic regression model where adult males accompanied by an estrous female were stronger predictors of fasting than solitary adult males. Breeding activity for polar bears occurs from March through June (Lønø 1970; Rosing-Asvid et al. 2002; Amstrup 2003). During this time, males search for estrous females and likely consume less food (Ramsay and Stirling 1986; Ramsay et al. 1991; Stirling et al. 1993). In support of this, Ramsay et al. (1991) reported that males consorting with females during the spring had significantly lower mean *U*/*C* values than solitary males. Similarly, reduced foraging by males during the mating season has been observed in black bears (Herrero 1983; Rogers 1987) and several species of seals (Anderson and Fedak 1985; Le Boeuf and Laws 1994; Coltman et al. 1997). Our results support the hypothesis that adult males eat less frequently during the breeding season, presumably because the need to find and maintain access to mates prevents effective hunting. The increased proportion of bears fasting in 2005–2006 could partially be due to more males breeding as recent declines in cub-of-the-year survival and recruitment (Regehr et al. 2006; Rode et al. 2007) would result in a higher number of solitary females available to breed.

Decreased food availability has been shown to coincide with decreases in average *U*/*C* values (Ramsay et al. 1991; Tryland et al. 2002). The results of our *U*/*C* value comparisons correspond with the conclusions of our logistic regression, with the exception of the lack of a significant difference between 1985 and 2005. However, comparisons of mean *U*/*C* values are likely less reliable than comparisons using a binary fasting/non-fasting classification due to the wide distribution of values occurring above 10. For instance, *U*/*C* values in Beaufort Sea polar bears ranged from 2.0 to 138.9. *U*/*C* values ≤ 10 indicate fasting in black bears (Nelson et al. 1984), and studies on polar bears found that fasting individuals also had values in this range (Lee et al. 1977; Nelson et al. 1983; Ramsay et al. 1991). However, the factors responsible for the wide range of *U*/*C* values above 10 are unclear. Serum *U*/*C* in bears may be dependent on a number of factors including renal function, protein intake, and protein catabolism (Lee et al. 1977; Hellgren et al. 1990; Atkinson et al. 1996; Lohuis et al. 2005). Many of these cannot be measured in the field and therefore comparisons of mean *U*/*C* values should be interpreted cautiously. Carefully designed studies on feeding and fasting captive polar bears would be useful to evaluate factors influencing *U*/*C* values >10.

An increase in the number of polar bears fasting would be expected to correspond with a decrease in body condition. However, even though the incidence of fasting was greater in 2005–2006, there was no detectable difference in estimated body mass among years. Polar bear body mass is dependent upon age and sex (Kingsley 1979; Derocher and Wiig 2002; Derocher et al. 2005) and caution must be used when comparing estimated masses among years. Even if body mass comparisons are done separately for each sex, the distribution of ages within a given year can introduce bias. To overcome this difficulty we compared deviances of estimated masses from male and female specific von Bertalanffy curves fitted to age and body mass (Derocher and Wiig 2002). However, the relationships used to determine mass estimate equations may not remain constant over time and this could have affected our ability to detect changes in body mass (Cattet and Obbard 2005). In addition, increases in the proportion of bears fasting in 2005–2006 relative to 1985–1986 may not have been great enough to cause overall declines in estimated body mass. Data collected between 1971 and 1994 indicates that ringed seal pup production in the Beaufort Sea was low during the mid 1980s, and coinciding decreases in polar bear natality were observed (Stirling 2002). Thus, polar bears captured during 1985–1986 were likely in poor body condition relative to years of higher ringed seal production. The increased proportion of individuals fasting in recent years may indicate that polar bears are having even more difficulty obtaining food than in the mid 1980s. Incorporating serum *U*/*C* measurements into long-term monitoring programs could prove useful in providing early indications of nutritional stress that may not be detectable in population level body mass comparisons.

This study was designed to examine variation in the spring feeding ecology of polar bears during two distinct time frames. However, logistical constraints involving weather, local sea ice, and tracking conditions prevented us from performing captures on precisely consistent days each year. Differences in mean capture dates occurring among some of the years could confound the observed year effect in polar bear fasting if feeding opportunity changed each spring. However, differences that occurred in mean capture dates were only 3–7 days and all of our capture periods had a high degree of overlap. Given that ringed seal pups are born throughout March and April (Stirling and McEwan 1975; Smith and Stirling 1975) it is unlikely that differences in mean capture dates $\leq$1 week would bias our results.

Serum *U*/*C* values are a useful physiological biomarker that can be used to monitor long-term patterns in polar bear feeding ecology. The increased proportion of individuals fasting in recent years is consistent with other observations regarding the feeding ecology of polar bears in the Beaufort Sea (Amstrup et al. 2006; Stirling et al. 2008a). Whether the apparent decrease in polar bear feeding is a short-term occurrence or an indicator of future conditions is unknown. Like all bear species, polar bears are long-lived animals with low reproductive rates (Bunnell and Tait 1981; Ramsay and Stirling 1988) and it is likely that population fluctuations lag behind environmental changes. Understanding the proximate mechanisms involved in population fluctuations and how they relate to environmental stressors, such as climate change, may provide timely indicators of future demographic responses.

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