

Comparative assessment of metrics for monitoring the body condition of polar bears in western Hudson Bay

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Abstract

Many species experience prolonged periods of fasting due to changes in habitat and food availability. Metrics that quantify energy reserves available during these periods allow for a better understanding of the interaction between environmental change and species survival. Body condition of polar bears has been assessed using morphometric and subjective indices, lipid content of adipose tissue, body composition models and, recently, bioelectrical impedance analysis (BIA). We assessed the utility of BIA and examined correlations among condition metrics for 134 free-ranging polar bears on shore in western Hudson Bay in fall 2012–2013 and spring 2013–2014. We also examined long-term inter-annual and seasonal trends from 736 bears handled in 2004–2014. Total body fat, as estimated from BIA, was correlated with adipose tissue lipid content, energy density and fatness index, but not storage energy or skull width. Body condition was higher in adult and subadult females than males, consistent with energetic demands of gestation and lactation. Adult females had higher body fat in the fall than spring, and body fat decreased with increasing number of dependent offspring. Long-term trends indicated a decline in body condition for all adult and subadult males and females. Although there were similar patterns among BIA and other established metrics, its limitations in the field suggest that BIA may not be the most efficient method of monitoring body composition in polar bears in comparison to other modeled metrics, such as energy density. Declines in polar bear body condition over time may be a reflection of contemporaneous changes in sea ice availability and population demography, and thus have implications for the long-term conservation of this subpopulation.

Introduction

Various measures of body condition are used in ecological research to assess the health and nutritional status of individuals, providing insight into biological interactions between organisms and their environment. Body condition in mammals is thought to improve with increased fat stores, which are used for the provision of energy during periods of food shortage (Pitts & Bullard, 1968; Lindstedt & Boyce, 1985). Condition has been quantified in a range of species to better understand relationships with heritability from parent to offspring (Gosler & Harper, 2000), reproductive success and breeding (Chastel, Weimerskirch & Jouventin, 1995; Simard *et al.*, 2014) and behavior and energetics (Gallagher *et al.*, 2014; Richard *et al.*, 2014). Given the close relationship between habitat quality and foraging success (Kitaysky, Wingfield & Piatt, 1999; Taylor *et al.*, 2001; Maceda-Veiga, Green & De Sostoa, 2014), body condition can serve as an early indicator of broad-scale ecological and environmental change, including reduction in habitat

quality or food availability. Accurately measuring body condition can thus provide important insights into fundamental ecological processes relevant to the conservation and management of wildlife populations.

Many mammalian species undergo considerable fluctuations in body composition as energy stores are accumulated and mobilized in response to seasonal conditions and life-history patterns. For example, mammalian overwinter survival is linked to fall body size and fat stores in both hibernating (Murie & Boag, 1984; Hilderbrand *et al.*, 2000) and non-hibernating species (Festa-Bianchet *et al.*, 1997; Cook *et al.*, 2004; Rödel *et al.*, 2004). Many species endure prolonged seasonal fasts, or periods of reduced foraging, associated with breeding and reproduction. Consequently, the acquisition of mates (Byers *et al.*, 2005; Byers, Byers & Dunn, 2006) and production and weaning of offspring (Farley & Robbins, 1995; Samson & Huot, 1995) may require large energy stores. Thus, fat and energy reserves in an organism are closely tied to biological fitness.

Morphometric relationships between body length and mass have been used as proxies of body condition in small mammals (Krebs & Singleton, 1993; Schulte-Hostedde, Millar & Hickling, 2001), large felids (Marker & Dickman, 2003), ungulates (Festa-Bianchet *et al.*, 1997) and ursids (Cattet *et al.*, 2002; Derocher, Wiig & Anderson, 2002; Rode, Amstrup & Regehr, 2010). Subjective indices of overall fatness, based on thickness of subcutaneous fat depots, have also been used in large mammals (Audige, Wilson & Morris, 1998; Stirling, Thiemann & Richardson, 2008; Wijeyamohan *et al.*, 2015). Adipocytes expand more rapidly than they proliferate during periods of lipid deposition, and shrink during fasting periods when lipid is mobilized (Schemmel, 1976; Pond, Mattacks & Ramsay, 1992a). Therefore, adipose tissue lipid content, relative to water and non-fat components, reflects overall fatness in birds (Johnson *et al.*, 1985), cetaceans (Aguilar & Borrell, 1990; Gómez-Campos, Borrell & Aguilar, 2011), pinnipeds (Beck, Smith & Hammill, 1993) and polar bears *Ursus maritimus* (Thiemann, Iverson & Stirling, 2006; McKinney *et al.*, 2014).

Measures of body composition can also quantify energy stores and provide a more detailed representation of body condition. Body composition measures may involve destructive techniques such as whole-body homogenization that prevent repeated measurements (Speakman, 2001; Wirsing, Steury & Murray, 2002). Conversely, non-lethal techniques, such as isotope dilution (Parker *et al.*, 1993; Farley & Robbins, 1994; Arnould, 1995) and mathematical models (Molnár *et al.*, 2009), allow for measurements of the same individual over time. Bioelectrical impedance analysis (BIA) has emerged as a relatively rapid, non-invasive and repeatable measure of body composition (Kushner, 1992; Gales, Renouf & Worthy, 1994). BIA is based on the principle that lean mass contains more water and electrolytes compared to fat (Lukaski *et al.*, 1986; Lukaski, 1987). Transmission of an electrical current through the organism will have greater resistance through fat tissue and more conductivity through lean mass (Hilderbrand, Farley & Robbins, 1998), with body water and body fat being inversely related (Farley & Robbins, 1994). BIA has been used to quantify fatness in a range of species, including humans (Lukaski *et al.*, 1985), porcupines *Erethizon dorsatum* (Barthelmeß, Phillips & Schuckers, 2006), pinnipeds (Gales *et al.*, 1994), skunks *Mephitis mephitis* (Hwang, Larivière & Messier, 2005), raccoons *Procyon lotor* (Pitt, Larivière & Messier, 2006), horses *Equus* species (Latman *et al.*, 2011) and ursids (Hilderbrand *et al.*, 2000; Gau & Case, 2002; Robbins *et al.*, 2012).

Similar to other ursids, polar bears alternate between periods of hyperphagia and fasting and experience seasonal cycles in fatness (Derocher *et al.*, 1990; Atkinson & Ramsay, 1995; Thiemann *et al.*, 2006). In the Western Hudson Bay subpopulation, individuals are forced to migrate to shore as sea ice habitat melts each summer. Progressively earlier sea ice breakup over the last several decades (Gough, Cornwell & Tsuji, 2004; Gagnon & Gough, 2005; Hochheim & Barber, 2014) has shortened the spring foraging period and negatively influenced body condition (Stirling, Lunn & Iacozza, 1999; Derocher, Lunn & Stirling, 2004; Regehr *et al.*, 2007). Simultaneously, progressively later freeze-up in the fall (Hochheim

& Barber, 2014) has extended the time bears spend on shore, without access to marine mammal prey. Several studies have reported terrestrial feeding during the onshore period (Derocher, Andriashek & Stirling, 1993; Gormezano & Rockwell, 2013) and have suggested that terrestrial foods could offset nutritional deficits from reduced on-ice foraging (Gormezano & Rockwell, 2015). However, empirical support for this hypothesis is still lacking (Hobson, Stirling & Andriashek, 2009; Rode *et al.*, 2015). Monitoring polar bear body condition over time may provide an indication of large scale ecological change in this subpopulation and inform bioenergetic models aimed at predicting the demographic effects of future climate change (Molnár *et al.*, 2010, 2011).

Despite its use in quantifying fatness in many species, BIA has yet to be applied to polar bears in western Hudson Bay. This technique may be useful as it directly quantifies total body fat in a manner that is relatively quick, non-invasive and non-destructive. The objectives of this study were to (1) comparatively assess BIA with other established condition metrics among age and sex classes and evaluate its utility and feasibility in the field; (2) assess potential contribution of terrestrial feeding to overall body condition on shore; and (3) evaluate inter-annual trends (2004–2013) in body condition in relation to polar bear life-history patterns and long-term changes in sea ice.

Materials and methods

Capture of free-ranging polar bears

Polar bears were captured in an approximate 12 000 km² area in northeastern Manitoba between the Churchill and Nelson Rivers and throughout Wapusk National Park of Canada during the fall open water (September) and spring ice covered (February–March) seasons 2004–2014. Spring captures consisted of family groups, with females and cubs exiting dens and migrating onto the sea ice. Bears were located from a Bell 206B helicopter and immobilized via remote delivery of a 1:1 combination of tiletamine hydrochloride and zolazepam hydrochloride (Telazol[®], Fort Dodge Laboratories, Fort Dodge, Iowa, USA or Zoletil[®], Virbac S.A., Carros, France) following standard protocols (Stirling, Spencer & Andriashek, 1989). Individuals were marked with uniquely numbered plastic tags in each ear and tattoos on the inside of the upper lip. A vestigial premolar was extracted for aging (Calvert & Ramsay, 1998) for independent bears not previously handled. Bears were classified into the following age classes: cub of the year (COY, <1 year), yearling (dependent 1–2 years), subadult (independent bears 2–4 years) and adult (5+ years). We measured axillary girth (cm), straight-line body length (tip of the nose to the last vertebra of the tail, cm) and zygomatic skull width (mm) on each bear in sternal recumbency. Skull measurements have been found to fluctuate with demographic and environmental factors (food availability, diet composition and habitat) in both subadult and adult life stages of brown bears *Ursus arctos* (Mowat & Heard, 2006; Zedrosser, Dahle & Swenson, 2006) and polar bears (Rode *et al.*, 2010). We scored each bear on a fatness index from 1 to 5 based on visual observation and palpation of subcutaneous fat on the dorsal side and

rump (Stirling *et al.*, 2008). Body mass was estimated using regression equations based on axillary girth and straight-line body length (Thiemann *et al.*, 2011). All bears (excluding spring COY) were sampled for adipose tissue lipid content using an 8 mm biopsy taken *c.* 15 cm lateral to the base of the tail. Samples were stored frozen (-20°C) in airtight cryogenic vials until analysis. We recorded evidence of terrestrial foraging (e.g. remnants of berries or vegetation around the mouth or presence of feces).

We collected BIA measurements on a subset of bears captured in fall 2012–2013 and spring 2013–2014 using a Quantum X analyzer (RJL Systems, Clinton Township, Michigan, USA) and following the protocol (snout-to-tail method) outlined by Farley & Robbins (1994). Briefly, immobilized bears were positioned on a plastic tarp when on damp ground or snow to prevent interference with the current. Bears were placed in sternal recumbency, with hind legs fully extended and forelimbs bent at 90 degrees. A 21 gauge, 1.5" vacutainer needle was inserted in the rump *c.* 3 cm on either side of the base of the tail. We attached alligator clips to both needles and on moistened gums above each canine. Resistance readings were taken twice and mean values were used for calculating per cent body water and body fat using equations derived by Farley & Robbins (1994). Because the Farley & Robbins (1994) model used snout-to-vent contour length to relate total body water to BIA resistance, we estimated snout-vent contour length (SVL) from straight-line body length (SLEN) using the relationship: $\text{SVL} = 1.11 \cdot \text{SLEN} - 13.65$ based on measurements from 109 live-captured polar bears in the Chukchi Sea (U.S. Fish and Wildlife Service, unpubl. data). We collected BIA readings prior to obtaining biological samples and noted any movement, irregular breathing patterns or vocalizations. Environmental conditions (e.g. precipitation, wet ground) were recorded. Bears with wet fur produced inconsistent readings and were omitted from analyses. Omitted bears included adults ($n = 11$), subadults ($n = 2$) and COY ($n = 6$). Bears measured for BIA were also weighed using an electronic load cell suspended from a tripod. Capture and handling procedures were reviewed and approved annually by the Animal Care and Use Committees at Environment Canada (Prairie and Northern Region) and York University.

Body condition measures and statistical analysis

Adipose tissue biopsies were weighed after removing attached skin or muscle. Lipid was quantitatively extracted (Iverson, Lang & Cooper, 2001; Budge, Iverson & Koopman, 2006) and total lipid content expressed as per cent total wet weight \pm standard error of the mean. As BIA was performed on bears only in fall 2012 and 2013 and spring 2013 and 2014, a comparative analysis of body condition metrics was limited to this time period and included total body fat (estimated from BIA), zygomatic skull width (mm), fatness index, adipose tissue lipid content and both storage energy (MJ) and energy density (MJ kg^{-1}), calculated following Molnár *et al.* (2009). Storage energy quantifies total energy in the individual allocated to

body maintenance, reproduction and growth and is derived from protein and fat. Storage energy will be affected by energy expenditure and intensity of foraging and may thus fluctuate both spatially and temporally in a population (Molnár *et al.*, 2009). Energy density accounts for the fact that, due to the costs of somatic maintenance, not all storage energy is available during fasting and is thus defined as the ratio of storage energy to lean body mass (Molnár *et al.*, 2009). Energy density has also been used to predict polar bear survival (Molnár *et al.*, 2010) and reproduction (Molnár *et al.*, 2011) as a function of body condition. We used principle component analysis (PCA) to explore relationships among six condition metrics. Spearman correlations were used to compare body condition measures and Kruskal–Wallis ANOVA and Mann–Whitney *U* post hoc tests were used to compare metrics across age and sex groups. We also used Mann–Whitney *U* tests to compare body condition between bears with and without evidence of terrestrial feeding.

Temporal trends in body condition and sea ice

We assessed trends in body condition (fall 2004–2013) using simple linear regression models for adult and subadult males and females. Adult females were further separated depending on reproductive status and body condition metrics were compared using Kruskal–Wallis ANOVA (fall/spring, 2004–2014): (1) solitary females (fall); (2) females with yearlings (fall); (3) females with COY (fall); (4) females with COY (spring). No solitary females were handled in the spring.

We used ArcInfo (Environmental Systems Research Institute, California) to extract sea ice concentrations from 25×25 km resolution passive microwave satellite raster imagery (NASA Team algorithm; Cavalieri *et al.*, 1996, 2012) from the National Snow and Ice Data Center (Boulder, Colorado) for 2004–2013. Each grid cell had an associated sea ice concentration value estimating the fractional amount of sea ice covering that cell (Cavalieri *et al.*, 1996). We calculated mean daily sea ice concentrations for the entire western Hudson Bay management zone. Two metrics were derived from mean daily sea ice concentration: (1) breakup, the ordinal date in spring when sea ice reached and remained below 50% concentration for at least three consecutive days (Etkin, 1991; Gagnon & Gough, 2005; Stirling & Parkinson, 2006); (2) freeze-up, the ordinal date in autumn when sea ice reached and remained above 10% concentration for at least three consecutive days (Cherry *et al.*, 2013).

We used multiple linear regression to assess relationships between sea ice and each body condition metric for age/sex classes. To ensure non-collinearity among predictors, we used variance inflation factor ($\text{VIF} < 2.5$) and tolerance values (> 0.10), which were supported with weak correlations between breakup and freeze-up. We used *P* values to assess if sea ice could significantly predict body condition and compared absolute standardized β coefficients of each predictor to assess its relative strength in the model. Positive or negative β coefficients provided relationship direction. Statistical analyses were

done using SPSS® version 22 for Windows® (IBM, Chicago, IL, USA).

Results

Comparison of body condition measures

PCA generated two principle components (PC) accounting for 72.6% of total variance. Metrics loaded onto PC1 (43.9% variance) were BIA, energy density, adipose tissue lipid content and fatness index, while PC2 (28.7% variance) included storage energy and skull width. Both BIA and energy density had the greatest loadings on PC1 (0.82 and 0.75 respectively) followed by adipose lipid and fatness index (0.70 and 0.58).

Lipid content in adipose tissue was positively correlated with total per cent body fat as estimated by BIA ($r^2 = 0.34$, $P = 0.01$) (Fig. 1). Lipid content increased with energy density ($r^2 = 0.43$, $P < 0.001$), but was negatively correlated with skull width ($r^2 = -0.22$, $P = 0.01$) and did not correlate with storage energy ($r^2 = -0.06$, $P = 0.46$). BIA was significantly correlated with energy density ($r^2 = 0.49$, $P < 0.001$), but not storage energy ($r^2 = 0.16$, $P = 0.23$) or skull width ($r^2 = -0.12$, $P = 0.37$) (Fig. 2). Fatness index scores across all immobilized bears varied from 1 to 4 in the fall, with the majority of handled bears scoring 2 and 3 (42 and 51% respectively). Fatness index scores were correlated with BIA (Spearman correlation, $r^2 = 0.33$, $P = 0.016$), but not with adipose tissue lipid content ($r^2 = 0.10$, $P = 0.25$).

All measures of body condition differed across males and females and typically increased with age class (Fig. 3). Both adipose tissue lipid content (Kruskal–Wallis, $\chi^2 = 38.8$, $P < 0.001$) and BIA ($\chi^2 = 10.58$, $P = 0.032$) differed across adult female, adult male, subadult female, subadult male and

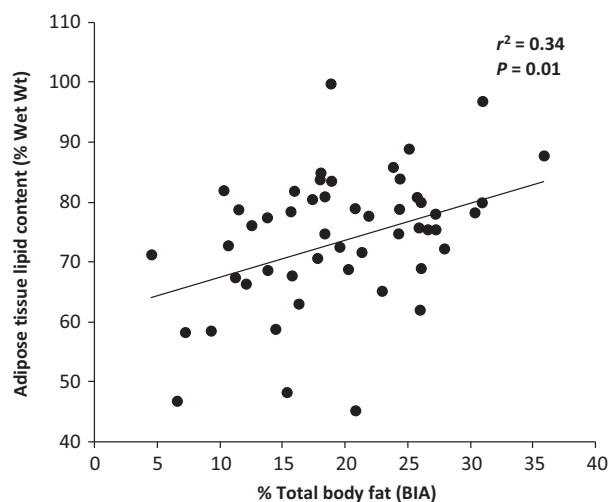


Figure 1 Relationship between adipose tissue lipid content (% wet weight) and per cent total body fat (calculated from bioelectrical impedance analysis, BIA) for $n = 52$ Western Hudson Bay polar bears in fall 2012 and 2013.

COY groups in the fall (2012–2013). Similarly, skull width ($\chi^2 = 116.6$, $P < 0.001$), storage energy ($\chi^2 = 99.3$, $P < 0.001$) and energy density ($\chi^2 = 58.9$, $P < 0.001$) also differed across age and sex groups. Both adult and subadult females had greater adipose tissue lipid content (Mann–Whitney U post hoc, $P < 0.001$ respectively) and energy density ($P < 0.001$ and $P = 0.02$ respectively) compared to adult males (Fig. 3). Skull width and storage energy also increased with age but were greater in adult male bears compared to both adult ($P < 0.001$ respectively) and subadult females ($P < 0.001$ respectively). Fatness index scores were nearly significantly different across age and sex groups ($\chi^2 = 8.64$, $P = 0.07$) (Fig. 3).

During the study, some individuals were noted to have been foraging on terrestrial food sources (i.e. berries and vegetation). For both adult and subadult groups, skull width (Mann–Whitney U, $P = 0.37$ and $P = 0.80$ respectively), fatness index ($P = 0.89$ and $P = 0.06$), adipose tissue lipid content ($P = 0.44$ and $P = 0.46$), BIA ($P = 0.17$ and $P = 0.38$), storage energy ($P = 0.21$ and $P = 0.34$) and energy density ($P = 0.74$ and $P = 0.18$) did not differ between bears with and without signs of terrestrial feeding. Similarly, dependent COYs did not differ in body condition metrics between terrestrial foragers and non-foragers for skull width ($P = 0.31$), fatness index ($P = 0.75$), adipose tissue lipid ($P = 0.18$) and storage energy ($P = 0.09$). Energy density, however, was greater in non-foraging COY (9.51 ± 0.48 MJ kg $^{-1}$, mean \pm SE) compared to those terrestrially feeding (8.32 ± 0.52 MJ kg $^{-1}$) ($P = 0.04$).

Adult female body condition

Body condition metrics were higher in solitary adult females than in females with COY or females with dependent yearlings for storage energy (Mann–Whitney U, $P < 0.001$), energy density ($P < 0.001$) and fatness index ($P < 0.001$) (Fig. 4). Solitary females had greater adipose tissue lipid content than females supporting COY ($P = 0.003$) and this was nearly significant for females supporting yearlings ($P = 0.07$). BIA was not significantly different between solitary females and those with COY ($P = 0.08$) or between solitary females and those with yearlings ($P = 0.61$), although patterns were similar to other metrics (Fig. 4). Skull width was greater in females with COY ($P = 0.01$) and females with yearlings ($P = 0.05$) compared to solitary adult females in the fall (Fig. 4). Females accompanied by dependent yearlings had greater storage energy ($P = 0.001$), energy density ($P = 0.001$) and fatness index ($P = 0.02$) than females accompanied by COY, but no difference in skull width ($P = 0.92$), adipose tissue lipid content ($P = 0.51$), or BIA ($P = 0.53$) (Fig. 4).

Adult female body condition was higher in fall than in spring for multiple metrics. Solitary females in the fall, females with COY in the fall and females with yearlings in the fall had significantly greater fatness index ($P < 0.001$, $P = 0.002$ and $P < 0.001$ respectively), adipose tissue lipid content ($P < 0.001$, $P = 0.002$ and $P = 0.002$ respectively), storage energy ($P < 0.001$) and energy density ($P < 0.001$) than females with COY in the spring. However, skull width

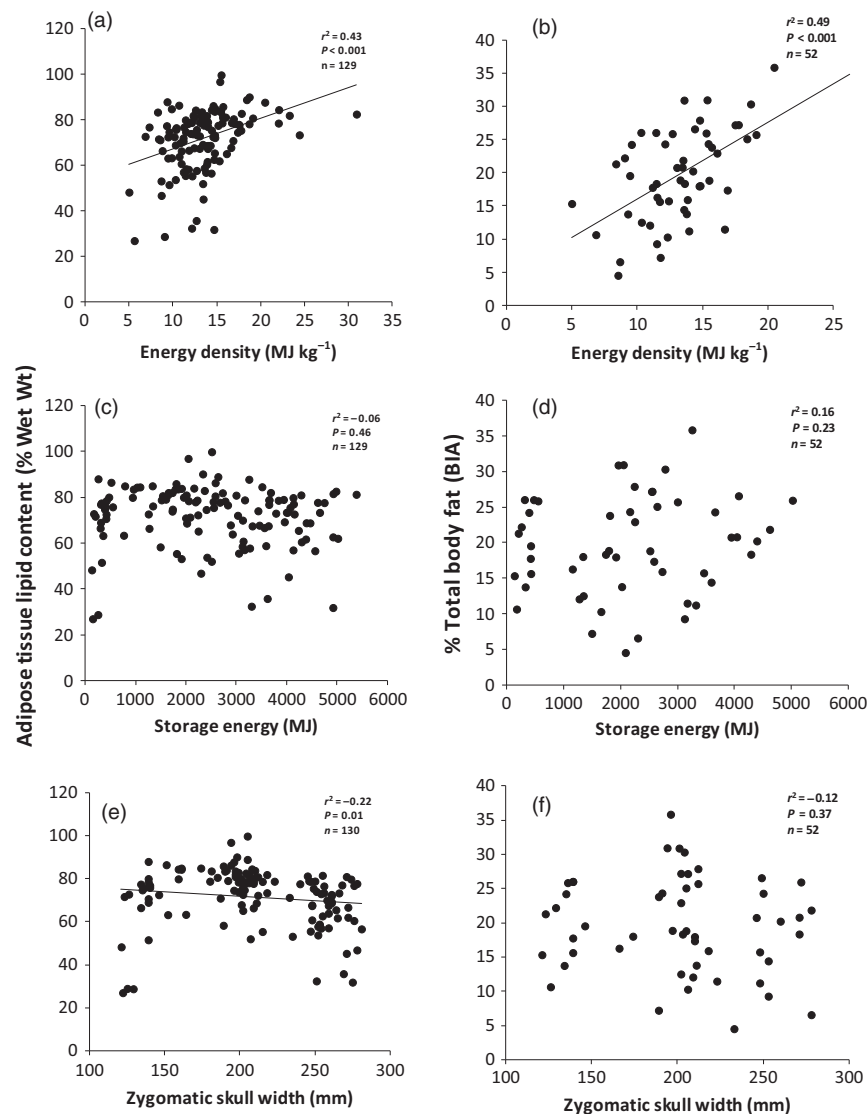


Figure 2 Relationship of adipose tissue lipid content (left) and total body fat (BIA) (right) with energy density (a and b), storage energy (c and d) and zygomatic skull width (e and f) for Western Hudson Bay polar bears in fall 2012 and 2013.

($P = 0.72$, $P = 0.06$ and $P = 0.11$ respectively) and total body fat via BIA ($P = 0.25$, $P = 0.77$ and $P = 0.82$ respectively) did not differ statistically across season, although seasonal patterns in BIA data were similar to other metrics (Fig. 4).

Body condition in adult females was further subdivided based on litter size (solitary, single offspring, or multiple offspring; yearlings and COY combined). Overall, adipose tissue lipid content (Kruskal–Wallis $\chi^2 = 9.01$, $P = 0.011$), energy density ($\chi^2 = 56.97$, $P < 0.001$) and storage energy ($\chi^2 = 55.62$, $P < 0.001$) decreased with a greater number of offspring. A similar but not significant pattern was evident for BIA ($\chi^2 = 4.74$, $P = 0.09$) (Fig. 5). Conversely, skull width was larger in females with one or more offspring compared to solitary females ($\chi^2 = 7.02$, $P = 0.03$) (Fig. 5). Fatness index scores were higher in solitary females than females with a single offspring (Mann–

Whitney U post hoc, $P < 0.001$) or females with multiple offspring ($P < 0.001$) and higher in single offspring than multiple offspring females ($P = 0.015$) (Fig. 5).

Inter-annual trends in body condition

Body condition of male polar bears decreased during 2004–2013 across each age class (Fig. 6). Energy density, adipose tissue lipid content and storage energy declined in adult male ($P < 0.001$ respectively) and subadult males ($P = 0.001$, $P = 0.017$ and $P = 0.001$ respectively) (Fig. 6), but skull width showed no change ($P > 0.05$) (Fig. 6). Similar trends were found in females across age class and status (Fig. 7). Energy density ($P = 0.015$), storage energy ($P = 0.001$) and skull width ($P = 0.015$) declined in solitary adult females, but

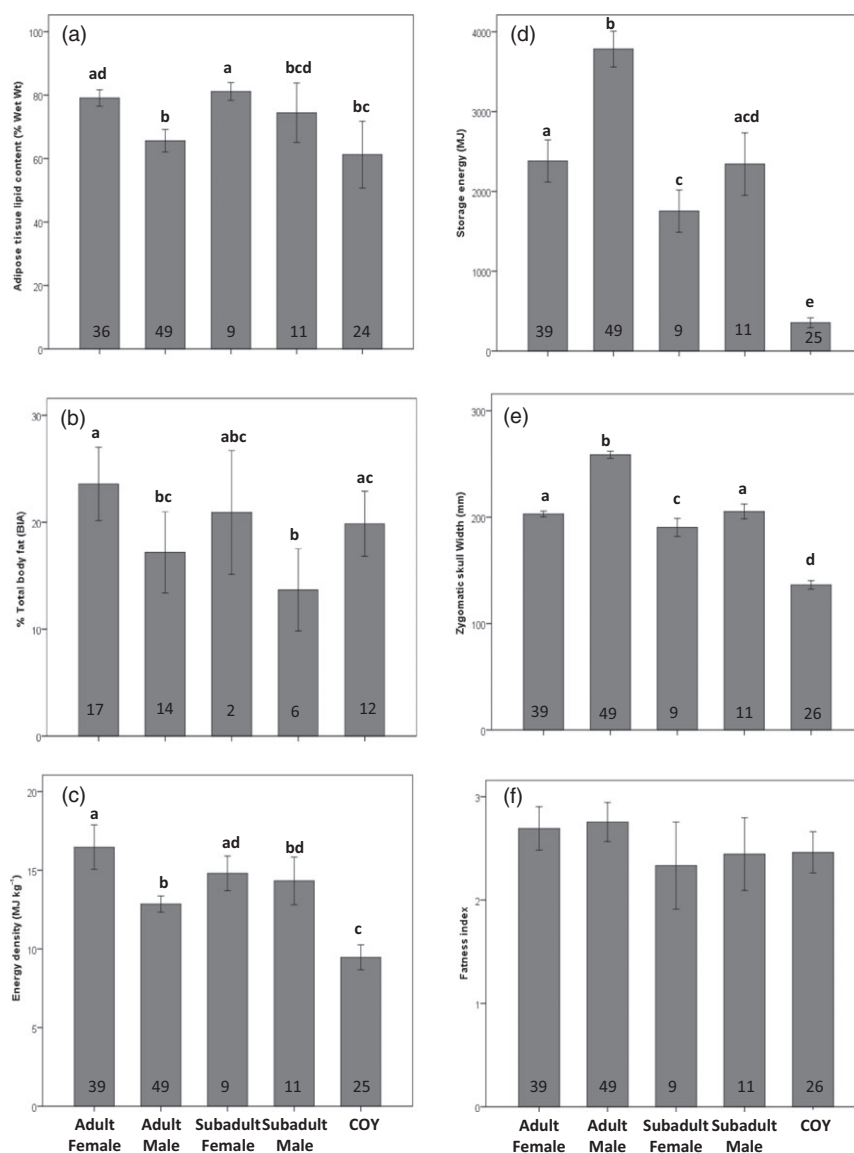


Figure 3 Mean (SE) measures of body condition of adult female, adult male, subadult female, subadult male and cub-of-the-year (COY) polar bears in the fall season in western Hudson Bay 2012 and 2013: (a) adipose tissue lipid content; (b) total body fat derived via BIA; (c) energy density; (d) storage energy; (e) skull width; (f) fatness index. Different letters indicate statistical differences between age and sex groups within each body condition metric. Numbers within bars indicate sample size.

lipid content did not ($P = 0.30$) (Fig. 7). Adult females with dependent offspring showed declines in adipose tissue lipid content ($P = 0.04$), energy density ($P < 0.001$) and storage energy ($P < 0.001$), but not skull width ($P = 0.35$) (Fig. 7). Similarly, subadult female bears declined in energy density ($P = 0.001$), adipose lipid content ($P = 0.007$) and storage energy ($P = 0.01$), but not skull width ($P > 0.05$).

Between 2004 and 2013, date of sea ice breakup varied from 5 June to 2 July and freeze-up from 18 November to 30 November, but showed no significant trends (linear regression, $P = 0.40$ and $P = 0.86$ respectively). Sea ice breakup and freeze-up significantly predicted lipid content ($P = 0.002$ and

$P < 0.001$) and energy density ($P < 0.001$ and $P = 0.008$) in adult males, while only breakup date predicted storage energy ($P < 0.001$) and skull width ($P = 0.004$) (multiple linear regression, Table S1, Supplementary Material). Breakup and freeze-up date also predicted lipid content in subadult males ($P = 0.011$ and $P = 0.043$), while sea ice breakup date predicted both storage energy ($P = 0.002$) and energy density ($P = 0.003$). Sea ice breakup also predicted energy density ($P < 0.001$) and storage energy ($P = 0.025$) in subadult females, while both breakup and freeze-up predicted lipid content ($P < 0.01$), but not skull width ($P > 0.05$). Only lipid content in solitary adult females was significantly predicted by

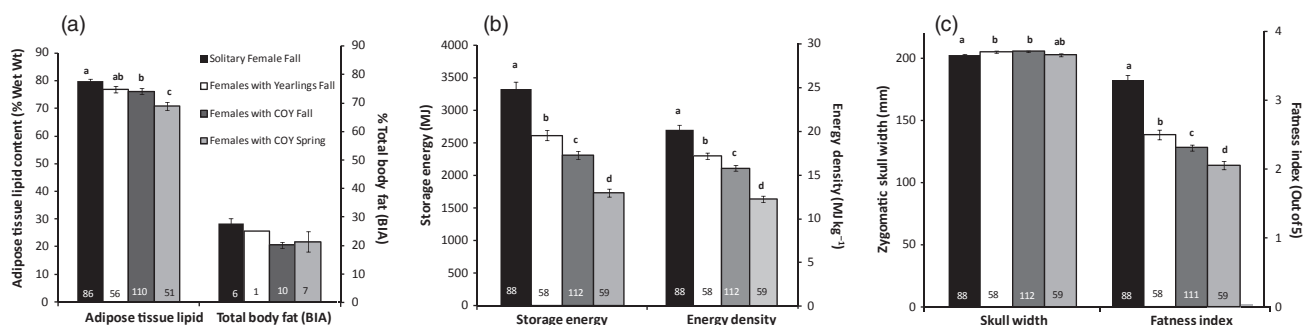


Figure 4 Mean (SE) measures of body condition of solitary female (fall), female accompanied by dependent yearlings (fall), female with COY (fall) and female with COY (spring) polar bears in western Hudson Bay (2004–2014) for: (a) adipose tissue lipid content and total body fat BIA; (b) storage energy and energy density; (c) skull width and fatness index. Total body fat (BIA) was measured in fall 2012 and 2013 and in spring 2013 and 2014. Statistical differences between female status/season within each body condition metric indicated by different letters and symbols. Numbers within bars indicate sample size.

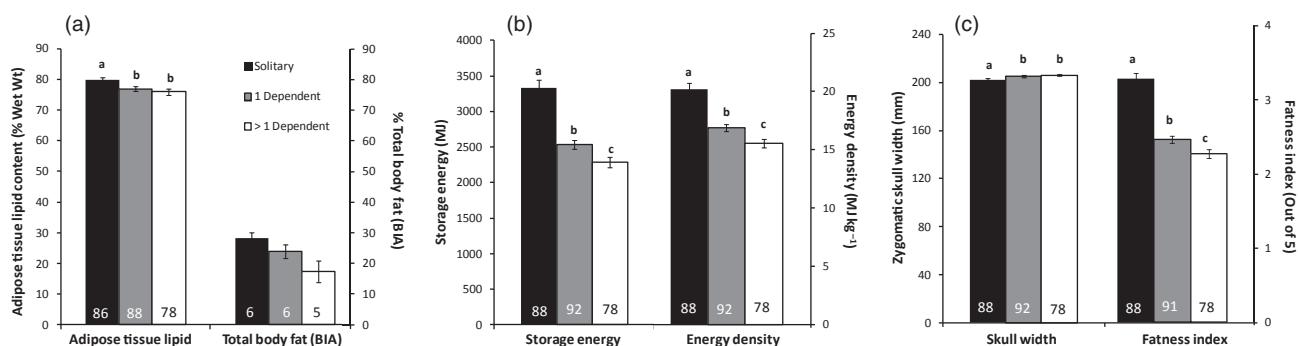


Figure 5 Mean (SE) measures of polar bear body condition for solitary females, females with 1 dependent offspring and females with >1 dependent offspring in the fall 2004–2013 in western Hudson Bay for: (a) lipid content and total body fat BIA; (b) storage energy and energy density; (c) skull width and fatness index. Total body fat (BIA) was measured in the fall 2012 and 2013. Statistical differences between females within each body condition metric are indicated by different letters and symbol. Numbers within bars indicate sample size.

both sea ice breakup and freeze-up ($P = 0.015$ and $P = 0.004$). Body condition of females with dependents was predicted by sea ice conditions for lipid content (Overall Model, $P = 0.001$), energy density ($P = 0.003$) and storage energy ($P = 0.017$) and more strongly affected by freeze-up date. Overall, body condition was positively related with later breakup and negatively related with later freeze-up (standardized β coefficients, Table S1, Supplementary Material).

Discussion

Body condition in mammals is a complex function of both extrinsic (e.g. resource availability) and intrinsic factors (e.g. energy demand). Although our data were broadly indicative of known patterns of polar bear life history in western Hudson Bay (Stirling *et al.*, 1999; Thiemann *et al.*, 2006; Regehr *et al.*, 2007), our results provide evidence that various metrics used to date differ in their sensitivity and utility when applied to free-ranging polar bears. Our results confirm that body condition in western Hudson Bay polar bears is highly dynamic and variable across age and sex classes, reproductive states,

seasons and years. Moreover, because polar bears in western Hudson Bay are adapted to prolonged seasonal and reproductive fasts, body condition reflects a mechanistic link between environmental conditions and demographic processes (Molnár *et al.*, 2011) and metrics of condition can serve as powerful predictors of future population trends (Molnár *et al.*, 2010).

BIA and body condition measures

We found that BIA followed similar patterns in body condition as other established metrics including adipose tissue lipid content (Thiemann *et al.*, 2006; McKinney *et al.*, 2014), energy density (Molnár *et al.*, 2009) and fatness index (Stirling *et al.*, 2008), however, correlations were relatively weak (r^2 ranged from 0.34 to 0.49) (Fig 2). Although our estimates of total body fat may have been affected by the estimation of snout-vent contour length from straight-line body length (see Methods), the close relationship between the two length measures ($r^2 = 0.88$; U.S. Fish and Wildlife Service, unpubl. data) suggests that any bias was minimal. Since BIA uses an electric current to measure resistance through body tissue, BIA was

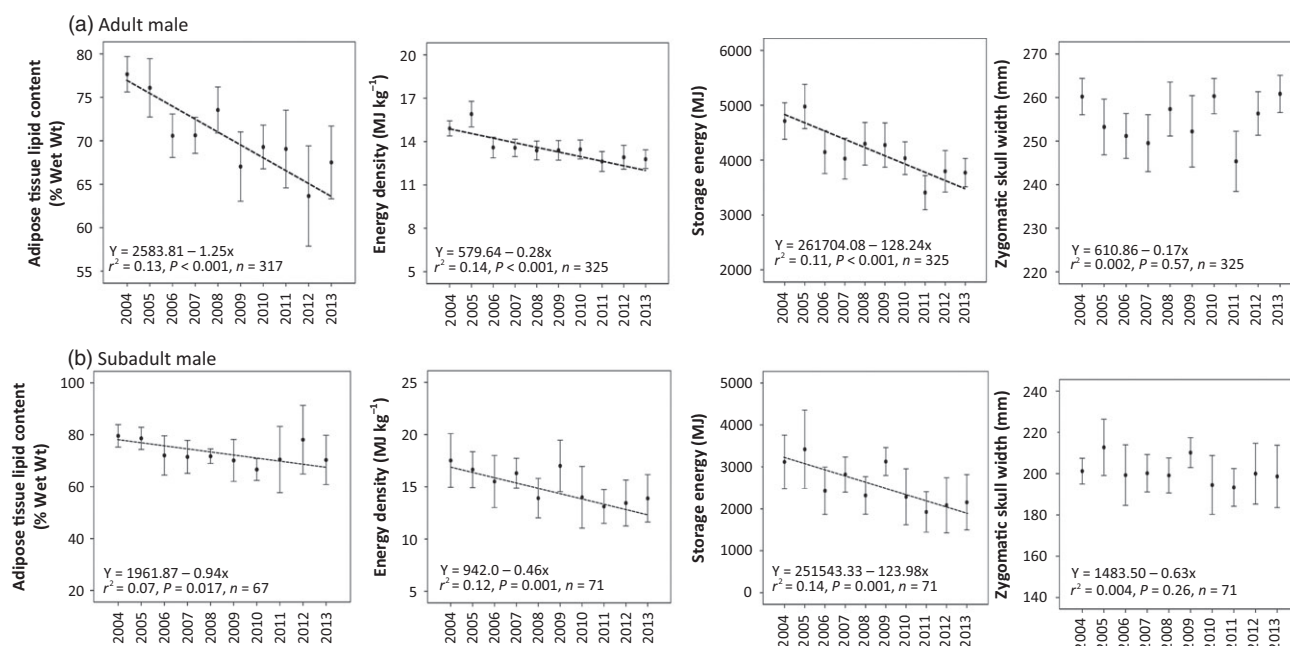


Figure 6 Temporal trends in mean (SE) body condition measures for (a) adult male and (b) subadult male (independent age 2–4 years) polar bears in western Hudson Bay in the fall 2004–2013.

more strongly correlated with metrics that quantify fat and energy stores (adipose tissue lipid content and energy density), compared to measures influenced by skeletal size (Figs 1 and 2). We also found similar patterns for BIA, adipose tissue lipid and energy density across age and sex classes (Fig. 3; Thiemann *et al.*, 2006; Stirling *et al.*, 2008), whereas morphometric-based measures, influenced by structural size, may not be representative of overall energy stores over shorter time scales (Pitt *et al.*, 2006; Barnett *et al.*, 2015). Although BIA did not differ across female reproductive status, this is likely attributable to lower sample sizes for these data. Specifically, BIA data were only available in the final 2 years of the study (2012–2014; Figs 4 and 5).

Superficial fat stores are often used as an indicator of body condition in mammals (Thiemann *et al.*, 2006; Stirling *et al.*, 2008; Robitaille *et al.*, 2012), however not all energy mobilized during fasting periods will be derived from superficial fat catabolism. Metrics that quantify total energy stores (e.g. energy density) may therefore be more useful in monitoring polar bear condition. In this study, energy density consistently identified differences across age and sex classes (Fig. 3), seasonal patterns (Figs 4 and 5) and inter-annual trends (Figs 6 and 7). Moreover, assessing condition using energy density models is arguably easier to implement as these models require only morphological measurements. In contrast to the subjective fatness index (Stirling *et al.*, 2008), which is based on palpation of superficial fat depots around the rump and hips, BIA quantifies both superficial and internal fat stores including intra-abdominal cavity and inter-muscular depots (Pond, 1992; Pond *et al.*, 1992a). Although inter-muscular depots expand minimally with increasing fatness, they remain

more metabolically active than larger superficial fat depots despite contrasting number and size of adipocytes between regions (Pond, 1992; Pond *et al.*, 1992a). Inter-muscular depots, for example, exhibit greater glucose and lipoprotein lipase activity (Pond, Mattacks & Sadler, 1992b) and are an important energy source for muscle activity (Pond, 1992). Smaller internal fat depots may be an important energy source for fasting organisms with daily energetic demands (e.g. movement) and can only be quantified by body composition analyses (e.g. BIA and energy density). Although BIA has been used in brown and black (*Ursus americanus*) bear studies to investigate relationships between body condition and hibernation, reproductive success (Hilderbrand *et al.*, 2000; Harlow *et al.*, 2002) and diet (Hilderbrand *et al.*, 1999; Schwartz *et al.*, 2014), our initial results suggest this technique reflects similar patterns in condition, but may not be easiest to implement on polar bears in the field.

We found that BIA measurements could be completed quickly (i.e. 5–10 minutes) and relatively non-invasively on immobilized polar bears, but readings were sensitive to capture conditions, including wet animals and wet ground. Similar to other studies (Farley & Robbins, 1994; Hilderbrand *et al.*, 1998), wet individuals generated erroneous readings due to increased conductivity around the body. The level of sedation and positioning was also found to be a factor affecting conductivity. Bears with head movement or vocalization gave variable readings, as previously reported in polar, black and brown bears (Farley & Robbins, 1994). As young bears (i.e. COY) are necessarily administered a relatively light dose of drug (due to small body size) and recover more quickly, accurate readings may be difficult to obtain; therefore, BIA should be

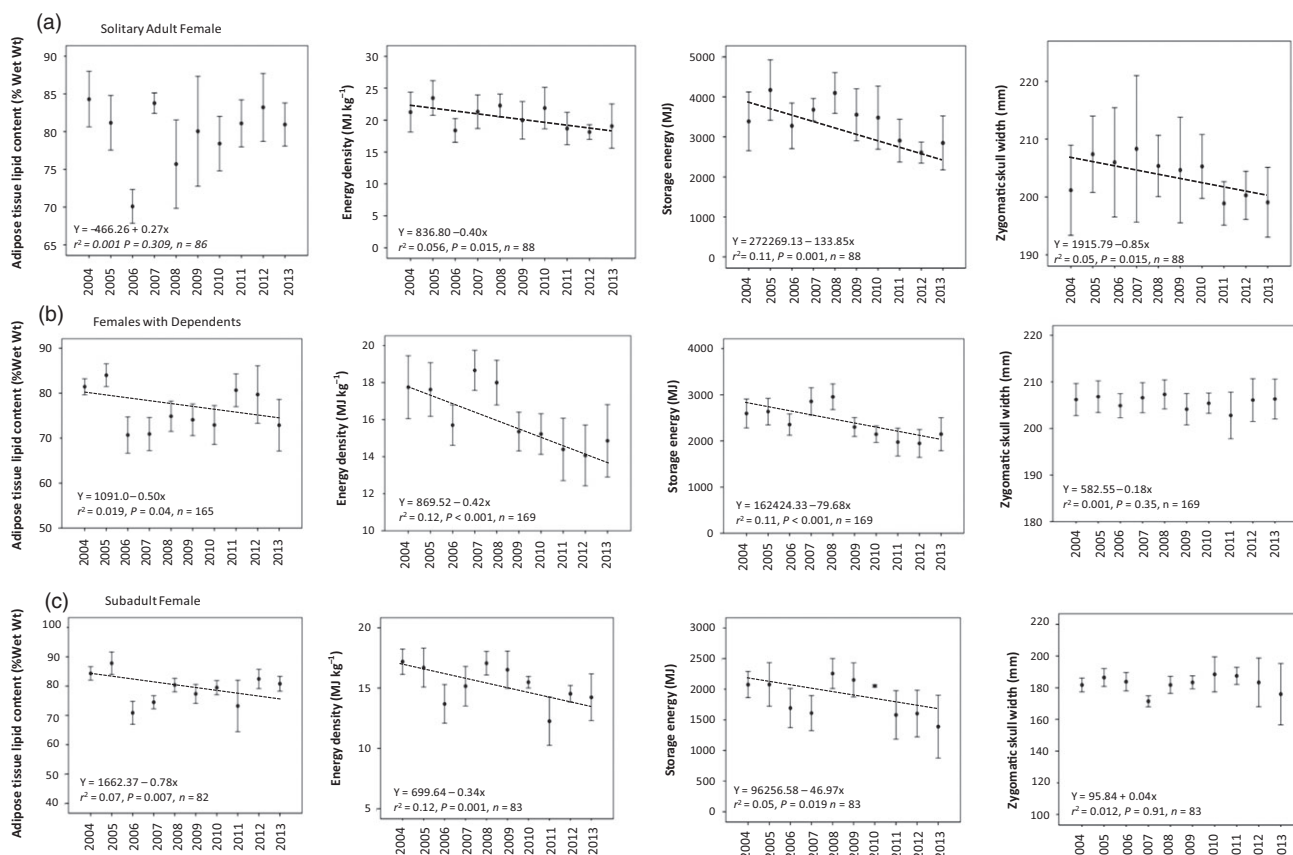


Figure 7 Temporal trends in mean (SE) body condition measures for (a) solitary adult female, (b) females with dependent offspring (both yearling and COY) and (c) subadult female (independent age 2–4 years) polar bears in western Hudson Bay in the fall 2004–2013.

collected from young individuals first. Gut fill was previously thought to affect BIA measures (Hilderbrand *et al.*, 1998), however this was not evident in our study. We used evidence of foraging based on remnants of vegetation around the mouth/anus as a proxy for gut fill and found no effect on BIA. However, polar bears in this study were probably fasting or consuming limited amounts of vegetation. Polar bears actively foraging on the sea ice can consume large amounts of material (e.g. up to 20% of body mass, Best, 1985) and BIA measures may thus be more strongly affected by gut fill if performed during periods of hyperphagia.

Although polar bears on shore during the ice free season are largely fasting (Stirling *et al.*, 1977; Ramsay & Stirling, 1988), some individuals forage on berries, kelp, goose eggs and other terrestrial foods (Lunn & Stirling, 1985; Ramsay & Hobson, 1991; Derocher *et al.*, 1993). Although the energetic value of terrestrial foods is minimal in comparison to marine mammal prey (Rode *et al.*, 2015), Gormezano & Rockwell (2015) argued that land-based food could offset the nutritional deficits arising from reduced foraging opportunities on the sea ice. We found no evidence to support this hypothesis as our results showed no relationship between body condition and terrestrial foraging. Our finding that energy density is lower in foraging COY suggests that terrestrial feeding may be associated with

smaller body size and reduced energy stores in younger, small bodied bears.

Adult female body condition

The consistently greater body condition of adult and subadult females across metrics (Fig. 3) suggests the potential for higher relative body fat stores in females as early as the subadult stage compared to males. It is possible that fat stores begin to accumulate earlier in females to better prepare for gestation and lactation that require large fat reserves (Ramsay & Stirling, 1986; Thiemann *et al.*, 2006). Moreover, male bears continue growth for longer periods before reaching maximum adult size compared to females (Derocher & Wiig, 2002), consequently fat store accumulation may not occur as early in life. Consistent with seasonal fasting and a *c.* 8-month onshore period associated with denning, body condition in adult females was higher in fall than spring and was higher in solitary females than those with dependent young in the fall (Atkinson & Ramsay, 1995; Hilderbrand *et al.*, 2000; Thiemann *et al.*, 2006; McKinney *et al.*, 2014).

Energy expenditure in mammals may increase with litter size (Konig, Riester & Markl, 1988; Kenagy *et al.*, 1990), and the effects of lactation (Arnould & Ramsay, 1994) appeared to

influence body condition of females supporting multiple cubs (Fig. 5). The extent of fat stores accumulated prior to fasting may dictate the likelihood of producing offspring (Atkinson & Ramsay, 1995; Samson & Huot, 1995; Belant *et al.*, 2006), date of parturition, rate of cub growth (Samson & Huot, 1995; Robbins *et al.*, 2012), litter size (Samson & Huot, 1995) and cub mass and survival (Derocher & Stirling, 1996, 1998). In contrast, skull size was smaller in solitary females compared to those supporting offspring. Skeletal features may be influenced by long-term nutrition (Zedrosser *et al.*, 2006; Rode *et al.*, 2010), and body size in bears can influence litter size and natality (Stringham, 1990). Thus, structurally larger females in our study population may have a reproductive advantage. Energy expenditures of adult females vary based on offspring needs, as storage energy, energy density and fatness index were greater in females with yearlings than COY (Fig. 4). Energetic demands of milk production for females supporting COY surpasses that of yearlings due to rapid COY growth rate and is reflected in the decline in fat content of milk over time (Arnould & Ramsay, 1994).

Inter-annual trends in body condition

Temporal trends in a suite of metrics revealed a long-term decline in polar bear body condition across age and sex classes. Although a fundamental adaptation of polar bear survival involves the ability to prioritize lipid catabolism during fasting, ongoing declines in sea ice habitat are likely reflected in measures of body condition. For example, declines in body condition were found in southern Beaufort Sea polar bears following years with reduced ice availability (Rode *et al.*, 2010). Polar bears in southern Hudson Bay have shown declines in body condition associated with a progressively longer ice-free season (Obbard *et al.*, 2016). Past studies in western Hudson Bay have documented declines in body condition of adult males and females associated with earlier sea ice breakup, suggesting that a reduced foraging period affects nutritional condition (Stirling *et al.*, 1999). Regehr *et al.* (2007) found juvenile, subadult and senescent (>20 years) polar bear survival to fluctuate based on timing of spring melt, while Lunn *et al.* (2016) identified trends in sea ice breakup dates to reflect survival of females across all age classes. Similarly, we found sea ice to influence body condition metrics across age and sex classes. The differing response of various metrics to changing ice conditions, however, suggests that timing of breakup and freeze-up may not be the sole factors involved in influencing polar bear body condition. For example, energy density, storage energy and skull width declined over time in solitary adult females (Fig. 7), but these metrics were not predicted by sea ice breakup or freeze-up dates. This suggests that other environmental factors, in conjunction with sea ice, may be collectively influencing body condition (Rode *et al.*, 2010), and environmental parameters that fluctuate with a changing climate may be more complex (Rode *et al.*, 2014; Bromaghin *et al.*, 2015). Although polar bear life history has evolved to enable populations to cope with fluctuating ice conditions, more frequent years of poor habitat can negatively influence body condition and survival (Stirling & Parkinson, 2006; Whiteman *et al.*, 2015).

The western Hudson Bay region is undergoing considerable environmental change. Spring air temperatures have increased and sea ice breakup occurs c. 3 weeks earlier than 30 years ago (Gagnon & Gough, 2005; Hochheim, Barber & Lukovich, 2010; Hochheim & Barber, 2014). Earlier ice melt reduces the foraging window and individuals come ashore in poorer condition (Stirling *et al.*, 1999; Regehr *et al.*, 2007). Our assessment of multiple metrics of body condition indicate that the climate-driven declines in polar bear body condition initially documented in western Hudson Bay in the mid-1990s (Stirling *et al.*, 1999) have continued. It is likely that sustained reductions in body condition resulting from ongoing changes in sea ice habitat driven by a warming climate will negatively affect population vital rates and subsequently, the abundance of polar bears in western Hudson Bay.

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Supporting Information

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

Table S1. Multiple linear regression results examining relationship between sea ice (breakup and freeze-up date) and adipose tissue lipid content, energy density, storage energy and skull width in different age/sex classes for polar bears captured during the fall season in western Hudson Bay from 2004 to 2013. Model F statistics, *P*-values and adjusted r^2 are reported along with standardized β coefficient values (and direction of relationship, positive or negative) for both breakup and freeze-up date in each model. * denotes a significant relationship between sea ice and each body condition metric. † indicates which predictor variable (breakup or freeze-up) had the greatest effect on the dependent variable (comparing β value). Sample sizes shown in Figs 6 and 7.