ARTICLE

Trends in body condition in polar bears (*Ursus maritimus*) from the Southern Hudson Bay subpopulation in relation to changes in sea ice

M.E. Obbard, M.R.L. Cattet, E.J. Howe, K.R. Middel, E.J. Newton, G.B. Kolenosky, K.F. Abraham, and C.J. Greenwood

Abstract: Sea ice is declining over much of the Arctic. In Hudson Bay the ice melts completely each summer, and advances in break-up have resulted in longer ice-free seasons. Consequently, earlier break-up is implicated in declines in body condition, survival, and abundance of polar bears (*Ursus maritimus* Phipps, 1774) in the Western Hudson Bay (WH) subpopulation. We hypothesised that similar patterns would be evident in the neighbouring Southern Hudson Bay (SH) subpopulation. We examined trends 1980–2012 in break-up and freeze-up dates within the entire SH management unit and within smaller coastal break-up and freeze-up zones. We examined trends in body condition for 900 bears captured during 1984–1986, 2000–2005, and 2007–2009 and hypothesised that body condition would be correlated with duration of sea ice. The ice-free season in SH increased by about 30 days from 1980 to 2012. Body condition declined in all age and sex classes, but the decline was less for cubs than for other social classes. If trends towards a longer ice-free season continue in the future, further declines in body condition and survival rates are likely, and ultimately declines in abundance will occur in the SH subpopulation.

Key words: body condition, climate change, Hudson Bay, polar bear, sea ice.

Résumé : La glace de mer baisse sur une grande partie de l'Arctique. Dans la baie d'Hudson, la glace fond complètement chaque été, et la dislocation de plus en plus précoce donne lieu à des saisons libres de glace plus longues. Par conséquent, la dislocation plus précoce est en cause dans les déclins de l'état corporel, de la survie et de l'abondance des ours polaires (*Ursus maritimus* Phipps, 1774) dans la sous-population de la baie d'Hudson Ouest (HO). Nous avons formulé une hypothèse que des tendances similaires seraient évidentes chez la sous-population voisine de la baie d'Hudson Sud (HS). Nous avons examiné les tendances de 1980 à 2012 des dates de dislocation et de la prise des glaces, et ce, pour toute l'unité d'aménagement de la baie d'Hudson Sud et pour les plus petites zones de dislocation et de la prise des glaces le long de la côte. Nous avons étudié l'évolution de l'état corporel de 900 ours capturés de 1984 à 1986, de 2000 à 2005 et de 2007 à 2009 et avons formulé l'hypothèse que l'état corporel soit corrélé avec la durée de la glace de mer. La saison libre de glace à la baie d'Hudson Sud s'est prolongée de 30 jours de 1980 à 2012. L'état corporel s'est dégradé pour tous les âges et sexes, mais le déclin fût moindre pour les oursons que

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pour les autres classes sociales. Si la direction générale vers une saison libre de glace plus longue se maintient à l'avenir, de plus amples dégradations de l'état corporel et des taux de survie sont probables, et en fin de compte des déclins de l'abondance se produiront chez la sous-population de la baie d'Hudson Sud.

Mots-clés : état corpore, changement climatique, Baie d'Hudson, ours polaire, glace de mer.

Introduction

Polar bears (*Ursus maritimus* Phipps, 1774) rely on sea ice as a platform for important life processes including mating, dispersal, and hunting their primary prey, ringed seals (*Pusa hispida* Schreber, 1775) and bearded seals (*Erignathus barbatus* Erxleben, 1777) (Stirling and Archibald 1977). However, the duration of sea ice has declined across much of the polar bear range (Stirling and Parkinson 2006), especially in seasonal sea ice regions (Amstrup et al. 2008) such as Hudson Bay (Gagnon and Gough 2005; Scott and Marshall 2010). For example, the open-water season in Hudson Bay has increased by about 3 weeks since 1996 (Hochheim and Barber 2014).

The Southern Hudson Bay (SH) subpopulation of polar bears occupies southern and east-ern Hudson Bay and James Bay, south of 60°N and east of 88.5°W (Fig. 1), the southernmost continuously occupied area of the worldwide range of polar bears (Obbard et al. 2010). Here, climate warming has already caused dramatic changes to the sea ice regime (Gagnon and Gough 2005), and changes to sea ice extent and duration are occurring more rapidly than elsewhere in the Arctic (Hochheim and Barber 2014). Consequently, it is predicted that polar bears may be extirpated from Hudson Bay due to loss of sea ice habitat by the end of the century (Amstrup et al. 2008).

Hudson Bay undergoes a complete cryogenic cycle each year (Etkin 1991); it is entirely cov-ered in ice by late December in most years but the ice melts in summer, so there is a 4–5 month ice-free period in summer and fall. During the ice-free period, all bears are forced ashore where they remain until ice forms again in late fall or early winter. While on land, polar bears generally survive on stored reserves acquired from hunting seals on the ice, although there has long been evidence that at least some bears exploit terrestrial food sources (Russell 1975; Derocher et al. 1993; Rockwell and Gormezano 2009; Gormezano and Rockwell 2013). Declines in sea ice affect polar bear populations by reducing the time avail-able to forage; the net result is expected to have both individual- and population-level effects, with individual-level effects being observable earlier than population-level effects (Stirling et al. 1999). In Hudson Bay, polar bears in the Western Hudson Bay (WH) subpopulation have already been affected by changes in sea ice with declines in body condition (Stirling et al. 1999) preceding a 22% decline in abundance from 1987 to 2004 (Regehr et al. 2007). More recent analysis suggests that from 2001 to 2010, there was a period of population stability in WH associated with temporary stability in sea ice conditions that affect survival rates of adult females (Lunn et al. 2016). Nevertheless, further changes in abundance are predicted as the ice-free season becomes longer. For example, Molnár et al. (2010, 2014) estimated that 2%–3% of adult males in WH would die before the end of a 120 day summer fasting period but 9%–21% would die if climate warming increased the fasting period to 180 days.

To assess the effects of climate change on the SH subpopulation, we examined trends in sea ice duration (1980–2012) and in body condition (1984–2009). We hypothesised that body condition of polar bears in SH would decline as a function of sea ice duration.

Materials and methods

Animal capture

In July–October 1984–1986 and September–October 2000–2005 and 2007–2009, we cap-tured polar bears of all age and sex classes along the Ontario coastline from Hook Point

Fig. 1. Recognized boundaries of Canadian polar bear subpopulations. SB, South Beaufort; NB, North Beaufort; VM, Viscount Melville; NW, Norwegian Bay; LS, Lancaster Sound; MC, M'Clintock Channel; GB, Gulf of Boothia; BB, Baffin Bay; DS, Davis Strait; FB, Foxe Basin; WH, Western Hudson Bay; SH, Southern Hudson Bay (Lunn et al. 2010).
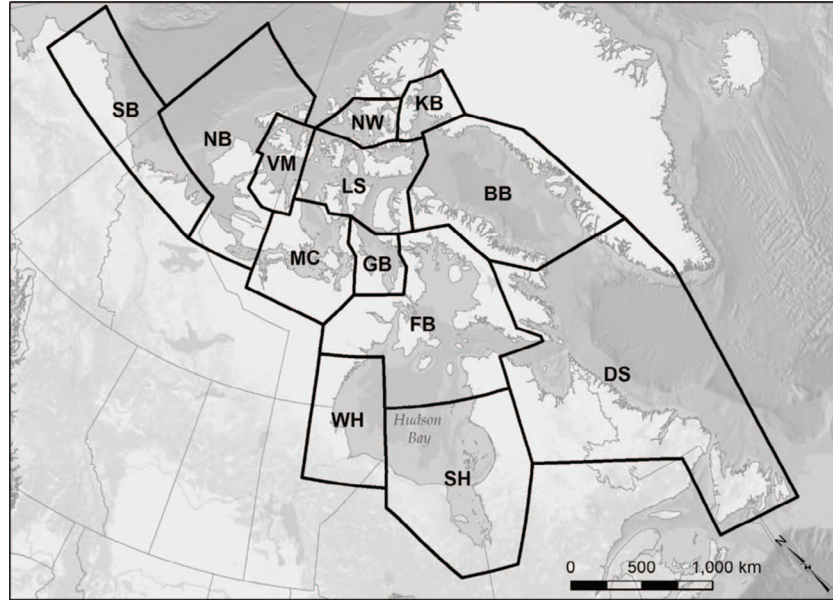
(54°50′N, 82°15′W) on northwestern James Bay to the Ontario–Manitoba border (56°50′N, 89°00′W) and up to 30 km inland (Fig. 2). We chemically immobilized bears from a helicopter by remote drug delivery using either a combination of ketamine hydrochloride and xylazine hydrochloride (KX) (1984–1986), zolazepam–tiletamine (ZT) (2000–2005), a combination of xylazine and zolazepam–tiletamine (XZT) (2007–09), or a combination of medetomidine and zolazepam–tiletamine (MZT) (2009). KX was administered as Ketaset® (Parke, Davis and Co., Inc., Brockville, Ontario, Canada) at a dosage of 7 mg/kg estimated body mass and Rompun® (Bayvet Division, Miles Laboratories Ltd., Mississauga, Ontario, Canada) at 7 mg/kg estimated body mass (Lee et al. 1981). ZT was administered as Telazol® (Fort Dodge Laboratories, Inc., Fort Dodge, Iowa, USA) at 8 mg/kg estimated body mass (Stirling et al. 1989). XZT was administered as xylazine (Cervizine 300®) (Wildlife Pharmaceuticals, Inc., Fort Collins, Colorado, USA) at 2 mg/kg and Telazol® (Fort Dodge Laboratories, Inc., Fort Dodge, Iowa, USA) at 3 mg/kg estimated body mass (Cattet et al. 2003). MZT was administered as medetomidine (Bow River Pharmaceuticals, Bow River, Alberta, Canada) at 0.06 mg/kg and Telazol® at 2 mg/kg (Cattet et al. 1997). At the conclusion of handling, we administered yohimbine hydrochloride (1984–1986) (Sigma Chemical Co., St. Louis, Missouri, USA) at 0.1 mg/kg to reverse the effects of xylazine (Ramsay et al. 1985) or atipamezole (2007–2009) (Antisedan®, Pfizer Bio-Pharmaceuticals and Animal Health, Mississauga, Ontario, Canada) at 0.20 mg/kg to reverse xylazine or 0.30 mg/kg to reverse medetomidine (Cattet et al. 1997, 2003). Bears <1 year of age were immobilized using a pole syringe. In order to avoid the influence of gut fill on body mass, and to ensure bears were not susceptible to aspiration of stomach contents, we did not attempt to handle bears if there was evidence that they might have recently fed (found near a carcass or with fresh blood on the rostrum or forelegs and chest).

Once bears were immobilized, we placed them in ventral (sternal) recumbency with the back legs extended behind and the front legs forward. We recorded pulse and respiratory rates, rectal temperature, and, from 2007 to 2009, haemoglobin oxygen saturation (Nellcor

Fig. 2. Location of study area in northern Ontario. Polar bears were captured between the Manitoba–Ontario border and Hook Point on James Bay and up to 30 km inland.
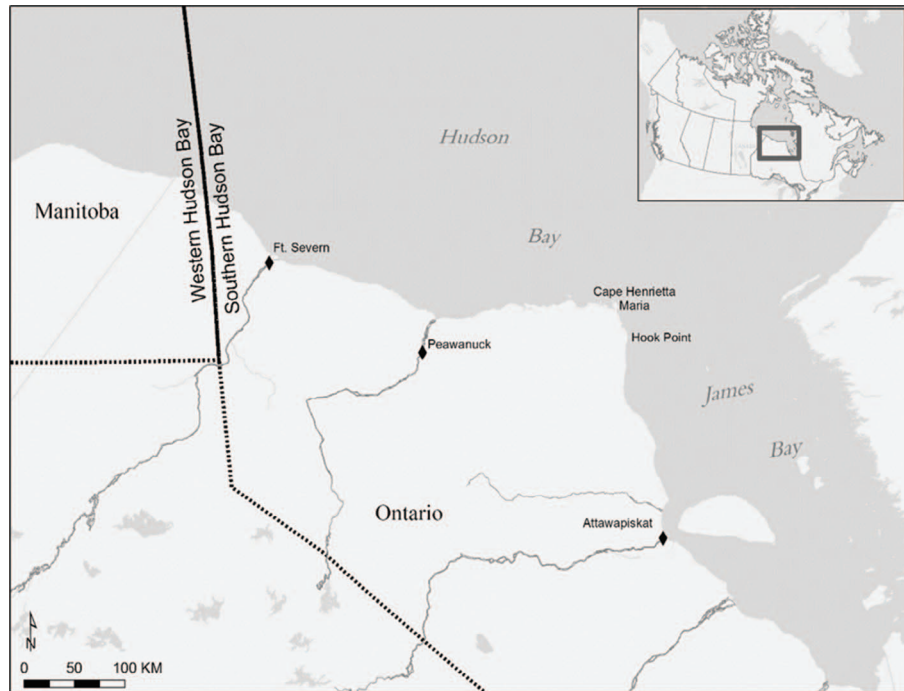
NPB-40 pulse oximeter) (Nellcor, Pleasanton, California, USA) at onset of handling and every 15 min thereafter. We protected the corneas of bears by applying 0.5% hydroxypropyl methyl cellulose eye drops (IsoptoTears®) (Alcon Canada Inc., Mississauga, Ontario, Canada) and protected the retinas by shielding the eyes with a cotton hood. We recorded standard morphometric measurements (straight-line body length, axillary girth, skull length, zygomatic width, and body mass). We measured body length to the nearest centimetre as the dorsal straight-line distance from the tip of the nose to the end of the last tail vertebra using a metal measuring tape extended above the bear in sternal recumbency. We recorded body mass to the nearest 500 g by suspending the bear from a spring-loaded weigh scale (1984–1986) or an electronic load cell (2000–2009) (Norac Ltd., Saskatoon, Saskatchewan, Canada) mounted below a tripod. During weighing, bears were secured in a semisupportive sling and lifted by chain hoist until clear of the ground. We subtracted the known weight of the supportive sling from the total weight to yield the final scale weight of the bear. We applied individually numbered ear tags and lip tattoos to each animal and removed a vestigial premolar from bears >1 year for aging based on counts of cementum growth layers (Calvert and Ramsay 1998).

All capture and handling procedures were approved annually by the Animal Care Committee of the Ontario Ministry of Natural Resources. Handling procedures followed the general guidelines of the Canadian Council for Animal Care (CCAC 2003) and the American Society of Mammalogists (Sikes and Gannon 2011).

Dates of freeze-up, break-up, and duration of ice cover

To describe ice cover on Hudson Bay and James Bay, we used ice concentration data at 25 km resolution available as satellite passive microwave data (SMMR/SSMI) obtained from the National Snow and Ice Data Center, Boulder, Colorado, USA (http://nsidc.org/).

We downloaded daily ice concentration data in bin format and processed the data to AI grid format using R version 2.15 (R Core Team 2012) and ArcGIS 9.3.1 (ESRI, Redlands, California, USA). We clipped the ice data to coincide with the boundaries of the SH subpopulation. We generated daily overall mean ice concentrations in Hudson Bay and James Bay for each year. The duration of ice cover each year is the period between freeze-up in late fall and break-up in early summer. Freeze-up and break-up have generally been defined, following navigation standards, as the period when average sea ice concentration reaches 50% (Etkin 1991). However, because this metric had low explanatory power in an earlier analysis that examined body condition in SH bears for the period 2003–2005 (Obbard et al. 2006), and because bears in WH were shown to both remain on the ice and return to the ice at lower ice concentrations (Cherry et al. 2013), we also explored whether break-up and freeze-up at lower thresholds of 40%, 30%, 20%, 10%, and 5% ice concentration were related to body condition levels. We defined freeze-up and break-up dates in each year as the first and last ordinal date, respectively, when the average ice concentration in Hudson Bay and James Bay reached the six thresholds and remained either above or below that level.

We tested for temporal trends during 1980–2012 in ordinal dates of freeze-up, break-up, and duration of ice cover at the six ice concentration thresholds within the entire SH management unit using Pearson's correlation. A counterclockwise current flow in Hudson Bay, combined with prevailing northwesterly winds, results in the last remaining ice in summer being concentrated north of the Ontario coast (Wang et al. 1994; Saucier et al. 2004). Because bears remain on this residual ice as it contracts towards the Ontario coast and return to the ice in fall before the entire management unit is ice-covered (Middel 2014), we also tested for trends in ordinal dates of freeze-up and break-up for the six ice concentration thresholds in smaller polygons along the Ontario coast of Hudson Bay and James Bay where ice accumulates during break-up in summer and where it forms first in late fall (Fig. 3). These smaller break-up and freeze-up coastal zones were defined in part by movement patterns of radio-collared bears (Obbard and Middel 2012; Middel 2014). For the coastal break-up zone, we used the July 30 polygon shown in Markham (1988) as being representative of the extent of residual ice off the Ontario coast in early summer in most years. To delimit the extent of the coastal freeze-up zone, we measured the distance from shore to the outer ice edge on the day that GPS-collared bears returned to the ice (2007–2010). Average ice extent on the date when bears ($n = 30$) returned to the ice was 47.05 km; therefore, we created a buffer of 50 km along the northern Ontario shoreline to create our coastal freeze-up zone. We report one-tailed P-values because we expected declines in ice coverage based on previous studies (Gagnon and Gough 2005; Hochheim et al. 2010; Hochheim and Barber 2014).

Trends in polar bear body condition over time

To estimate a body condition index (BCI) required three steps. First, we tested several models (e.g., linear, logarithmic, inverse, power, quadratic, etc.) using the Curve Estimation command in IBM SPSS Statistics version 23 (IBM Corporation 2015) to determine which model best described the relationship between body mass and body length in female and male polar bears in our study population. Next, using the best-fitting, sex-specific models, we calculated predicted body mass values and then the residuals as the observed minus predicted body mass values. Finally, following Cattet et al. (2002), we standardized the residuals using a Z-transformation and used the standardized residuals as our BCI values. Cattet et al. (2002) validated the standardized residual as an index of body condition in polar bears by confirming its strong association with true body condition, defined as the combined mass of fat and skeletal muscle relative to body size, in 31 hunter-killed polar bears.

Fig. 3. Hudson Bay and James Bay showing the orientation of surface currents and the Southern Hudson Bay management unit boundaries with our defined coastal break-up and freeze-up zones.
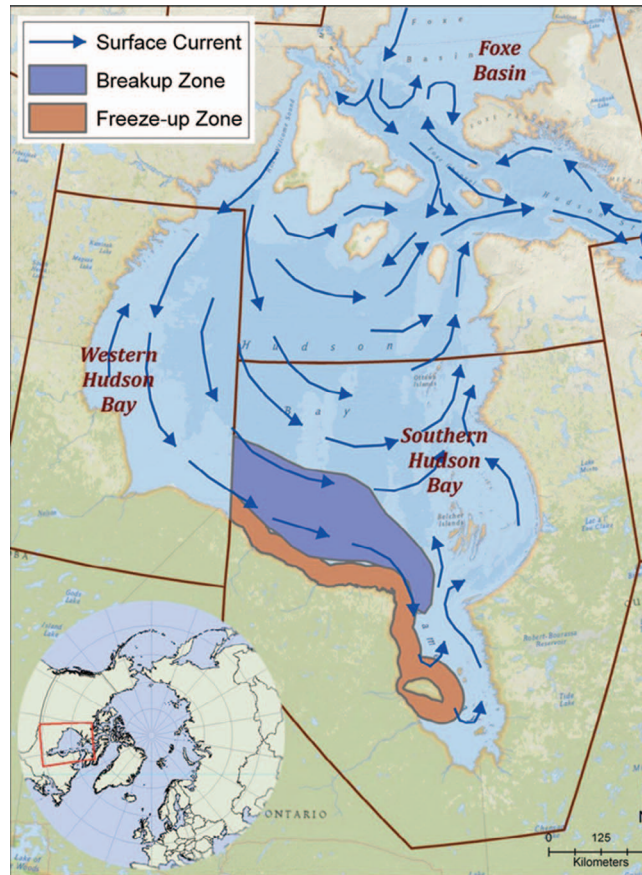
We tested for a linear trend in BCI across years and differences in BCI among polar bear capture periods (1980s = 0, 2000s = 1) and social classes (adult (≥5 years) males, adult females accompanied by young, solitary adult females, subadults (2–4 years), yearlings, and cubs) by comparing linear mixed-effects models (with bear as the only random effect) using AIC_c (Hurvich and Tsai 1989). We evaluated support for a difference between the capture period in the 1980s and the capture period in the 2000s. Most solitary adult females were deemed pregnant at the time of capture based on body mass, but this category likely also included some nulliparous females aged >4 years, senescent females, and reproductive-age females that were not accompanied by young but may not have been pregnant in the year of capture. We evaluated the effect of two covariates that represented the length of time bears spent on shore because we expected body condition to decrease between the dates that bears came ashore and date of capture in fall (Derocher and Stirling 1995). These covariates were the ordinal date of capture, *odc*, and estimated number of days ashore since breakup, *dashore* (*odc* − ordinal date of breakup at 5% ice concentration), transformed to begin at "day 1." Both variables were standardized by subtracting the mean and dividing by 2 standard deviations (Gelman and Hill 2007). Loss of body mass, and therefore a decrease in BCI, is proportional to body temperature and metabolic expenditure (McCue 2010), and polar bear body temperature declines throughout the summer and fall seasons (Whiteman et al. 2015; M.E. Obbard, unpublished data). Therefore, to account for the possibility that polar

bear body condition could decline in a nonlinear fashion throughout the duration of the season, we also included a quadratic term for both *odc* and *dashore*; these were standardized after squaring.

We included models with interactions between year or capture period and social class because we expected that changes in BCI over time might differ among social classes. We also included models with interactions between social class and *odc*, or *dashore*, and their quadratics, because different social classes could have different physiological strategies throughout the season in response to food deprivation. At this stage, we retained all bears for which BCI values were available (1071 observations of 900 individuals; Table S1[1]), including dependent offspring. The condition of the offspring likely depended on that of their mothers, so observations may not have been completely independent, but we included data from dependent offspring here because we were interested in differences in BCI and changes in BCI over time, among all age classes including cubs and yearlings. Models were fitted by maximizing the full rather than the restricted likelihood because we were interested in selecting among models with different fixed effects as opposed to random effects (Bolker 2008). When calculating AIC_c values, we set the number of observations to the number of unique individuals rather than the total number of observations. In total, 50 models were included in the candidate set; *odc* and *dashore* and their related quadratics were never included in the same model because the two variables were collinear. Similarly, year and capture period were never included in the same models.

Next, we limited the data set to independent bears (i.e., excluded dependent offspring) and tested for a linear trend through time in years, differences between capture periods, and effects of variables describing ice cover on BCI of independent bears (738 observations of 608 bears; Table S2). Ice variables for the year that BCI was measured were ordinal dates of break-up that year and freeze-up in the previous year as well as the duration of ice cover from freeze-up the previous year to break-up in the current year at each of 50%, 40%, 30%, 20%, 10%, and 5% average ice concentration, both within the entire SH management unit and in our smaller defined break-up and freeze-up zones. For ice in the break-up and freeze-up zones, we further included ice durations with all crossed combinations of ice concentrations (e.g., duration of ice cover from freeze-up at 50% ice concentration in fall until break-up at 50%, 40%, 30%, 20%, 10%, and 5% ice concentration the following spring). The large number of covariates describing ice cover would have led to a very large number of fitted models if we included all subsets of potential covariates, so we adopted a quasi-stepwise approach to model selection as follows. In Step 1, we initially fit 14 models to confirm that body condition was a function of social class and ordinal date of capture or number of days on shore since breakup at 5% and their quadratics and interactions, similar to the analysis with dependent bears described above, but without including year or capture period covariates. In Step 2, we fit a set of 71 models containing the top model(s) from Step 1 (i.e., with ΔAIC_c values <2; Burnham and Anderson 2002); the rest of the models included all variables present in the top model(s) and one covariate describing variation among years (either an ice covariate, a linear trend across years, or a difference between capture periods). For Step 3, we added six more models to the set of 71. These models were similar to the six top-ranked models in Step 2, but we included an interaction with the covariate of variation among years for that particular model (year, capture period, or ice covariate) with social class because large interaction effects are likely to occur when main effects are also large (Gelman and Hill 2007). We report results for the final set of 77 models in Step 3. We fit models by maximizing the full likelihood and set the total number

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[1]Supplementary material is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/as-2015-0027.

of observations to the number of unique individuals when calculating AIC_c values as above. All analyses were performed in R version 3.2.2 (R Core Team 2015). Mixed-effects models were fitted using functions implemented in the lme4 package (Bates et al. 2014). We report the conditional R^2 for top models in each analysis, $R^2_{GLMM(c)}$. The conditional R^2 is a measure of the variance explained by both the fixed and random factors and can be considered an indication of the goodness-of-fit of each model (Nakagawa and Schielzeth 2013).

Results

Dates of freeze-up, break-up, and duration of ice cover

Within the entire SH management unit, ordinal date of freeze-up was positively correlated with year ($P < 0.001$), break-up was negatively correlated with year ($P < 0.05$), and the duration of ice cover was negatively correlated with year ($P < 0.005$) at all ice concentrations. For the coastal break-up and freeze-up zones, ordinal date of freeze-up was positively correlated with year ($P < 0.05$) at all ice concentrations, break-up was negatively correlated with year ($P < 0.05$) at all concentrations except at 50% ($P = 0.06$), and duration of ice cover was negatively correlated with year ($P < 0.01$) at all ice concentrations. For both the entire management unit and the coastal freeze-up and break-up zones, relationships were stronger at lower ice concentrations; therefore, we report trends in freeze-up and break-up for the 5% ice concentration threshold only. We do not imply that polar bears occupy areas with ice concentration as low as 5%. Rather, the concentration is a mean of all 25 km × 25 km pixels in the defined region (90 pixels for our coastal freeze-up zone, 144 pixels for our coastal break-up zone, and 741 pixels for the entire SH management unit). For example, at break-up, even in our smaller coastal zone, much of the area will be open water and bears will occupy the residual ice that has much higher ice concentration than 5%; nevertheless, the mean for the entire polygon is 5% ice concentration.

At 5% ice concentration, ordinal dates of freeze-up and break-up changed by approximately 0.5 day/year on average ($\beta = 0.53$, SE 0.12, and $\beta = -0.61$, SE 0.21, for freeze-up, and break-up, respectively, in the entire SH management unit and $\beta = 0.52$, SE 0.20, and $\beta = -0.47$, SE 0.27, respectively, in the freeze-up and break-up zones near the coast) such that the duration of ice cover decreased by approximately 1 day/year ($\beta = -1.11$, SE 0.25, in the entire SH management unit and $\beta = -1.09$, SE 0.40, in the freeze-up and break-up zones). Weaker relationships with break-up dates than freeze-up dates may be attributable to greater variability in break-up dates after 1990 (Figs. 4 and 5). Results were similar when we excluded data from 1992, when break-up was particularly late due to the effects of the eruption of Mt. Pinatubo in 1991 (Parks et al. 2006).

Trends in polar bear body condition over time

The top-ranked model of variation in BCI through time and among social classes fit to the full data set (including dependent offspring) had almost twice as much support as the second-ranked model (Table 1). The top model included an effect of the ordinal date of capture, the quadratic term for ordinal date of capture, differences among social classes, the interaction between quadratic ordinal date of capture and social classes, and capture period (Table 1). The second-ranked model was similar to the top model, except that it did not include a quadratic term for *odc*; instead, it included an interaction between social class and *odc*. The third model was also similar to the top model, but included a covariate for an interaction between social class and capture period. The top models had similar goodness-of-fit values; however, the fit of the third model was slightly higher than those of the first and second. Although the third- and fourth-ranked models explained more variance in BCI than the top two models, they had a greater number of parameters and therefore lower AIC_c weights (Table 1). Other top models were similar to the top four models in that they included interactions between an *odc* variable and social class, but they included covariates for a change in BCI across years

Fig. 4. Ordinal dates of freeze-up (shaded circles) and break-up (open circles), and the duration of ice cover (solid circles), all to 5% ice concentration, within the Southern Hudson Bay polar bear management unit,1980–2012. Text labels show Pearson's correlation coefficients for the linear relationships depicted, all of which were significant at $\alpha = 0.05$.
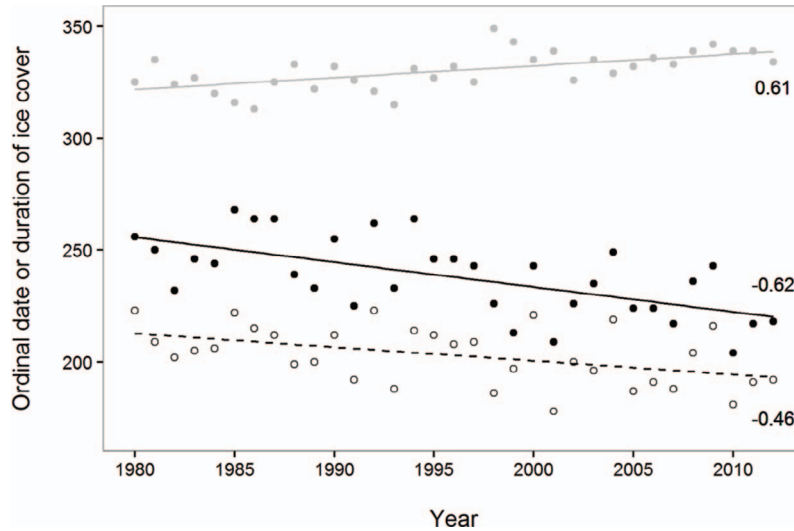

Fig. 5. Ordinal dates of freeze-up (shaded circles) and break-up (open circles), and the duration of ice cover (solid circles), all to 5% ice concentration, for the coastal break-up and freeze-up zones off the northern Ontario coast and coast of James Bay in Ontario, Canada, 1980–2012. Text labels show Pearson's correlation coefficients for the linear relationships depicted, all of which were significant at $\alpha = 0.05$.
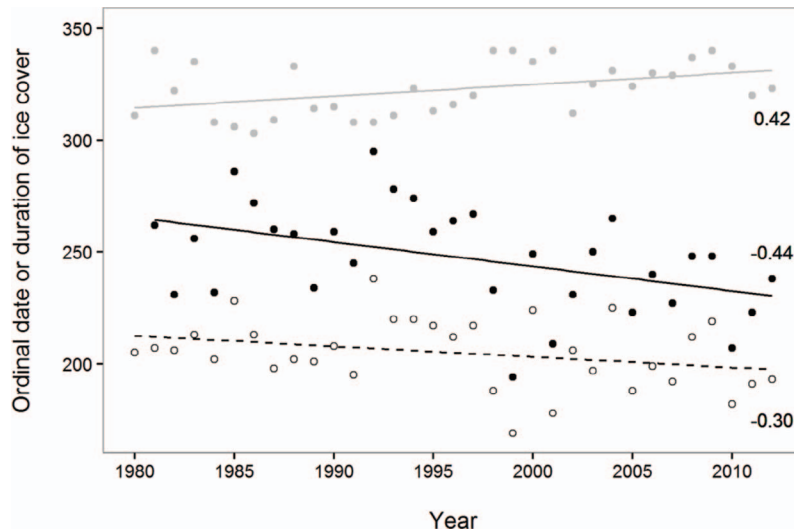
rather than between capture periods, or for an interaction between social classes and the linear relationship across years (Table 1). Neither the *dashore* term (estimated number of days ashore) nor its quadratic was supported in the top models.

Body condition decreased significantly for all social classes between the 1980s and 2000s by about 1 standard deviation of the mean in the three top-ranked models, translating to a loss in body mass of approximately 45 kg for males and 31 kg for females (Table 2; Fig. 6).

Table 1. Model selection results for the top ranked of 50 models of variation in body condition index of polar bears and their dependent offspring in the Southern Hudson Bay subpopulation, 1984–1986 (capture period = 0) and 2000 – 2009 excluding 2006 (capture period = 1).

Model	Parameters	AIC_c	ΔAIC_c	w_i	$R^2_{GLMM(c)}$
$odc + odc^2 \times soc$ + capture period	16	2615.59	0	0.44	0.534
$odc \times soc$ + capture period	15	2616.82	1.23	0.24	0.534
$odc + odc^2 \times soc + soc \times$ capture period	21	2618.06	2.47	0.13	0.536
$odc \times soc + soc \times$ capture period	20	2619.04	3.45	0.08	0.537
$odc \times soc$ + year	15	2619.19	3.6	0.07	0.534
$odc + odc^2 \times soc$ + year	16	2621.17	5.58	0.03	0.533
$odc \times soc + soc \times$ year	20	2623.19	7.6	0.01	0.531
$odc + odc^2 \times soc + soc \times$ year	21	2625.14	9.55	0.00	0.531
$odc + odc^2 + soc \times$ capture period	16	2632.58	16.99	0.00	0.517
$dashore + dashore^2 + soc \times$ year	16	2632.71	17.12	0.00	0.513
$odc + soc \times$ year	15	2633.85	18.26	0.00	0.516
$odc + odc^2 + soc \times$ year	16	2634.95	19.35	0.00	0.516
$odc + soc \times$ capture period	15	2635.73	20.14	0.00	0.517

Note: In model names: odc, ordinal date of capture; dashore, odc, ordinal date when ice concentration at breakup was at 5%; soc, social class (adult male, adult female accompanied by young, solitary adult female, subadult, yearling, cub) A multiplication sign indicates interactions between main effects; "year" was modeled as a linear relationship.

The third-ranked model included an interaction between social class and capture period, suggesting that body condition declined between capture periods at different rates among social classes (Table 2; Fig. 7). In the third model, body condition of cubs declined less rapidly than that of adult males; the rate of change in BCI between capture periods for adult females, subadults, and yearlings was not significantly different from that of adult males (Table 2; Fig. 7).

In terms of time spent ashore, interaction effects precluded interpretation of main effects of social class, odc, and odc^2 (Table 2); however, the body condition of adult females and subadults declined more quickly throughout the ice-free season than did body condition of adult males. The decline in BCI for solitary adult females was especially pronounced over the ice-free season (Table 2; Fig. 6). The seasonal trend in BCI for yearlings and cubs was not significantly different from that of adult males.

Factors affecting body condition of independent polar bears

When we excluded dependent offspring and included ice covariates in the models to explain variation in BCI over time, the same model of variation in BCI minimized AIC_c as in the previous analysis (Table 3). Rates of decline in BCI after bears came ashore, between capture periods, and differences among social classes in the rate of change in BCI throughout the season were similar to when dependent offspring were included (Tables 2 and 4). The decline in BCI between capture periods for independent bears translated to approximately 49 kg for males and 34 kg for females. Although a decline in BCI between capture periods provided a more parsimonious fit to our BCI data than any of the ice covariates we evaluated, models with an ice covariate for ordinal dates of freeze-up at low ice concentrations in the SH management unit or the coastal zone were supported over models with other ice covariates. Therefore, the observed decline in body condition was apparently more closely related to later freeze-up than to earlier break-up or shorter ice duration.

Discussion

We showed that at the lowest ice concentration value of 5%, break-up advanced and freeze-up was delayed by about 0.5 day/year each on average; therefore, as a result, length of the ice-free period in our study area increased by about 1 day/year between 1980

Table 2. Parameter estimates for factors affecting body condition of polar bears and their dependent offspring in the Southern Hudson Bay subpopulation, 1984–1986 and 2000–2009 (excluding 2006), with standard errors and approximate *P* values calculated using Satterthwaite-approximated degrees of freedom (Kuznetsova et al. 2015) for the three top-ranked models.

	Model								
	$odc + odc^2 \times soc + cp$			$odc \times soc + cp$			$odc + odc^2 \times soc + soc \times cp$		
Effect	β	SE	P	β	SE	P	B	SE	P
Intercept	0.6482	0.0814	<0.0001*	0.6117	0.0793	<0.0001*	0.7804	1.3474	<0.0001*
odc	2.3377	1.3455	0.0826	0.0858	0.1191	0.4714	2.1468	1.3457	0.1114
odc^2	−2.2345	1.3401	0.0957				−1.9405	0.2131	0.1496
Encumbered adult females	−0.1992	0.0842	0.0183*	−0.2072	0.0843	0.0142*	−0.2504	0.2763	0.2402
Solitary adult females	1.2345	0.1222	<0.0001*	1.2457	0.1223	<0.0001*	0.9062	0.1573	0.0011*
Subadults	−0.0870	0.0770	0.2587	−0.0793	0.0771	0.3036	−0.1676	0.2167	0.2870
Yearlings	−0.0194	0.0941	0.8369	−0.0254	0.0942	0.7872	−0.2348	0.2111	0.2787
Cubs	0.0473	0.0816	0.5623	0.0414	0.0817	0.6122	−0.4396	0.1613	0.0375*
cp	−0.9129	0.0801	<0.0001*	−0.8622	0.0757	<0.0001*	−1.1026	0.2172	<0.0001*
Encumbered adult females × odc^2	−0.7507	0.1591	<0.0001*				−0.7905	0.3243	0.0003*
Solitary adult females × odc^2	−1.0793	0.2548	<0.0001*				−1.3507	0.1843	<0.0001*
Subadults × odc^2	−0.3862	0.1543	0.0125*				−0.4569	0.2384	0.0133*
Yearlings × odc^2	−0.1430	0.1786	0.4234				−0.3152	0.2165	0.1864
Cubs × odc^2	0.1089	0.1561	0.4855				−0.2671	1.3474	0.2176
Encumbered adult females × *odc*				−0.7648	0.1589	<0.0001*			
Solitary adult females × *odc*				−1.1345	0.2565	<0.0001*			
Subadults × *odc*				−0.4125	0.1541	0.0076*			
Yearlings × *odc*				−0.1555	0.1786	0.3840			
Cubs × *odc*				0.1145	0.1556	0.4621			
Encumbered adult females × *cp*							0.0852	0.2634	0.7463
Solitary adult females × *cp*							0.4589	0.3422	0.1802
Subadults × *cp*							0.1165	0.1987	0.5577
Yearlings × *cp*							0.3063	0.2760	0.2673
Cubs × *cp*							0.6409	0.2586	0.0134*

Note: Adult males were the reference class. *odc*, ordinal date of capture; *soc*, social class; *cp*, capture period.

and 2012. The net result was that polar bears from the SH subpopulation were forced to spend about 30 days longer on land in 2012 than bears did in 1980. This is similar to earlier estimates of advances in break-up of 3–4 weeks in the western half of Hudson Bay between 1971 and 2003 based on coarser temporal resolution Canadian Ice Service data (Gagnon and Gough 2005), but suggests that the trend has continued. A similar trend to earlier break-up and later freeze-up was documented for northern regions of Hudson Bay in Foxe Basin and Hudson Strait (Sahanatien and Derocher 2012). Variability in the trend in ordinal dates of freeze-up and break-up was greater for our defined coastal zones than for the entire SH management unit, which reflects the increased temporal variability in the immediate physical environment that bears in SH now face when either returning to or leaving the sea ice. Increasing variability in the physical environment is one of the general predictions from climate change models (IPCC 2007). It seems that polar bears in SH will be faced with an increasingly unpredictable sea ice regime in the future.

Fig. 6. Standardized body condition index (BCI) values and top-model regression lines by social class and capture period for polar bears, including dependent offspring, in the Southern Hudson Bay subpopulation, 1984–1986 and 2000–2009 (excluding 2006).
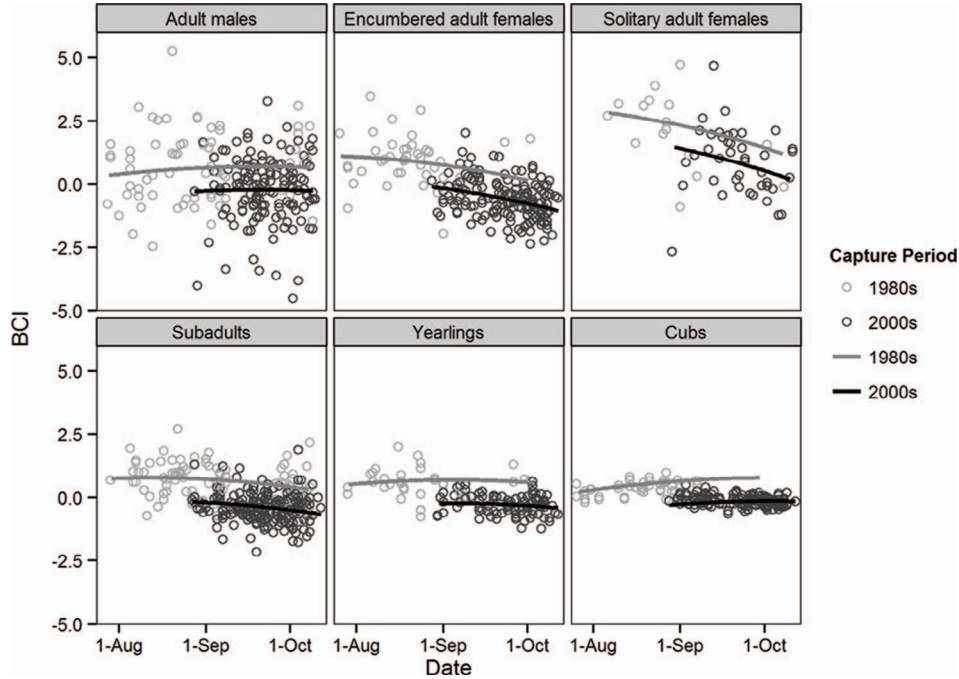

Fig. 7. Interaction between social class and two capture periods, 1984–1986 and 2000–2009 (excluding 2006), as predicted by the third model describing variation in standardized body condition index (BCI) values for polar bears, including dependent offspring, in the Southern Hudson Bay subpopulation. Ordinal date of capture was held constant at the median date of capture of 19 September.
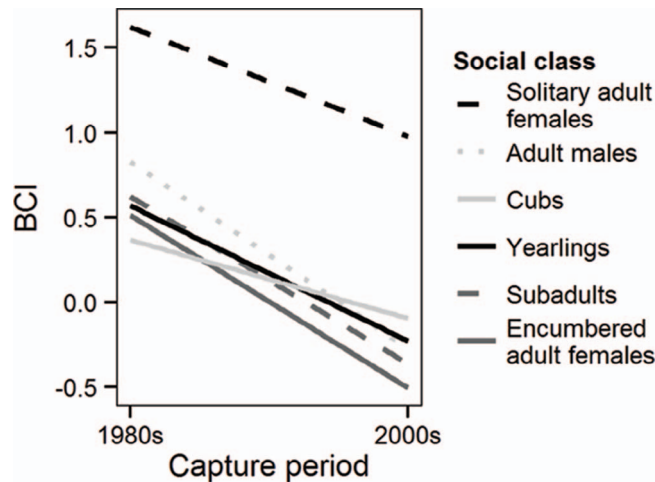
We showed that body condition in all social classes of bears of the SH subpopulation declined significantly between 1984 and 2009 — strong evidence for individual-level effects having occurred in this subpopulation. The trends in BCI between capture periods for yearlings, subadults, encumbered adult females, and solitary adult females were similar to the

Table 3. Model selection results for the top ranked of 77 models of variation in body condition index of independent polar bears (i.e., excluding dependent offspring) in the Southern Hudson Bay subpopulation, 1984–1986 (capture period = 0) and 2000–2009, excluding 2006 (capture period = 1).

Model	Parameters	AIC_c	ΔAIC_c	w_i	$R^2_{GLMM(c)}$
$odc + odc^2 \times soc$ + capture period	12	2034.95	0	0.84	0.596
$odc + odc^2 \times soc$ + year	12	2039.57	4.63	0.08	0.589
$odc + odc^2 \times soc + soc$ × capture period	15	2040.05	5.10	0.07	0.594
$odc + odc^2 \times soc + soc$ × year	15	2043.83	8.89	0.01	0.586
$odc + odc^2 \times soc$ + SHMU freeze-up (5%)	12	2085.55	50.60	0.00	0.564
$odc + odc^2 \times soc + soc$ × SHMU freeze-up (5%)	15	2091.18	56.24	0.00	0.566
$odc + odc^2 \times soc$ + SHMU freeze-up (20%)	12	2092.83	57.88	0.00	0.575
$odc + odc^2 \times soc$ + SHMU freeze-up (10%)	12	2095.15	60.21	0.00	0.570
$odc + odc^2 \times soc$ + SHMU freeze-up (40%)	12	2095.76	60.81	0.00	0.574
$odc + odc^2 \times soc$ + SHMU freeze-up (30%)	12	2098.41	63.47	0.00	0.576
$odc + odc^2 \times soc$ + coastal freeze-up (20%)	12	2098.85	63.91	0.00	0.578
$odc + odc^2 \times soc + soc$ × SHMU freeze-up (20%)	15	2098.93	63.98	0.00	0.572
$odc + odc^2 \times soc$ + coastal freeze-up (40%)	12	2100.73	65.79	0.00	0.580

Note: In model names: odc, ordinal date of capture; soc, social class (adult male, adult female accompanied by young, solitary adult female, subadult). A multiplication sign indicates interactions between main effects; "year" was modeled as a linear relationship.

Table 4. Parameter estimates for the top-ranked model for factors affecting body condition of independent polar bears (i.e., excluding dependent offspring) in the Southern Hudson Bay subpopulation, 1984–1986 and 2000–2009 (excluding 2006), with standard errors and approximate P values calculated using Satterthwaite-approximated degrees of freedom (Kuznetsova et al. 2015).

	Model: $odc + odc^2 \times soc$ + capture period		
Effect	β	SE	P
Intercept	0.6962	0.1037	<0.0001*
odc	1.7606	1.9131	0.3577
odc^2	−1.6252	1.9050	0.3939
Encumbered adult females	−0.1979	0.1001	0.0484*
Solitary adult females	1.2564	0.1430	<0.0001*
Subadults	−0.0698	0.0912	0.4442
Capture period	−0.9873	0.1083	<0.0001*
Encumbered adult females × odc^2	−0.7416	0.1829	0.0001*
Solitary adult females × odc^2	−1.0942	0.2892	0.0002*
Subadults × odc^2	−0.3805	0.1775	0.0324*

Note: Adult males were the reference class. odc, ordinal date of capture; soc, social class.

trend for adult males. However, some models suggested that the decline in body condition was less for cubs than for adult males (Fig. 7). Given that cub body condition declined at a slower rate than that of their mothers, because of the declines in body mass of adult females, they may be allocating a proportionally greater amount of energy to their dependent young in recent years such that the energetic cost to themselves is proportionally higher than in the 1980s. If that is the case, this portends further declines in body condition of reproductive-age females and subsequent declines in reproductive success. Declines in body condition between capture periods for solitary females may have been less than that for encumbered females, which also may reflect the proportional increase in energetic costs of reproduction for lactating females in recent years due to their declining body mass (Table 2; Fig. 7). However, the solitary female class had small sample sizes in some years and also likely included nulliparous adult females, older unencumbered adult females that may

not have been pregnant, and senescent females, leading to greater variability in the data and subsequent large SE associated with the parameter estimates. This meant that we could not distinguish the trend for solitary females from that for encumbered females.

There were interesting differences among social classes in trends of body condition during time ashore (Fig. 6). Compared to adult males, the greater rate of decline in body condition for subadults presumably represents the energetic costs of somatic growth. The relatively greater declines for encumbered adult females presumably reflect the energetic costs of lactation, although by late September, few adult females in this subpopulation are still lactating (M.E. Obbard, unpublished data). The trend for solitary adult females may be more an artefact of small samples sizes and subsequent high variability in the data. The trend for cubs and yearlings did not differ from that for adult males, and the pattern suggests that, at least for the late summer and early fall period, many cubs and yearlings are still benefitting from nursing.

It has been suggested that exploiting terrestrial food sources may ameliorate declines in body condition in polar bears (e.g., Gormezano and Rockwell 2015), although the importance of terrestrial foraging in offsetting lost opportunities to hunt seals remains controversial (e.g., Rode et al. 2015). Bears in WH have been documented feeding on various terrestrial food sources (Derocher et al. 1993; Rockwell and Gormezano 2009; Gormezano and Rockwell 2013). Similarly, SH bears were reported to exploit terrestrial foods during the ice-free season as far back as the 1970s (Russell 1975) and more recently (Smith and Hill 1996). However, the current extent and opportunities for terrestrial feeding are not well understood for the SH subpopulation. It is uncertain how important terrestrial feeding may be for these bears in the future, but body condition declined since the 1980s while bears have had opportunities to exploit terrestrial food sources.

Declines in individual-level traits can be expected to presage declines in population-level traits, especially in long-lived animals such as bears where females can control reproductive effort through delayed implantation (Wimsatt 1963; Hellgren 1998). In both the WH and Southern Beaufort Sea subpopulations, declines in body condition preceded declines in survival rates and litter production rates (Stirling et al. 1999; Regehr et al. 2007, 2010; Rode et al. 2010, 2012), and these negative trends were correlated with declines in sea ice duration and distribution. For example, Regehr et al. (2007) suggested that survival of juveniles, subadults, and senescent-adult polar bears in WH was correlated with spring sea ice break-up date, which was variable among years and occurred approximately 3 weeks earlier in 2004 than in 1984. The authors argued that this correlation provided evidence for a causal association between earlier sea ice break-up (due to climatic warming) and decreased polar bear survival, resulting in a decline in abundance (Regehr et al. 2007).

Based on results of capture–recapture studies conducted in SH from 1984 to 1986 and from 2003 to 2005, Obbard et al. (2007) showed that survival rates tended to decline between the two capture periods, although point estimates were not significantly different because of the overlap in confidence intervals. Recently, results of intensive aerial surveys conducted in 2011 in WH (Stapleton et al. 2014) and SH (Obbard et al. 2015) suggested that reproductive output, as measured by average litter size and proportion of cubs and yearlings in the sample, was greater in SH than in WH. This suggests that, despite the demonstrated declines in body condition and the suggestion of declines in survival rates, reproductive output in SH is still better than that of the neighbouring subpopulation. In contrast with the situation in the WH subpopulation, no decline in abundance was detected in the SH subpopulation between the mid-1980s and 2012 (Obbard et al. 2015). Nevertheless, if these trends in body condition and survival rates continue, declines in abundance seem inevitable. Because no change in abundance has yet been detected in the SH subpopulation, it seems unlikely that density-dependent factors are influencing body condition of bears.

Rather, it seems more likely that declines in body condition in SH are related to changes in the physical environment, that is, to decreases in the length of time Hudson Bay is ice-covered and providing a suitable platform for hunting.

Date of freeze-up had a stronger influence on subsequent body condition than date of break-up in our study. Although models with date of freeze-up were supported over models with other ice covariates, we acknowledge that lower variability in freeze-up dates than in ice duration or break-up dates could have influenced the model selection process. Nevertheless, we suggest that a stronger effect of date of freeze-up may be because even though break-up has advanced by up to 3–4 weeks in portions of Hudson Bay, it still occurs no earlier than late June or early July so does not yet interfere with opportunities to feed on neonate ringed seal pups that are born in March–April in eastern Hudson Bay (Chambellant 2010). Therefore, losing days or weeks of hunting opportunities during June and July deprives polar bears of the opportunity to feed on adult seals, but does not deprive them of the critical spring period (Watts and Hansen 1987) when they are truly hyperphagic. No doubt, the loss of hunting opportunities to kill adult seals has a negative effect on body condition, but it appears that for bears in SH, a forced extension of the fast in late fall has a greater negative effect on subsequent body condition. Because the bears now return to the ice in poorer condition than in previous decades, they have a greater energy deficit to recover during a now shorter hunting season. The additive effects of continued declines in the time available to acquire energy stores on long-lived animals such as polar bears will eventually have negative outcomes. An even longer ice-free season will result in further reduced access to prey, lowered fat stores, greater physiological stress, and eventually effects on survival and reproductive success (Derocher et al. 2004; Molnár et al. 2010, 2011; Stirling and Derocher 2012).

Molnár et al. (2010, 2011) predicted that an ice-free period ≥180 days would cause large declines in survival rates and reproduction for polar bears in WH. Based on these predictions, Castro de la Guardia et al. (2013) defined critical years for polar bears in this subpopulation as those with ≥180 ice-free days and projected changes in the ice cycle and in sea ice concentration in spring under three IPCC greenhouse gas emissions scenarios (B1, A1B, and A2). Under all three scenarios, critical years were more common after 2050; from 2051 to 2100, eight critical years were predicted to occur under the B1 scenario, 35 under the A1B scenario, and 41 under the A2 scenario (Castro de la Guardia et al. 2013). Therefore, in two emissions scenarios, polar bear habitat will deteriorate rapidly after 2050 and the polar bears in WH will be increasingly less likely to persist. However, if greenhouse gas emissions can be reduced (B1 scenario), sea ice habitat will deteriorate less rapidly and polar bears should persist through the 21st century (Castro de la Guardia et al. 2013). Future research on polar bears in SH should address forecasting when sea ice changes can be expected to greatly reduce survival and reproduction. Analysing detailed fine-scale temporal and spatial data from polar bears fitted with GPS radiocollars would improve our understanding of the ice conditions when polar bears abandon the ice platform and return to land in spring and when they return to the ice in fall. This information is critical to understanding the marginal sea ice conditions that polar bears will continue to use as a hunting platform.

Acknowledgements

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