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# Significance of Autumn and Winter Food Consumption for Reproduction by Southern Beaufort Sea Polar Bears, *Ursus Maritimus*

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## Original Publication Citation

**ORIGINAL PAPER**

# Significance of autumn and winter food consumption for reproduction by Southern Beaufort Sea polar bears, *Ursus maritimus*

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## Abstract

Polar bears (*Ursus maritimus*) in the southern Beaufort Sea experience long annual periods when preferred seal prey are scarce or are unavailable. Consumption of bowhead whale (*Balaena mysticetus*) carcasses from native Alaskan subsistence hunting is increasingly common for onshore polar bears, yet the energetic consequences of this consumption remain unclear. We use data on bears captured repeatedly over periods that encompassed autumn and winter, combined with calculations, to show that adult female bears likely consume an average of at least 4 seal equivalents during both autumn and winter periods and that considerable variation in energy intake exists across individual bears. We further show that subsistence-caught whale carcasses provide an upper threshold of > 4000 seal equivalents, which could potentially meet mean consumption needs of ~ 80% of the southern Beaufort Sea bear subpopulation during autumn and winter periods. Finally, we modify an existing model to show that observed mass changes over autumn and winter could substantially alter spring foraging habitat choice by females with cubs and the chance that a female with reduced energy reserves would abort a pregnancy or abandon cubs in favor of increasing her own survival; these behaviors could potentially influence population vital rates. Our study highlights the importance of mass dynamics over the autumn and winter months, points to the need for additional data on foraging and energetics over this period, and indicates that the recent declines in polar bear body condition in some subpopulations could have complex effects on reproduction.

**Keywords** Baleen whale carcass · Optimal behavior · Polar bear · Seal equivalents · Subsistence hunting · *Ursus maritimus*

## Introduction

Polar bears (*Ursus maritimus*) experience strong seasonal fluctuations in food availability and feeding activity. The most intense feeding period is during spring when ringed seal (*Pusa hispida*) pups are abundant and sea ice conditions are amenable (Stirling et al. 1975; Pilfold et al. 2012, 2015). Based on historic autumn habitat use (Ferguson et al. 2000; Durner et al. 2004) and relatively high autumn body mass (Durner and Amstrup 1996), it has been assumed that bears in the southern Beaufort Sea (SBS) likely also have a peak foraging period in autumn, when sea ice returns to the continental shelf (Schliebe et al. 2008), the preferred

habitat of ringed seals. Despite the considerable dietary flexibility of polar bears (Thiemann et al. 2008), feeding during ice-free summer periods and during winter freeze-up is generally thought to be less common (Stirling and Øritsland 1995). During these periods, polar bears may seek alternative, terrestrial foods, including items from landfills (Lunn and Stirling 1985), caribou (*Rangifer tarandus*) (Gormezano and Rockwell 2013), beached whale carcasses (Laidre et al. 2018), and eggs within bird colonies (Divoky et al. 2015; Bourque et al. 2020; Jagielski et al. 2021).

The most prominent alternative food item accessed on land by SBS polar bears appears to be beach-cast bowhead whale (*Balaena mysticetus*) carcasses from subsistence hunting. Subsistence whaling occurs out of whaling villages along the coasts of the Bering, Chukchi, and Beaufort Seas during early fall (late August to early September) with some spring hunting also occurring out of Utqiagvik, AK (Ashjian et al. 2010). Bears congregate at the "bone piles" where these carcasses are deposited (Herreman and Peacock 2013; Pongracz and Derocher 2017; Lillie et al. 2019) and

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bear density is often higher near bone piles than elsewhere onshore during the autumn (Miller et al. 2006; Schliebe et al. 2008; Gleason and Rode 2009). Further, polar bear onshore abundances are higher in years when subsistence whale carcasses are more available (Schliebe et al. 2008). Stable isotope analysis indicates that for polar bears near shore, the contribution of bowhead whale to the diet is seasonally variable, peaking at 40–70% during summer (Rogers et al. 2015; Whiteman et al. 2018) and falling to 11–26% during winter (Bentzen et al. 2007). Diet estimates based on fatty acids are slightly lower, suggesting that for the SBS subpopulation overall, bowhead whale represents 10–15% (Bourque et al. 2020; Florko et al. 2020) of the annual diet. The benefits of whale consumption appear to be clear: shore bears consuming whale retain more body protein (Whiteman et al. 2018) and have better body condition than those that do not (Mckinney et al. 2017b). Whale consumption is also likely increasing over time: as a result of sea ice loss, more polar bears are spending longer periods near the coast and on land (Atwood et al. 2016; Pongrancz and Derocher 2017). Declining mercury concentrations in polar bear tissues are consistent with a decrease in their trophic level, which could be caused by increasing consumption of bowhead whale, which are at a lower trophic level than the seals that polar bears normally eat (Mckinney et al. 2017a).

Whale consumption is therefore likely a key factor driving variation in body condition of SBS polar bears in coastal habitat. Despite this, population models often make simplifying assumptions that ignore the dynamics of this food source. For example, a recent model that explored the influence of energy balance on optimal reproductive strategy in polar bears (Reimer et al. 2019) made the assumption that during autumn and winter, SBS individuals maintain energy balance by consuming just enough food to maintain body mass until the onset of the prime seal hunting season in spring. However, this assumption is not consistent with whale consumption by some individuals, and with physiological evidence of highly dynamic changes in body mass and condition during autumn and winter (Pagano et al. 2018; Whiteman et al. 2018; Galicia et al. 2020). It therefore remains unclear how individual differences in mass gains or losses over autumn and winter periods may influence the optimal fitness strategies of different polar bears.

Here, we address three questions to help clarify variation in energy dynamics of bears during the autumn and winter periods and the implications for individual fitness. First, we use longitudinal data on recaptured SBS adult female bears to examine changes in their body mass during the autumn and winter periods, and we use expected mass loss (based on metabolic patterns) to project the amount of food that would need to be consumed in order to affect the observed body mass changes. Second, we calculate the overall amount of energy available to bears in bone piles from subsistence

whale hunts to determine the possibility that whale carcasses could meet the consumption levels predicted from observed changes in bear mass. Third, to explore the fitness consequences of variation in these shore-based energy dynamics across individual bears, we build upon a previously developed dynamic state variable model (Reimer et al. 2019) to examine how inclusion of observed changes in body mass over autumn and winter may influence optimal maternal reproductive decisions.

## Methods

### Mass change of bears over autumn and winter

We used archived data from SBS polar bears that were captured multiple times between autumn 2008 and spring 2010 during a series of ecophysiological studies (Whiteman et al. 2015, 2018, 2019; Durner et al. 2017). Captures occurred via helicopter darting on shore between Utqiagvik, AK, and the Alaska-Canada border, or on sea ice ≤ 700 km offshore. We focused on adult female bears that did not enter maternity dens during the study period, and that were captured over intervals that primarily encompass autumn and/or winter periods when their foraging is expected to be minimal. Table 1 gives the capture interval and the mass at each capture for each bear. For each bear ($n = 17$), we determined the observed mass change ($\Delta m_{obs}$) as the difference between the first ($m_i$) and second ($m_f$) capture dates:

$$\Delta m_{obs} = m_f - m_i \tag{1}$$

We then calculated the expected mass change of each bear over this same capture interval ($\Delta m_{exp}$) based on metabolic rate, their mass at first capture, the time of year, and the duration of time until their second capture, as described below. We assumed that daily mass loss reflected no food intake (i.e., fasting) and seasonally dependent field metabolic rates (FMR), which we estimated for each bear based on movement rates (see Fig. 3B in Pagano et al. 2018). Of the 17 bears in our study, we had hourly GPS locations for eight of them throughout the capture interval (Whiteman et al. 2015), from which we directly calculated average daily movement rates (km h$^{-1}$). For two additional bears, we used ~ hourly Doppler locations to determine whether the bears were on land or on sea ice, because movement rates differ on these two substrates (Whiteman et al. 2015). For the remaining seven bears, we assumed that they were on land for portions of the capture interval from August to October, and on sea ice for portions of the capture interval from November to May. We estimated movement rates for the eight bears without GPS data using the monthly mean movement rates for bears on land or on sea ice (Whiteman

**Table 1** Capture dates and mass of polar bears (*Ursus maritimus*) at sequential captures

| Bear ID | Primary time of year | Capture interval (# days) | Mass at initial capture (kg) | Mass at recapture (kg) | Mass change (kg) |
|---|---|---|---|---|---|
| 6810 | Autumn | 8/29/08–10/17/08 (49) | 234 | 288 | 54 |
| 20414 | Autumn | 8/5/09–10/10/09 (66) | 220 | 242 | 22 |
| 20562 | Autumn | 8/4/09–10/7/09 (64) | 238 | 211 | − 27 |
| 20586 | Autumn | 8/23/08–10/19/08 (57) | 270 | 323 | 53 |
| 20735 | Autumn | 8/29/09–10/18/09 (50) | 217 | 331 | 114 |
| 20741 | Autumn | 8/23/08–10/26/08 (64) | 226 | 177 | − 49 |
| 20966 | Autumn | 8/10/08–10/20/08 (71) | 288 | 263 | − 24 |
| 20977 | Autumn | 8/23/08–10/19/08 (57) | 185 | 210 | 24 |
| 20977 | Autumn | 8/6/09–10/6/09 (61) | 245 | 236 | − 10 |
| 32255 | Autumn | 8/26/08–10/8/08 (43) | 218 | 187 | − 30 |
| 32282 | Autumn | 8/25/08–10/10/08 (46) | 273 | 291 | 18 |
| 20413 | Winter | 10/9/08–4/24/09 (197) | 293 | 225 | − 67 |
| 20414 | Winter | 10/10/09–4/13/10 (185) | 242 | 165 | − 77 |
| 21024 | Winter | 10/7/09–3/26/10 (170) | 226 | 201 | − 25 |
| 20586 | Winter | 10/19/08–4/9/09 (172) | 323 | 215 | − 107 |
| 20132 | Winter | 8/18/08–4/29/09 (253) | 186 | 160 | − 26 |
| 21045 | Winter | 10/12/09–4/10/10 (298) | 298 | 220 | − 78 |

Data are reproduced from archived data collected previously (Whiteman et al. 2015, 2018, 2019; Durner et al. 2017)

et al. 2015). We then used these movement rates to calculate the daily FMR in KJ kg$^{-1}$ day$^{-1}$ (Pagano et al. 2018, $R^2 = 0.82$):

$$FMR = 167.3 \times movement\ rate + 153.3 \tag{2}$$

We then multiplied the daily FMR by the initial mass at the start of that day ($m_d$) to determine the total energy lost that day ($E_d$).

$$E_d = FMR \times m_d. \tag{3}$$

A single bear engaged in a long-distance swim during the capture interval (bear ID 20741) (Durner et al. 2011), which would incur a different metabolic cost than the FMR estimated for the other bears. We therefore used the estimated metabolic rate during this swim (Griffen 2018) to determine the associated energy loss, and we used GPS locations to estimate its daily *FMR* for the rest of the sample interval, in the same manner as described above for the other bears.

To convert this energy lost per day to mass loss, we calculated the amount of fat and lean tissue that are metabolized, since the metabolism of these two tissue types yield different amounts of energy. The relative amount of fat and lean tissue metabolized depends on the proportion of body mass that is fat (Atkinson et al. 1996), which was determined using bioelectrical impedance analysis, conducted on 14 of the 17 bears at the initial capture (Whiteman et al. 2018). For the three bears without these data, we estimated values based on bears in the database with similar body mass at the same time of year.

We then used this initial proportional body fat ($P_F$) and the relationship given in Atkinson et al. (1996) to determine the contribution of fat (met$_F$) and lean (met$_L$) tissue to metabolism ($R^2 = 0.70$):

$$met_F = 1.8325 \times P_F - 0.3239, \tag{4}$$

$$met_L = 1 - met_F. \tag{5}$$

Finally, we combined the energy lost per day, the proportion of this loss that was fat or lean tissue, and the energy liberated from metabolizing fat ($c_F = 39.3$ MJ kg$^{-1}$) and lean tissue ($c_L = 23.6$ MJ kg$^{-1}$) (following Atkinson et al. 1996) to determine the total mass loss:

$$x' = \frac{E_d \times met_F}{c_F} + \frac{E_d \times met_L}{c_L}. \tag{6}$$

Using these methods, for each day of the capture interval, we iteratively calculated the mass loss and updated the mass ($x$) as follows:

$$\Delta m_{exp} = f(d) = x - x' \quad d \in \mathbb{Z}, d_i \leq d \leq d_f, \tag{7}$$

where $d_i$ and $d_f$ are the days of the initial and final captures.

## Seal equivalents needed to account for mass changes

We determined the amount of consumption required during the capture interval to account for differences between observed mass changes and expected mass changes. Not knowing the type of food consumed by each bear during this interval, we standardize this by determining consumption in 'ringed seal equivalents.' First, we determined the apparent energy gain ($E_g$) as the difference between the observed mass change and expected mass losses, converting mass to energy by again using the calculated proportion of mass loss that is fat and lean tissue and using the same conversion factors ($c_F$ and $c_L$) as above:

$$E_g = (\text{met}_F \times c_F + \text{met}_L \times c_L) \times (\Delta m_{obs} - \Delta m_{exp}). \quad (8)$$

Given our use of 'ringed seal equivalents', we assumed that any mass not lost (i.e., less mass loss than expected) was a result of ringed seal consumption. Based on seasonal variation in ringed seal body composition and the proportions of seal age groups consumed by polar bears, previous estimates are that polar bears consume ~16 kg of tissue per seal ($m_{seal}$) (Laidre et al. 2018). We likewise assumed ~16 kg of tissue per seal and that 80% of consumed tissue was blubber ($\%_{blubber}$), with the remaining 20% consumption reflecting lean tissue ($\%_{lean}$) (Stirling and McEwan 1975; Erlenbach et al. 2014). We used digestion and assimilation ($a_F$ and $a_L$, respectively) of energy from blubber (97.3%) and from lean muscle tissue (83.7%) as measured following consumption by polar bears (Best 1985). The values of energy gained from blubber ($E_{blubber}$) and lean tissue ($E_{lean}$) were combined as follows to estimate the amount of energy assimilated per seal consumed ($E_{seal}$):

$$E_{blubber} = m_{seal} \times \%_{blubber} \times a_F \times c_F, \quad (9)$$

$$E_{lean} = m_{seal} \times \%_{lean} \times a_L \times c_L, \quad (10)$$

$$E_{seal} = E_{blubber} + E_{lean}. \quad (11)$$

This yielded a total of 553 MJ of energy assimilated per seal consumed. We therefore divided the consumed energy required to account for the observed mass change by 553 to get the number of seal equivalents consumed by each bear.

## Seal equivalents of subsistence bowhead whale carcasses

We calculated the energy available to polar bears from bowhead whale carcasses (in ringed seal equivalents)

using the approach of Lairdre et al. (2018). To make the most realistic estimates possible, we focus only on subsistence-harvested bowhead whales and account for butchering before the carcass becomes available to bears. Between 2000 and 2010, $39.0 \pm 7.7$ (mean $\pm$ S.D) bowhead whales were caught annually in the region (Suydam et al. 2010). In 2010, 29 whales were caught in the SBS region. For these 29 whales, we used an empirically based equation ($n = 8$, $R^2 = 0.945$; George 2009) to calculate whale mass ($m_{body}$) based on length (Suydam et al. 2010):

$$m_{body} = 50.33 \text{length}^{2.45}. \quad (12)$$

We also calculated whale bone mass ($m_{bone}$) as a function of body length, using an equation ($R^2 = 0.975$) based on 170 baleen whale specimens (Anderson et al. 1979):

$$m_{bone} = 0.024 \text{length}^{1.107}. \quad (13)$$

We then determined the non-skeletal (i.e., consumable) mass ($m_{consumable}$) as the difference between the body mass and bone mass for each whale:

$$m_{consumable} = m_{body} - m_{bone}. \quad (14)$$

Due to butchering by whalers, not all of this consumable tissue would be available to bears. To estimate the consumable tissue left on the bones following butchering and therefore available for consumption by bears, we used data from a single butchering event of an 11-m, 14,797 kg bowhead whale during a subsistence harvest (Kishigami 2013). The mass of each body part included: tongue (893.0 kg, 6% of body mass), skin and blubber (6601.9 kg, 44%), muscle (2428.0 kg, 16%), baleen (595.5 kg, 4%), tail (217.7 kg, 1.5%), flippers (349.2 kg, 2.4%), kidney (97.9 kg, 0.7%), heart (95.2 kg, 0.6%), and intestines (223.8 kg, 1.5%). We assumed that the same percentages of body mass were butchered and distributed for all 29 whales captured in 2010 (Suydam et al. 2010). The remaining soft body tissue (i.e., $m_{consumable}$ minus the masses of each of these individual body parts) was the consumable tissue for polar bears.

We divided the amount of consumable mass after butchering (i.e., the consumable mass available to bears) of each of the 29 whales from the 2010 hunt (Suydam et al. 2010) by 16 kg to determine ringed seal equivalents. This calculation assumes that the energetic contents of whale carcasses and of ringed seals are equivalent. While our assumption is that bears only consume 16 kg of a seal (Laidre et al. 2018), we acknowledge that scavenging of the remainder of the seal may occur (Derocher et al. 2000), in which case, our calculations overestimate the seal equivalents from a single bowhead whale carcass.

## Expected behavioral and fitness impacts of mass changes during autumn and winter

We examined the behavioral and fitness consequences of variable changes in autumn and winter mass dynamics by modifying a previously developed dynamic state variable model that explored behavior by SBS adult female bears as a function of age, body condition, and reproductive status (Reimer et al. 2019). This model assumed that adult females went through a period of mass loss during summer, followed by a period of mass neutrality where consumption during autumn and winter was sufficient only to maintain a constant body mass throughout these periods. Reimer et al. (2019) assume that summer fasting periods encompassed the period from ice breakup (assumed to be July 17) until ice freeze-up (assumed to be October 8). This differs from the seasonal terminology used here. Based on the resampling data described above, we refer to 'autumn' as the period where foraging by onshore bears increases, influencing mass changes. We therefore use autumn as the period from mid-August to October. As summer, autumn, and winter are encompassed in a single time step within the model (Reimer et al. 2019), all mass changes during this period occur in the model during a single time step, and this semantic difference therefore does not influence our results.

The Reimer et al. (2019) model predicted two key aspects of behavior: first, whether females should optimally select "fast ice" or "active ice" for spring foraging. Fast ice, which is adjacent to land and frozen in place, provides greater safety for cubs because adult male polar bears, which may commit infanticide, are less common in this habitat (Derocher and Wiig 1999; Amstrup et al. 2006); also, there is less open water and thus less risk of hypothermia during swimming (Blix and Lentfer 1979; Pilfold et al. 2014). However, fast ice offers relatively poor foraging. Active ice, which is more distant from land and includes pack ice and the floe edge, is more risky for cubs but has improved foraging relative to fast ice. Second, the model also predicted which reproductive strategy—abort/abandon their offspring, or continue the pregnancy or cub care—would optimize lifetime reproductive success.

We modified this model to incorporate the changes in polar bear mass observed here. We found that the amount of mass lost by adult female bears during the winter varied in proportion to autumn body mass (see Results). We therefore used this relationship to modify their over-winter function, $w_\eta$ (see section S2 of Supplementary Information, Reimer et al. 2019), where the subscript $\eta$ can take one of four values indicating reproductive state (1 = lone female, 2 = pregnant female, 3 = female with cubs-of-the-year, and 4 = female with dependent cubs). For stages 1, 3, and 4, we modified the total energy loss ($w_\eta$) by subtracting

the mass-specific energy loss to yield the modified over-wintering mass ($w_\eta^*$):

$$w_\eta^* = w_\eta - \left(\text{met}_F \times c_F + \text{met}_L \times c_L\right) \times (-0.544x + 78.683),$$
(15)

where $x$ is initial autumn body mass, and $\text{met}_F$, $\text{met}_L$, $c_F$, and $c_L$ are as defined above. For females in reproductive state 2, we did not adjust the original model, because mass losses associated with metabolism and lactation of these denning bears during this period of fasting were already accounted for in the model (Reimer et al. 2019).

We found that mass changes during autumn were variable, with some bears gaining and some bears losing mass (see Results). We assumed that these divergent results reflected a combination of differences among bears in energy expenditure and in the degree of foraging success, whether on subsistence whale bone piles or other sources. We therefore used the average value of mass change for bears that gained or lost mass, respectively, as the additional mass change expected for bears during autumn. We again assumed that all mass changes were due to a combination of fat and lean tissue metabolism. We therefore ran the model twice, once adding to $w_\eta^*$ the mean energy gain of bears that gained body mass during autumn (1244 MJ) and once subtracting from $w_\eta^*$ the mean energy loss of bears that lost body mass during autumn (−758 MJ).

We did not make any additional changes to the original model. We obtained the published Matlab code from the original model and made the modifications described above to their code. We then used this modified code to solve the model for the optimal reproductive strategy using backward iteration, as previously described (Reimer et al. 2019). This yielded new optimal strategies, which we then qualitatively compare to the strategies predicted by the original model.

## Results

### Mass change of bears over autumn and winter

Each of the adult female bears whose resampling dates encompassed the winter months experienced mass loss over this period. The amount of mass lost differed considerably across bears and increased with body mass during the initial capture in the autumn (linear model, $P = 0.02$, Fig. 1A). In contrast, for bears whose capture interval only occurred during autumn, some bears lost mass while other bears gained mass, and there was no relationship with initial capture mass (linear model, $P = 0.68$, Fig. 1B). For both autumn and winter capture intervals, all bears experienced less mass loss (or more mass gain) than expected based on FMR (Fig. 1), consistent with food consumption during the capture intervals.
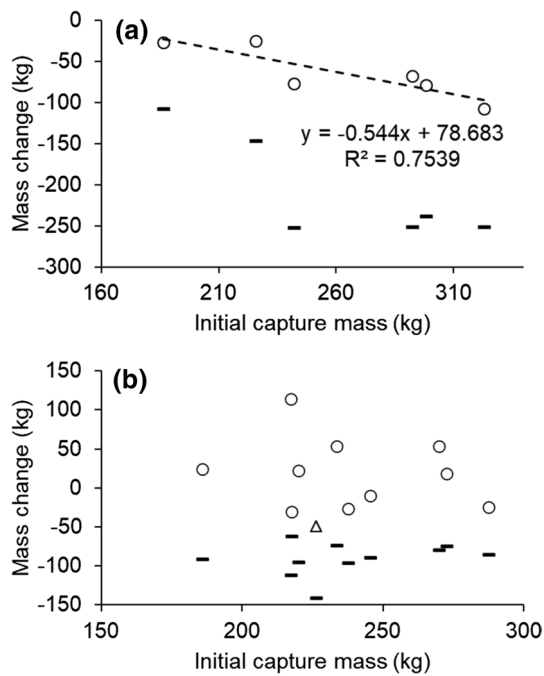
**Fig. 1** Mass changes by polar bears *Ursus maritimus* between captures. Mass changes by female adult polar bears between an initial autumn capture and a final spring capture (**a**), or between an initial early autumn and late autumn capture (**b**). Circles show observed mass change and dashes show calculated expected mass changes over the capture interval if no food consumption had occurred. The single triangle shows the observed mass change for the bear that engaged in a long-distance swim during the capture interval (see Methods). The dashed line, equation, and $R^2$ in part A show the significant relationship

## Seal equivalents needed to account for mass changes

Individual bears would have needed to consume from 1 to ~ 11 ringed seal equivalents to affect the mass changes that were observed across both autumn and winter, as opposed to expected mass loss based on *FMR* (Fig. 1). The range of seal equivalent consumption did not differ considerably during winter and autumn capture intervals, while the range of mass changes was very different (Fig. 1). This reflects the longer capture intervals associated with winter periods compared to autumn and therefore the greater potential for mass loss (Fig. 2).

## Seal equivalents of subsistence bowhead whale carcasses

Seal equivalents of bowhead whales captured via subsistence hunting increased allometrically with the length of the whale according to the following equation:
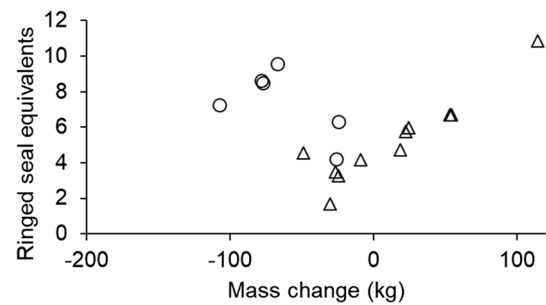


**Fig. 2** Ringed seal (*Pusa hispida*) equivalents consumed by polar bears *Ursus maritimus*. Estimated ring seal equivalents to have been consumed by female adult polar bears *Ursus maritimus* to account for observed mass changes between an initial autumn capture and a final spring capture (circles), or between an initial early autumn and late autumn capture (triangles). The single filled triangle shows the bear that engaged in a long-distance swim during the capture interval (see Methods)

$$\text{seal equivalents} = 0.6678\text{length}^{2.3434}. \tag{16}$$

Based on the lengths of the 29 whales captured in 2010 in the SBS region (Suydam et al. 2010), each whale provided ~ 50 to > 400 ringed seals. The total seal equivalents, representing food resources available to terrestrially scavenging polar bears during that single year, would have been ~ 4400 (upper threshold).

## Expected behavioral and fitness impacts of consumption during autumn and winter

Incorporating mass-dependent mass loss over the winter, and average mass loss or gain during the autumn, altered the optimal foraging and reproductive strategies originally reported by Reimer et al. (2019) (original model results reproduced in Fig. 3a). Specifically, these mass changes altered the optimal habitat selection by females with cubs. When bears gained mass through successful foraging over autumn, the use of safer, but less profitable fast ice during the spring foraging season was more common (Fig. 3b). In contrast, when bears lost mass through less successful foraging over autumn, the use of active ice that is more profitable but riskier for cubs was more common during the spring foraging season (Fig. 3c).

Similarly, adding autumn average mass gain or loss and winter mass loss altered the optimal reproductive strategies compared to the original model reported by Reimer et al. (2019) (original model results reproduced in Fig. 4a). Specifically, when bears gained mass over autumn and lost mass over winter, the state space where aborting a pregnancy is the optimal strategy for pregnant bears was extended (including more bears with smaller energy reserves; Fig. 4b), and the state space where keeping cubs is the optimal strategy for females with COY was extended

**Fig. 3** Model-predicted optimal foraging habitat selection for female polar bears *Ursus maritimus*. Predicted optimal habitat selection for foraging as a function of date during the spring foraging season (*x*-axis) and energetic condition (*y*-axis). **a** Original results from Reimer et al. (2019); note that the spacing of the *y*-axis between $x_{crit}$ and 2500 MJ has been corrected here to be consistent with the spacing on the remainder of the *y*-axis. **b** Model results when winter mass loss is included and when bears have average mass gains during autumn. **c** Model results when winter mass loss is included and when bears have average mass losses during autumn
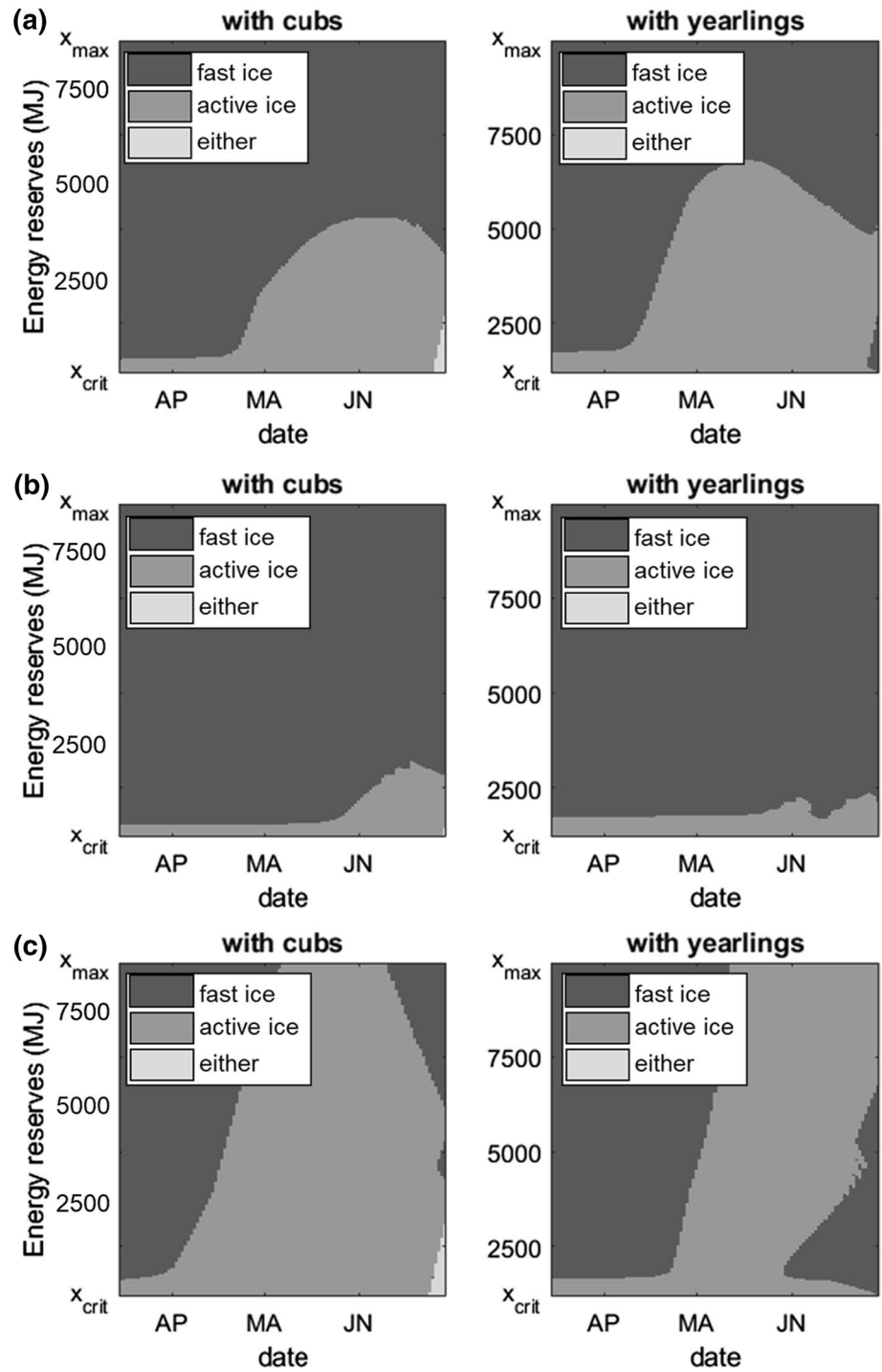


(again including more bears with smaller reserves; Fig. 4b). Conversely, adding autumn average mass loss and winter mass loss completely eliminated the state space where aborting a pregnancy is optimal, replacing it with the space where aborting or continuing a pregnancy are equivalent because the mother's energy reserves are low enough such that survival over the ice-free summer is not possible, so reproductive decisions do not matter (Fig. 4c). For females with COY, adding autumn and winter mass loss greatly increased the state space where cub abandonment is the optimal strategy, at the expense of reducing the space where keeping the cubs is optimal (Fig. 4c).

**Fig. 4** Model-predicted optimal reproductive strategy for female polar bears *Ursus maritimus*. Predicted optimal reproduction as a function of maternal age (*x*-axis) and energetic condition (*y*-axis). **a** Original results from Reimer et al. (2019); note that the spacing of the *y*-axis between $x_{crit}$ and 2500 MJ has been corrected here to be consistent with the spacing on the remainder of the *y*-axis. **b** Model results when winter mass loss is included and when bears have average mass gains during autumn. **c** Model results when winter mass loss is included and when bears have average mass losses during autumn
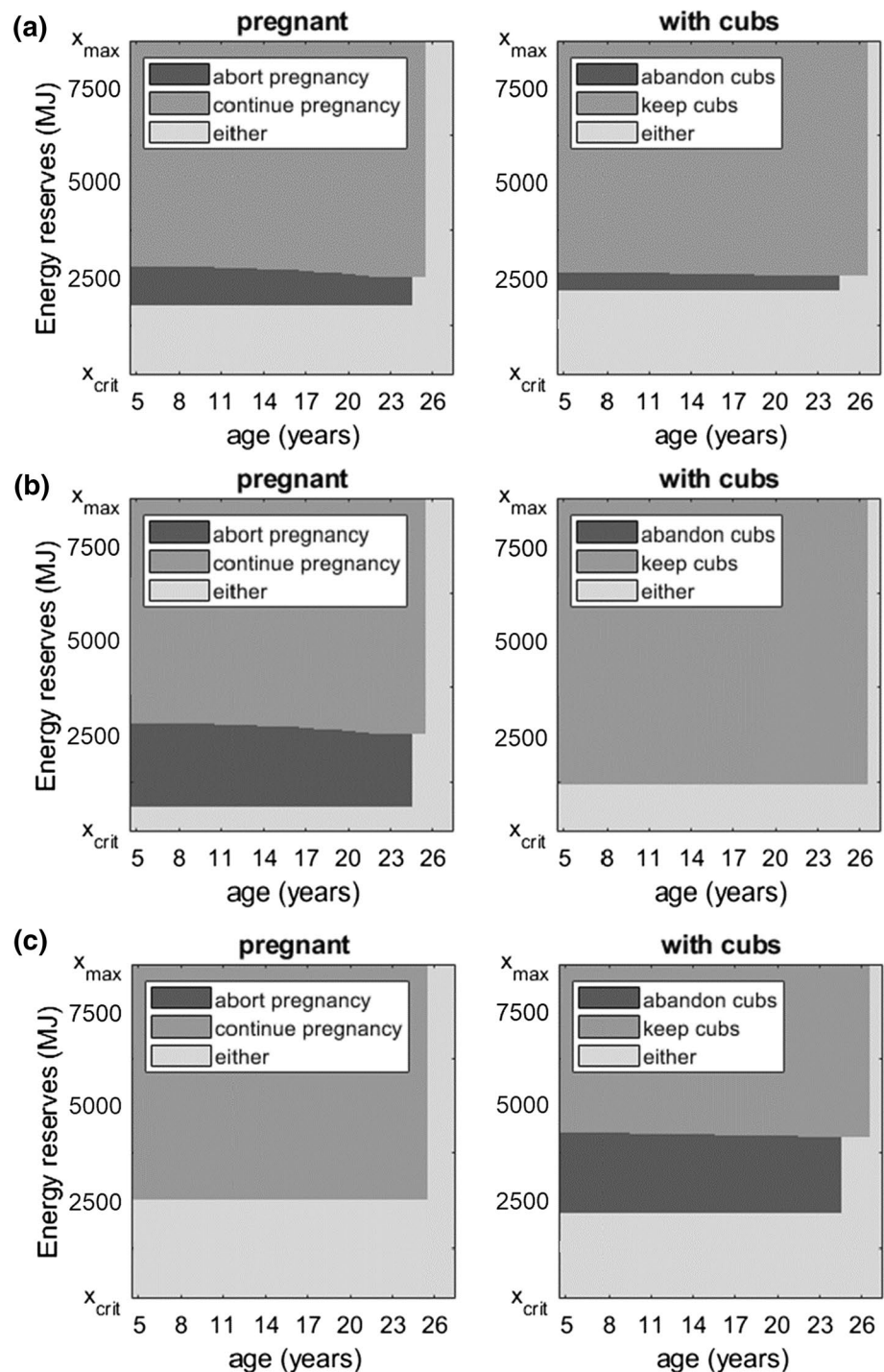


## Discussion

We found that mass loss in adult female polar bears over winter periods is considerable but is less than expected based on metabolism if no food consumption had occurred. Mass changes during autumn were more variable, with some bears losing mass and others gaining mass, but as with the winter period, all mass changes were consistent with food consumption occurring. We calculated that whale bone piles can provide thousands of ringed seal equivalents per year in the SBS region, emphasizing that this is a substantial food resource. Finally, when the observed mass changes in polar bears were incorporated into an existing model (Reimer et al. 2019), the optimal habitat selection and reproductive behavior became influenced by autumn and winter body mass. For example,

autumn mass gain made foraging on fast ice optimal for mothers with cubs for all but the most energy-stressed females and eliminated the optimality of ever abandoning cubs, whereas autumn mass loss made the use of active ice the optimal foraging strategy over a much broader range of maternal body condition and substantially increased the optimality of cub abandonment until the last three years before reproductive senescence.

## Seal equivalents of subsistence hunted bowhead whales

Based on our observed mass changes, polar bears consumed ~6 seal equivalents per bear during the autumn or winter periods. Using this average, and our calculation that individual whale carcasses in the SBS provided ~50 to >400 ringed seal equivalents, we estimate that bone piles could have supported the autumn and winter foraging of >700 bears, which represents ~80% of the current estimated size of the SBS subpopulation (Bromaghin et al. 2015). These calculations included many assumptions and there is variation across whales based on body composition, the effectiveness of butchering, and the amount that is taken post-butchering by harvest participants or returned unused.

During the 2010 bowhead whale hunt, 71 whales were struck by harpoon while only 45 were landed (Suydam et al. 2010). The fate and location of the 26 whales that were struck but not landed is uncertain. If these whales eventually died from the wounds incurred by this hunt, some of their carcasses could potentially have washed ashore and would therefore have been available to bears, providing tissue amounts (without butchering) as previously calculated (Laidre et al. 2018). Thus, because of the possibility of mortality following unsuccessful hunting attempts, some of the provisioning of food from beached whales previously reported (Laidre et al. 2018) may not be completely independent from subsistence hunting.

Our estimate of the number of polar bears that could be supported energetically by bowhead whale carcasses is a theoretical maximum. In reality, multiple factors can constrain this number, including changes in whale abundance and movement patterns, changes in subsistence hunting effort and success, environmental conditions, and conspecific and human-polar bear conflict at bone piles (Laidre et al. 2018). Importantly, polar bears are highly specialized toward a life on the sea ice (Harington 2008; Cahill 2021) and approximately 70–80% of the Southern Beaufort Sea subpopulation chooses ice habitat during summer and autumn, despite the potential benefits of using bone piles (Pongracz and Derocher 2017; Lillie et al. 2019; Pagano et al. 2020). It will be important for future studies to directly test for links between bone pile use and reproductive outcomes.

## Optimal strategy

Our resampling results demonstrate a range of possible energy outcomes for bears over the summer–autumn–winter period, with some bears losing considerable mass and other bears gaining considerable mass. The assumption used in the original model by Reimer et al. (2019)—that mass loss occurs during summer at a rate consistent with resting metabolic rate and that food consumption during autumn and winter is sufficient only to maintain body mass—falls within this range, but is only one possible outcome. Our results highlight that individual bears can have a range of possible optimal strategies based on their individual mass dynamics during parts of the year when foraging is less prominent. The winter mass losses we report are congruent with Galicia et al. (2020) reporting that lipid content of adipose tissue reaches a nadir in late winter and early spring in other subpopulations. Furthermore, our observed mass changes over winter should be viewed as conservative, given that recaptured bears in the spring may have replaced lost mass via foraging before their capture.

Prey capture on fast ice is lower than on active ice, and the model modified here assumes that daily mortality risk on active ice is 1.1× greater than on fast ice (Reimer et al. 2019). Thus, the model predicts that females in poor body condition should trade cub safety for improved foraging success. If this difference in mortality were to be removed, the model would no longer predict the use of fast ice because food acquisition would be the predominant factor determining habitat use. However, the 1.1× greater mortality risk is only an estimate, highlighting the need to empirically quantify relative cub mortality risk on active versus fast ice, as this assumption has substantial impacts on optimal habitat use by female bears with cubs. Greater use of fast ice could feasibly help explain why bears are staying on land more in the summer, as previously reported (Atwood et al. 2016). Bears remaining on fast ice close to shore in the spring ice-melt period eventually face the choice of either moving to shore for the summer or performing a long-distance swim to the retreating edge of the active ice. Given the heavy metabolic costs of long swims (Griffen 2018), this latter choice can impose significant risks. For example, 2012 was a year with rapid sea ice melting in the Beaufort Sea. This rapid rate of open water gain resulted in ~70% of adult female bears engaging in long-distance swims (Pilfold et al. 2017). Survival rates of COY and year-old cubs were anomalously low in the SBS during 2012 (Bromaghin et al. 2015), likely in part due to these long swims. Years such as 2012 cause elevated survival risks for bears that choose to stay on the sea ice rather than staying on shore and using bone piles and other coastal resources. This may provide a population-level mechanism for increasing the prevalence of the behavioral trait of staying near shore.

Results of our model modifications suggest that this mass-dependent pattern of winter mass loss is compensated for when bears gain considerable mass in autumn. However, when we modeled combined autumn and winter mass loss, the resulting predicted mortality for bears that enter the summer with < 2500 MJ of energy reserves eliminates any benefit from abortion because future reproductive output is curtailed. Simultaneously, abandonment of cubs is predicted to increase substantially, as females entering the summer with < ~4000 MJ of energy reserves can improve their own survival and maintain future reproductive opportunities. Similarly, variability in autumn mass changes, with some bears losing considerable mass and others gaining considerable mass, is consistent with previous data on autumn variation in body mass in this population (Durner and Amstrup 1996).

The data described above, combined with model predictions, suggest that winter and autumn nutritional stress is a critical influence on polar bear reproduction. Polar bear body condition is declining in association with sea ice loss in several regions of the Arctic (Rode et al. 2010, 2012; Obbard et al. 2016). In these regions, abortion may become more rare while cub abandonment, cub mortality from use of dangerous active ice habitat, and adult female mortality may all become more common. These changes could influence population vital rates and demographic structure. Such possibilities highlight the need for additional data on polar bear nutrition and physiology during autumn and winter to fully understand reproductive strategies and the impacts of climate change on those strategies.

It should be noted that this model assumed that mass dynamics were fixed throughout the life of a bear. One reality of climate change is increased variation from year to year in the environmental conditions that influence mass dynamics. As climate change enhances variation and reduces predictability, polar bears and other organisms are faced with a continually shifting baseline on which to base evolutionary responses (Reed et al. 2010). Evolving and predicting optimal strategies under such variable conditions may become increasingly difficult as climate change progresses, and we may expect to see reliance on behavioral and physiological strategies that have evolved to past conditions which increasingly differ considerably from the variable conditions animals now face.

**Data availability** The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Ethical approval** All methods for capturing and sampling bears were approved by IACUC at the University of Wyoming and USGS Alaska Science Center and permitted by US Fish and Wildlife Service (MA690038); see Whiteman et al. (2015) for details.

**Consent to participate** NA

**Consent for publication** NA

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