

# Modeling the metabolic costs of swimming in polar bears (*Ursus maritimus*)

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**Abstract** Climate change is expected to increase the frequency and duration of long-distance swims by polar bears (*Ursus maritimus*). The energetic costs of such swims are assumed to be large, however, no estimates of metabolic costs of swimming for polar bears are available. Here, I use data on internal body temperature and external ambient temperature for two swimming polar bears, combined with mathematical modeling of heat production and of heat conduction to the surrounding water, to estimate the metabolic rate of swimming. Using this metabolic rate, I then examine the relative heat production and heat loss for bears of a range of sizes and body conditions. I calculated overall mean metabolic rate for a swimming bear to be  $2.75 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ , which is generally higher than metabolic rates previously reported for walking polar bears. When compared at the same movement rate, the cost of transport for swimming was estimated to be approximately  $5\times$  that of walking. I further show that for small bears (less than approx. 145 cm body length or 90 kg) and bears in poor body condition, heat loss while swimming in cold Arctic waters should exceed heat production, and long swims should therefore not be thermodynamically sustainable. These results support previous claims that increasing frequency and duration of long-distance swims in polar bears is energetically stressful. Energetic and

thermodynamic costs of long swims may be further exacerbated by recent declines in body condition that have been documented due to climate warming.

**Keywords** Bioenergetics · Body heat · Energetics · Oxygen consumption · Thermal

## Introduction

The impacts of climate change are apparent in ecological systems globally, but these impacts are perhaps most apparent in polar regions (Turner et al. 2005; Post et al. 2009). The Arctic in particular has experienced rapid reductions in seasonal sea ice extent and thickness over the previous several decades (Stroeve et al. 2007, 2012; Frey et al. 2015). Many of the species that inhabit this region are ecologically tied to sea ice dynamics, and these changing dynamics have consequently altered their behavior (e.g., Hamilton et al. 2016), the timing of important life history events (e.g., Gaston et al. 2005), as well as their individual physiological condition (e.g., Crawford et al. 2015). Polar bears (*Ursus maritimus*) are one such species that has been heavily impacted with changes to sea ice dynamics. Recent studies implicate reductions in sea ice as the cause of shifting spatiotemporal habitat use by polar bears (Durner et al. 2008; Cherry et al. 2016), altered timing (Derocher et al. 2011) and location of denning (Olson et al. 2017), smaller litter sizes (Molnár et al. 2011), and decreased body condition (Obbard et al. 2006, 2016).

These negative impacts of reduced sea ice on polar bears stem largely from energetic constraints. Polar bears rely on the ice as their primary hunting platform, from which they capture seals that also use this platform for resting, molting, and seasonal reproduction (Stirling 1974). Reductions

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in sea ice therefore ultimately reduce food availability during periods of intense foraging, particularly in the spring months (Hamilton et al. 2016), and simultaneously lengthen the summer fasting period when ice is less available over productive waters of the continental shelf (Obbard et al. 2016; de la Guardia et al. 2017). Temporal patterns of feasting and fasting have shaped the evolution of polar bear behavior (Stirling and Derocher 1990) and physiology (Liu et al. 2014), and contemporary changes to these patterns associated with climate change, therefore, present energetic challenges to the polar bear that it appears to be ill-adapted to face (Derocher et al. 2004). Understanding the impacts of climate change on polar bears, therefore, depends on understanding the energetic implications of sea ice reductions.

One oft-cited implication of declining sea ice is an increase in the occurrence of long-distance swims by individual polar bears (Derocher et al. 2004; Monnett and Gleason 2006; Durner et al. 2011; Pagano et al. 2012; Stirling and Derocher 2012; Pilfold et al. 2017). Polar bears are accomplished swimmers capable of swimming very long distances. For instance, Pilfold et al. (2017) examined 135 bears in the Beaufort Sea and in the Hudson Bay and found that 45% of bears examined engaged in long-distance swims ranging from 1.3 to 9.3 days (median duration 3.4 days) and covering 71–566 km (median distance 125 km). While swimming in polar bears is common, Pilfold et al. (2017) also demonstrate that the length and frequency of swims appears to vary between populations as a result of spatial differences in seasonal sea ice dynamics and landscape morphology. Based on their findings, it appears that the Southern Beaufort Sea subpopulation has experienced considerable increases thus far in documented swims, and these swims are expected to continue to increase for this subpopulation in both frequency and length. Potential increases in long-distance swimming in most other subpopulations have not yet been examined. Previous studies define long-distance swims as those > 50 km (Pagano et al. 2012; Pilfold et al. 2017). Here I use this term to refer to extended swimming events without any specific definition or cutoff for duration or distance.

Long-distance swims present multiple problems for polar bears. First, longer swims may increase the potential for a swimming bear to encounter rough seas, which could lead to increased risk of drowning (Monnett and Gleason 2006). This risk is likely to increase with projected changes to weather patterns in the Arctic associated with climate change (Serreze et al. 2000; Serreze and Barry 2005; Simmonds et al. 2008). Secondly, increasing frequency and length of swims present an energetic stress for individual bears. Several authors have posited that polar bears are likely inefficient swimmers and that swimming is likely much less efficient than walking (Derocher et al. 2004;

Monnett and Gleason 2006; Durner et al. 2011; McCall et al. 2016). This stems from comparison of polar bear swimming mechanics with other paddle swimmers (e.g., mink, Videler and Nolet 1990) and the calculated inefficiency of this swimming mode for other species (Fish and Baudinette 1999). Third, swimming in cold Arctic waters present a thermodynamic challenge for bear cubs and puts them at risk of hypothermia (Scholander et al. 1950; Øritsland 1970; Blix and Lentfer 1979). Consequently, mothers with young cubs avoid open water areas (Stirling et al. 1993; Freitas et al. 2012; Pilfold et al. 2014) and are less prone to undertake long swims (Pilfold et al. 2017). Females may even carry cubs on their backs to reduce their immersion in cold water (Aars and Plumb 2010). Here I address the second and third of these issues.

If, as expected, long-distance swims continue to increase in frequency and distance for polar bears, then determining the metabolic costs of swimming is essential to fully understand the metabolic costs of climate change for this species. Ideally the metabolic rates of swimming bears could be directly measured and then compared with rates of walking and resting bears. Unfortunately, these data for swimming bears are not available and would likely be logistically challenging to collect. However, the metabolic rate may instead be estimated for swimming bears using a proxy. Previous studies have examined cardiac frequency, stride frequency, core body temperature, and respiratory frequency as metabolic rate proxies (Best et al. 1981). A subsequent study demonstrated the utility of body temperature and provides an empirically-derived relationship between heat production and metabolic rate for active polar bears (Hurst et al. 1982). I therefore use heat production to estimate the metabolic rate. I first use thermal data for two bears that engaged in swimming after having been fitted with thermal and GPS data loggers (previously reported in Durner et al. 2011 and Whiteman et al. 2015). I then use this estimated metabolic rate and calculated heat loss via conduction to explore the body size and fat storage levels where heat production would exceed heat loss while swimming in cold Arctic waters, allowing bears to successfully undertake long swims. In addition, I directly compare the metabolic cost of moving a set distance (cost of transport) for swimming and walking. Finally, I also use the calculated metabolic rate to determine the likely mass loss experienced by one of the two bears during its > 9-day swim.

## Methods

### Description of bears used in this study

Durner et al. (2011) document a single event in 2008 where an adult female polar bear (hereafter referred to as 20741, following Durner et al. 2011) that had been fitted with a collar undertook a 9-day, 687 km swim from the Alaskan coast to the offshore sea ice. Information collected during the bear's swim included its location, reported as hourly GPS coordinates, the ambient water temperature, reported from a sensor located on the collar, and the internal body temperature of the bear, measured using a sensor surgically implanted just below the subcutaneous fat layer on the rump. Durner et al. (2011) report that over the course of the 9-day swim, collar temperature (i.e., ambient temperature, assumed here to be water temperature) decreased, rump temperature decreased, and activity level increased, and that the decrease in collar and rump temperatures were correlated. In addition, at the time of initial capture, they measured the straight-line body length of the animal (185 cm, G.M. Durner pers. com.) and the initial body mass (226 kg, Durner et al. 2011).

Whiteman et al. (2015) document several bears that had temperature loggers implanted either in their abdomen or in their rump, as described for the bear above. A single bear (bear 20414, 211 cm straight-line body length, 220 kg body mass) with the logger inserted in its abdomen subsequently undertook four separate swims (see Whiteman et al. 2015, Fig. 3 for details on how swimming bouts were identified). The first lasted 1 h 40 min, taking the bear approximately 420 m from shore. The second lasted approximately 4 h 25 min, extending up to 280 m from shore. The third swim lasted 1 h 30 min and extended approximately 1 km from shore. And the final swim lasted just 40 min and covered a distance of up to 1 km (*pers. comm.* JP Whiteman). As with other marine vertebrates (Ponganis et al. 2003), polar bears may be capable of regional heterothermy that limits heat loss through the extremities via vasoconstriction (Durner et al. 2011; Whiteman et al. 2015). Consequently, estimated metabolic rates may differ when based on body heat measured at the core (bear 20414) and at the extremities (bear 20741). For this reason, I modeled the metabolic rates of both bears using the same methods described below to allow for direct comparison.

### Metabolic rate of a swimming polar bear

I calculated the metabolic rate of these swimming bears as follows. Ultimately, the metabolic rate of exercising polar bears can be deduced from the change in internal body

temperature during exercise (Hurst et al. 1982). However, for a swimming polar bear, changes in body temperature come not just from the buildup of metabolic heat energy, but also from the reduction in heat energy due to dissipation of heat to the surrounding water. Thus, the *effective* temperature change is a combination of the measured actual temperature change, combined with the additional temperature change that would have occurred had the bear not dissipated heat to the surrounding water. The first step was therefore to calculate the amount of heat energy lost to the surrounding water. To do this, several pieces of information were needed, including the storage and structural mass of the bear, its surface area, and the average thickness of its subcutaneous fat layer. I first determined the structural mass ( $M_{STR}$ ) of the bear, defined as all non-storage body components, using the following equation from Molnár et al. (2009):

$$M_{STR} = \rho_{STR} k L^3, \quad (1)$$

where  $\rho_{STR}$  is the structural density ( $\text{kg m}^{-3}$ ),  $k$  is a dimensionless parameter that accounts for the irregular shape of the animal, and  $L$  is straight-line body length (m). Molnár et al. (2009) estimated the product of  $\rho_{STR}$  and  $k$  for polar bears to be  $14.94 \text{ kg m}^{-3}$ . Next, again following Molnár et al. (2009), I determined the storage mass ( $M_{STO}$ ) as:

$$M_{STO} = M - M_{STR}, \quad (2)$$

where  $M$  is overall body mass (226 kg for bear 20741 and 220 kg for bear 20414). Storage mass is composed of fat and proteins that may be used as an energy source, plus body water, and ash associated with these materials (Molnár et al. 2009). However, the modeling approach here does not model storage for its ability to provide energy, but rather for its ability to retain heat and impede its dissipation from the bear to the surrounding sea water. Since each component of the storage mass can hold heat and impede its dissipation, I do not differentiate between the different components here and refer to them collectively as fat.

Best (1976) measured the surface area of 18 bears ranging from 11 to 275 kg and developed a predictive equation for skin surface area ( $R^2 = 0.99$ ) that I used to determine the surface area ( $A$ ) of the bears based on their overall body masses:

$$A = 0.09M^{0.67}. \quad (3)$$

I next calculated the average thickness of the subcutaneous fat layer of the bears. Fat storage in polar bears is not uniform, but varies in thickness across the body (Øritsland 1970). However, because heat loss used in calculating metabolic rate increases linearly with average thickness of the superficial fat layer (see below), heat loss that is greater in body regions with a thinner fat layer and lower in body

regions with a thicker fat layer (Best 1982) combines linearly and so can be averaged using the mean storage mass thickness across the whole body. I therefore calculated the total fat volume ( $V_F$ ) as:

$$V_F = \frac{M_{STO}}{\rho_{STO}}, \quad (4)$$

where  $\rho_{STO}$  is the approximate density of the stored fat. No estimates are available for polar bear fat density. However, previous work on polar bear fat tissue assumed a value of  $900 \text{ kg m}^{-3}$  (Pond et al. 1992), and I use this value here. I then used the fat volume given by Eq. (4), together with the surface area of the bear, to calculate the mean storage mass thickness ( $d$ , given in meters):

$$d = \frac{V_F}{A}. \quad (5)$$

This calculation assumes that  $M_{STO}$  is comprised entirely of subcutaneous mass stores that provide a barrier to heat loss.

I next calculated the amount of heat loss from the polar bear via dissipation to the surrounding water as it was swimming. Polar bear fur provides excellent insulation against heat loss on land or ice; however, heat loss through polar bear skin and fur increases by a factor of 20–25 when submerged in calm water, and by a factor of 45–50 in agitated water, as would occur during swimming (Scholander et al. 1950). I therefore assumed that the subcutaneous fat stores provided the only barrier to heat loss (see below for relaxation of this assumption). For each of the two bears, ambient (assumed water) temperature was recorded hourly over the course of their swims, and internal temperature was recorded every 10 min. For the analysis here, the internal temperature over the six adjacent 10-min intervals was averaged, yielding a single mean internal temperature during each hour of the swim. For each of the hourly intervals ( $x$ ) during each of the swims, I calculated the heat loss ( $Q_x$ , given in watts) using Fourier's Law for heat conduction in one dimension across a barrier (Lienhard and Lienhard 2017):

$$Q_x = \frac{AC(T_{Ix} - T_{Ax})}{d}, \quad (6)$$

where  $A$  is body surface area from Eq. (3) above,  $C$  is thermal conductivity,  $T_{Ix}$  and  $T_{Ax}$  are, respectively, the internal and ambient temperatures (Kelvin) during time interval  $x$ , and  $d$  is mean mass storage thickness from Eq. (5) above. In using this equation, I assume that heat transferred through the fat layer by conduction is in equilibrium with convective heat loss (Ryg et al. 1993), so that as the swimming bear moves through the cold Arctic water, convective heat loss maintains the exterior of the bear's skin approximately at ambient temperature, thus

maintaining the temperature gradient across the fat layer. The uniformity in the composition of adipose tissue between the inner and outer sides of superficial fat stores in polar bears suggests that the primary role of these stores is as an energy reserve rather than as a thermal barrier (Pond et al. 1992; Thiemann et al. 2006). Nevertheless, heat exiting the polar bear body must first traverse the fat deposits, and the efficiency of this process will be determined by the thermal conductivity of this adipose tissue. Thermal conductivity for polar bear fat is not known, I therefore used the value of  $0.28 \text{ (W m}^{-1} \text{ K}^{-1}\text{)}$  measured across four fur seal (*Arctocephalus*) species, a group of species that, similar to polar bears, relies on fur for thermal insulation and uses fat deposits primarily as an energy reserve (Liwanag et al. 2012).

Heat loss via conduction to the surrounding water ultimately would influence the core body temperature, though the extent that this occurs should depend on the resistance of body tissues to temperature change. This in turn depends on the specific heat of the different body tissues. The specific heat for different polar bear tissues is not known. I therefore used an available database from the Foundation for Research on Information Technologies in Society (IT'IS) for the thermal, physical, and dielectric properties of various body tissues in humans (*Homo sapiens*) (Database V3.1, IT'IS 2016), making the assumption that the specific heat of various tissues is similar across mammal species. Based on this database, the specific heats of various tissues that comprise the structural mass (blood, brain, cartilage, muscle, small and large intestines, stomach) are very similar (range  $3421\text{--}3690 \text{ J kg}^{-1} \text{ }^\circ\text{C}^{-1}$ , mean  $3596.6$ ), while the specific heat of bone is much lower ( $2274 \text{ J kg}^{-1} \text{ }^\circ\text{C}^{-1}$ ). Consequently, I dealt with bone separately and with all other tissues as an aggregate. To do this, I first determined bone mass for each bear. Cattet et al. (2002) provide the relationship between straight-line body length ( $L$  in cm) and skeletal mass ( $M_{Bone}$ ) for polar bears (their Fig. 2). I digitized the data in their Fig. 2 using WebPlotDigitizer and used the digitized data to determine the following relationship ( $R^2 = 0.89$ ), which I used to calculate skeletal mass (kg):

$$\ln(M_{Bone}) = 2.548 \times \ln(L) - 9.9311. \quad (7)$$

I then combined the specific heat of the bone ( $H_{Bone}$ ) with the specific heat of the rest of the internal structural mass ( $H_{Tissue}$ ) to determine the total internal specific heat ( $H_{Total}$ ) as:

$$H_{Total} = \frac{M_{Bone}}{M_{STR}} \times H_{Bone} + \frac{M_{STR} - M_{Bone}}{M_{STR}} \times H_{Tissue}. \quad (8)$$

Next, I determined the total amount of heat generated during each time interval ( $x$ ) by each bear ( $T_{Gen_x}$  in  $^\circ\text{C}$ ) by combining the heat loss during each time interval ( $Q_x$  from

Eq. 6), the time interval of interest expressed as seconds ( $t = 1800$  s, or the equivalent of 30 min), the total specific heat of the internal tissues ( $H_{\text{Total}}$ ) and the structural body mass ( $M_{\text{STR}}$ ) as:

$$T_{\text{Gen}_x} = \frac{Q_x \times t}{H_{\text{Total}} \times M_{\text{STR}}}. \quad (9)$$

This total amount of heat generated during each time interval  $x$  was then combined with half of the actual change in internal temperature of the bear during that time interval, as measured by the surgically implanted internal temperature logger, to give the net *effective* internal temperature change ( $T_{\text{Change}_x}$ ):

$$T_{\text{Change}_x} = T_{\text{Gen}_x} + \left( \frac{T_{I_{x+1}} - T_{I_x}}{2} \right). \quad (10)$$

Only half of the actual temperature change was used (i.e., the second term in Eq. 10 includes division by 2) because the temperature change was measured at hourly intervals, while the metabolic rate, to be consistent with Hurst et al. (1982), was calculated for 30 min intervals. This assumes that changes in body temperature during each 1-h interval progressed at a constant rate.

The final step in calculating the metabolic rate was to convert this *effective* change in temperature during each time interval into a metabolic rate. Several factors have been investigated as proxies for metabolic rate in polar bears (Best et al. 1981), with core body temperature providing an accurate proxy (Hurst et al. 1982). Hurst et al. (1982) measured changes in core body temperature in walking bears and provide an equation linking changes in body temperature over 30 min of treadmill exercise to metabolic rate (their Eq. 3,  $R^2 = 0.88$ ). Here I assume that this relationship derived from walking bears is applicable to swimming bears as well and use it to convert the net *effective* internal temperature change to metabolic rate ( $R$  in  $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ):

$$R = 0.516T_{\text{Change}_x} + 0.987. \quad (11)$$

I determined the mean metabolic rate over the course of each swim ( $R^*$ ) as the mean of the metabolic rates calculated for each of the  $x$  time intervals.

Two other factors that could influence the estimate of metabolic rate should be noted. First, respiration is also used by polar bears to remove metabolic heat (Best et al. 1981). However, this was not included in the above calculations because it would already have been accounted for in the conversion of temperature change to metabolic rate given by Eq. (11), since polar bears walking on treadmills that were used to derive this relationship also would have been ventilating to remove body heat. Second, heat loss may further be impeded by the insulative capabilities of the hide, though these are minor (Scholander et al. 1950). I

repeated the above calculations by including the hide as an additional layer of thermal protection and by modifying Eq. (6) above to include multiple insulative layers in series by including  $R = R_1 + R_2$  (Lienhard and Lienhard 2017), where  $R_1$  and  $R_2$  are the fat and the hide:

$$R_n = \frac{d}{C_n A_n}, \quad (12)$$

where  $d$ ,  $C$ , and  $A$  are as defined above for Eq. (6), and assuming total hide thickness (skin + fur) of 60 mm (Scholander et al. 1950), and calculating  $C$  for the hide from the conductance of polar bear hides in water, measured to be  $0.0015 \text{ cal m}^{-2} \text{ s}^{-1} \text{ }^\circ\text{C}^{-1}$  as measured by Frisch et al. (1974). However, including this additional layer of insulation only altered the calculated mean metabolic rate by 0.025%. For simplicity, I therefore focus on results that include only fat insulation here.

### Heat loss as a function of body size and fat storage

I generalized these results so that they could be applied to bears across a broad range of sizes and body conditions. To do this, I used the equations above to calculate the influence of body size and fat storage on heat loss and heat production in order to determine the body size and condition where it is thermodynamically feasible for bears to engage in long-distance swims. In terms of heat loss, I made the following calculations for a range of bear sizes (25–250 cm straight-line body length). For each body size, I first used Eq. (1) above to calculate the structural body mass ( $M_{\text{STR}}$ ). For bears of body lengths throughout this range, I then determined the storage body mass ( $M_{\text{STO}}$ ) and total body mass ( $M$ ) needed to produce bears where 5, 20, 35, or 50% of their body mass was fat storage (i.e.,  $M_{\text{STO}}/M = 0.05, 0.2, 0.35, \text{ or } 0.5$ ). For each of these body masses, I then calculated the body surface area using Eq. (3), the total volume of fat using Eq. (4), and then combined these to determine the thickness of the fat layer using Eq. (5). For each level of fat storage and for the range of bear sizes given above, I then used Eq. (6) to calculate the heat loss for swimming bears, in watts, assuming that their internal body temperature is  $37^\circ\text{C}$  and the water temperature is  $2^\circ\text{C}$ .

In terms of heat production, I made the following calculations. I used the mean metabolic rate calculated above (the average of  $R^*$  for bear 20741 and of  $R^*$  from all 4 swims for bear 20414) and then made a series of unit conversions from  $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$  to  $\text{mg O}_2 \text{ g}^{-1} \text{ h}^{-1}$  (based on  $1 \text{ mg O}_2 = 0.7 \text{ ml O}_2$ ), then to  $\text{cal g}^{-1} \text{ h}^{-1}$  (based on the energetic equivalents of  $3.28 \text{ cal mg}^{-1} \text{ O}_2$  for fat metabolism, Elliott and Davison 1975), then to  $\text{joules kg}^{-1} \text{ s}^{-1}$ . I then multiplied this value by the structural mass ( $M_{\text{STR}}$ ) for the range of body sizes examined above to yield

the energy production in watts. I then used graphical analysis to compare the heat loss by diffusion and heat production for the range of sizes of bear examined and for each of the four levels of fat storage indicated above. Bears that produce more heat energy than they lose should be capable of long-distance swims, while those that lose heat more rapidly than they produce it would be susceptible to hypothermia. Two measurements commonly made on captured bears are body length and body mass. I therefore express results of these analyses in terms of both of these two metrics.

The calculation of relative heat production and heat loss described in the preceding paragraphs predicted the lower size limit below which bears would be susceptible to hypothermia because heat loss in cold Arctic waters exceeds heat production. I next determined the ages at which these lower size limits are likely to be reached. Derocher and Wiig (2002) parameterized the von Bertalanffy growth curves for both straight-line length and weight in polar bears from Svalbard. I rearranged the von Bertalanffy equations to solve for the age ( $a$  in years) at which a bear should achieve a given length ( $l_a$  in cm) or mass ( $w_a$  in kg), yielding:

$$a = \frac{\ln(1 - \frac{l_a}{L})}{-k} + A, \quad (13)$$

or

$$a = \frac{\ln(1 - \sqrt[3]{\frac{w_a}{W}})}{-k} + A, \quad (14)$$

where  $L$  and  $W$  are respectively the asymptotic body length (cm) and weight (kg),  $k$  is a growth rate constant ( $\text{year}^{-1}$ ), and  $A$  is the theoretical age (years) at which the bear would have 0 length or mass. I then set  $l_a = 145$  or  $w_a = 90$  (based on results presented below) and used the mean parameter values provided by Derocher and Wiig (2002) for the other parameters. I then used these equations to determine the age at which swimming should be feasible based on the need to thermoregulate.

### Comparing the metabolic costs of swimming and walking

Next, I directly compared the cost of transport via swimming and walking by comparing the mass-specific metabolic cost of moving a given distance at the same rate. To do this, I calculated the mean distance traveled during each of the 232 1-h intervals that bear 20741 swam using the latitude and longitude GPS collar data. I made this calculation using the `distm` function of the `geosphere` package in R. This provided the speed of travel ( $D$ ) in each interval ( $\text{m h}^{-1}$ ). There were 5 location data points that were missing over the course of this swim. For simplicity, I

estimated these locations by interpolating from the locations at the time points before and after the missing data point and assuming a constant movement speed during that time. I then combined the speed traveled with the mean metabolic rate,  $R^*$ , during these same time intervals to determine the cost of transport by swimming ( $\text{COT}_s$ ):

$$\text{COT}_s = R^* \div D. \quad (15)$$

Gormenzano et al. (2016) combined all the data available in the published literature for the metabolic cost of walking in polar bears to demonstrate that metabolic rate is influenced by bear size and by walking speed. I used their equation to calculate the metabolic rate ( $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) of bear 20741 based on its mass (226 kg) and walking speed ( $S$ , assumed to be the same as the average swimming speed of bear 20741, or  $3 \text{ km h}^{-1}$ , to facilitate direct comparison with swimming):

$$\text{Metabolic rate} = (1.056 \times \text{mass}^{-0.25}) \times e^{0.2626 \times S}. \quad (16)$$

Finally, I divided this by the distance traveled per hour of walking (same as  $D$  above) to yield the metabolic cost of transport by walking ( $\text{COT}_w$ ). For ease of comparison with other species, I represent these costs for swimming and walking as a ratio ( $\text{COT}_s:\text{COT}_w$ ).

### Weight loss by bear 20741

The body mass of bear 20741 was measured upon initial capture (23 August 2008) and was found to be 226 kg. Its mass was then measured again two months later (26 October 2008) upon recapture, revealing that in the interval the bear had lost 22% of its body weight, with a recapture weight of 177 kg. Durner et al. (2011) hypothesized that this weight loss may have resulted primarily from a high energetic cost of swimming, with subsequent replenishment of depleted energy stores via feeding while on the pack ice at the end of the swim, but before recapture. Alternatively, they hypothesize that the weight loss could have resulted from the swim, combined with reduced feeding during the subsequent 6-week walk across the pack ice. Here I use the metabolic rate calculated above to estimate the loss of body mass that would have resulted from the recorded swim. I started with the mean metabolic rate over the course of the swim ( $R^*$ ) and then converted this to  $\text{cal kg}^{-1} \text{ h}^{-1}$  using the same conversion described above. I then multiplied this value by the structural mass of bear 20741 ( $M_{\text{STR}}$ ) and by the number of hours of the swim (232 h) to yield the total number of calories burned during the swim. These calories are thermodynamic calories (i.e., the amount of energy needed to raise a gram of water by  $1^\circ\text{C}$ ). I therefore converted these to “food” calories, or kilocalories, by dividing by 1000. I then converted this into mass loss in lbs, using the conversion that

3500 kcal  $\approx$  1 lb of body fat (Finkelstein et al. 2010; Smith et al. 2010), which I then converted to kg mass loss.

## Results

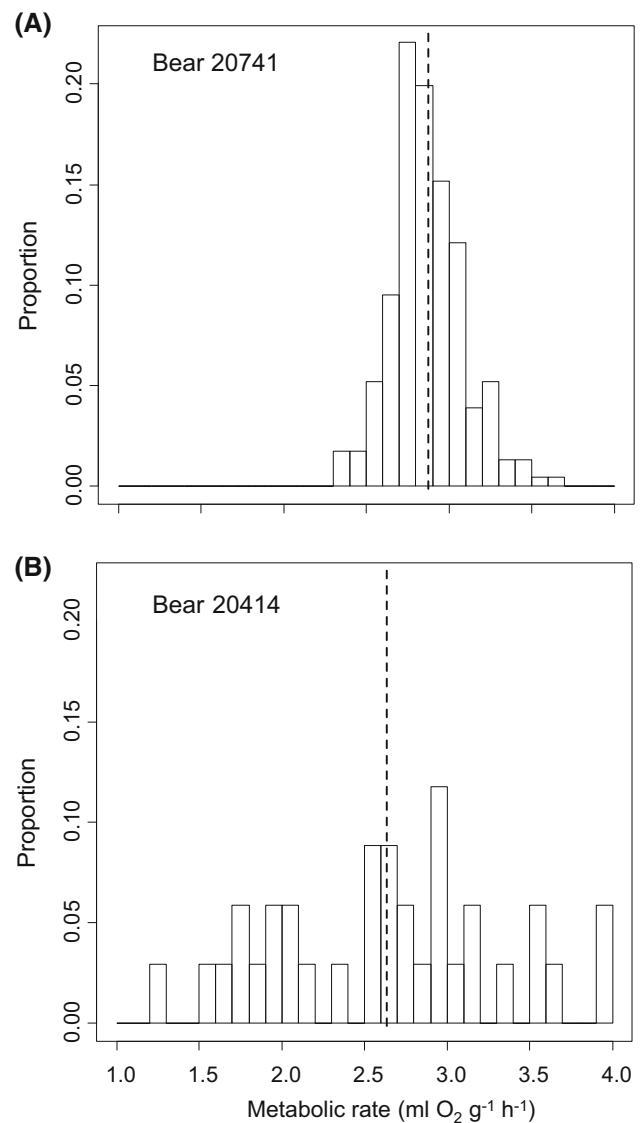
Using the relationships given above in Eqs. (1)–(5), and based on the initial body mass and length, I calculated that bear 20741 had a structural mass of approximately 94.6 kg, a storage mass of 131.4 kg, a surface area of 3.4 m<sup>2</sup>, and a layer of storage mass that was on average 0.043 m thick. Further, its internal temperature as given by data from the logger implanted in its rump was  $33.0 \pm 0.7$  °C (mean  $\pm$  SD), while the external temperature based on the collar data was  $5.4 \pm 1.1$  °C. Similarly, I calculated that bear 20414 had a structural mass of 140.3 kg, a storage mass of 79.7 kg, a surface area of 3.3 m<sup>2</sup> and a layer of storage mass that was on average 0.027 m thick. Based on the data logger implanted in its abdomen, its internal temperature was  $36.4 \pm 0.5$  °C, while the external temperature based on collar data was  $13.6 \pm 6.9$  °C.

### Metabolic rate of a swimming polar bear

I calculated that during the course of its 9-day swim, bear 20741 had metabolic rates that ranged from 2.32 to 3.61 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>, with a mean of 2.87 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> (Fig. 1a). For bear 20414, calculated metabolic rates were more variable over the course of all 4 swims, ranging from 1.20 to 3.92 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>, with a mean that was 8.2% lower than the mean for bear 20741, at 2.63 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> (Fig. 1b). The overall average estimated metabolic rate obtained by averaging these separate estimates from these two bears is therefore 2.75 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>.

### Heat loss as a function of body size and fat storage

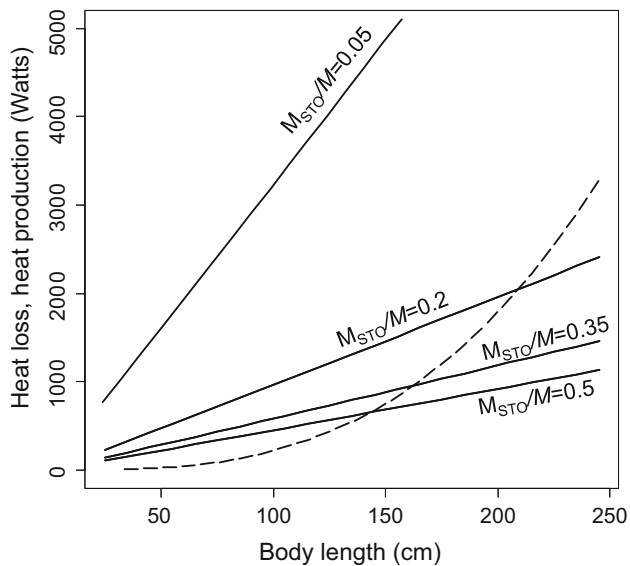
Based on metabolic relationships calculated here, polar bear heat loss increases linearly with straight-line body length, with the rate of that heat loss being inversely proportional to the thickness of the fat layer, which itself increases with storage mass ( $M_{STO}$ ) (Figs. 2, 3). The heat retention benefit of fat storage shows a diminishing returns, as the incremental rate of additional heat retention declines with increasing fat storage (Figs. 2, 3), while heat production increases steadily with structural body mass ( $M_{STR}$ ), and is a constant value regardless of fat storage (Fig. 2). As a result, small bears (less than ca. 145 cm length, or less than ca. 90 kg for bears where half of their body weight is storage mass) should not be expected to undertake long-distance swims because heat loss exceeds heat production, while large bears (greater than 200 cm length) should be able to engage in long-distance swims



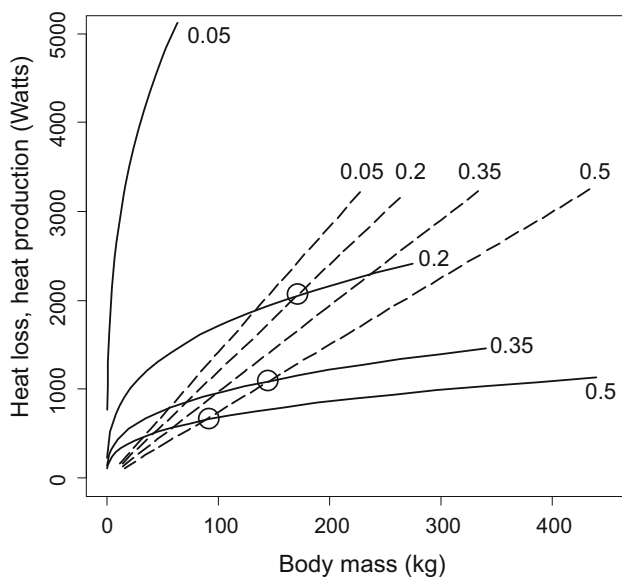
**Fig. 1** Frequency histogram of calculated metabolic rates by polar bear (*Ursus maritimus*) 20741 during its 9-day swim and by bear 20414 during four separate shorter swims. The dashed vertical line indicates the overall mean metabolic rate for each bear

without losing body heat even at fairly modest levels of fat storage.

Results here predict that, based on length (Eq. 13), cubs less than approximately 1.5 years old should not be able to swim without losing more heat than they generate and therefore should not engage in long-distance swims, while the same calculations based on mass (Eq. 14) predict that cubs should not be able to swim long distances when less than approximately 2 years of age.



**Fig. 2** Calculated heat production (dashed line) and heat loss (solid lines) as a function of body length (x-axis) and body condition (separate lines showing proportion of body weight made up of stored fat,  $M_{STO} M^{-1}$ ) for polar bears (*Ursus maritimus*)



**Fig. 3** Calculated heat production (dashed lines) and heat loss (solid lines) as a function of body mass (x-axis) and body condition for polar bears (*Ursus maritimus*). Body condition shows four different levels of proportion of body weight made up of fat storage ( $M_{STO} M^{-1}$ ): 0.05, 0.2, 0.35, and 0.5

### Comparing the metabolic costs of swimming and walking

The ratio of the metabolic cost of transport at  $3 \text{ km h}^{-1}$  via swimming ( $COT_s$ ) and via walking ( $COT_w$ ) was 4.8, indicating that the cost of swimming a given distance is

nearly  $5\times$  greater for polar bears than walking the same distance.

### Weight loss by bear 20741

I calculated that bear 20741 may have lost approximately 37 kg of body fat during the course of its 9-day swim, or more than 16% of its overall body mass. This suggests that the remaining 6% of initial body mass lost prior to recapture, as reported by Durner et al. (2011), was estimated to have been lost as a result of a food shortage while walking on the pack ice.

### Discussion

I have used relative changes in ambient water and internal body temperatures, as measured for two bears during swims, to estimate the metabolic rate for swimming polar bears. The overall average value estimated here,  $2.75 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ , is near the upper range of metabolic rates measured for bears engaged in relatively fast walking. For instance, Hurst et al. (1982) measured rates ranging from approx.  $1.3$  to  $2.3 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$  for bears walking on a treadmill at  $5.4 \text{ km h}^{-1}$ , and Watts et al. (1991) measured rates ranging from approx.  $2.1$  to  $3.1 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$  in two subadult bears walking at  $7.9 \text{ km h}^{-1}$  following a disturbance. Thus, the cost of swimming is similar to metabolic rates for walking at the fastest rates ever observed. Whiteman et al. (2015) also suggested that the metabolic cost of swimming may be similar to that of walking for polar bears. However, when converted to metabolic cost of traveling at the same rate of  $3 \text{ km h}^{-1}$ , the cost of transport was nearly  $5\times$  higher for swimming than for walking, supporting previous suggestions that swimming is an inefficient mode of travel energetically (Derocher et al. 2004; Monnett and Gleason 2006; Durner et al. 2011; McCall et al. 2016). Because the metabolic cost of walking decreases with bear size (Gormenzano et al. 2016), this ratio should correspondingly increase with bear size. However, this relationship may be complicated as the cost of swimming may also decrease with bear size because of improved buoyancy of bears in good body condition (see below). It should also be noted that the cost of transport via walking was examined during treadmill walking where the precise distance traveled was known, while the cost of transport for swimming is based on hourly snapshots of the swimming bear's location. As a result, the linear distance traveled during a time interval is a minimum estimate of the actual distance traveled, as travel paths between two locations are not necessarily straight. In addition, energetic costs of travel while swimming may also reflect movement



that is impeded or assisted, depending on the direction of prevailing currents.

Previous work has suggested that polar bears are capable of regional heterothermy (Durner et al. 2011; Whiteman et al. 2015). The mean metabolic rate of bear 20741 (logger implanted in the rump) was 8.2% higher than the mean metabolic rate of bear 20414 (logger implanted in the abdomen). It is unclear what proportion of this higher mean metabolic rate was due to regional heterothermy, or was due to individual variation in metabolic rate (Speakman et al. 2004). Other unknown factors may also have contributed to the difference in metabolic rates between these two bears. For instance, bear 20741 was initially captured with a cub and was lactating. This cub was lost at some point between the initial and subsequent capture, and the time of its loss is unknown. But given that the bear began its long swim only 3 days after its initial capture (Durner et al. 2011), it is likely that the bear was still lactating during the swim, and this would have contributed to higher metabolic costs.

Some of the calculations used here included parameters (fat density, fat thermal conductivity, specific heat of body tissues) that are unknown for polar bears. As described above, for fat density and thermal conductivity I used values from other marine mammals. Specifically, I used a fat density of  $900 \text{ kg m}^{-3}$  that comes from harp seals and that has previously been assumed for polar bears (Pond et al. 1992). Fat density and thermal conductivity vary across species (e.g., Parry 1949; Kvasdheim et al. 1994). Specific heat also varies across tissues and species and here I used values measured for humans. Best (1982) assumed similar (but somewhat different for adipose tissue) values in calculating thermoregulation for polar bears; however, it is unclear where the values used by Best (1982) came from. Sensitivity analysis indicated that a change in any of these metrics by 5% altered the estimated metabolic rate by < 2.9%. The model predicted metabolic rates calculated here are, therefore, fairly robust to changes in these unknown parameters. Still, precise measurements for these metrics in polar bear tissues would increase the accuracy of model estimated metabolic rates given here.

For simplicity, I also assumed that the mass of fat storage remained constant throughout the swim (Eqs. 4 and 5). For bear 20741, Durner et al. (2011) hypothesized that declining rump temperatures throughout the course of the swim may have reflected declining fat stores. This change in fat thickness would cause the estimates of metabolic rate here to be progressively more conservative as the swim progressed. I estimated above that bear 20741 may have lost as much as 37 kg of body mass during the course of its 9-day swim. This estimated potential amount of mass loss during the swim is equivalent to  $4.1 \text{ kg d}^{-1}$ , which is more than  $3\times$  higher than the median rate of mass loss of

$1.3 \text{ kg d}^{-1}$  for inactive, fasting female bears with cubs of the year (Pilfold et al. 2016). Repeating the calculations above (Eqs. 1–11), but allowing body mass, and thus fat thickness, to decline steadily from 226 to 189 kg over the course of the swim, produces a mean estimated metabolic rate of  $2.96 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ , an increase of approximately 3% compared to the rate calculated assuming constant body mass. This high cost of transportation via swimming that is nearly  $5\times$  higher than the cost of walking indicates that the energetic cost of swimming for 9 days by bear 20741 would have been equivalent to the energetic cost of walking for as much as 6 weeks. This agrees reasonably well with the estimate given here that bear 20741 lost ca. 37 kg during its swim and the other 13 kg over the next 7 weeks on the sea ice.

I have determined the approximate size cutoff ( $\sim 145 \text{ cm}$ ,  $\sim 90 \text{ kg}$ ) below which bear cubs should not be expected to endure long-distance swims (in waters around  $2 \text{ }^\circ\text{C}$ ) because of excessive heat loss. Due to the many factors that can influence body condition, considerably more variation exists in the parameter estimates as given by Derocher and Wiig (2002) for the growth-age relationship for mass (Eq. 14) than for length (Eq. 13). But using either metric, based on thermoregulation, cubs should not be expected to endure long-distance swims in cold Arctic waters until 1.5–2 years of age. The only published data available on a swimming cub is for a single 80 kg cub swimming in 0 and  $2 \text{ }^\circ\text{C}$  water. At both water temperatures, the core body temperature, as measured by a swallowed data logger, equalized at  $38.5 \text{ }^\circ\text{C}$  during the 20 and 80 min swims, respectively, whereas the core temperature of the same bear was  $37.4 \text{ }^\circ\text{C}$  when asleep (Øritland 1969). The mass of this bear is close to the minimum size cutoff predicted here. However, the predicted minimum ages for maintaining body heat during a swim seem high. One reason for these relatively high predictions may be that the calculations here to produce Figs. 2 and 3 used a single metabolic rate for swimming bears, regardless of bear size. For walking, heat accumulation declines linearly with body size, since walking is more efficient for larger bears (Hurst et al. 1982). A similar relationship between efficiency and body size may occur for swimming. If so, increased heat production during swimming for small bears would further compensate for the increased heat loss because of their larger surface area to volume ratio. In this case, this may alter the estimate of body size at which long-distance swimming becomes thermodynamically feasible. More data on heat loss by cubs of different size while swimming in cold waters would be useful for further refining this model.

Lastly, results presented here suggest that, even for adults, long-distance swims may result in the loss of more heat than can be generated if body condition is poor.

Additional data are needed to understand the influence of body condition on swimming.

### Factors that influence swimming efficiency in polar bears

Previous studies have posited that polar bears are inefficient swimmers based on their paddle swimming style and making comparisons to efficiency measurements in Australian water rats (Fish and Baudinette 1999). And indeed, when compared to efficiency of swimming methods used by fully aquatic animals, like fish or dolphins, paddle swimming is an inefficient swimming mode (Videler and Nolet 1990). However, polar bears have multiple adaptations that increase their swimming efficiency relative to that of other paddle swimmers. I discuss two of these here.

First, polar bears have large paws relative to their body size, reaching up to 30 cm in diameter, that are partially webbed (Lister 2014). These large paws spread the bear's weight while walking on snow and ice, but also increase the efficiency of the paddle swimming method used by this species. For paddle swimmers, the propulsive force is determined by the size of the paddle, and the size of the paddle determines the energy costs of paddling. Giving a small amount of water a large velocity change requires more kinetic energy than giving a large amount of water a small velocity change (Toussaint and Beek 1992). Thus the same propulsive force can be generated at very different costs using either a large, slow paddle (relatively low costs) or a small, fast paddle (relatively large costs). For example, studies with competitive swimmers using only their arms (with the feet buoyed by floatation, i.e., directly analogous to a swimming polar bear) demonstrate that attaching paddles to the swimmer's hands increases the swimming distance per stroke by an amount proportional to the difference in size between the paddle and the hand alone (Toussaint et al. 1991). Further, increased paddle size not only increases swimming speed, but also increases swimming efficiency, resulting in reduced metabolic energy expenditure to swim a given distance (Ogita and Tabata 1993).

Second, polar bears store large amount of fat on their rump (Øritsland 1970), thus increasing the buoyancy of their back end during swimming. Resistance to swimming organisms comes from drag, which at high Reynolds numbers (i.e., for large animals like polar bears) is dominated by pressure drag, or the resistance to pushing a large body through the water (Toussaint et al. 1988). The magnitude of this pressure drag increases proportionally with the projected frontal area of the swimming body, which is determined by the combination of the size of the organism and its angle relative to the direction of movement (Zamparo et al. 2008). Thus, the buoyant nature of the polar

bear's rear end keeps its body horizontal with the surface of the water (i.e., in line with its direction of movement), thereby minimizing the projected frontal area and resulting pressure drag. The buoyancy of polar bears likely increases with fat storage, and, therefore, the benefits of this buoyancy for swimming efficiency may increase with body condition.

While their large paws and horizontal orientation in the water may increase swimming efficiency in polar bears, swimming at the water surface greatly decreases their efficiency due to surface drag. Total drag can be 4–5 times higher for organisms moving across the water surface compared to those moving under the water (Hertel 1966), leading to relatively high costs of transport for semiaquatic marine mammals, such as polar bears, compared to fully aquatic marine mammals (Williams 1999). Overall, polar bears appear to be somewhat less efficient than other paddle swimmers. The cost of swimming for polar bears given here was nearly 5× the cost of walking. This is high compared to other surface paddle swimmers, such as the pelvic-paddling Australian water rat (*Hydromys chryso-gaster*) (Fish and Baudinette 1999) and the quadrupedal-paddling North American mink (*Mustela vison*) (Williams 1983a, b), both of which have swimming to walking cost ratios of 1.3. Therefore, despite the adaptations described above to facilitate swimming, this appears to be a relatively inefficient mode of transportation for polar bears.

### Conclusions

Previous studies posit that polar bears are inefficient swimmers and that the increased length and frequency of long-distance swims caused by climate warming will therefore have negative impacts on polar bear energetics and survival (Derocher et al. 2004; Monnett and Gleason 2006; Durner et al. 2011; Pagano et al. 2012; Stirling and Derocher 2012; Pilfold et al. 2017). I have used heat flux modeling to demonstrate that the metabolic costs of swimming in polar bears is high compared to the cost of walking. These results suggest that the depletion of energy stores and decreased survival during long-distance swims could come from a combination of inefficient swimming and the long periods of concerted exercise without the opportunity for rest. Further, results here suggest that swimming efficiency may decline with climate warming because of reduced body condition that appears to be associated with declining ice levels and associated hunting opportunities (Obbard et al. 2006, 2016). Reduced body condition will reduce swimming efficiency by making individuals less buoyant and by increasing heat loss to the surrounding water. Reduced body condition should also lead to an increase in the minimum size at which cubs can

swim without losing more heat than they generate. These impacts, combined with greater length and frequency of long-distance swims with climate warming (Pilfold et al. 2017) could greatly increase the costs and risks for swimming polar bears.

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