

# The influence of sea ice dynamics on population energetics of Western Hudson Bay polar bears

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## Abstract

The Arctic marine ecosystem has experienced extensive changes in sea ice dynamics, with significant impacts on ice-dependent species such as polar bears (*Ursus maritimus*). We used abundance estimates, age/sex structure, and body condition data to estimate population energy density and storage energy in Western Hudson Bay polar bears from 1985 to 2018. We examined intra-population variation in energetic patterns, temporal energetic trends, and the relationship between population energetics and sea ice conditions. Energy metrics for most demographic classes declined over time in relation to earlier sea ice breakup, most significantly for solitary adult females and yearlings, demonstrating their vulnerability to nutritional stress. Population energy metrics declined significantly over time in relation to earlier breakup and longer lagged open water periods, suggesting multi-year effects of sea ice decline. This study provides insights into ecological mechanisms linking population responses to sea ice decline and highlights the utility of long-term bioenergetics research.

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Data accessibility statement : If the manuscript is accepted, the data supporting the results will be archived in an appropriate public repository and the data DOI will be included at the end of the article.

## 1. Introduction

Population and ecosystem dynamics are key ecological processes to monitor as ecosystems undergo anthropogenic alterations due to habitat fragmentation and loss (Fahrig 2003; Mantyka-Pringle et al. 2012) and climate warming (Parmesan & Yohe 2003; Scheffers et al. 2016). Species have responded through changes in ecological processes including shifts in phenology (Parmesan & Yohe 2003; Visser & Both 2005), changes to foraging behaviour (Mahan & Yahner 1999), altered habitat use/distribution (Mantyka-Pringle et al. 2012; Kortsch et al. 2015), and reduced reproductive/survival rates with resulting declines in population abundance (Fahrig 2003; Scheffers et al. 2016). These changes in species abundances and distributions can lead to altered community structure and trophic interactions (Rall et al. 2010; Molinos et al. 2015; Scheffers et al. 2016) as well as regime shifts (Petchey et al. 1999; Kortsch et al. 2014), with implications for ecosystem function and stability (de Ruiter et al. 1995; Neutel et al. 2002; Rall et al. 2010). Changes in community structure are especially critical to ecosystems where higher trophic levels are vulnerable to anthropogenic change because altered top predator population dynamics can cause cascading effects (Shackell et al. 2010).

Examining energy dynamics over time can provide insights into ecological responses to both natural and anthropogenic change. Bioenergetics has been studied at individual/species levels using ingestion and assimilation rates (Bailey & Mukerji 1977; Cressa & Lewis 1986), prey consumption estimates (Lantry & Stewart 1993), and metabolism (Lam et al. 1991). Furthermore, broader-scale energetics studies have documented patterns in population energetic requirements (Markussen & Øritsland 1991; Ryg & Øritsland 1991; Ernest et al. 2003) and ecosystem energetic dynamics across trophic levels (Sakshaug et al. 1994). Bioenergetics research at various scales is useful for monitoring ecological patterns given that alterations in individual energetic balances may lead to changes in population dynamics (Yodzis & Innes 1992; Humphries et al. 2004). Thus, understanding temporal dynamics in energetics and relationships to environmental conditions may provide insights into the mechanisms influencing population dynamics and improve our ability to predict how populations may respond to future stressors.

The Arctic marine ecosystem has experienced rapid and extensive changes in sea ice in response to climate warming (Comiso 2002; Stirling & Parkinson 2006; Stroeve & Notz 2018; IPCC 2019). In particular, reduced sea ice extent and earlier sea ice breakup are major factors that influence the life history of many Arctic marine species (Comiso 2002; Stirling & Parkinson 2006; Meier et al. 2014), especially sea ice-dependant marine mammals (Laidre et al. 2008, 2015; Post et al. 2009; Wassman et al. 2011). For example, polar bears (*Ursus maritimus*) are particularly vulnerable to sea ice decline (Stirling et al. 1999; Stirling & Derocher 2012) because they rely on sea ice for movement, reproduction, and as a platform from which to hunt their main prey, ice-associated seals (Stirling & Archibald 1977; Smith 1980). As both a top predator and a species sensitive to sea ice conditions, polar bears are particularly useful for monitoring changing Arctic marine ecosystem dynamics. The Western Hudson Bay (WH) polar bear population is an example of a long-term monitoring program where individuals have been captured and measured over three decades, which provides a unique opportunity to examine energetic dynamics relative to sea ice habitat. Declines in WH polar bear body condition (Sciullo et al. 2016), reproductive rates (Stirling et al. 1999), survival (Regehr et al. 2007), and abundance (Lunn et al. 2016) have all been associated with climate warming. Such changes to population dynamics are influenced by individual condition and energy balances (Yodzis & Innes 1992; Humphries et al. 2004), which in turn are driven by alterations in energy intake and expenditure (Pagano et al. 2018). The open water period Hudson Bay, during which polar bears fast on land, has lengthened (Stern & Laidre 2016) and an increase to a 180 day fasting period is predicted to result in increased starvation and mortality rates (Molnár et al. 2010, 2014; Pilfold et al. 2016). It is therefore important to examine energetic dynamics at various levels and long-term monitoring can provide important insights into top predator bioenergetic responses to climate warming and implications for ecosystem dynamics.

Energetics has been examined in polar bear populations using a fat condition index (Stirling et al. 2008), metabolic rates (Pagano et al. 2018), body condition metrics and fasting (Atkinson & Ramsay 1995; Robbins et al. 2012; Rode et al. 2018), and lipid content (Sciullo et al. 2016). Additionally, the use of body measurements to estimate individual energetic stores can provide insights into energetic dynamics. For example, storage energy and energy density have been used to quantify energy budgets for individual polar bears (Molnár et al. 2009, 2010; Sciullo et al. 2016). Storage energy represents the energy that is available for maintenance, reproduction, and growth, and is influenced by energy intake and expenditure (Molnár et al. 2009, 2010; Sciullo et al. 2016). However, because not all energy is available for use when individuals are fasting, energy density is another useful metric as it accounts for the energy content per unit mass (Molnár et al. 2009, 2010; Sciullo et al. 2016). These measures are both informative for understanding changes in individual energy balances, as well as predicting changes in population dynamics in response to future conditions.

We used data on population abundance, age/sex structure, and morphometrics collected from WH polar bears to estimate the population energy density and storage energy from 1985 to 2018. Our objectives were to: 1) examine temporal dynamics of energy in the WH population, 2) assess the influence of environmental conditions on population energy, and 3) explore lagged effects of environmental variables. In addition, we analyzed energy dynamics within the population to provide insights into intra-population variation and examine the vulnerability of different age/sex classes based on energy balances. This research increases our understanding of the temporal and intra-population energetic patterns of a top predator experiencing habitat

loss due to climate warming, as well as potential implications for Arctic marine ecosystem dynamics.

## 2. Materials and methods

### 2.1 Field sampling

Hudson Bay is an inland sea that is seasonally ice covered (autumn to spring) and ice free in summer (Hoccheim et al. 2010; Fig. 1). When sea ice retreats in summer, WH polar bears come ashore along the western coast of the Bay in northeastern Manitoba, Canada and remain on land until sea ice freeze-up (Stirling et al. 1999; Lunn et al. 2016). Polar bears were captured in the core summering area of the WH population (Fig. 1) in late August to early October from 1985 to 2018 following standard methods (Stirling et al. 1989). Bears were measured (straight-line body length and axillary girth), marked with uniquely numbered ear-tags and tattoos, and released. Age was determined from an extracted vestigial premolar (Calvert & Ramsay 1988). Bears were categorized into seven age, sex, and reproductive classes: adult male ([?] 5 years), solitary adult female ([?] 5 years), adult female with offspring ([?] 5 years and accompanied by offspring), subadult male (2-4 years), subadult female (2-4 years), yearling (ca. 20-22 months), and cub-of-the-year (COY, ca. 8-10 months). All capture and handling techniques were in accordance with the Canadian Council on Animal Care ([www.ccac.ca](http://www.ccac.ca)) guidelines and approved by the University of Alberta BioSciences Animal Care and Use Committee and Environment and Climate Change Canada's Western and Northern Animal Care Committee. Research was conducted under wildlife research permits issued by the Government of Manitoba and the Parks Canada Agency.

### 2.2 Environmental data

Annual dates of sea ice breakup and freeze-up for the WH management zone were extracted from 323 grid cells with 25 x 25 km resolution passive microwave satellite raster imagery from the National Snow and Ice Data Center (Cavalieri et al. 1996). The first ordinal date in spring when sea ice concentration was [?] 50% for three consecutive days was used as the date of sea ice breakup, while the first ordinal date in autumn when sea ice was [?] 10% for three consecutive days was used as the date of freeze-up (Etkin 1991; Stirling et al. 1999; Lunn et al. 2016). The length of the open water period (i.e., when bears are on land) was calculated as the date of freeze-up minus the date of breakup, then further subtracting 25 days due to the bears arriving onshore approximately 21 to 28 days after breakup (Stirling et al. 1999; Castro de la Guardia et al. 2017; Johnson et al. 2019). In addition, the Arctic Oscillation winter index (AOw) and the North Atlantic Oscillation winter index (NAOw) were extracted for each year to examine broad climate variability. The AO affects sea ice distribution (Stroeve et al. 2011) and is related to polar bear reproduction rates and diet (Derocher 2005; McKinney et al. 2017), while NAO influences sea ice extent and is related to polar bear stress hormones (Bechshoft et al. 2013). AOw was calculated as the mean of January to March AO in each year (National Ocean and Atmospheric Administration; [https://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily\\_ao\\_index/ao.shtml](https://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao.shtml)). NAOw was calculated as the winter index (December to March) from the National Centre for Atmospheric Research (Hurrell 2012). To account for the influence of environmental conditions of the previous year, we also calculated lagged environmental variables in each year.

### 2.3 Age/sex class energy patterns

Individual body measurements collected at capture were used to estimate energetic metrics for each bear. Straight-line body length and axillary girth were used to estimate body mass using regression equations in Table 2 from Thiemann et al. (2011b) and then energy density ( $\text{MJ kg}^{-1}$ ) and storage energy (MJ) were calculated using equations 18 A-E from Molnar et al. (2009).

Energy density and storage energy trends over time for each demographic class were analyzed using linear regression models. In addition, multiple linear regression models (Table S1 in Supporting Information) were defined *a priori* based on ecological hypotheses and were used to assess the relationship between energy

density or storage energy for each class and the environmental variables (sea ice breakup, length of the open water period, AOW, NAOw, and lagged effects). Environmental variables were assessed for collinearity and variables that were correlated ( $r > |0.6|$ ) were not included in the same model (Table S2). Model selection was determined using Akaike's Information Criterion (AIC).

As the energy density and storage energy values were non-normally distributed (Shapiro-Wilk test,  $P [?] 0.05$ ) and standard transformations did not improve normality, we used Kruskal-Wallis ANOVA and Dunn's non-parametric tests to examine differences among age/sex classes.

## 2.4 Estimating population energy density and storage energy

Total population energy density and storage energy were calculated based on population structure, abundance estimates, and individual body measurements. Capture records from 1985 to 2018 were used to estimate population structure; however, variation in yearly sample sizes (e.g., low numbers of bears caught from certain age classes in certain years) necessitated the use of bootstrapping over a five-year moving window to estimate yearly percentages of each age/sex class. Therefore, step one of the population energy estimation process involved calculating the mean percentage of each class in the five-year window around the year of interest from 2000 bootstrap iterations (sampling with replacement) using the *boot* package in R (Canty & Ripley 2019) to represent yearly population structure.

Abundance estimates were calculated in the program MARK using the POPAN formulation (Schwarz & Arnason 1996; Appendix S1). To account for uncertainty in MARK estimates, step two involved drawing a random value from a normal distribution (based on the MARK values) to estimate the annual abundance. The numbers of bears of each class were then calculated in step three by multiplying the bootstrapped age/sex class structure by the estimated annual abundance.

In step four, the yearly mean energy density and storage energy per class were calculated from 2000 bootstrap iterations (sampling with replacement) using the *boot* package in R (Canty & Ripley 2019). Step five involved calculating the yearly total energy density and storage energy for each class by multiplying the number of bears in that class by the mean energy of that class.

In step six, the yearly total population energy density and storage energy were calculated by summing the energy values across classes. To account for uncertainty in this process, steps 1-6 were conducted 10,000 times and the resulting mean and SE were used as the total population energy density and storage energy estimates in further analyses.

## 2.5 Temporal dynamics of population energy and environmental analyses

We examined temporal trends (1985-2018) in total population energy density, storage energy, and temporal dynamics of sea ice variables using linear regression models. We used multiple linear regression analysis to examine the relationship between total population energy values and environmental variables (Table S1). Model selection was conducted using AIC and the top model was used to make predictions about population energy given potential future environmental conditions (i.e., 180 day fasting period; Molnar et al. 2010, 2014; Pilfold et al. 2016). All statistical analyses were conducted in R v.3.6.1 (R Core Team 2019).

## 3. Results

There were 4346 captures from 1985 to 2018 of 2533 individual bears, with a mean of 127.8 bears (SE = 11.3) captured per year (Table S3). There were 1159 adult male, 540 solitary adult female, 807 adult female with offspring, 296 subadult male, 331 subadult female, 393 yearling, and 820 COY captures (Table S4).

### 3.1 Age/sex class energy patterns

Energy density declined significantly over time for solitary adult females (linear regression,  $P = 0.015$ ) and declined non-significantly over time for the other classes, except adult males and adult females with offspring (linear regression,  $P > 0.05$ ; Fig. 2). Storage energy declined significantly over time for solitary adult females and yearlings (linear regression,  $P = 0.001, 0.041$  respectively) and declined non-significantly over time for the other classes, except adult females with offspring (linear regression,  $P > 0.05$ ; Fig. 3).

Energy density was significantly lower at earlier sea ice breakup dates for adult males and subadult females (multiple linear regression,  $P = 0.020, 0.034$ ; Fig. S1; Tables S5, S6) and non-significantly lower at earlier breakup dates for the other classes (multiple linear regression,  $P > 0.05$ ; Fig. S1; Table S6). Storage energy was significantly lower at earlier sea ice breakup dates for adult males, subadult males, subadult females, and COY (multiple linear regression,  $P = 0.004, 0.014, 0.012, 0.029$  respectively; Fig S2; Tables S7, S8) and non-significantly lower at earlier breakup dates for the other classes (multiple linear regression,  $P > 0.05$ ; Fig. S2; Table S8). A longer lagged open water period was associated with significantly reduced storage energy and non-significantly lower energy density for solitary adult females (multiple linear regression,  $P = 0.028$  and  $P = 0.074$ , respectively; Figs. S3, S4; Tables S6, S8).

Energy density was significantly different among classes (Kruskal-Wallis,  $\chi^2 = 958.35$ ,  $df = 6$ ,  $P < 0.001$ ). Solitary adult females had significantly higher energy density than all other classes (Dunn's test,  $P [?] 0.05$ ; Tables S4, S9). COY and adult females with offspring had significantly lower energy density than all other classes, while adult males, subadult males/females, and yearlings had intermediate energy density. Storage energy was also significantly different among classes (Kruskal-Wallis,  $\chi^2 = 3398.2$ ,  $df = 6$ ,  $P < 0.001$ ). Adult males had significantly higher storage energy than all other classes, followed by solitary adult females (Dunn's test,  $P [?] 0.05$ ; Tables S4, S10). Subadult males/females and adult females with offspring had intermediate storage energy. Yearlings and COY had significantly lower storage energy than all other classes.

### 3.2 Temporal dynamics of population energy

From 1985 to 2018, the total population energy density declined by 53% and population storage energy declined by 56% (linear regression,  $P < 0.001$  and  $P < 0.001$  respectively; Fig. 4). There was a significant positive correlation between yearly population abundance estimates and both population energy density and storage energy (Spearman's correlation, coefficient = 0.69,  $P < 0.001$  and coefficient = 0.68,  $P < 0.001$  respectively).

### 3.3 Population energy and the environment

Sea ice breakup varied from 17 May to 10 July and occurred significantly earlier from 1985 to 2018, with mean breakup occurring 5.5 days/decade earlier (linear regression,  $P [?] 0.05$ ; Fig. S5). Sea ice freeze-up varied from 4 Nov to 7 Dec and occurred significantly later over time, with mean freeze-up occurring 4.3 days per decade later (linear regression,  $P [?] 0.001$ ; Fig. S5). The length of the open water period varied from 102 days to 166 days and significantly lengthened over time, with a mean increase of 9.9 days per decade (linear regression,  $P [?] 0.001$ ; Fig. S5).

The top ranked models for population energy density and storage energy included sea ice breakup and the lagged open water period, while AOw, NAOw, and their lagged effects were not included in the top models (Table S11). Total population energy density was significantly lower when sea ice breakup occurred earlier and the lagged open water period was longer (multiple linear regression,  $P < 0.001$  and  $P = 0.001$ , respectively; Fig. 5, Table 1). The top multiple linear regression model predicted that at the earliest breakup (ordinal date 137) and 180 day lagged open water period, total population energy density would be 8303.0 MJ kg<sup>-1</sup> (58% lower than the mean energy density value that was calculated in our study, 19944.8 MJ kg<sup>-1</sup>).

Similarly, total population storage energy was significantly lower when sea ice breakup occurred earlier and the lagged open water period was longer (multiple linear regression,  $P < 0.001$  and  $P < 0.001$  respectively;

Fig. 5, Table 4). At the earliest breakup (ordinal date 137) and 180 day lagged open water period, population storage energy was predicted to be 838781 MJ (63% lower than our mean estimated storage energy, 2270218 MJ).

## 4. Discussion

We examined intra-population variation in energy density and storage energy, temporal dynamics in energetics, and the influence of sea ice dynamics on WH polar bear population energetics from 1985 to 2018. All age/sex classes, except adult males and adult females with offspring declined in energy density over time, all classes except adult females with offspring declined in storage energy over time, and reduced energy values were associated with earlier sea ice breakup across classes. Furthermore, we found that the WH population energy density and storage energy both declined significantly over time in relation to earlier sea ice breakup and longer lagged open water periods. This research is important for monitoring trends in individual physiological condition, understanding implications for population dynamics, and predicting future responses of polar bears to climate warming.

### Age/sex class patterns

We found variation in energetic dynamics from 1985 to 2018 among WH polar bear age/sex classes. All classes except adult males and adult females with offspring showed decreases in energy density over time, and all classes except adult females with offspring declined in storage energy over time, with the most significant declines for solitary adult females and yearlings. Energy density is determined as the ratio of storage energy to body mass (Molnár et al. 2009) and was less variable than storage energy. In contrast, storage energy indicates the total amount of energy in an individual (Molnár et al. 2009) and is therefore more sensitive to changes in body condition given that the amount of storage energy is lower at smaller body sizes. Decreases in storage energy indicate that the bears had less energy available for maintenance, growth, and survival (Molnár et al. 2009; Sciullo et al. 2016). These results are similar to Sciullo et al. (2016) where WH polar bear storage energy declined from 2004-2013 across classes. Due to the relationship between energy reserves/body condition and fitness (Jakob et al. 1996; Sciullo et al. 2016), the observed reductions in available energy will influence survival and reproduction, with consequences for individual fitness. The significant reduction in energy density and storage energy over time for solitary adult females and the significant reduction in storage energy for yearlings further indicates the vulnerability of these classes to future environmental changes. The small body size, dietary constraints, energetic demands of growth, and inexperienced hunting skills of younger bears make them more vulnerable to reductions in sea ice and thus prey availability (Rode et al. 2010; Thiemann et al. 2011a; Pilfold et al. 2016; Johnson et al. 2019; Laidre et al. 2020). In contrast, adult males can best buffer against sub-optimal conditions given their larger body size, broader diets, more effective hunting skills, and ability to take kills away from smaller bears (Stirling 1974; Regehr et al. 2007; Thiemann et al. 2011a; Pilfold et al. 2016; Johnson et al. 2019). These patterns highlight the importance of continued monitoring of the condition of young bears.

The reproductive status of adult female polar bears in WH influenced their energy patterns. Solitary adult females had higher energy density and storage energy than adult females with offspring, but solitary females experienced significant declines in both energy metrics over time whereas females with offspring had lower but relatively stable energy values. These results are consistent with observations that solitary adult females have higher body condition due to their accumulation of body fat in preparation for the energetic requirements of gestation and lactation (Atkinson & Ramsay 1995; Thiemann et al. 2006; Sciullo et al. 2016). The amount of energy a solitary adult female accumulates before denning determines the likelihood of successfully producing cubs as well as subsequent cub survival (Atkinson & Ramsay 1995; Derocher & Stirling 1994, 1996, 1998) and litter size (Laidre et al. 2020). Decreases in solitary adult female condition can therefore translate into a decline in cub survival and reproductive success, both of which have already been observed in WH (Derocher & Stirling 1995; Stirling et al. 1999). The observed declines in solitary adult female energy may

reflect difficulty in accumulating sufficient resources. In contrast, females with offspring have lower energy reserves due to lactational energetic demands (Derocher et al. 1993; Arnould & Ramsay 1994; Atkinson & Ramsay 1995). There is likely a threshold of energetic reserves that is required to successfully reproduce (Molnár et al. 2010; Reimer et al. 2019). For instance, Derocher et al. (1992) found that the lowest weight of an adult female that was known to have successfully reproduced was 189 kg, while Robbins et al. (2012) indicated that females require 20% body fat when entering a den to successfully produce cubs. Similarly, our results indicated that adult females with offspring had relatively stable energy density (median: 19.8 MJ kg<sup>-1</sup>; Fig. 2) and storage energy (median: 2241 MJ; Fig. 3), suggesting energetic thresholds for reproduction. In agreement with Robbins et al. (2012), our results highlight the vulnerability of females with offspring due to their already-reduced energetic reserves, as well as the sensitivity of solitary adult females that need to accumulate sufficient energy in preparation for future reproductive events yet are nutritionally stressed.

Our study also demonstrated the association between age/sex class energetic patterns and environmental conditions. Reduced energy density and storage energy were associated with earlier sea ice breakup and this relationship was most significant for adult males, subadult males/females, and COY. These results are consistent with the relationship between earlier breakup and reduced body condition in WH (Stirling et al. 1999; Sciullo et al. 2016). Our finding that the lagged open water period was an important predictor for solitary adult female storage energy suggests that the previous year's sea ice conditions influenced the ability of solitary females to accumulate energy reserves in preparation for reproduction. Similarly, Derocher & Stirling (1994) found that an adult female's condition in the previous year was a strong determining factor for reproductive success in WH. In addition, the previous year's breakup date influenced body condition of Davis Strait polar bears, whereby earlier breakup in the previous year forced bears ashore earlier, resulting in poorer body condition (Galicia et al. 2019), while Baffin Bay polar bear body condition was associated with the previous ice-free period (Laidre et al. 2020). Our observed decline in solitary adult female energy and the relationship with the lagged open water period suggests that females may not be able to recover from poor conditions in previous years, which may build up over time and affect lifetime reproductive success. Overall, our results indicate that polar bear energetic balances are negatively affected by sea ice declines and that vulnerable demographic groups include younger bears and adult females.

## Population trends

WH total population energy density and storage energy declined significantly over the 34 year study period. Both energy metrics were correlated with estimated abundance, which indicates that the population energy decline was related to reduced population abundance. The WH population has declined from approximately 1185 to 806 bears over the period of 1987 to 2011 (Lunn et al. 2016) with a continued decline in recent years (ECCC unpublished data, 2019); furthermore, WH body condition has also declined over time (Derocher & Stirling 1995; Stirling et al. 1999; Sciullo et al. 2016). Reduced population abundance in addition to declining body condition of individuals may both contribute to the observed decline in the total energy stored in this population. Declines in individual energy balances and subsequent consequences for survival and reproduction illustrate the mechanism linking climate change and population dynamics (Yodzis & Innes 1992; Humphries et al. 2004; Molnár et al. 2009, 2010; Pagano et al. 2018). Understanding the ecological mechanisms behind demographic change is important for wildlife management and can improve our predictions about how populations may respond to future climate warming (Cherry et al. 2009; Pagano et al. 2018; Reimer et al. 2019).

We found that western Hudson Bay experienced significant long-term change in sea ice dynamics, with a lengthening of the open water period by approximately 9.9 days per decade. WH polar bear population energy density and storage energy were both significantly reduced when sea ice breakup was earlier and the lagged open water period was longer, demonstrating a linkage between declining sea ice and reduced energetic balances. Sea ice is probably the most important single mechanism influencing polar bear demographic responses in the changing Arctic marine ecosystem. Our results are consistent with the association between earlier breakup/late freeze-up and declining body condition (Stirling et al. 1999; Obbard et al. 2016; Sciullo

et al. 2016; Laidre et al. 2020), altered foraging ecology (McKinney et al. 2009; Johnson et al. 2019), and reduced reproduction/survival rates and abundance (Regehr et al. 2007; Rode et al. 2010; Lunn et al. 2016; Obbard et al. 2018) in various polar bear populations including WH, Southern Beaufort Sea, Southern Hudson Bay, and Baffin Bay. Changes to energetic intake and expenditure in response to sea ice dynamics have consequences for energetic balances (Pagano et al. 2018). Polar bear energetic intake is reduced when breakup occurs earlier and freeze-up occurs later because the spring hunting period is shortened and bears are forced to fast on land for longer periods in poorer condition (Cherry et al. 2009, 2013; Rode et al. 2014, 2018). Meanwhile, energetic expenditure increases due to declines in optimal habitat (Durner et al. 2009; Stern & Laidre 2016), increasingly fragmented and drifting sea ice (Mauritzen et al. 2003; Sahanatien & Derocher 2012; Auger-Méthé et al. 2016; Durner et al. 2017), and long-distance swims as a result of more open water (Durner et al. 2011; Pagano et al. 2012; Pilfold et al. 2017). We found that the open water period increased from 105 days in 1985 to 145 days in 2018, with a maximum of 166 days in 2015. An increase in the fasting period from 120 days in the 1980s to 165 days was predicted to lead to higher starvation rates for adult male polar bears in WH (Robbins et al. 2012), while 180 day fasting was predicted to lead to additional increases in starvation and mortality rates (Molnár et al. 2010, 2014; Pilfold et al. 2016). Similarly, our predictions indicated that at 180 day previous fasting period, population energy density and storage energy would decline to 58% and 63% lower than the mean estimated values, respectively. Decreases in the length of the spring foraging period are predicted to lead to declines in female polar bear expected fitness (Reimer et al. 2019) and higher fasting rates have occurred concurrently with reductions in survival and abundance (Cherry et al. 2009; Rode et al. 2014, 2018). Our predicted declines in WH population energy at longer fasting periods would have implications for individual fitness, population vital rates, and productivity. Moreover, the importance of the lagged open water period suggests that there are cumulative effects of prior conditions that affect the ability of bears to recover from previous nutritional stressors. Hudson Bay is expected to undergo continued sea ice loss in the future and WH polar bears are therefore at risk of further declines to energetic balances leading to reduced survival rates for young bears and decreased reproductive success, which may ultimately result in a functionally extinct population (Castro de la Guardia et al. 2013; Pilfold et al. 2016).

## Ecosystem implications

While the Arctic marine ecosystem has already experienced various alterations due to climate warming (Wassman et al. 2011), our observed decline in population energy of a top predator may have further implications for ecosystem dynamics. Altered top predator population dynamics have the potential to cascade through ecosystems and influence trophic interactions and food web dynamics (Pace et al. 1999; Schmitz et al. 2000; Frank et al. 2005). For example, reduced body size of top predators has been associated with a weakening of predation pressure on lower trophic levels (Shackell et al. 2010). A potential consequence of reduced WH polar bear energetic balances is therefore altered trophic interactions with their primary prey species, ringed seals (*Pusa hispida*). However, Hudson Bay ringed seals have similarly shown population declines over time (Young et al. 2015; Ferguson et al. 2017); thus, our limited understanding of changing predator-prey interactions in the Arctic would benefit from long-term monitoring of ecological parameters across multiple trophic levels. Our study provides insights into potential mechanisms linking WH polar bear population dynamics and sea ice decline. As the Arctic continues to warm, polar bears can act as an indicator species to improve our understanding of changing ecosystem dynamics (Rode et al. 2018). Our research reinforces the importance of long-term monitoring of individual physiological condition and broad population patterns.

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# Figures

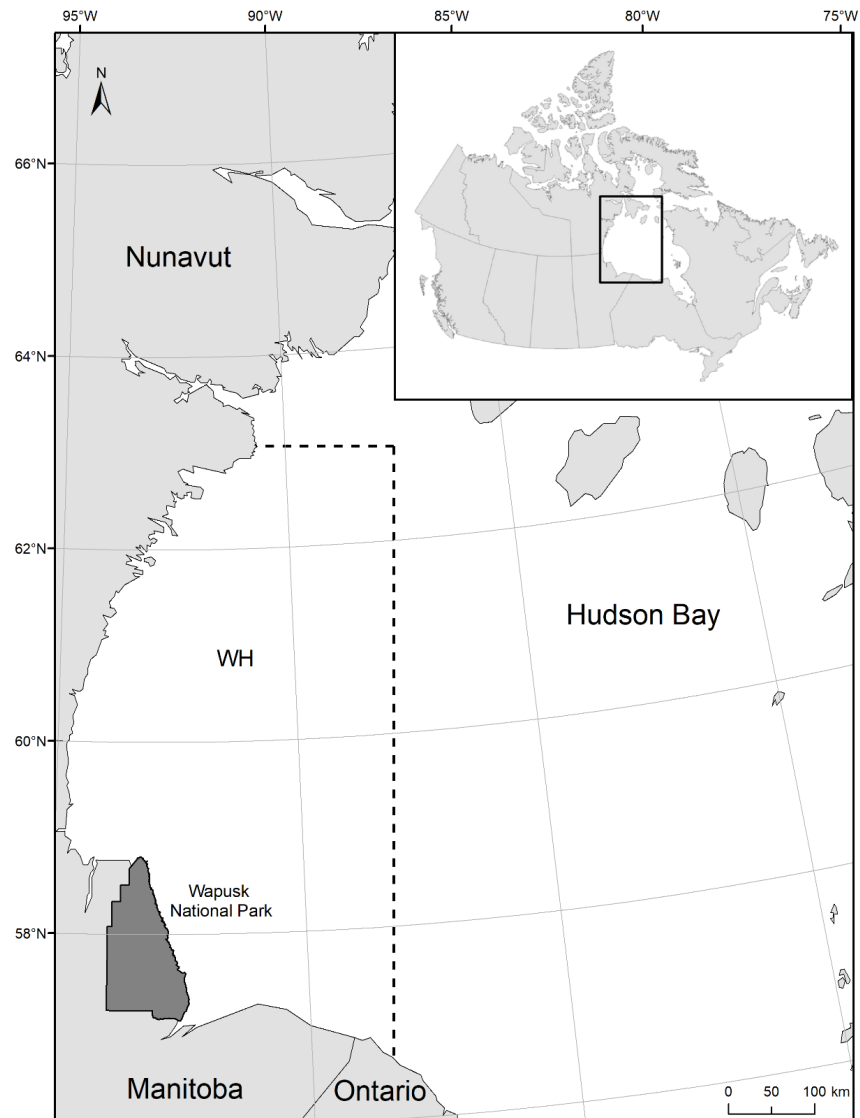


Figure 1. Western Hudson Bay, Canada, where polar bears were captured in the core summering area (Wapusk National Park) from 1985-2018. The management boundary of the Western Hudson Bay (WH) population is indicated by the dashed line.

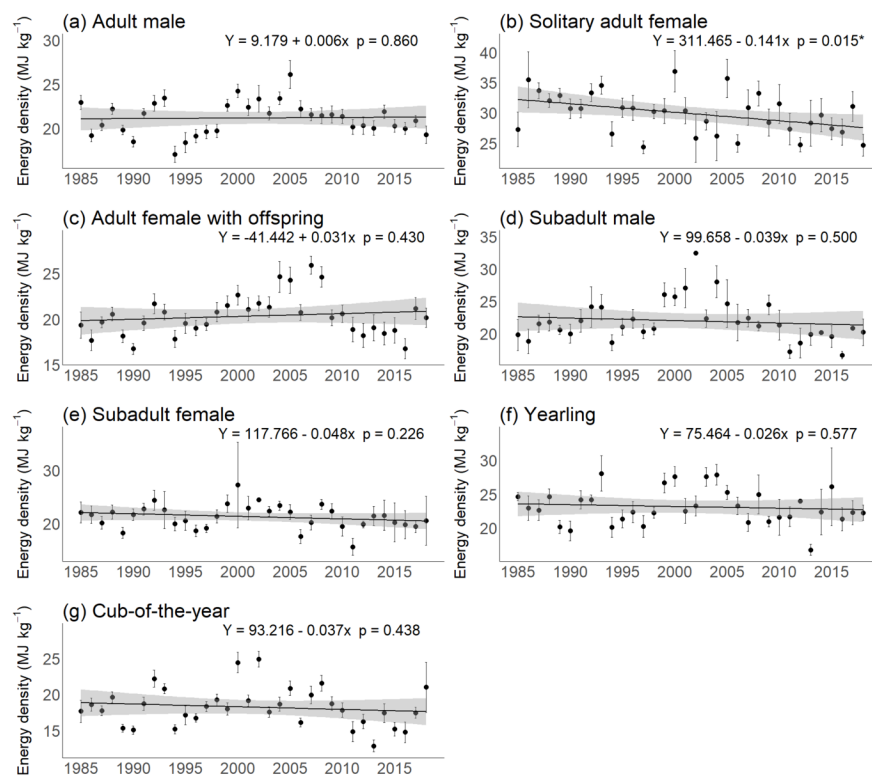


Figure 2. Mean energy density over time for each age/sex class of Western Hudson Bay polar bears: adult male (a), solitary adult female (b), adult female with offspring (c), subadult male (d), subadult female (e), yearling (f), and cub-of-the-year (g). \* indicates significant ( $p \leq 0.05$ ).



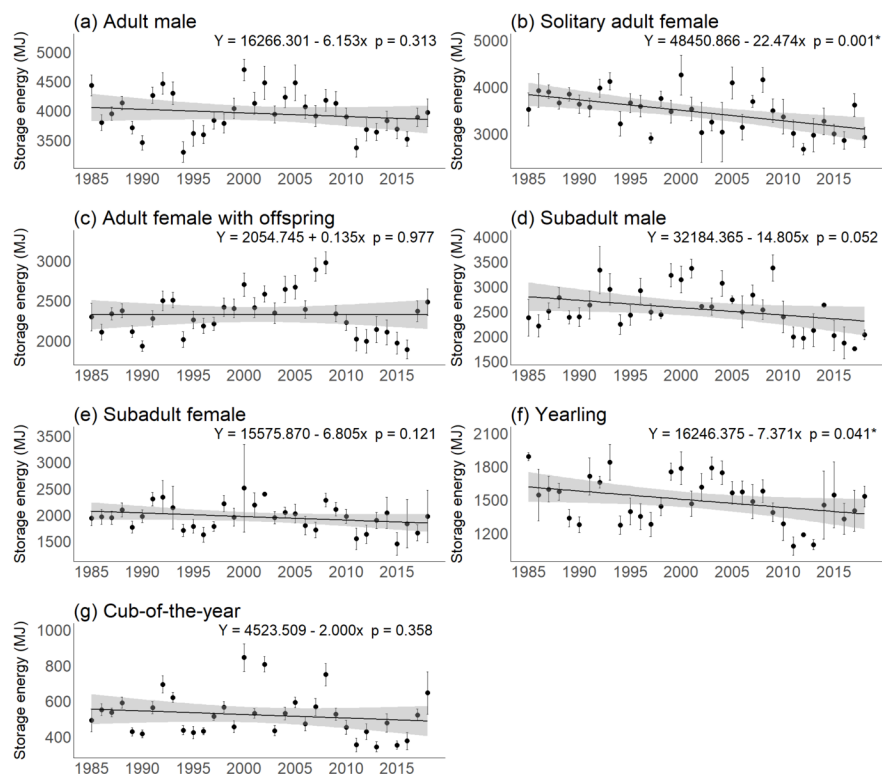


Figure 3. Mean storage energy over time for each age/sex class of Western Hudson Bay polar bears: adult male (a), solitary adult female (b), adult female with offspring (c), subadult male (d), subadult female (e), yearling (f), and cub-of-the-year (g). \* indicates significant ( $p \leq 0.05$ ).

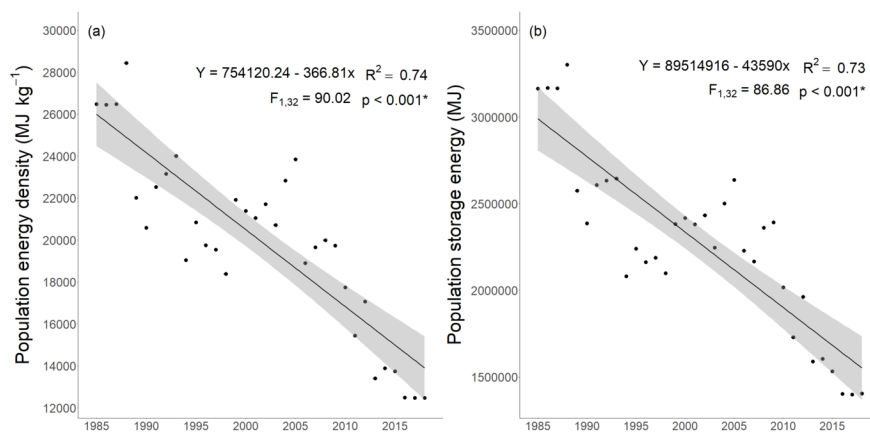


Figure 4. Estimated total population energy density (a) and population storage energy (b) for Western Hudson Bay polar bears from 1985 to 2018. \* indicates significant ( $p \leq 0.05$ ).

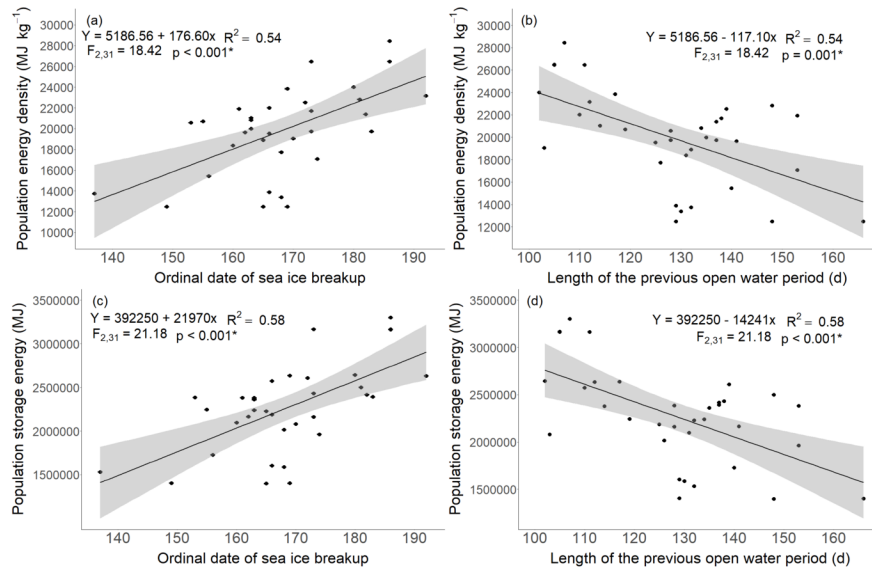


Figure 5. Estimated total population energy density (a, b) and storage energy (c, d) with sea ice breakup and the length of the previous open water period (lagged by one year) for Western Hudson Bay polar bears from 1985 to 2018. \* indicates significant ( $p \leq 0.05$ ).

## Tables

Table 1. The top multiple regression models for total population energy density and storage energy with the environmental covariates for Western Hudson Bay polar bears from 1985 to 2018. The model F-statistic,  $R^2$ ,  $\beta$  coefficients ( $\beta$ ), standard error (SE), and p-values ( $p$ ) are included. \* indicates significant ( $p \leq 0.05$ ). Model number corresponds to Table S1.

Response	Model no.	Covariates	F	$R^2$	Intercept $\beta$	$\beta$	SE	$p$
Energy density	7	Breakup	18.42	0.543	5186.56	176.60	45.82	<0.001*
		OpenWater_Lag				-117.10	33.59	0.001*
Storage energy	7	Breakup	21.18	0.578	392250	21970	5261	<0.001*
		OpenWater_Lag				-14241	3857	<0.001*