

# Spring fasting behavior in a marine apex predator provides an index of ecosystem productivity

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## Abstract

The effects of declining Arctic sea ice on local ecosystem productivity are not well understood but have been shown to vary inter-specifically, spatially, and temporally. Because marine mammals occupy upper trophic levels in Arctic food webs, they may be useful indicators for understanding variation in ecosystem productivity. Polar bears (*Ursus maritimus*) are apex predators that primarily consume benthic and pelagic-feeding ice-associated seals. As such, their productivity integrates sea ice conditions and the ecosystem supporting them. Declining sea ice availability has been linked to negative population effects for polar bears but does not fully explain observed population changes. We examined relationships between spring foraging success of polar bears and sea ice conditions, prey productivity, and general patterns of ecosystem productivity in the Beaufort and Chukchi Seas (CSs). Fasting status ( $\geq 7$  days) was estimated using serum urea and creatinine levels of 1,448 samples collected from 1,177 adult and subadult bears across three subpopulations. Fasting increased in the Beaufort Sea between 1983–1999 and 2000–2016 and was related to an index of ringed seal body condition. This change was concurrent with declines in body condition of polar bears and observed changes in the diet, condition and/or reproduction of four other vertebrate consumers within the food chain. In contrast, fasting declined in CS polar bears between periods and was less common than in the two Beaufort Sea subpopulations consistent with studies demonstrating higher primary productivity and maintenance or improved body condition in polar bears, ringed seals, and bearded seals despite recent sea ice loss in this region. Consistency between regional and temporal variation in spring polar bear fasting and food web productivity suggests that polar bears may be a useful indicator species. Furthermore, our results suggest that spatial and temporal ecological variation is important in affecting upper trophic-level productivity in these marine ecosystems.

## KEYWORDS

Beaufort Sea, Chukchi Sea, creatinine, feeding, predation, ringed seals, sea ice, urea

## 1 | INTRODUCTION

Arctic sea ice loss has resulted in significant ecosystem effects (Post et al., 2013) and is expected to continue into the future (Laidre et al., 2015). However, the effects of declining Arctic sea ice on ecosystem productivity appear to vary inter-specifically, spatially, and temporally and are not well understood (Hoegh-Guldberg & Bruno, 2010; Kovacs, Lydersen, Overland, & Moore, 2011; Moore & Huntington, 2008; Post et al., 2013). This variation, in part, is a result of varying rates of sea ice loss across the circumpolar Arctic. For example, the Barents Sea, Laptev Sea, East Siberian Sea, Beaufort Sea, Chukchi Sea (CS), Hudson Bay, and East Greenland Sea are undergoing some of the greatest declines in summer sea ice extent (Laidre et al., 2015; Markus, Stroeve, & Miller, 2009; Stern & Laidre, 2016), yet species-specific effects vary depending on local bathymetry, community composition, and other factors (Kovacs et al., 2011; Rode, Regehr, Douglas, et al., 2014). Primary productivity has been predicted to increase in the Arctic as sea ice loss continues (Arrigo, van Dijken, & Pabi, 2008). However, global warming is expected to result in highly variable and difficult to predict changes in productivity of regional seas due to spatial variation in ice cover, stratification, and wind patterns (Grebmeier, Moore, Overland, Frey, & Gradinger, 2010; Kovacs et al., 2011; Slagstad, Ellingsen, & Wassmann, 2011).

Effects on upper trophic-level fauna from declining sea ice are also not well understood. Pelagic organisms are expected to increase in abundance, whereas benthic organisms are expected to decline (Cooper et al., 2013; Grebmeier, 2012). Cold-water species, such as Arctic cod (*Boreogadus saida*) are predicted to be displaced by warmer-water species (Mueter et al., 2009) as a result of warming ocean temperatures and changes in sea ice distribution (Gaston, Woo, & Hipfner, 2003). Changes in the timing of primary production are expected to negatively affect the zooplankton that Arctic cod rely on (Post et al., 2013), but empirical data suggest some variation in that pattern. For example, in the southern Beaufort Sea, ringed seal (*Pusa hispida*), beluga whale (*Delphinapterus leucas*), and black guillemot chicks (*Cephus grylle*) that rely heavily on Arctic cod were observed to decline in body condition, growth rates, and/or reproductive success while bowhead whales (*Balaena mysticetus*) which are more dependent on pelagic plankton communities exhibited improvement (Harwood et al., 2015). Furthermore, Arctic char (*Salvelinus alpinus*) exhibited a shift from consumption of Arctic cod to other alternative forage fish (Harwood et al., 2015). In contrast, ringed and bearded seals (*Erignathus barbatus*) in the neighboring, and more southerly extending CS, have increased consumption of Arctic cod, suggesting that cod have not yet been displaced or declined with warming, despite substantial declines in sea ice extent (Crawford, Quakenbush, & Citta, 2015). Understanding marine mammal responses to sea ice loss depends on understanding trophic cascading effects of changing ecosystems (Hoegh-Guldberg & Bruno, 2010; Kovacs et al., 2011), including direct effects on abundance and distribution, as well as prey behavior.

As an apex marine predator occupying a relatively simplified ecosystem (Murphy et al., 2016), polar bears (*Ursus maritimus*) may

be a useful indicator of changes in species productivity at lower trophic levels. The ability of a polar bear to hunt depends directly on seal abundance and behavior, and the sea ice conditions that promote successful predation (i.e., encounter and capture). Although much attention has been placed on the loss of summer sea ice as a platform for hunting seals (Derocher, Lunn, & Stirling, 2004; Rode et al., 2015; Whiteman et al., 2015), studies in the Beaufort Sea suggest that reductions in polar bear foraging efficiency are occurring during seasons when sea ice loss has been less dramatic. Cherry, Derocher, Stirling, and Richardson (2009) documented reduced spring (i.e., March–April) foraging success evidenced by a greater frequency of fasting over the previous 7 days or more in 2005–2006 compared to 1985–1986. Furthermore, Rode, Pagano, Bromaghin, et al. (2014) and Rode, Regehr, Douglas, et al. (2014) documented that frequencies of fasting in the southern Beaufort Sea (SB) were much higher than those observed in the adjacent CS in recent years. These observations were concurrent with documented declines in polar bear body condition, cub survival, and population size in the SB between the 1980s and 2000s, and with maintained or improved body condition and cub survival in the CS—all during a time when both subpopulations were experiencing substantial summer sea ice loss (Rode, Regehr, Douglas, et al., 2014). However, there has been little change in spring sea ice extent between periods or across regions (Douglas, 2010; Frey, Moore, Cooper, & Grebmeier, 2015), suggesting that other factors related to ecosystem productivity (e.g., seal and Arctic cod abundance) and function (i.e., seal behavior) or the quality of sea ice as a hunting platform (i.e. the availability of pressure ridge, lead systems, stalking cover, etc.), may be influencing spring polar bear feeding behavior.

Spring is the most important, if not critical, foraging period for polar bears in which they gain mass lost over the previous winter (Rode, Regehr, Douglas, et al., 2014), particularly for females emerging from dens with newborn cubs (Pilfold, Derocher, Stirling, Richardson, & Andriashek, 2012; Stirling & McEwan, 1975; Stirling & Øritsland, 1995). Ringed and bearded seals haul-out to molt and pup in the spring, making them more accessible to polar bears than during any other time of the year. Several studies have estimated that adult polar bears need to capture a ringed seal every 5 days during the peak foraging period in late spring and early summer to build up fat reserves to support reproduction and survival during the following winter (Pagano et al., unpublished data; Stirling & Øritsland, 1995). A recent study that tracked the feeding behavior, energetic costs, and body mass change of nine adult females in the SB found that the three that did not eat over a 9-day period lost 10% or more of their body mass (Pagano et al., unpublished data). Thus, reduced frequency of feeding in the springtime appears to have meaningful consequences for individual condition.

Although nearly 40% of the ringed seals killed by polar bears in the Beaufort Sea are pups, older age classes of prey are also important contributors to total biomass consumed (Pilfold et al., 2012). Adult seals are typically killed when hauled out rather than at lairs in the spring (Pilfold et al., 2012), thus factors affecting their haul-out

patterns may be important in affecting polar bear predation success. Sea ice availability and quality, prey behavior, and ecosystem productivity may be important factors that combine to determine polar bear predation success.

Here, we examine spring fasting behavior (*i.e.*, not having fed for  $\geq 7$  days) based on blood serum and creatinine ratios of polar bears in three recognized subpopulations (the Northern Beaufort (NB), SB, and CS) over three decades (1983–2016) as potential indicators of the sea ice and ecosystem changes in these regions. Our objectives were to (i) determine whether the frequency of spring fasting has changed over time or differs among these subpopulations (Rode, Regehr, Douglas, et al., 2014; Stirling, McDonald, Richardson, Regehr, & Amstrup, 2011) which have exhibited different responses to recent sea ice loss, (ii) determine whether environmental and ecological conditions which could affect fasting have changed over time and differ among subpopulations, and (iii) attempt to identify which factors may affect the frequency of fasting including indices of seal productivity, variables related to seal haul-out behavior, and measures of sea ice and weather conditions that could affect local foraging success.

## 2 | MATERIALS AND METHODS

### 2.1 | Sample collection and analysis

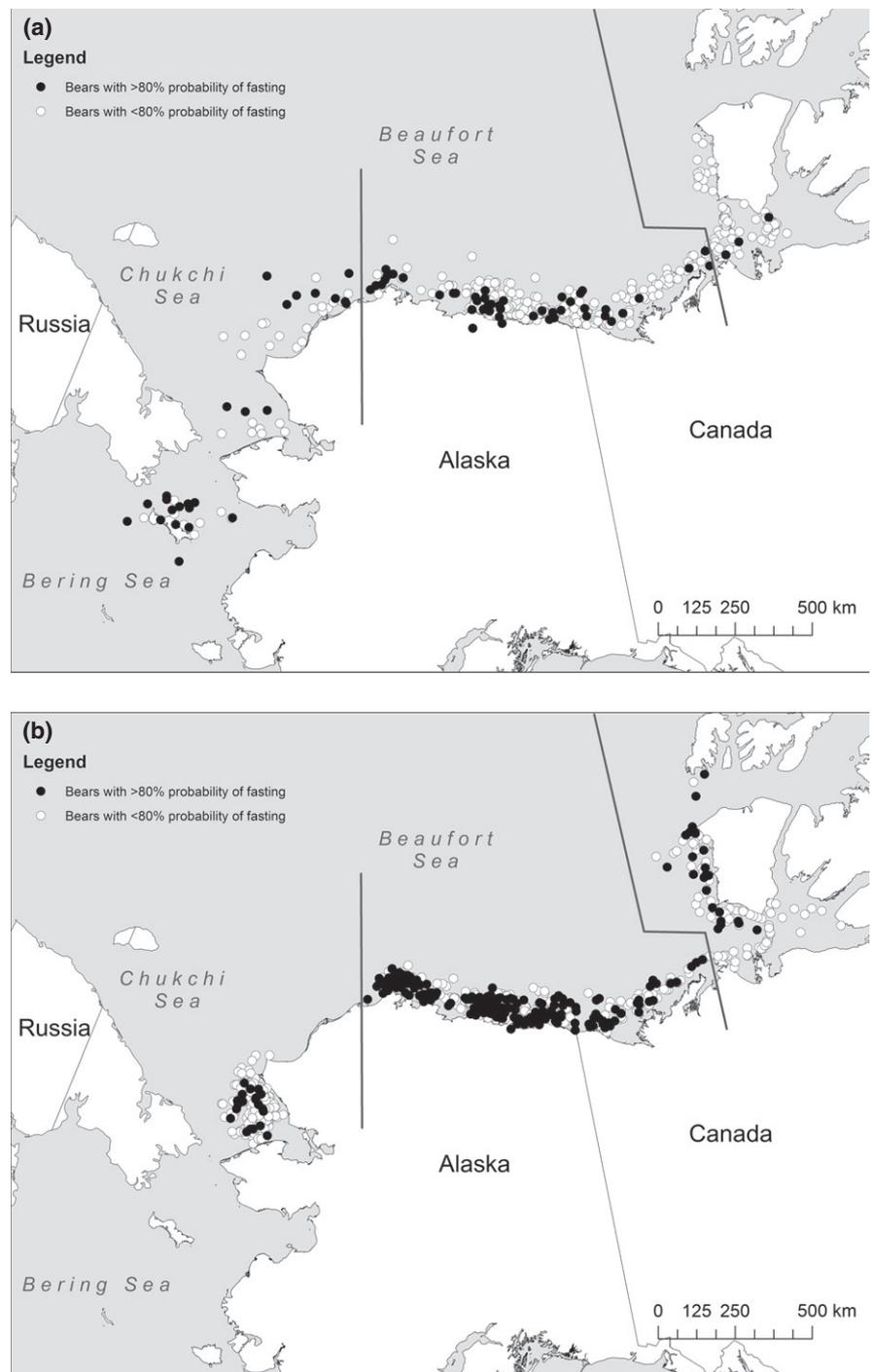
We analyzed serum samples from polar bears handled during capture–recapture studies between mid-March and early May, in 1985–1996 and 2005–2006 in the NB, 1983–2016 in the SB, and 1987–1993 and 2008–2016 in the Alaska portion of the CS (Figure 1). Polar bears were located from a helicopter and immobilized with a rapid-injection dart (Palmer Cap-Chur Equipment, Douglasville, GA, USA) containing zolazepam-tiletamine (Telazol<sup>®</sup> or Zoletil<sup>®</sup>) 1987–2016, or Sernylan, M-99, or phencyclidine prior to 1987. Bears were captured on the sea ice with the exception of 7 of 1448 samples collected from bears on land during the early years of the study (Figure 1). Land-based bears were likely to have denned, but denning effects on fasting were accounted for as described below. In the CS 2008–2016 and in the NB and SB during all years, all sex and age classes were equally targeted for sampling whereas in the CS, capture efforts 1987–1993 targeted primarily adult females (55 of 62 bears captured were females). Studies were conducted under USFWS research permits MA 690038 and 046081 and followed protocols approved by Animal Care and Use Committees of the USGS and the USFWS.

Bears were classified to subpopulations based on range patterns from satellite collar data and ecological features that were associated with range patterns. Bears captured west of  $-160^\circ$  longitude were classified as belonging to the CS polar bear subpopulation, bears captured east of  $-160^\circ$  and west of  $-128.2^\circ$  were classified to the SB subpopulation, and bears captured east of  $-128.2^\circ$  were classified to the NB subpopulation. The International Union for the Conservation of Nature's Polar Bear Specialist Group (PBSG) boundary between the CS and SB occurs at approximately  $-163^\circ$  longitude

(Figure 1), but satellite location data from adult females captured between  $-160^\circ$  and  $-163^\circ$  longitude ( $n = 11$ ) suggest they remain primarily in the area designated as the CS subpopulation (Amstrup, McDonald, & Durner, 2004; USGS and USFWS, unpublished data). Similarly, although the SB/NB subpopulation boundary is defined by the PBSG as  $-121^\circ$ , bear movement patterns and habitat conditions vary east and west of Ballie Island in response to the Cape Bathurst polynya (Galley, Else, Howell, Lukovich, & Barber, 2012; Stirling, Richardson, Andriashek, & Derocher, 2006) and there have been discussions to change the PBSG subpopulation boundary. Therefore, bears were assigned to the NB subpopulation if their capture location was east of  $-128.2^\circ$  and south of  $71.5^\circ$  or east of  $-132.0^\circ$  and north of  $71.5^\circ$  ( $n = 150$  bears of 241 assigned to the NB that would have been assigned to the SB subpopulation based on the current IUCN boundary).

A vestigial premolar was extracted for age determination upon first capture, except for dependent young which were aged based on size and dentition. We classified senescent adults as  $\geq 20$  years old (Lunn et al., 2016), prime-age adults as 5–19 years old, subadults as independent (*i.e.*, without their mother) bears 2–4 years old, and dependent young as cubs age 0–2 years accompanying their mother. Blood was collected in no-additive tubes and centrifuged to separate blood serum from red blood cells. Serum was initially stored in the field for up to 4 weeks at  $-3$  to  $-5^\circ\text{C}$  and then stored at  $-80^\circ\text{C}$  until processing. Urea and creatinine are stable in blood during long-term storage at  $-80^\circ\text{C}$  (see Appendix S1 for a detailed discussion of this topic). However, we examined the potential for previous thawing of samples during long-term storage to affect UC ratios by comparing paired previously thawed and not thawed samples collected from five individuals on the same capture date (Appendix S1). Levels of blood urea nitrogen (BUN) and creatinine were measured in serum using comprehensive rotors with an Abaxis vetScan (Abaxis, Inc., Union City, CA, USA) or via methods described in Cherry et al. (2009). Serum urea was calculated by multiplying  $\text{BUN} \times 0.466$  (Nelson, Beck, & Steiger, 1984) and divided by serum creatinine to determine a urea:creatinine ratio (hereafter UC ratio); a metric that is commonly used to identify fasting status in polar bears (Cherry et al., 2009; Derocher, Nelson, Stirling, & Ramsay, 1990; Nelson et al., 1984).

Previous studies have used UC ratios of  $\leq 10.0$  as indicative of bears that have fasted for  $\geq 7$  days (Cherry et al., 2009; Nelson et al., 1984). However, data from captive studies of feeding and fasting polar bears suggest that ratios  $>10.0$  commonly occur when bears are fasting and that there is considerable variation around mean UC ratios for fasting bears (Derocher et al., 1990). Furthermore, recently collected video-collar and body mass data on wild polar bears in the SB demonstrated at least one bear that did not feed for 9 days and had a UC ratio of 10.7 (Pagano et al., in review). Therefore, rather than creating a binary dataset classifying bears as having fasted or not fasted for a  $\geq 7$  day period, we used a Bayesian mixture model to estimate the probability of fasting for each bear in our data set (see Statistical analyses).



**FIGURE 1** Polar bear capture locations in spring (March–May) during 1983–1999 (a) and 2000–2016 (b) in the Beaufort and Chukchi Seas (CSs). Bears whose serum urea to creatinine ratios were associated with a >80% estimated probability of fasting are shown as closed circles and those with <80% probability of fasting are shown as open circles. This threshold was used to aid in visualizing distribution of bears that were likely to be fasting and differences in distribution between time periods that are discussed in the text. Black lines represent delineation between the CS (bears captured west of  $-160^{\circ}$ ), southern Beaufort (bears captured between  $-160^{\circ}$  and  $-128.2^{\circ}$ ), and northern Beaufort (bears captured east of  $-128.2^{\circ}$  and south of  $71.5^{\circ}$  or east of  $-132.0^{\circ}$  and north of  $71.5^{\circ}$ ) subpopulations

## 2.2 | Objective 1: Spatial and temporal patterns in fasting behavior

Our first objective was to determine whether the frequency of fasting differed among the three polar bear subpopulations and/or changed over time. We compared the frequency of fasting among subpopulations and between two time periods: before 2000 and from 2000 to 2016. We chose this period separation for several reasons. There were no data collected in the SB 1993–1997, NB 1986–2004, or in the CS 1994–2007, so a gap in the data set occurred in the mid-late 1990s for all subpopulations. Consistent anomalies in

the length of the melt season and availability of summer ice habitat began to occur in approximately 2000 in the Beaufort Sea (Bromaghin et al., 2015; Frey et al., 2015; Pagano, Durner, Amstrup, Simac, & York, 2012; Petty, Hutchings, Richter-Menge, & Tschudi, 2016) and declines in the body condition of beluga whales, ringed seals, and black guillemot chicks occurred between the 1990s and 2000s (Harwood et al., 2015). Polar bear capture locations were similar between the two periods compared in the NB and SB, but differed somewhat in the CS with more bears captured around St. Lawrence Island in Alaska and along the CS/SB subpopulation boundary in the early period compared to the later period. The

**TABLE 1** Variables included in models

Variable	Definition
Age	Categorical variable based on a bear's age: subadult = 2–4 years old, adult = 5–19 years old; senescent adult $\geq 20$ years
Sex	Binary variable of a bear's sex: F = female, M = male
Capture date	Ordinal day in which a bear was captured and sampled
Mating	Binary variable of whether a bear exhibited mating behavior or not at the time of capture
Denning	Binary variable of whether a bear denned or not during the prior winter
Population	Categorical variable classifying the subpopulation to which a bear was assigned based on its capture location
Period	Binary variable of an early time period prior to 2000 and a later time period of $\geq 2000$
Mean ice conc	Mean ice concentration (%) within a 100 km radius of a bear's capture location over the 7 days prior to capture
SD ice conc	Standard deviation of ice concentration within a 100 km radius of bear's capture location over the 7 days prior to capture
Mean drift	Mean sea ice drift in km/day within a 100 km radius of a bear's capture location over the 7 days prior to capture
SD drift	Standard deviation in sea ice drift within a 100 km radius of a bear's capture location over the 7 days prior to capture
Temp anomaly	The difference between air temperature 2 m above sea level surrounding a bear's capture location averaged over the 7 days prior to capture and the mean temperature on those 7 days for 1980–2016 ( $^{\circ}\text{C}$ )
Wind speed	Wind speed (km/hr) at 10 m above sea level surrounding a bear's capture location averaged over the 7 days prior to capture
Pressure	Pressure (mb) at 2 m above sea level surrounding a bear's capture location averaged over the 7 days prior to capture
Seal pups	Annual % of pups in the open water ringed seal harvest in east Amundsen Gulf of the eastern southern Beaufort Sea from Harwood et al. (2012); Data available 1992–2010 only
Seal ovulating	Annual ovulation rate of mature adult female ringed seals in east Amundsen Gulf of the eastern southern Beaufort Sea from Harwood et al. (2012); Data available 1992–2010 only
Seal index	Annual body condition index based on teeth annuli of ringed seals in the Canadian Beaufort Sea from Nyugen et al. (2017); 1983–2006
Scatterometry	Mean daily difference in qscat horizontally polarized scatterometry images over 7 days prior to capture within a 100 km radius of a bear's capture location. Data available 2000–2013 only
winterAO	Binary variable indicating whether the winter phase (Jan–Mar) of the Arctic Oscillation was negative or positive
AOO	Binary variable indicating whether the Arctic Ocean Oscillation was negative or positive

potential effects of capture location were considered when interpreting differences in the probability of fasting between periods in the CS.

There were several factors that we accounted for that could affect fasting behavior, including age, sex, mating behavior, denning, and capture date. We included age as a categorical variable (categories described under *Sample collection* and in Table 1) and excluded dependent young from the analysis because their feeding status is likely correlated with their mother. Because male polar bears are known to reduce or forego feeding during the mating season (Cherry et al., 2009) which coincides with the spring foraging period (April–June; Stirling, Spencer, & Andriashek, 2016), we included mating as a binary variable. A bear was classified as mating if they were observed pursuing a mate (i.e., for males they were either following the tracks of a female or with a female) or being pursued (a male was observed with a female) or if they were in estrus at the time of capture (females). Subadults and females with cubs or yearlings were assumed not to be mating. Because recording of estrus was not consistent across the study and males that were not observed pursuing a mate at the time of capture may have been involved in mating, many bears had an unknown mating status. We therefore used a Bayesian data imputation procedure (Gelman,

Carlin, Stern, & Rubin, 2004) to assign mating status to bears with an unknown status (see Statistical analyses).

Denning throughout the winter occurs almost exclusively by lone females who are presumed to be pregnant and emerge from land or ice-based dens in April. Because females emerging from a den are more likely to exhibit a UC ratio consistent with fasting, we identified females that denned during the prior winter as those with cubs-of-the-year or those wearing radio-collars which demonstrated a winter temperature signature consistent with denning (Fischbach, Amstrup, & Douglas, 2007; Olson et al., 2017). However, lone females that were not collared and observed without cubs could have denned during the prior winter, lost their cubs, and recently emerged from a den. Similar to our method for contending with mating uncertainty, we used a Bayesian data imputation procedure to assign mating status to bears with an unknown status (see Statistical analyses).

We included ordinal capture date as a potential factor affecting the frequency of fasting because ringed seals give birth to and nurse their pups and increasingly haul-out in subnivean lairs and later on the surface of the ice as the spring progresses (Smith 1987; Kelly et al., 2010) which affects polar bear predation success (Pilfold et al., 2012).

## 2.3 | Objectives 2 & 3: Environmental and ecological factors affecting fasting behavior

We hypothesized that ice and weather conditions that affect seal haul-out behavior (Frost, Lowry, Pendleton, & Nute, 2002) and access to seals, and annual variation in seal productivity could affect fasting behavior. Therefore, we examined air temperature, atmospheric pressure, and wind speed, as well as sea ice concentration, ice drift (km/day), and day-to-day changes in radar scatterometry ice imagery (described more below and in Appendix S1), at each capture location during the 7 days before capture (Table 1; Appendix S1). Weather data at each capture site were obtained from the North American Regional Reanalysis (Mesinger et al., 2006) using the Env-DATA portal (Dodge et al., 2013) at [www.movebank.org](http://www.movebank.org) (accessed November 2016). Sea ice characteristics were quantified within a 100-km radius around each capture location, the average net distance (plus one standard deviation) that polar bears move in 7 days during March and April, excluding the first 7 days post-capture (see Appendix S1; Rode, Pagano, Bromaghin, et al., 2014). Mean (and SD) daily sea ice concentration (%) and sea ice drift (km/day) during the week prior to capture were derived for each capture location using 25 km × 25 km resolution grids obtained from the National Snow and Ice Data Center (see Appendix S1). Because ice concentration data alone afford a limited representation of the sea ice environment, we used scatterometry data as an additional metric related to the magnitude of short-term (7 day) sea ice habitat change that may have implications on polar bear foraging success. Scatterometers have been used to characterize sea ice drift, age, surface melt status, and to better resolve small-scale geographic features such as leads and polynyas (see details in Appendix S1). In addition, we examined more broad-scale variables including annual metrics of ringed seal ovulation rates and pup production (Harwood, Smith, Melling, Alikamik, & Kingsley, 2012; Nyugen et al., 2017), as indicators of the health and abundance of ringed seals, winter Arctic Oscillation index (AO Jan–Mar), and Arctic Ocean Oscillation (AOO index, annual average). Ringed seal data collected by Harwood et al. (2012) were sampled in Amundsen Gulf in the eastern Beaufort Sea, whereas samples collected by Nyugen et al. (2017) were from the Canadian portion of the Beaufort Sea. Data on ringed and bearded seal abundance were not available for the Chukchi and Beaufort Seas nor were there comparable (i.e., data collected using the same methods) condition metrics for ringed seals in the Alaska portion of the Beaufort Sea or the CS. See Appendix S1 for more detail on the covariates included in the models.

The available data on ice conditions, weather patterns, and ringed seal ovulation rates and pup production varied spatially and temporally requiring that we examine relationships with spring fasting behavior among several separate models. Although data on patterns of ringed and bearded seal reproduction are available for the CS, both the time scale of available data (2003–2012; Crawford et al., 2015) and differences in the methods used in comparison to the Beaufort Sea prevented inclusion of these variables in a model across all three study regions. Furthermore, scatterometry data were not available until 2000. Therefore, our first model examining environmental and ecological factors affecting fasting included bears from all three regions

across the broadest time frame (1983–2016), but excluded indices of seal ovulation rates and measures of sea ice conditions derived from scatterometry data. We ran two additional models with bears in the NB and SB where seal data were available. The two sources of seal productivity data (Harwood et al., 2012; Nyugen et al., 2017) spanned different timeframes (1992–2010 and 1983–2006, respectively) and were potentially correlated. Thus, they were included in separate models. Finally, because scatterometry data were only available starting in 2000, we ran a fourth model including scatterometry data for all three populations during this truncated timeframe.

We ensured that collinearity was controlled for by measuring variance inflation factors (VIF) for all variables, ensuring that no variable had a VIF > 5 (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

## 2.4 | Statistical analyses

We used a Bayesian mixture model to determine what factors influenced the probability of fasting in polar bears between the three subpopulations. We modeled UC as a mixture of two gamma distributions dependent on the fasting status of individuals ( $i$ );

$$UC_i \sim \begin{cases} \text{gamma}\left(\frac{\mu_f^2}{\sigma_f^2}, \frac{\mu_f}{\sigma_f^2}\right), & \text{if } p_i = 1 \\ \text{gamma}\left(\frac{\mu_{nf}^2}{\sigma_{nf}^2}, \frac{\mu_{nf}}{\sigma_{nf}^2}\right), & \text{if } p_i = 0 \end{cases} \quad (1)$$

where  $p_i$  represents the fasting status of individual  $i$  (0 = non-fasting, 1 = fasting),  $\mu_f$  and  $\mu_{nf}$  are the mean UC for fasting (f) and non-fasting (nf) bears, respectively, and  $\sigma_f^2$  and  $\sigma_{nf}^2$  are the variances of UC for fasting and non-fasting bears, respectively. We used informed priors for the mean and variance parameters in equation 1, based on data found in Derocher et al. (1990) for UC values obtained from wild-caught but captive polar bears with known fasting status (i.e., 1 day post-feeding [non-fasting], and an average of 40-days post-feeding [fasting]). In Derocher et al. (1990), UC values were obtained from 13 bears in 2 years which were used to inform the variability in both the mean and standard deviation of the UC ratios. We modeled the prior of  $\mu_{nf}$  and  $\sigma_{nf}$  as;

$$u_{nf} \sim \text{gamma}\left(\frac{46.6^2}{20.6^2}, \frac{46.6}{20.6^2}\right) \quad (2)$$

and

$$\sigma_{nf} \sim \text{gamma}\left(\frac{19.1^2}{18.0^2}, \frac{19.1}{18.0^2}\right). \quad (3)$$

We modeled the priors of  $\mu_f$  and  $\sigma_f$  as;

$$u_f \sim \text{gamma}\left(\frac{13.4^2}{3.4^2}, \frac{13.4}{3.4^2}\right) \quad (4)$$

and

$$\sigma_f \sim \text{gamma}\left(\frac{6.1^2}{1.2^2}, \frac{6.1}{1.2^2}\right) \quad (5)$$

where the numerator of  $u$  and  $\sigma$  are determined from the mean UC ratios and standard deviations, respectively, and the denominator from the standard deviation of the UC ratios and standard

deviations of non-fasting (nf) and fasting (f) bears in Derocher et al. (1990).

To address study objective 1 (identifying spatial and temporal variation in spring fasting behavior), we modeled the probability that an individual was fasting as a function of population, time period, a population–period interaction, sex, age, mating status, denning status, and capture date (defined in Table 1);

$$\text{logit}(p_i) = \beta_0 + \beta \mathbf{x}_i + \varepsilon_i \quad (6)$$

where  $\beta_0$  is an intercept term,  $\beta \mathbf{x}_i$  is the vector of coefficient estimates multiplied by their associated variable values for individual  $i$ , and  $\varepsilon_i$  is a random effect (Table 2). All  $\beta$  and  $e$  were given a vague normal prior with mean 0, and variance 10. Objective 3 was addressed via the four models (explained above) with covariates listed in Table 3.

We developed a predictive model for the probability of a bear denning based on the set of bears with known denning status ( $d$ ), with population, period, and capture date serving as predictors;

$$\text{logit}(d_i) = \beta_{d0} + \beta_d \mathbf{x}_i \quad (7)$$

We then estimated the denning status for those bears with missing values with a Bernoulli distribution (i.e., Bernoulli( $d_i$ )). Our predictive model for mating status was similar to that of the denning status model, except that we also included denning status and sex as explanatory variables in the model. Based on the estimated probability of mating ( $m$ ), we then determined the mating status of an

individual, again with a Bernoulli distribution (i.e., Bernoulli( $m_i$ )). All  $\beta$  for the permutation procedure were given a vague normal prior with mean 0, and variance 10.

Estimates of denning and mating status of bears with missing values were computed iteratively in the Markov Chain Monte Carlo (MCMC) procedure to account for the uncertainty in both factors.

We estimated the posterior distribution for each parameter with MCMC using the package “rjags” (Plummer, 2015) to run the program JAGS (Plummer, 2003) from the R language and environment for statistical computing (R Core Development Team, 2014). We initialized two chains with separate starting values and allowed a burn-in period of 50,000 iterations. We then obtained 50,000 iterations from each chain, and thinned each by 50, resulting in a total of 2,000 samples from the posterior distribution (Appendix S1). We visually assessed each parameter for convergence. We did not employ model selection, based on reasons similar to those outlined in Hobbs, Andr n, Persson, Aronsson, and Chapron (2012). We were not seeking to create the most parsimonious model, but rather to include all parameters known to potentially affect fasting (e.g., mating and capture date, sex, and age; Pilfold, Derocher, Stirling, & Richardson, 2015) and to test hypothetical factors that may affect fasting based on polar bear and seal ecology (as described above). We assessed the importance of each variable based on whether the 95% credible interval (CI) overlapped zero, similar to Hobbs et al. (2012). We standardized all continuous covariates to aid in model convergence and to allow for easier interpretation of the magnitude of influence among covariates. We performed posterior predictive checks (Chambert, Rotella, & Higgs, 2014) to determine how well the model fit our observed data (i.e., UC ratios). We calculated Bayesian  $p$  values for four test statistics (i.e., mean, standard deviation, discrepancy, and goodness of fit) and considered  $p$  values for test statistics between 0.1 and 0.9 to indicate a good fit between the model and observed data for a given test statistic (Hobbs & Hooten, 2015). All of the above statistical analyses were conducted in R version 3.3.2.

To better understand whether environmental and ecological conditions experienced by bears during the 7 days prior to capture differed between periods and regions, we ran general linear models with population and period as fixed effects, capture date as a covariate, and a population–period interaction. Capture date were removed from the model if it was not significant at  $p < .05$ . Models were run in SPSS version 24.0.

**TABLE 2** Mean and 95% credible intervals for coefficient estimates from a Bayesian mixture model examining potential changes over time and differences among three populations in the probability of fasting

Parameter	Probability of fasting	
	Mean	95% C.I.
Intercept	−0.45	−2.58 to 1.60
Population (CS)	−0.39	−2.35 to 1.47
Population (NB)	0.60	−1.61 to 2.64
Period	1.39*	0.40 to 2.44
Sex	−2.56*	−3.59 to −1.67
Capture date	−1.93*	−2.46 to −1.41
Mating	2.28*	0.92 to 3.67
Denning	3.68*	2.30 to 5.28
Population (CS) × Period	−3.24*	−5.33 to −1.01
Population (NB) × Period	−0.79	−3.18 to 1.67
Age (adult)	−0.96	−2.42 to 0.58
Age (subadult)	−2.87*	−4.66 to −1.12

CS, Chukchi Sea; NB, Northern Beaufort. Population coefficient estimates are relative to the southern Beaufort subpopulation and for age are relative to senescent adults. A negative coefficient for sex indicates a lower probability of fasting in females. Probability of fasting declined with capture date and was higher for bears involved in mating or that had denned the prior winter than those that did not. “\*” indicates that the 95% credible interval for a parameter’s estimation did not overlap 0 and is therefore, important in the model

## 3 | RESULTS

### 3.1 | Objective 1: Spatial and temporal variation in fasting behavior

The final data set included urea and creatinine levels from 1,448 serum samples from 1,176 individual adult and subadult bears captured in the CS ( $n = 296$  samples) 1987–1993 and 2008–2016, SB ( $n = 911$ ) 1983–1992 and 1998–2016, and NB ( $n = 241$ ) 1985–1996 and 2005–2006. Mating status (i.e., mating or not mating) was known from field observations for 551 of 692 adult female and 164

**TABLE 3** Mean and 95% credible intervals for coefficient estimates from a Bayesian mixture model of factors affecting the probability of spring fasting for four models incorporating various environmental and ecological variables described in Table 1

Covariates	Model							
	All pops (1983–2016) <i>n</i> = 1448		Beaufort Sea pops with Harwood et al. (2012) seal data (1992–2010) <i>n</i> = 675		Beaufort Sea pops with Nyugen et al. (2016) seal data (1983–2006) <i>n</i> = 831		All pops and scatterometry data (2000–2013) <i>n</i> = 839	
	Mean	95% C.I.	Mean	95% C.I.	Mean	95% C.I.	Mean	95% C.I.
Intercept	0.28	−2.09 to 2.52	−0.44	−3.89 to 3.04	−0.15	−2.87 to 2.43	−0.326	−4.66 to 3.73
Sex	−2.79*	−3.92 to −1.80	−2.25*	−3.80 to −0.79	−2.16*	−3.64 to −0.85	−1.64*	−2.50 to −0.91
Capture date	−1.73*	−2.32 to −1.22	−2.20*	−3.25 to −1.32	−1.72*	−2.59 to −0.96	−2.05*	−3.33 to −1.01
Mating	2.85*	1.25 to 4.66	2.78*	0.36 to 5.36	3.09*	1.16 to 5.22	4.25*	2.28 to 6.62
Denning	4.75*	3.12 to 6.61	4.13*	1.93 to 6.64	4.03*	2.09 to 6.25	5.09*	3.06 to 7.60
Mean ice conc	0.21	−0.33 to 0.76	−0.31	−1.22 to 0.61	0.32	−0.49 to 1.20	−0.18	−1.02 to 0.67
SD ice conc	−0.20	−0.74 to 0.37	−0.12	−1.08 to 0.86	0.10	−0.69 to 0.93	0.50	−0.32 to 1.31
Mean drift	−0.23	−1.08 to 0.53	0.43	−1.03 to 1.80	−0.36	−1.53 to 0.72	0.98	−0.26 to 2.27
SD drift	−0.09	−0.87 to 0.68	−0.85	−2.19 to 0.40	−0.09	−1.23 to 1.07	−1.00	−2.21 to 0.12
Temp anomaly	−0.05	−0.52 to 0.41	0.04	−0.63 to 0.74	0.19	−0.47 to 0.85	−0.28	−0.93 to 0.34
Wind speed	0.61*	0.10 to 1.15	0.19	−0.57 to 1.00	0.40	−0.28 to 1.10	0.21	−0.40 to 0.90
Pressure	−0.04	−0.51 to 0.42	−0.24	−0.93 to 0.44	0.10	−0.50 to 0.72	−0.47	−1.14 to 0.14
winterAO	−0.62	−1.52 to 0.26	0.04	−1.49 to 1.50	1.32	−0.09 to 2.94	−1.78*	−2.93 to −0.64
AOO	−0.53	−1.81 to 0.79	0.20	−2.96 to 3.24	−0.06	−1.76 to 1.68	−0.40	−4.60 to 3.75
Age (adult)	−0.75	−2.29 to 0.82	−0.70	−2.85 to 1.56	−0.70	−2.70 to 1.33	−0.99	−2.87 to 0.89
Age (subadult)	−2.92*	−4.86 to −1.10	−3.39*	−6.84 to −0.50	−2.45*	−4.70 to −0.18	−3.99*	−6.80 to −1.50
Seal pups	–	–	−0.85	−2.08 to 0.31	–	–	–	–
Seal ovulating	–	–	−0.02	−1.08 to 1.01	–	–	–	–
Seal Index	–	–	–	–	−1.30*	−2.05 to −0.63	–	–
Scatterometry	–	–	–	–	–	–	−1.80*	−4.14 to −1.07

Only the “All pops” models include data from all three bear subpopulations, whereas all other models include data from only the Northern and Southern Beaufort Sea subpopulations. Age class coefficients are relative to senescent adults. Different timeframes of data were used to match available data for different covariates of interest (e.g., seal body condition indices, scatterometry data). “\*” indicates that the 95% credible interval for a parameter's estimation did not overlap 0 and is therefore, important in the model

of 489 adult male samples. Using our data imputation procedure, we assigned an additional 139 (95% CI = 92–181) adult bears of unknown mating status as “mating” at the time of capture (Table S1) and the remaining 334 bears as not mating. Similarly, denning status was known from field observations for 401 of 692 adult females sampled. We assigned an additional 173 (95% CI = 167–181) adult females as having denned prior to capture (Table S1) and the remaining 157 females as not having denned based on data imputation. We estimated that females traveled  $51.6 \pm 47.0$  (SD) km over a 7 day period ( $n = 13,241$  movement measurements). Collar-based movement data were not available for males in this region, but Laidre et al. (2012) found no difference in movement rates of males and females in the spring.

There was no difference in either the serum urea nitrogen ( $p = .3$ ) or creatinine ( $p = .7$ ) using a Wilcoxon signed rank paired test suggesting that if thawing had unknowingly occurred it was unlikely to bias our results.

We estimated mean UC ratio for bears identified as fasting and non-fasting to be  $12.6 \pm 6.8$  (mean  $\pm$  SD; 95% CI = 11.3–13.8) and

$48.6 \pm 32.2$  (95% CI = 45.1–52.7), respectively (Figure 2). The percent of bears fasting differed among the three subpopulations and two periods (Table 2). The percent of adult females fasting declined from 53% (42%–64%;  $n = 55$ ) to 10% (6%–17%;  $n = 106$ ) in the CS and increased from 30% (22%–39%;  $n = 136$ ) to 42% (34%–49%;  $n = 293$ ) and from 13% (3%–27%;  $n = 40$ ) to 33% (22%–44%;  $n = 99$ ) in the SB and NB, respectively (Figure 3). The percent of males fasting increased from 44% (34%–55%;  $n = 55$ ) to 66% (59%–74%;  $n = 257$ ) and from 27% (12%–40%;  $n = 39$ ) to 40% (27%–55%;  $n = 62$ ) between periods in the SB and NB, respectively (Figure 3). The sample size for CS males was too low ( $n = 7$ ) in the early period for comparison, but was large enough in the recent period to estimate at 34% (24%–44%;  $n = 128$ ; Figure 3). Sex, denning status, mating status, age class, and capture date also affected fasting (Table 2). Bears that had denned (adult females only) or were involved in mating (adults only) had higher probabilities of fasting than non-denning and non-mating bears, respectively. Males ( $51.3 \pm 38.7\%$ ; mean  $\pm$  SD;  $n = 628$ ) had a higher probability of fasting than females ( $33.0 \pm 35.9\%$ ;  $n = 820$ ). Senescent adults were

most likely to be fasting ( $49.3 \pm 39.3\%$ ;  $n = 85$ ), followed by adults ( $44.4 \pm 38.7\%$ ;  $n = 1096$ ), and subadults ( $23.8 \pm 30.7\%$ ;  $n = 267$ ). Finally, polar bears captured later in the year had lower probabilities of fasting than bears captured earlier (Table 2). The model appeared to fit the data well, with Bayesian  $p$  values for each of the four metrics indicating a good fit; mean ( $p = .48$ ), standard deviation ( $p = .25$ ), discrepancy ( $p = .21$ ), and goodness of fit ( $p = .52$ ; Table S2).

### 3.2 | Objective 2: Spatial and temporal variation in weather and sea ice conditions

Mean sea ice concentration experienced by bears during the 7 days prior to capture was higher in the SB ( $96.4 \pm 3.4\%$ ) than the CS ( $93.1 \pm 4.3\%$ ) or NB ( $93.4 \pm 4.3\%$ ; population–period interaction:  $F_{1,1441} = 11.7$ ,  $p < .0001$ ) but several metrics suggested greater variability in sea ice conditions in the CS than the SB or NB. The standard deviation of sea ice concentration was higher in the CS ( $2.5 \pm 1.5\%$ ;  $n = 296$ ) than the SB ( $1.7 \pm 1.6\%$ ;  $n = 972$ ) or NB ( $1.7 \pm 0.9\%$ ;  $n = 180$ ) ( $F_{2,1443} = 38.4$ ,  $p < .0001$ ) as was 7 day variation in scatterometer images (CS:  $0.53 \pm 0.32$ ;  $n = 179$ ; SB:  $0.35 \pm 0.15$ ,  $n = 615$ ; NB:  $0.34 \pm 0.12$ ,  $n = 100$ ;  $F_{2,890} = 71.3$ ,  $p < .0001$ ). Similarly, mean sea ice drift was highest in the CS ( $3.1 \pm 1.3$  km/hr,  $n = 262$ ) compared to the SB ( $2.9 \pm 2.2$  km/hr;  $n = 920$ ) and NB ( $2.3 \pm 1.0$  km/hr;  $n = 115$ ; population–period interaction:  $F_{2,1290} = 3.1$ ,  $p = .047$ ) and there was only a marginal difference between subpopulations in the standard deviation of drift (CS:  $2.0 \pm 0.9$  km/hr, SB:  $2.0 \pm 1.5$  km/hr, NB:  $1.5 \pm 0.9$  km/hr;  $F_{2,1292} = 3.0$ ,  $p = .05$ ). The NB exhibited the greatest temperature anomalies in the most recent time period (NB:  $1.9 \pm 2.6^\circ\text{C}$ ,  $n = 100$ ), followed by the CS ( $0.96 \pm 0.31^\circ\text{C}$ ,  $n = 234$ ) and SB ( $0.4 \pm 3.2^\circ\text{C}$ ,  $n = 667$ ; population–period interaction:  $F_{2,1441} = 13.8$ ,  $p < .0001$ ). There was no difference in wind speed between subpopulations ( $F_{1,1443} = 0.05$ ,  $p = .95$ ). Pressure was lowest in the CS ( $1013.6 \pm 8.8$ ;  $n = 296$ ), higher in the SB ( $1018.0 \pm 7.1$ ,  $n = 972$ ), and highest in the NB ( $1021.1 \pm 7.0$ ;  $n = 180$ ;  $F_{2,1444} = 39.6$ ,  $p < .0001$ ).

Mean sea ice concentration around polar bear capture sites increased 1% in the CS and 2.8% in the NB between periods, but exhibited no change in the SB (population\*period interaction:

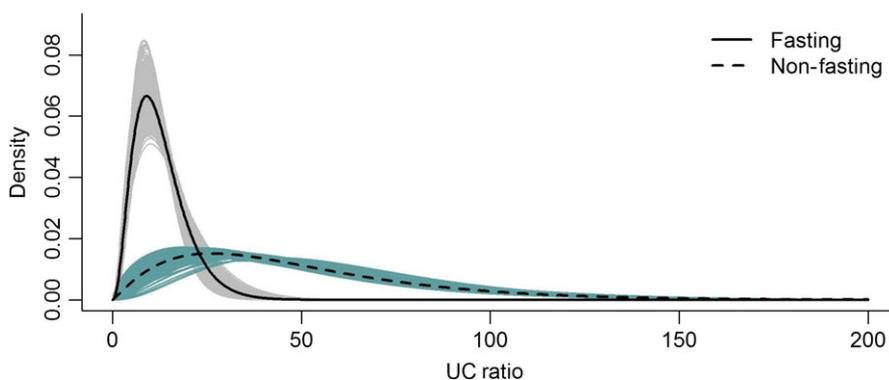
$F_{2,1441} = 11.7$ ,  $p < .0001$ ). Sea ice drift decreased in the CS by 0.4 km/hr and increased in the NB and SB by 0.3 and 0.5 km/hr, respectively, between time periods (population\*period interaction:  $F_{2,1290} = 3.1$ ,  $p = .05$ ). The standard deviation in sea ice concentration and sea ice drift increased between periods (ice concentration:  $\beta = 0.33 \pm 0.09\%$ ,  $F_{2,1443} = 38.4$ ,  $p < .0001$ ; drift: period\*population interaction:  $F_{2,1290} = 3.1$ ,  $p = .05$ ). There was a shift from negative to positive temperature anomalies experienced by bears in all three subpopulations (population\*period interaction:  $F_{2,1441} = 13.8$ ,  $p < .0001$ ), but this shift was most pronounced in the NB where anomalies averaged  $-2.4^\circ\text{C}$  in the early period and  $1.9^\circ\text{C}$  in the latter period. Wind speeds were also 0.4 km/hr higher across all regions in the most recent time period compared to the past ( $\beta = 0.39 \pm 0.20$ ;  $F_{1,1445} = 3.9$ ,  $p = .049$ ). There was no change in pressure ( $F_{1,1443} = 0.77$ ,  $p = .38$ ). Scatterometer data were not available in the early time period for comparison.

### 3.3 | Objective 3: Relationships between weather, sea ice conditions, seal availability, and polar bear fasting behavior

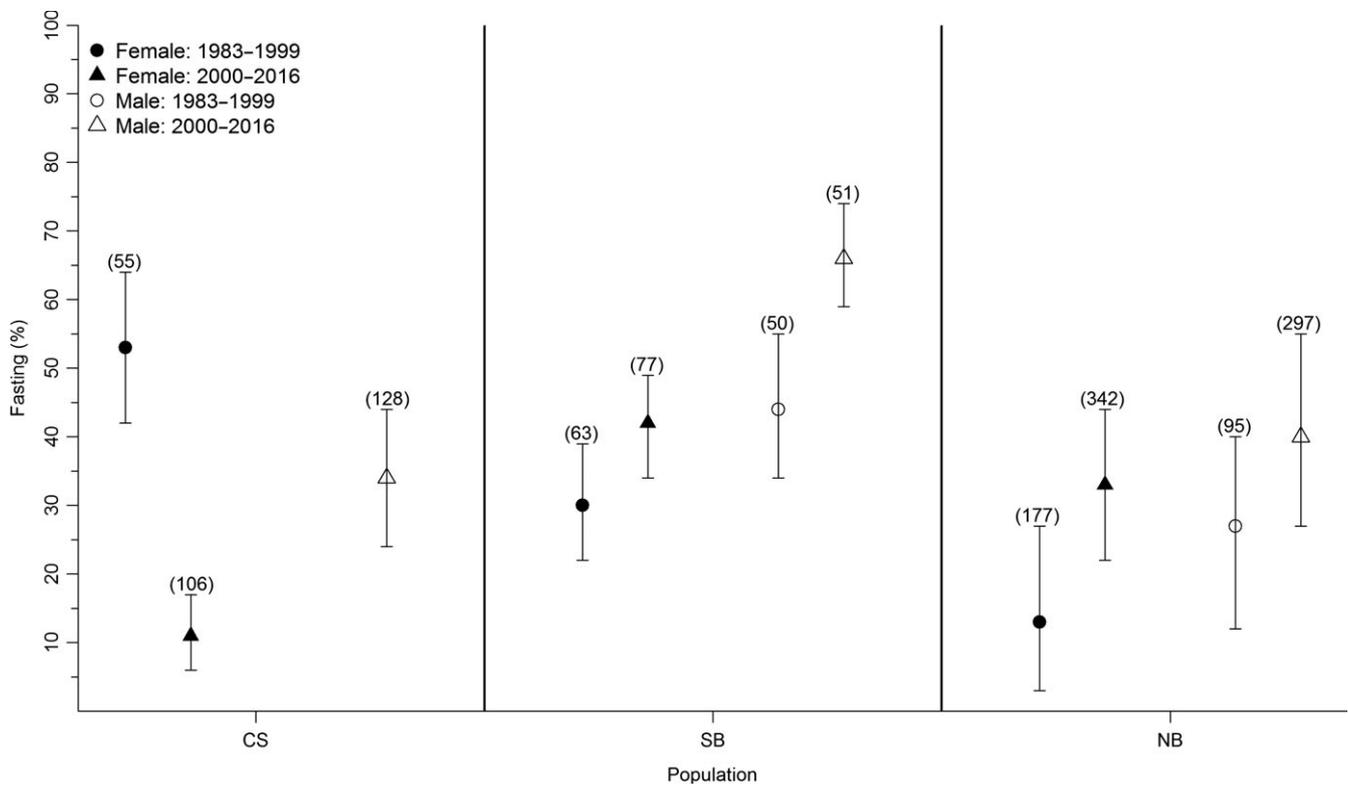
Similar to the model comparing the probability of fasting across time periods and populations, all models examining environmental and ecological variables in the SB and NB included effects of sex, capture date, mating, denning, and age (Table 3). Of the environmental and ecological variables examined (Tables 1 and 3), wind speed, an index of seal body condition (Nyugen et al., 2017), variation in scatterometer measures of ice conditions, and the winter AO were important in models of fasting (i.e., confidence intervals of coefficient estimates did not overlap zero, Table 3). Bayesian  $p$  values indicated good model fits to the data for all metrics except for goodness of fit, which only fit model 1 well (Table S2).

## 4 | DISCUSSION

Marine mammals have been identified as important sentinels of marine ecosystems (Laidre et al., 2015; Moore et al., 2014). Their broad spatial distribution, long lifespans, and position at higher trophic levels mean that changes in their overall reproductive success,



**FIGURE 2** Modeled distribution of fasting and non-fasting probabilities based on serum urea and creatinine levels in 1448 samples from subadult and adult polar bears captured in the Chukchi and Beaufort Seas 1983–2016



**FIGURE 3** The percent of male and female polar bears identified as fasting (%) based on urea:creatinine ratios within blood serum in the Chukchi (CS), Northern Beaufort, and southern Beaufort seas during two time periods, 1983–1999 and 2000–2016

survival of age classes, and population size may be indicative of regional scale changes in the ecosystems in which they reside. Polar pelagic food webs consist of a small number of species where energy flows to higher trophic levels via fewer pathways than more complex systems (Murphy et al., 2016). This results in Arctic systems being sensitive to changes in abundance of keystone species, such as Arctic cod which link lower and higher trophic levels (Murphy et al., 2016). Spring fasting of the three polar bear subpopulations in this study varied temporally and spatially consistent with observed variation in measures of primary productivity and the health of prey and other species within their Arctic food web. Thus, their foraging behavior appeared to track change in the food web during a season when sea ice extent was near its annual maximum. Collectively, these results point to changes in polar bear foraging behavior that are associated with ecosystem productivity. A lack of data on Arctic cod distribution and abundance at region-wide and decadal scales and on other potential ecosystem drivers preclude identification of the proximate mechanisms affecting ecosystem variation.

In the Beaufort Sea, increases in spring fasting behavior of polar bears occurred concurrent to observed declines in the body condition, growth rates, and/or reproductive success of polar bears (Rode, Amstrup, & Regehr, 2010), ringed seals (Harwood et al., 2012; Nyugen et al., 2017), and three other species linked to the pelagic food web (Harwood et al., 2015). Similarly, in our study, polar bear fasting was directly related to an index of ringed seal body condition. The Beaufort Sea is characterized by a narrow continental shelf that

limits benthic habitat for bearded seals and has lower benthic-pelagic coupling, benthic biomass, and chlorophyll-a concentrations in comparison to the CS (Dunton, Goodall, Schonberg, Grebmeier, & Maidment, 2005). Additionally, estimates of ringed seal densities are generally lower and more variable (1.01–1.85 seals/km<sup>2</sup>; Frost et al., 2002) than those in the CS (1.62–1.91 seals/km<sup>2</sup>; Bengtson, Hirukiraring, Simpkins, & Boveng, 2005). Higher percentages of bears fasting in the SB compared to the NB are consistent with reduced and stable polar bear populations, respectively (Bromaghin et al., 2015; Stirling et al., 2011). Greater reductions in the western Beaufort Sea ice cover compared to the eastern Beaufort (Hutchings & Rigor, 2012) could play a role in affecting both spring fasting behavior and population status (Stirling et al., 2011).

In the CS, low percentages of fasting polar bears are consistent with evidence that it is one of the most productive regions in the Arctic Ocean (Grebmeier, Cooper, Feder, & Sirenko, 2006) and has experienced increases in primary productivity in recent years as indicated by chlorophyll-a concentrations (Frey et al., 2016). This productivity is believed to be supported by the extensive continental shelf that covers most of the CS in combination with warm water and nutrient influxes from the Bering Sea (Frey et al., 2016; Grebmeier et al., 2006). Polar bears, ringed seals, and bearded seals appear to have maintained or improved body condition in the CS despite recent sea ice loss (Crawford et al., 2015; Rode, Regehr, Douglas, et al., 2014) perhaps buffered by the primary productivity of the region. The observed similarities in patterns of polar bear

fasting with those of ocean primary productivity during a time of year when sea ice is not limiting suggest that polar bears could be useful in monitoring the productivity of species within their food chain. Moore et al. (2014) similarly suggested that the diets and condition of upper trophic-level Arctic species can provide evidence of variability in ecosystem productivity.

Declines in the percent of CS females fasting in our study suggest that feeding conditions may have improved over our period of observation. Crawford et al. (2015) documented increased ringed seal condition including thicker blubber and faster growth during 2003–2012 compared to 1975–1984 the former of which affects reproduction (Harwood et al., 2012) and thereby may signal increased seal abundance. These trends may have contributed to the observed decline in fasting of female polar bears over a similar period. However, patterns in fasting relative to capture location (Figure 1) may have inflated the apparent decline. During the early period, bears were captured north of 70° along the SB/CS subpopulation boundary and south of 65° near St. Lawrence Island (Figure 1), areas that were not sampled in the more recent period. Including bears only captured in the same study area during both periods resulted in an apparent decline in the fasting in CS females from 39% to 10%, a pattern that corresponds with increased condition of their prey.

Although the status of prey populations appears to be an important contributor to polar bear spring fasting behavior, scatterometry measures also contributed to observed variation. Greater variability between day-to-day scatterometry images may reflect habitat dynamics such as the opening and closing of leads, drift, and the creation of pressure ridges. Scatterometry and standard deviation in ice drift and mean ice concentration were all higher in the CS compared to the Beaufort Sea. These results support the hypothesis that some variability in ice conditions (i.e., more active ice conditions) are beneficial to successful predation and that ice concentration and extent alone are insufficient to fully characterize foraging habitat quality for polar bears. Further study is needed to identify the specific ice and snow conditions measured in scatterometry data, including the use of higher-resolution data that may be important for polar bears.

Several other factors explained variance in the probability of fasting. Wind speed exhibited relationships with fasting probability when all years (1983–2016) and regions (CS and Beaufort Sea) were combined. Although wind speed did not vary across subpopulations, speed increased between periods and could affect polar bear fasting behavior via declines in haul-out duration of seals (Carlens, Lydersen, Krafft, & Kovacs, 2006) or disruption of polar bears' olfactory cues (Togunov, Derocher, & Lunn, 2017). Pilfold et al. (2015) similarly documented impacts of wind speed on polar bear predation success and wind has been documented as an important factor for successful predation in other species (Funston, Mills, & Biggs, 2001; Nevitt, Losekoot, & Weimerskirch, 2008). The probability of a predation event for polar bears and ringed seal body condition from the eastern Beaufort Sea have both been shown to have significant relationships with the AO and AOO (Pilfold et al., 2015; Nyugen et al.,

2017). These results are consistent with our finding that the winter AO in the Beaufort Sea was correlated with fasting probability.

Fasting varied as a result of both sex and age. Fasting probability may have been higher in males because males were more likely to be fasting ( $77.2 \pm 28.9\%$ ) when they were pursuing mates than females that were classified as mating based on estrus ( $38.1 \pm 35.4\%$ ). A higher frequency of fasting among senescent adults is likely related to aging effects on the ability to successfully capture seals. Senescent adults have been shown to be in poorer condition than younger adults and have lower rates of survival (Derocher & Stirling, 1994; Lunn et al., 2016). We expected that subadults might show higher fasting probabilities because their hunting skills are still developing. However, subadults may be more likely to obtain food via scavenging. Previous studies suggest that polar bears do not always consume the entirety of their kills (Stirling & McEwan, 1975) which may be likely when prey are large, such as bearded seals which are more commonly preyed upon by adult males (Cherry, Derocher, Hobson, Stirling, & Thiemann, 2011; Thiemann, Iverson, & Stirling, 2008) and when foraging occurs simultaneous to mating (i.e., males may leave prey to pursue mates) as it does in the spring. Compared to subadults, adult females may scavenge less from adult males as a result of habitat segregation (Ferguson, Taylor, & Messier, 1997) to avoid infanticide or conflicts associated with mating season. Although subadults exhibited the lowest probabilities of fasting, our analysis estimated whether a bear fed or not, and not how much they ate. Consequently, even small amounts of scavenging could create a UC ratio indicative of feeding. Pagano et al. (in review) observed that an adult female that scavenged from an old carcass on 1 of 8 days had a UC ratio of 26.1 but lost 12% of her body mass during the same period. Declines in subadult survival in the Beaufort Sea (Bromaghin et al., 2015) suggest that, despite our results of lower probabilities of fasting, this age class may not be faring well in the SB.

Our approach of estimating fasting probabilities and using the distribution of those probabilities to identify fasting and non-fasting bears resulted in higher fasting probabilities than reported in previous studies that used an absolute UC ratio threshold of  $\leq 10.0$  to identify fasting behavior (Cherry et al., 2009). However, the mean UC ratios we identified for fasting bears (12.6) were within the range measured by Derocher et al. (1990) of 11.0 and 15.8 for polar bears that had fasted for an average of 44 and 36 days, respectively. Similarly, UC ratios of three video-collared females that did not feed for 7–9 days in the SB were 10.7, 9.5, and 8.9 (Pagano et al., in review). Thus, our approach of estimating fasting probabilities rather than using a specific UC-ratio as a cutoff for identifying fasting and non-fasting bears appears to accurately reflect some of the variability in UC-ratios associated with feeding versus fasting.

Reduced foraging success by bears in the SB may be a contributing factor to a recently observed subpopulation decline (Bromaghin et al., 2015). Pagano et al.'s (in review) observation that bears that did not feed for 9 days and subsequently had serum UC values of 11 or less lost weight, suggests that fasting as defined in our study is likely to be associated with declines in body condition.

Observations of polar bears digging through solid sheets of rafted sea ice to access seals (Stirling, Richardson, Thiemann, & Derocher, 2008), cannibalism events (Amstrup, Stirling, Smith, Perham, & Thiemann, 2006), observations of starved bears (Regehr, Amstrup, & Stirling, 2006), and declines in ringed seal population productivity (Nyugen et al., 2017) provide supporting evidence for reductions in the availability of prey in the Beaufort Sea and increased fasting probabilities observed in the latter part of our study.

Declines in Arctic sea ice extent have occurred more in the summer than during other times of the year (Grebmeier et al., 2010; Stroeve et al., 2012). Accordingly, much attention has been placed on the role of summer sea ice loss in affecting Arctic ecosystems (Laidre et al., 2015; Slagstad et al., 2011). Because polar bears rely year-round on sea ice as a platform to hunt their primary prey, ice-associated seals, many studies have focused on the direct effects of decreased sea ice extent on polar bear behavior and population dynamics (Regehr, Lunn, Amstrup, & Stirling, 2007; Rode et al., 2010; Rode, Pagano, Bromaghin, 2014; Rode, Regehr, Douglas, et al., 2014; Rode et al., 2015; Whiteman et al., 2015). Our results suggest that spatial and temporal ecological variation is important in affecting upper trophic-level productivity in these marine ecosystems and that sea ice loss may have both direct and indirect effects at upper trophic levels. Understanding the role that sea ice loss may play in observed variation in Arctic food webs will be important in predicting the impacts of continued, projected Arctic sea ice loss. Polar bears may be a useful indicator species for tracking broad-scale changes in food web dynamics under the sea ice.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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