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Seal body condition and atmospheric circulation patterns influence polar bear body condition, recruitment, and feeding ecology in the Chukchi Sea

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## Abstract

Polar bears (*Ursus maritimus*) are experiencing loss of sea ice habitats used to access their marine mammal prey. Simultaneously, ocean warming is changing ecosystems that support marine mammal populations. The interactive effects of sea ice and prey are not well understood yet may explain spatial-temporal variation in the response of polar bears to sea ice loss. Here, we examined the potential combined effects of sea ice, seal body condition and atmospheric circulation patterns on the body condition, recruitment, diet, and feeding probability of 469 polar bears captured in the Chukchi Sea, 2008-2017. The body condition of ringed seals (*Pusa hispida*), the primary prey of females and subadults, was related to dietary proportions of ringed seal, feeding probability, and the body condition of females and cubs. In contrast, adult males consumed more bearded seals (*Erignathus barbatus*) and exhibited better condition when bearded seal body condition was higher. The litter size, number of yearlings per adult female, and the condition of dependent young were higher following winters characterized by low Arctic Oscillation (AO) conditions, consistent with a growing number of studies. Body condition, recruitment, and feeding probability were either not associated or negatively associated with sea ice conditions, suggesting that, unlike some subpopulations, Chukchi Sea bears are not currently limited by sea ice availability. However, spring sea ice cover declined 2% per year during our study reaching levels not previously observed in the satellite record and resulting in the loss of polar bear hunting and seal pupping habitat. Our study suggests that the status of ice seal populations is likely an important factor that can either compound or mitigate the response of polar bears to sea ice loss over the short-term. In the long-term, neither polar bears nor their prey are likely robust to limitless loss of their sea ice habitat.

KEYWORDS: Arctic oscillation, bearded seal, diet, ringed seal, QFASA, sea ice, *Ursus maritimus*

## 1. INTRODUCTION

Identifying environmental and ecological factors that influence wildlife population dynamics is critical to maintaining viable populations (Fuentes et al., 2016; Smith & Beck, 2017; Schuyler et al., 2018). Understanding these relationships has become increasingly important in managing species affected by environmental change associated with global warming (Milligan et al., 2009; Van Hemert et al., 2015; McRae et al., 2016). For these species, factors that had once

been stable are now exhibiting directional change, often at relatively fast rates (Mahlstein et al., 2013). This is particularly true in the Arctic where global warming is amplified resulting in increases in surface air temperatures that are twice the global average (Serreze & Barry, 2011; Previdi et al., 2020). Warming has led to substantial declines in the extent and thickness of Arctic sea ice (Cavalieri et al., 1997; Cohen et al., 2014). Minimum September sea ice extent declined 12.4% per decade between 1979 and 2010 (Stroeve et al., 2011) and in the summer of 2012 reached half the average from 1979-2000 (Overland and Wang, 2013). Similarly, mean winter ice thickness declined from 3.7 m in 1980 to 1.8 m by 2008 (Kwok & Rothrock, 2009). These changes have the potential to affect many of the species that live in marine Arctic ecosystems (Kovacs et al., 2010; Laidre et al., 2015).

Polar bears are useful indicators of ecosystem health because they occur throughout the circumpolar Arctic and are the only apex predator that lives on the sea ice surface (Kirk et al., 2010; Moore, 2008). Polar bears depend on a robust under-ice ecosystem that supports their primary prey, ringed (*Pusa [Phoca] hispida*) and bearded seals (*Erignathus barbatus*), as well as regionally variable secondary prey, such as beluga whales (*Delphinapterus leucas*) and walrus (*Odobenus rosmarus*) (Thiemann et al., 2008). Changes that occur within the ecosystem, including regional contaminant levels and reductions in sea ice algae, can be detected in polar bears (McKinney et al., 2011; Brown et al., 2018). Furthermore, in places where polar bears have exhibited population declines, other species within the system have also exhibited declines in body condition and vital rates (Harwood et al., 2014, 2015; Ferguson et al., 2017).

Many polar bear studies have related their habitat use, behavior, ecology and population dynamics to sea ice conditions in part because data on sea ice concentration and the area of coverage are readily available via satellite. In some parts of the Arctic, the seasonal availability of sea ice is directly related to variability in polar bear populations. For example, in western Hudson Bay where all sea ice melts in summer and polar bears summer onshore, longer ice-free seasons have been associated with declines in body condition and survival (Stirling et al., 1999; Lunn et al., 2016). However, in other areas, such as the Chukchi Sea where most bears remain on the sea ice year-round, substantial reduction in summer sea ice extent occurred without apparent impacts on polar bear body condition, reproduction or survival (Rode et al., 2014; Regehr et al., 2018). Similarly, in the adjacent Beaufort Sea, sea ice as well as other factors appear to influence survival (Regehr et al., 2010; Bromaghin et al., 2015). The paucity of

concurrent, long-term data on polar bears and their prey has limited our understanding of the mechanisms by which sea ice conditions and prey abundance and health interact to influence polar bear body condition and vital rates. Stirling (2002) documented low polar bear natality and subadult survival in response to declines in the reproduction and density of ringed seals in the eastern Beaufort Sea. In Davis Strait, increased abundance of harp seals was associated with increased polar bear survival and reproduction (Peacock et al., 2013). Elsewhere, however, data on the abundance and condition of seals are lacking, precluding determination of the effects prey have on polar bear population dynamics. Where available, ecological and environmental data have been used to infer factors important to polar bear population dynamics. For example, in the eastern Beaufort Sea, Pilfold et al. (2015) described relationships between polar bear kill rates and ringed seal reproduction, ice concentration, and large-scale atmospheric circulation patterns (i.e., the winter Arctic Oscillation (AO)) and concluded that kill rates are influenced by a combination of abiotic and biotic factors.

In this study, we examined relationships between sea ice conditions, seal body condition (as an indicator of seal biomass), a climatic index, and the annual body condition, recruitment, diet and spring feeding probability (i.e., the probability of having fed in the past 7-10 days) of polar bears in the Chukchi Sea using 8 years of capture-based measurements and samples collected during the period 2008-2017. The Chukchi Sea polar bear subpopulation ranges throughout an expansive area of sea ice over productive shallow continental shelf waters (Sakshaug, 2004) between the northwest coast of Alaska and northeast coast of Russia in the Bering, Chukchi, and east Siberian seas (Fig. 1). Each summer, the sea ice in this region retreats northward and the duration between retreat and return has increased by 9 days per decade since the 1980s (Douglas, 2010; Stern & Laidre, 2016; Molnár et al., 2020). Optimal polar bear habitat was estimated to have declined by 8% per decade between 1979 and 2006 (Durner et al., 2009). Additionally, Wilson et al. (2016) documented a 75% reduction in the area of preferred summer sea ice habitat during the same time period. In response, some polar bears are spending more of the summer on land rather than on the sea ice (Rode et al., 2015; Atwood et al., 2016). Based on radio-collared females, 40% of Chukchi Sea bears spent an average of 60 days on land in the summers of 2008-2013 (Rode et al., 2015). Onshore, collared females were estimated to spend >90% of their time resting (Ware et al., 2017), although some scavenge marine mammal carcasses (Laidre et al., 2018). Except for pregnant females that enter dens, polar bears remain

on the sea ice during the winter months to hunt. Although the extent of sea ice over which polar bears can hunt for prey is substantially reduced in the summer, most of the Chukchi Sea bears' range is ice-covered the rest of the year. Thus, the amount of prey available to polar bears, independent of sea ice, may be an important factor affecting bear condition and recruitment.

In the absence of data on seal density and abundance, we used seal body condition as a proxy for seal biomass within the Chukchi Sea ecosystem. We also considered the potential for the winter AO to affect polar bear recruitment, body condition, diet, and feeding probability because the AO appears to capture aspects of environmental conditions important to polar bear feeding ecology that are not reflected directly in the limited sea ice and prey metrics available (i.e., Derocher, 2005; Pilfold et al., 2015; McKinney et al., 2017; Rode et al., 2018). When the winter AO index is lower, older thicker ice occurs in the central Arctic (Rigor et al., 2002) and lower AOs have been associated with higher densities and body condition in ringed seals (Ferguson et al., 2005; 2020). Although the seasonal extent of sea ice can be quantified via satellite data, there are likely other features of sea ice (e.g., the availability of leads and thickness) that affect polar bear predation rates, some or all of which may be indicated by the winter AO. Our objectives were to: (a) determine if polar bear body condition and recruitment exhibited a trend from 2008 to 2017 and (b) evaluate whether sea ice cover and concentration, seal body condition, and the winter AO were associated with polar bear body condition, recruitment, diet, and spring feeding probability.

## **2. MATERIALS AND METHODS**

### **2.1 Polar bear capture and sampling**

Polar bears were captured and released on sea ice in the Chukchi Sea off the northwest coast of Alaska between mid-March and late April in 2008-2011, 2013, and 2015-2017 (Fig. 1). Captures were conducted from a helicopter and all bears encountered were sampled if conditions were safe to do so (e.g., no open water hazards, sufficient helicopter fuel, bear was not visibly injured).

Polar bears were immobilized with zolazepam-tiletamine (Telazol®) administered by a dart. Immobilized bears were weighed to the nearest kilogram (kg). Age of independent bears (i.e., bears that had been weaned and were not with their mother) was determined by counting cementum annuli in a vestigial premolar extracted during capture (Calvert & Ramsay, 1998). Cubs in this subpopulation remain with their mothers for approximately 2.5 years. Thus, females

captured in the spring could be accompanied by dependent cubs-of-the-year (COY; <6 months old), yearlings (< 18 months old), or by two-year-old cubs that would be soon weaned.

However, we rarely observed females with COY because key denning areas for the Chukchi Sea subpopulation occur in Russia (e.g., Rode et al., 2015), approximately 650 km from our study area. COY are identifiable based on size, whereas yearlings and two-year-olds overlap in size and were distinguished based on dentition.

Adipose tissue biopsies and blood samples were collected from all independent bears for fatty acid-based diet analyses (Thiemann et al., 2008) and quantification of serum urea and creatinine ratios to determine the probability that a bear had fed in the past 7-10 days (feeding probability) (Rode et al., 2018). A 6-mm biopsy punch was placed approximately 15 cm lateral to the base of the tail to collect an adipose sample. Blood was drawn from femoral vasculature in one of the rear legs and collected in no-additive tubes and centrifuged the same day to remove serum.

Starting in 2009, we visually assessed whether a bear had fed just prior to capture to determine whether gut fill might influence the body mass measurement (Rode et al., 2020). We used gut palpitation, direct observations of feeding prior to capture, and fecal sampling to determine the potential for a bear to have food in their digestive tract at the time they were weighed. “Full” bears were identified based on tight extended bellies and observations of feeding prior to capture and “empty” bears were those that were not observed feeding prior to capture, had bellies that could be palpitated with no apparent sounds or movement of a recent meal, did not defecate during capture, and had no fecal material in their rectum (Rode et al., 2020) or had serum urea and creatinine ratios  $\leq 10.0$  (Derocher et al., 1990; Rode et al., 2018). Bears between these two categories were identified as “partially full”.

## **2.2 Body condition and recruitment**

We used residual body mass to quantify bear body condition (hereafter referred to as “body condition”) based on the difference between measured body mass and predicted mass from a modified von Bertalanffy growth curve fit to the relationship between age and body mass using sex-specific curves that accounted for gut fill (Rode et al., 2014; 2020; see Supplemental Methods; Fig. S1a & b). Body mass has been identified as an indicator of reproductive success and survival in bears (Derocher & Stirling, 1996; Hertel et al., 2017; Folio et al., 2019; Rode et al. 2020). The residual body mass measures accounted for age effects on body mass so that

bears of different ages could be included in the same analyses. Gut fill was also accounted for in estimating residual body mass because a bear's stomach contents at capture can contribute meaningful weight to body mass measures (Rode et al., 2020).

We used four indices of recruitment for polar bears: 1) the body condition of dependent young because cub mass has been linked to cub survival (Derocher & Stirling, 1996; Rode et al., 2020), 2) the litter size of females observed with yearlings, 3) the percent of females accompanied by yearlings as an annual summed metric, and 4) the number of yearlings per the total number of adult females ("yearlings per female") in the annual capture samples which combines cub production, first year cub survival, and litter size into a single metric and has been commonly used to assess reproductive success in polar bears (Derocher, 2005; Rode et al., 2014; Regehr et al., 2018). Litter size and the percent of females accompanied by yearlings are components of yearlings per female (index 4). Because females with COY are under-represented in our sample, we excluded the 3 females captured with COY from recruitment measures.

### **2.3 Dietary prey proportions**

We used quantitative fatty acid analysis (QFASA) to estimate the contribution of different prey species to polar bear diets. Fatty acids were measured in adipose tissue samples collected from independent polar bears and in blubber samples from prey species. Fatty acids in polar bear adipose tissue completely turnover within ~100 days (Iverson et al., 2004; Thiemann et al., in review). Therefore, adipose tissue collected from polar bears in this study from mid-March to early May would represent diet from approximately December through the date of spring capture. Based on species overlap and observational data described in the Supplementary Methods, we included the following prey in QFASA models: ringed seal pups, ringed seal non-pups (i.e., all sex/age classes except pups), bearded seal non-pups, beluga whales (*Delphinapterus leucas*) and bowhead whales (*Balaena mysticetus*). Details of the QFASA model are provided in Supplemental Methods.

### **2.4 Feeding probability**

Serum urea and creatinine levels from blood were used to determine the probability that a bear had fed during the 7-10 days prior to capture. Previous studies with both captive and wild polar bears have shown that serum urea declines simultaneous to increases in serum creatinine when bears fast, such that bears that have not fed in 7-10 days have serum ratio of urea to creatinine approximately  $\leq 10.0$  (Nelson et al., 1984; Derocher et al., 1990; Cherry et al., 2009;

Rode et al., 2017). Rather than creating a binary dataset classifying bears as having fed or not fed based on serum urea to creatinine ratios, we used a Bayesian mixture model as described below and in Rode et al. (2018) to estimate the probability of feeding (i.e., feeding probability) for each bear in our data set. We then examined relationships between feeding probability, year, and ecological and environmental variables. Urea nitrogen (BUN) and creatinine were measured in blood serum samples using an Abaxis VS2 analyzer (Abaxis, Union City, CA, USA). Ratios of serum urea to creatinine (i.e., urea:creatinine ratios) were calculated as urea nitrogen/0.466/creatinine (Nelson et al., 1984).

## **2.5 Sea ice, atmospheric circulation, and seal body condition**

We examined annual variability in polar bear body condition, recruitment, feeding probability, and diet in relation to indices of sea ice conditions, prey biomass, and a climatic index across multiple spatial-temporal scales. These included specific measures of sea ice availability from satellite data over seasonal timeframes hypothesized to affect feeding and energetics, indices of prey availability seasonally and annually, and the winter AO index (i.e., the average of monthly AO indices for January to March, as provided by the National Ocean and Atmospheric Administration's Climate Prediction Center; <https://www.climate.gov/news-features/understanding-climate/climate-variability-arctic-oscillation>)(Table 1).

We included three sea ice metrics derived from satellite data in models of body condition, recruitment, diet and feeding probability (Tables 1 & 2). Ice metrics were based on aspects of sea ice that are selected by polar bears or related to polar bear behavior (Durner et al., 2006; Wilson et al., 2014; Rode et al., 2015; Stern & Laidre, 2016) and included: (1) the mean daily percentage of the Chukchi/Bering Seas continental shelf covered by sea ice of  $\geq 15\%$  concentration summed from March to May (*MarMayIce*) during the same year (t) that bears were measured and sampled, (2) the same mean daily percentage from June to November of the prior year (year t - 1) (*JunNovIce*), and (3) the number of days with sea ice during the prior calendar year (year t -1) (*DaysIce*; i.e. the days prior to sea ice breakup + the days after sea ice advance) as defined in Stern and Laidre (2016) within the IUCN Polar Bear Specialist (PBSG) group subpopulation boundary (Table 1). Further explanation of these metrics is provided in Supplementary Methods.

Because *WinterAO* is correlated with surface air temperature and sea ice conditions through most of the subsequent year (Rigor et al., 2002), we considered *WinterAO* of the year in



which a bear was captured (since bears were captured mid-March through the end of April) and that of the prior year (*PriorWinterAO*) (Table 1).

Seal body condition was used as proxy for prey biomass available to polar bears because annual data on seal density and abundance were not available in the Chukchi Sea. Blubber thickness of ringed and bearded seals was provided by Alaska Native subsistence hunters from 11 coastal communities in northwestern Alaska as part of an Alaska Department of Fish and Game Ice Seal Biological Monitoring program. Residual blubber thickness of seals was quantified as the mean blubber thickness for a given year relative to the average across all years while accounting for season and seal age. Blubber thickness residuals (hereafter referred to as ringed seal or bearded seal “body condition”) from the prior fall for ringed seals (year  $t - 1$ ; collected in all 8 of the study years) and for the current spring for bearded seals (year  $t$ ) were included in candidate models of spring polar bear body condition (year  $t$ ; collected in 7 of the 8 years in which polar bear data were available). These seasonal measures were used because they were available for more years in which polar bear data were collected than data collected on fall bearded seal and spring ringed seal blubber thickness.

## **2.6 Temporal trends in polar bear body condition and recruitment**

To determine if polar bear body condition and recruitment exhibited a trend over the 10-year study period, we modeled each dependent variable using the model type and covariates identified in model sets 1-5 (Table 2) with year as the only explanatory variable (i.e., without sea ice, seal body condition, or AO). Temporal trends were identified based on the  $\chi^2$  and p-value of the coefficient for year in the model.

## **2.7 Relating polar bear body condition, recruitment, diet and feeding probability to sea ice, seal body condition, and AO**

Prior to analyses, we evaluated annual trends in sea ice, seal body condition, and AO using a linear regression with year. We examined Pearson correlations among sea ice, seal body condition, and AO variables to identify pairs of variables that were highly correlated. Collinearity diagnostics specific to candidate models were conducted as described below.

Our focus was to identify variables that were associated with polar bear body condition, recruitment, diet and feeding probability, rather than build predictive models. Table 2 identifies the dependent variable in each analysis, the type of model used (e.g., general linear, logistic), the

covariates included to account for effects that were not of interest (e.g., *Age*, *Sex*, date in which a bear was captured - *Cdate*), and the ecological and environmental independent variables.

## **2.8 Models of polar bear body condition and recruitment**

We used general linear models to examine relationships between the body condition of independent bears and sea ice metrics, seal body condition, and AO. Independent females and males were analyzed separately (Model sets 1 and 2, Table 2). Age class was included in all candidate models of bear body condition for both sexes as a three-level categorical variable and defined based on growth curves and sexual maturity: (1) subadults were independent bears aged 2-4 that were not sexually mature and exhibit substantial structural growth with age; (2) young adults were bears ages 5-10 that were sexually mature with moderate increases in structural size with age; and (3) adults were bears ages 11+ that were sexually mature and exhibit a reduced or negligible increase in mass and length with age. Female bears captured in the spring that denned the previous winter exhibit lower body condition than females of other reproductive classes (Rode et al., 2020). Thus, we included a binary variable (*CoY*) in all models of female body condition (Table 1). Bear body condition does not differ among females with yearlings, females with two-year-olds, and lone females or relative to the litter size of cubs accompanying a female (Rode et al., 2010; 2020).

The body condition of dependent young was analyzed separately from independent bears and included only yearlings and two-year-olds because only 3 COY were captured during the 8 years of data collection (Model set 3, Table 2). A nested age(sex) effect was included in all candidate models of dependent young to allow body condition to vary and coefficients to be estimated for the four age and sex classes of dependent young (Table 2). Capture date was included in all models of dependent young body condition (Table 2) because sampling occurred over a 5-6 week period between mid-March and late April when dependent young grow rapidly.

We used a binary logistic regression to examine whether yearling litter size of individual females was related to ice metrics, ringed seal fall body condition, and winter AO (Model set 4, Table 2). Litter sizes of 1 and 2 or more were used as the dependent variable because only 3 of 46 females with yearlings had litter sizes of 3. General linear models were used to examine relationships between other recruitment variables (the number of yearlings per female, or the percent of females with yearlings, summed in annual samples) and ice metrics, ringed seal fall body condition, and winter AO (Models set 5 & 6, respectively, Table 2).

All possible combinations of independent factors listed in Table 2 were included in candidate models, except combinations in which variables were identified as being collinear based on diagnostics described below. An intercept-only model was included as a candidate model and intercepts were included in all candidate models. We did not consider interactions among main effects because we did not have specific hypotheses for interactions and samples size were relatively small (8 years of data). We identified collinear variables as those with eigenvalues near 0, variance proportions of 0.50 when condition indices  $> 15$  (here, condition index is a statistical term for a collinearity diagnostic that is unrelated to bear body condition), or with variance inflation factors  $> 5$  (Belsley, 1991; Douglass et al., 2003; Midi et al., 2010). Collinear variables were included in separate models only. We identified variables that influenced bear body condition or recruitment as those occurring in models with  $\Delta AIC_c \leq 2.0$  (referred to as “top models”; Burnham & Anderson, 2002). AIC model weights ( $w_i$ ) were summed for each variable among the top models. However, it is important to note that weights for collinear variables may be biased because the variables are used less frequently in candidate models and thereby have a reduced opportunity to acquire weight across models (Smith et al., 2009; Freckleton, 2011). Because our objective was to identify influential variables, we focused on identifying the variables that occur in top models and focused less on comparisons among top models when interpreting results. In the supplementary material we present all models with  $\Delta AIC_c \leq 7.0$ , because models with  $\Delta AIC_c > 7.0$  have little to no support (Burnham & Anderson, 2002). We report the model coefficients ( $\beta$ )  $\pm$  standard error (SE) and p-values. For linear models we used  $\chi^2$  and p-values to compare fit relative to an intercept-only model (i.e., significant differences suggest improved fit from the intercept-only model), and for binary logistic regression we used Hosmer-Lemeshow  $\chi^2$  and p-values (i.e., significant differences confirm adequate model fit) to confirm model fit. All analyses of polar bear body condition and recruitment indices were conducted in IBM SPSS statistical software Version 27.0.0.0.

Spring bearded seal body condition data were available for 7 of the 8 years in which polar bear data were collected. As a result,  $AIC_c$  values could not be compared between models of polar bear body condition or feeding probability because  $AIC_c$  values are affected by sample size. Therefore, relationships with polar bear variables and spring bearded seal body condition were examined in separate models based on the parameter  $\chi^2$  and p-value for linear models and whether the 95% credible interval on the parameter estimate overlapped 0 for Bayesian mixture

models. Spring bearded seal body condition was not included among the variables that were related to diet (Table 2).

## **2.9 Relationships with polar bear diet**

We used a redundancy analysis to examine relationships between the percent each prey species contributed to individual polar bear diets and combinations of ice metrics, seal body condition, AO, and year variables (Model set 7, Table 2) similar to the approach described by Florko et al. (2020). A Hellinger transformation (square root of each dietary proportion; Florko et al., 2020) was used to reduce skewness in the data associated with variability in the prominence of some prey versus others. A forward stepwise procedure was used to identify the suite of variables that influenced prey proportions using the “vegan” package (Oksanen et al., 2019) of R (R Core Team, 2020, version 4.0.3). Probabilities of 0.025 and 0.030 were used as thresholds for variables to be added or removed from the model, respectively.

## **2.10 Models of polar bear feeding probability**

Relationships between the probability that a bear fed in the past 7-10 days (as a dependent variable) and ice metrics, seal body condition, winter AO, and year were examined using Bayesian mixture models in which urea:creatinine ratios were modeled as a mixture of two gamma distributions dependent on the feeding status of individuals (as described in Rode et al., 2018)(Model set 8, Table 2). Informed priors for the mean and variance parameters were based on data from Derocher et al. (1990) in which the urea:creatinine ratios of 13 fasting and feeding captive polar bears were measured. We modeled the probability that an individual bear had fed in the past 7-10 days as a function of variables known to affect feeding behavior, including capture date, age class, and sex (i.e., Rode et al., 2018), and combinations of ice metrics, ringed seal fall body condition, and winter AO. Watanabe Akaike Information Criteria (WAICs) were used to identify top models. Capture date, age class, and sex were included in all candidate models and alone in a candidate model for comparisons with models that included ice metrics, ringed seal fall body condition, and winter AO. A separate model with capture date, age class, sex, and year was used to determine if there was a trend in feeding probability over the 10 years of the study. Relationships between feeding probability and model variables were determined by comparing models with ice, seal, and AO variables to those with capture date, age class, and sex only. We also examined the significance of variables based on whether mean  $\beta$ -values

(coefficients) overlapped the 95% credible interval (Rode et al., 2018). Models of feeding probability were conducted in R (R Core Team 2020, version 4.0.3).

### 3. RESULTS

#### 3.1 Temporal trends and correlations among ice, seal body condition, and AO

Although there has been a long-term temporal trend of declining summer sea ice extent in the Arctic (Fig. 2), there was no temporal trend in sea ice extent in the Chukchi Sea between June and November during our study (*JunNovIce*:  $r = 0.11$ ,  $p = 0.76$ ; Fig. 3a). However, spring ice extent (*MarMayIce*) over the continental shelf declined during the study ( $r = -0.84$ ,  $p < 0.01$ ; Fig. 3b). No other ice, seal body condition, or AO metrics exhibited temporal trends during the study period.

Fall ringed seal body condition (*RSFallBodyCondition*) was lower when sea ice extent was high over the continental shelf during June–November ( $r = -0.85$ ,  $p < 0.01$ ; Fig. 4a) and bearded seal spring body condition was positively correlated with *PriorWinterAO* ( $r = 0.76$ ,  $p < 0.01$ ) (Fig. 5a). The *DaysIce* was lower during years preceding a higher winter AO ( $r = -0.71$ ,  $p = 0.05$ ).

#### 3.2 Temporal trends in bear body condition and recruitment

There was no temporal trend in female (*Year + AgeClass + Coy*:  $\beta = 0.21 \pm 0.85$ ,  $\chi^2 = 0.06$ ,  $p = 0.80$ ), male (*Year + AgeClass*:  $\beta = 2.7 \pm 1.5$ ,  $\chi^2 = 3.4$ ,  $p = 0.07$ ), or dependent young (*Year + Age(Sex) + Cdate*:  $\beta = -0.71 \pm 0.75$ ,  $\chi^2 = 0.88$ ,  $p = 0.35$ ) body condition during 2008–2017. There was also no temporal trend in three recruitment indices including the number of yearlings per female in the annual capture sample (model with year only:  $\chi^2 = 0.46$ ,  $p = 0.50$ ; mean across all years  $\pm$  stdev:  $0.62 \pm 0.33$ ), the percent of females with yearlings in the annual capture sample (model with year only:  $\chi^2 = 0.23$ ,  $p = 0.63$ ), and yearling litter size (*Age + Year*:  $\chi^2 = 0.10$ ,  $p = 0.75$ ).

#### 3.3 Relationships between body condition of independent bears and ecological and environmental variables

The top models of independent female bear body condition (in spring of year  $t$ ;  $n = 143$  bears) indicated negative relationships with *JunNovIce* (Fig. 4b; combined  $w_i$  of top models including *JunNovIce* = 0.43;  $\beta = -1.9 \pm 0.5$ ,  $p < 0.01$ ), *DaysIce* (in year  $t - 1$ ; combined weight = 0.27;  $\beta = -0.6 \pm 0.2$ ,  $p < 0.01$ ), *winterAO* (in year  $t$ ; combined weight = 0.70;  $\beta = -4.4 \pm 2.1$ ,  $p = 0.04$ ), and *PriorWinterAO* (in year  $t - 1$ ; combined weight = 0.29;  $\beta = -3.2 \pm 2.5$ ,  $p = 0.20$ ); and a

positive relationship with *RSFallBodyCondition* (in year t - 1; Fig. 4c; combined weight = 0.27;  $\beta = 8.4 \pm 6.4$ ,  $p = 0.19$ ) (Tables 3 & S1; Fig. 5b). *DaysIce* was collinear with *MarMayIce* and AO (positively related). Thus, these variable pairs were not included in the same models. All top models exhibited improved fit compared to the intercept-only model ( $\chi^2 > 18.0$  and  $p < 0.01$ ). A body mass value for one female was identified as an outlier and removed from the data set prior to generating the predicted mass curve. Spring bearded seal body condition was not related to female body condition in a separate linear model that included the 7 years of spring bearded seal body condition with *AgeClass* and *Coy* ( $\beta = 9.1 \pm 13.1$ ,  $n = 131$ ,  $\chi^2 = 0.5$ ,  $p = 0.49$ ).

The top model of independent male bear body condition ( $n = 185$ ) included a positive relationship with *PriorWinterAO* ( $\beta = 9.9 \pm 4.2$ ,  $p = 0.02$ ; Fig. 5b) and negative relationship with *JunNovIce* ( $\beta = -2.2 \pm 0.9$ ,  $p = 0.02$ ) ( $w_i = 0.26$ ; Tables 3 & S2). Only one other model had a  $\Delta AIC_c \leq 2.0$  which included a positive relationship with *PriorWinterAO* and a negative relationship with *DaysIce* ( $\beta = -0.5 \pm 0.2$ ,  $p = 0.03$ ;  $w_i = 0.12$ ). Male body condition was positively related to spring bearded seal body condition in the same year (year t) based on a separate model with the smaller data set (*Ageclass + BSSpringCondition*:  $\beta = 66.4 \pm 24.4$ , 114.3,  $n = 165$ ,  $\chi^2 = 7.4$ ,  $p < 0.01$ ; Fig. 5c). *PriorWinterAO* and *BSSpringCondition* were positively related (Fig. 5a). All top models exhibited improved fit compared to the intercept-only model ( $\chi^2 > 20.0$  and  $p < 0.01$ ). Body condition was low for six males that were age 23 and older (Fig. S1b), consistent with potential senescent decline in body condition (Derocher et al., 2005). We removed these six individuals prior to generating the predicted mass curve for males to avoid a negative bias in body condition during years in which these individuals were sampled.

### **3.4 Relationships between recruitment and ecological and environmental variables**

All three models with  $\Delta AIC_c \leq 2.0$  for body condition of 113 yearlings and two-year-olds indicated that bear body condition was higher during years with lower winter AOs (combined  $w_i$  of the 3 models = 0.83;  $\beta = -6.5 \pm 1.7$ ,  $p < 0.01$ ) (Tables 4 & S3). A positive relationship with *RSFallCondition* was identified in two of the top models (combined  $w_i = 0.55$ ;  $\beta = 18.2 \pm 8.0$ ,  $p = 0.02$ ) and a negative relationship with *PriorWinterAO* occurred in the model with the lowest  $AIC_c$  but no other top models ( $w_i = 0.40$   $\beta = -5.3 \pm 2.5$ ,  $p = 0.03$ ). *MarMayIce* and *DaysIce*, *RSFallCondition* and *JunNovIce*, *WinterAO* and *DaysIce*, and *WinterAO* and *MarMayIce* were collinear and not included in the same models. Yearling females had the lowest body condition

( $\beta = 27.3 \pm 6.4$  kg lower than male two-year-olds;  $p < 0.01$ ) followed by yearling males ( $\beta = 29.7 \pm 5.7$  kg lower than male two-year-olds;  $p < 0.01$ ), and two-year-old females ( $\beta = 7.0$  kg lower than male two-year-olds;  $p < 0.01$ ). Body condition increased with spring capture date ( $\beta = 0.40 \pm 0.19$ ,  $p = 0.04$ ). There was no relationship with bearded seal spring body condition when included in a separate model with *Age(Sex)* and capture date ( $\beta = -11.3 \pm 10.8$ ,  $\chi^2 = 1.1$ ,  $n = 109$ ,  $p = 0.30$ ). All top models exhibited improved fit compared to the intercept-only model ( $\chi^2 > 32.0$  and  $p < 0.01$ ).

The model of yearling litter size with the lowest  $AIC_c$  included *WinterAO* but the model weight was low (0.17) and five other models (of 21 total models) containing different variables had  $\Delta AIC_c \leq 2.0$  (Tables 4 & S4). Among top models, Hosmer-Lemeshow  $\chi^2 > 3.0$  and p-values  $> 0.25$  suggested adequate model fit, but low weights among a suite of different variables indicated large model-selection uncertainty. Variables in all models had p-values  $> 0.05$ .

The annual number of yearlings per adult females in the capture sample (which combines litter size and presence/absence of yearlings) was negatively related to *WinterAO* ( $\Delta AIC_c = 0$ ,  $w_i = 0.76$ ,  $\beta = -0.19 \pm 0.06$ ,  $n = 113$  females captured during 8 years;  $p = 0.02$ ; Fig. 6a; Table 4). All other models (27 total models) had  $\Delta AIC_c$  values  $> 2.0$  and much lower weights ( $w_i \leq 0.05$ ) (Table S5). The same pattern was apparent for the percent of females accompanied by yearlings. The top model included *WinterAO* ( $\Delta AIC_c = 0$ ,  $w_i = 0.66$ ,  $\beta = -8.7 \pm 3.3$ ,  $p < 0.01$ ; Figs. 6b; Table 4) and all other models (27 total models) had  $\Delta AIC_c$  values  $> 2.0$  and much lower weights ( $w_i \leq 0.06$ ) (Table S6).

### 3.5 Diet

Prey species contributions to Chukchi Sea polar bears diets based on QFASA modeling are provided in Table 5. Estimated calibration coefficients are provided in Table S7. Adult male diets were comprised mostly of bearded seals (40%), followed by beluga whale (21%), and non-pup (17%) and pup (13%) ringed seals. Adult female diets were mostly non-pup ringed seal (57.5%) followed by equal percentages of bearded seal and beluga whale (13%). Bowhead whales comprised  $< 8.5\%$  of the diet of all sex and age classes. The percent of ringed seal non-pups in diets were higher following falls when ringed seal body condition was higher (Fig. 7). The percent of ringed seal pups in the diet were also higher during years with a more positive AO index and greater ice extent from March until May (*MarMayIce*). The percent of bearded seals in diets were positively related to the amount of sea ice from June to November

(*JunNovIce*). *DaysIce* was excluded from the stepwise modeling process due to high collinearity (variance inflation factor >5).

### 3.6 Feeding probability

The top model of feeding probability included *RSFallCondition*, *DaysIce*, and *PriorWinterAO* ( $\Delta\text{WAIC}_c = 0$ ,  $w_i = 0.35$ ;  $n = 296$  subadult and adult male and female bears) and had a substantially lower  $\text{WAIC}_c$  value compared to the null model ( $\Delta\text{WAIC}_c = 25.1$ )(Table S8). Bears had a higher feeding probability when *RSFallCondition* was higher the prior fall ( $\beta = 1.51$ , 95% credible interval: -0.02, 3.27; Fig. 8), when *PriorWinterAO* was higher (0.34; 95%CI: -0.88, 1.51) and when duration of ice cover was lower (*DaysIce*: -0.37, 95%CI: -1.43, 0.64)(Table S5). The only other model with a  $\Delta\text{WAIC}_c \leq 2.0$ , included *RSFallCondition* with no other variables ( $\Delta\text{WAIC}_c = 1.36$ ,  $w_i = 0.18$ )(Table S8). A separate model identified that feeding probability was higher when *BSSpringCondition* was higher based on the 7 years of available data ( $\beta = 1.36$ ; 95%CI = -0.42, 2.31). The probability of feeding was 4.27 times (95%CI: 2.60, 6.28) higher in females than males consistent with reduced male feeding during spring breeding which occurs throughout the timeframe in which polar bears were sampled in this study (Rode et al. 2018). Feeding probability also increased with capture date during our 5-6 week spring field season ( $\beta = 1.97$ , 95%CI = 1.04, 2.99). There was no apparent trend in feeding probability over the 8 years in which data were collected (year:  $\beta = 0.06$ ; 95%CI = -0.78, 0.89).

Body condition and recruitment data, polar bear adipose tissue and seal blubber fatty acid data, and polar bear serum urea/creatinine data are available in Rode (2020), USGS Alaska Science Center Polar Bear Program (2017), and USGS Alaska Science Center Polar Bear Program (2021).

## 4. DISCUSSION

Polar bears have evolved to be a specialized predator feeding on marine mammals that they access from the sea ice. Throughout their circumpolar range, the majority of their diets are composed of 1-2 seal species (Thiemann et al., 2008; this study) which is not unlike other specialized predators, such as lynx (*Lynx lynx*), whose population status is closely associated with that of their prey (Tyson et al., 2010). In our study, the probability that a bear had recently fed in the spring was higher during years in which bearded and ringed seals were in better condition (Table 6). Dietary proportions of ringed seal consumed by adult females and subadults and the body condition of adult females and dependent young were higher during years with



higher ringed seal body condition (Tables 5 & 6). Males similarly exhibited higher body condition when bearded seal were in better condition consistent with bearded seals being their primary prey (40% of the diet; Tables 5 & 6). Thus, local and regional variation in the status of ice seals is likely an important factor that can either compound or mitigate the response of polar bears to sea ice loss over the short-term. Because seal body condition is associated with biomass and blubber content (Stirling & McEwan, 1975; Ryg et al., 1990) and corresponds with pup production (Harwood et al., 2012), years with higher seal body condition are likely reflective of increased total prey biomass, particularly because pups are also a seasonally important prey item (10-13% of winter-spring diets, see Table 5; Pilfold et al., 2012). In several regions where prey availability or biological productivity has increased in the Arctic simultaneous to sea ice loss, polar bear populations appear to have been unaffected or minimally affected (e.g., Foxe Basin: Galicia et al., 2016; Davis Strait: Peacock et al., 2013; Kane Basin: Laidre et al., 2020), whereas in regions where prey reproduction or body condition have declined simultaneous to sea ice loss, even if temporarily, polar bear populations have declined (e.g., southern Beaufort Sea; Bromaghin et al., 2015; Hudson Bay: Ferguson et al., 2017).

When polar bears lose sea ice habitat, they lose the platform from which they access prey. However, bears are capable of fasting for long periods (Atkinson & Ramsay, 1995) and the amount of sea ice required over the course of a year to support polar bear body condition, recruitment, and survival is dependent on the nutritional gains bears can make when on the sea ice (Molnár et al., 2010, 2020; Robbins et al., 2012). During the recent decades, sea ice loss has predominately occurred in summer (Stern & Laidre, 2016; Stroeve & Notz, 2018). But despite summer sea ice loss, over half the Chukchi Sea polar bear population remains on the sea ice throughout the year as it retreats toward the pole (Rode et al., 2015). Thus, unlike some parts of the Arctic where sea ice loss has lengthened the period in which populations lack access to prey during the summer (e.g., Hudson Bay), at least a portion of the Chukchi Sea subpopulation may retain access to prey throughout all or most of the year. Longitudinal studies suggest that between 1985 and 2011, Chukchi Sea polar bears did not exhibit declines in body condition and recruitment, despite declines in summer sea ice extent (Rode et al., 2014) and increased numbers of bears summering on land and spending longer durations there (Rode et al., 2015) where they primarily rest (Ware et al., 2017). Similarly, during the 10-year period of this study, we did not find evidence for a positive relationship between three sea ice metrics and polar bear body

condition and recruitment, which suggests that sea ice may not currently be limiting polar bears' ability to meet their annual nutritional requirements in this region. These results are consistent with Rode et al. (2014) and with recent energetics modeling (Molnár et al., 2020) suggesting that declines in summer sea ice extent have not yet negatively affected this subpopulation.

Body condition of male and female polar bears were higher following years with less sea ice cover during June-November (Table 6). These relationships are likely associated with the strong negative correlation between ringed seal body condition and June-November sea ice cover ( $r = -0.85$ ), which is consistent with previous studies that have shown improved ringed seal body condition and pup production following and during years with lower sea ice cover or earlier spring breakup (Crawford et al., 2015; Harwood et al., 2012, 2020; Nguyen et al., 2017). Thus, heavy ice conditions do not appear to be optimal for seals such that some degree of reduced sea ice extent increases seal productivity. However, both ringed and bearded seals are reliant on sea ice for pupping and molting in the spring and early summer. During our study, spring sea ice cover declined 2% per year to levels not previously observed within the satellite record (Fig. 3b) and consistent with patterns across the Arctic in which spring and winter sea ice have exhibited the greatest declines in recent years (Stroeve & Notz, 2018). In 2018 and 2019, spring sea ice was sufficiently reduced such that polar bears could not be safely captured and sampled in our study area and were the lowest years of spring sea ice coverage since 1985 (Fig. 2). Consequently, polar bears lost a large area of habitat in which they typically hunt, and ringed and bearded seals lost habitat used for pupping and molting.

Winter AO appears to encapsulate variability in sea ice and prey conditions that are important to polar bears. We identified that indicators of recruitment were higher during, or following, years with lower winter AOs (Table 6, Fig. 6) consistent with previous studies that have similarly shown increased frequency of predation (Pilfold et al., 2015; Rode et al., 2018), increased proportions of ringed seal in adult female and juvenile diets (McKinney et al., 2017), and lower hair cortisol levels (Bechshoft et al., 2013) during years with lower winter AOs. Lower winter AOs have also been associated with increased abundance and productivity of ringed seals (Nguyen et al., 2017; Ferguson et al., 2020) and may represent aspects of sea ice conditions important to polar bear foraging, such as sea ice thickness (Rigor et al., 2002; Park et al., 2018), that are not reflected in satellite data of sea ice area and concentration. In Svalbard, body mass of adult male and female polar bears, cubs per female per year, and the proportion of

females accompanied by cubs were similarly negatively correlated with the AO (Derocher, 2005) suggestive that the winter AO may be an important factor influencing cub production, survival, or both across Arctic systems. Further research is needed to understand the mechanistic relationships among the winter AO, surface air temperatures, sea ice extent and effects on various biotic trophic levels within Arctic marine systems.

Unlike indicators of recruitment, male body condition was higher when the prior winter AO was higher (rather than lower; Fig. 5b). However, this relationship was influenced by a single year (the winter of 2009–2010) in which the prior winter AO was the lowest on record since 1951 (Stroeve et al., 2011; Fig. 5c). The low AO year corresponded with the third lowest sea ice extent on record, counter to conditions typical of low AOs (Cohen et al., 2010; Stroeve et al., 2011) and had the lowest bearded seal body condition of any year of our study (Fig 5a). Although it is possible that males exhibit patterns with the AO that are opposite of those exhibited by females and young bears due to differences in diet, the relationship between male body condition and the prior winter AO may be an artifact of an anomalous year during our study.

## 5 CONCLUSIONS

Our results support that, wherever possible, monitoring both the annual availability of sea ice and the status of prey populations will give a more thorough indication of the status of polar bears. Male and female polar bears are likely responsive to different aspects of the Arctic ecosystem. In the Chukchi Sea, bearded seal and beluga whale made up 61% of the winter-spring male diet whereas females and subadults primarily ate ringed seals, a pattern common throughout the Arctic (Thiemann et al., 2008). We limited the prey species included in our diet models to those we believed were available to polar bears during the winter and spring when they deposited the adipose fat we sampled, but in the summer, gray whale carcasses (*Eschrichtius robustus*; Laidre et al., 2018) and walrus (*Odobenus rosmarus*; Kochnev, 1999; Ovsyanikov, 2005) are available and this prey diversity could also play a role in buffering the short-term effects of summer sea ice loss on the condition and recruitment of bears in this subpopulation. Monitoring patterns in broader atmospheric metrics such as the winter AO and understanding how those metrics affect polar bears regionally, will further aid in assessing the near-future status of polar bears. For example, increasing frequency of high winter AOs would be a potential warning sign of negative effects on polar bear recruitment. Finally, conditions in

the Arctic are changing rapidly. In the long-term, even in places like the Chukchi Sea where polar bears have maintained body condition and recruitment while summer sea ice loss has occurred, the dependence of polar bears and seals on sea ice suggests they are not robust to limitless loss of sea ice habitat. Studies have shown that there are thresholds at which effects become apparent (Castro de la Guardia, 2013; Molnár et al., 2020), and determining population-specific thresholds continues to be an important area of research. Our study suggests that monitoring prey simultaneous to sea ice availability and continuing investigation into links with atmospheric circulation patterns will be important in determining when compounding factors are likely to negatively affect polar bear populations.

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**TABLE 1.** Descriptions of variables included in models examining relationships with polar bear body condition, recruitment, diet, and feeding probability. Models are described in Table 2.

Variable Name	Description
<i>Cdate</i>	The day of the year in which a bear was captured and measured
<i>Sex</i>	A binary variable indicating whether a bear was a male or female
<i>Age</i>	A bear's age. This variable was used only for distinguishing yearlings and two-year olds in models of dependent young body condition.
<i>AgeClass</i>	Categorical variable used to indicate subadults (1: age 3-4 years), young adults (2: age 5-10 years), and adults (3: age > 10 years)
<i>Coy</i>	A binary variable indicating whether a female was accompanied by cubs-of-the-year (i.e. first year cubs; 1) or not (0)
<i>Year</i>	Calendar year
<i>Litsize</i>	A binary variable of 1 cub or more than 1 cub.
<i>MarMayIce</i>	The percent of the Chukchi/Bering Seas continental shelf covered by sea ice of $\geq 15\%$ concentration between March and May of the current year
<i>JunNovIce</i>	The percent of the Chukchi/Bering Seas continental shelf covered by sea ice of $\geq 15\%$ concentration from June to November of the previous year
<i>DaysIce</i>	The number of days between advance of sea ice in the fall of the previous year and the retreat of sea ice during the current year. Date of advance and breakup were determined as described in Stern and Laidre (2016) within the IUCN Polar Bear Specialist Group boundary for the

	Chukchi Sea subpopulation. This boundary includes the northern Bering and Chukchi Sea and does not occur only over the continental shelf.
<i>RSFallCondition</i>	Residual blubber thickness (cm) of ringed seals (excluding pups) harvested by 11 communities in the Bering and Chukchi seas in the fall prior to polar bear sampling and measurement.
<i>BSSpringCondition</i>	Residual blubber thickness (cm) of bearded seals (excluding pups) harvested by 11 communities in the Bering and Chukchi seas in the spring of the same year in which polar bears were sampled and measured.
<i>PriorWinterAO</i>	Winter Arctic oscillation index determined as the mean for the months of Jan-March the year prior to polar bear sampling and measurement.
<i>WinterAO</i>	Winter Arctic oscillation index determined as the mean for the months of Jan-March for the year in which polar bears were sampled and measured.

**TABLE 2.** Prey, ice, and AO metrics (i.e., factors), covariates (variables included in all models to account for sources of variation that were not parameters of interest), and model descriptions used to address study objectives. “Ice metrics” include *MarMayIce*, *JunNovIce*, and *DaysIce* (see Table 1). Seal body condition includes *RSFallCondition* and *BSSpringCondition* (see Table 1). “AO” includes the Arctic Oscillation index from the prior year (*PriorWinterAO*) or current year (*WinterAO*; see Table 1). Variables that were identified as being collinear (per diagnostics described in the text) were not included in the same candidate models. Spring residual blubber thickness of bearded seals (i.e. “seal body condition”) were not available for all years. Thus, relationships with that variable was considered in separate models or analyses. GLM indicates general linear model. Variables are defined in Table 1.

Model set	Dependent variable	Model type	Covariates (not parameters of interest)	Factors
1	Independent female residual body mass (body condition)	GLM	<i>AgeClass, Coy</i>	<i>Ice metrics, Seal body condition, AO</i>
2	Independent male residual body mass (body condition)	GLM	<i>AgeClass</i>	<i>Ice metrics, Seal body condition, AO</i>
3	Residual mass of dependent yearlings and two-year-olds (body condition and recruitment)	GLM	<i>Cdate, Age(Sex)</i>	<i>Ice metrics, Seal body condition, AO</i>
4	Yearling litter size (1 or $\geq 2$ ) (recruitment)	Binary logistic regression	<i>Age (of mothers)</i>	<i>Ice metrics, Seal body condition, AO</i>



5	Annual yearlings per female (recruitment)	GLM		<i>Ice metrics, Seal body condition, AO</i>
6	% females with yearlings (recruitment)	GLM		<i>Ice metrics, Seal body condition, AO</i>
7	The percent of each prey item in the diet (diet)	Redundancy analysis		<i>Ice metrics, Ringed seal fall body condition, AO</i>
8	Feeding probability	Bayesian mixture model	<i>AgeClass, Sex, Cdate</i>	<i>Seal body condition, Ice metrics, AO</i>

**TABLE 3.** Model selection results for female and male polar bear body condition (i.e., model sets 1 and 2, respectively as identified in Table 2) and their associations with sea ice conditions, indices of seal body condition, and the winter Arctic Oscillation index (*PriorWinterAO* and current *WinterAO*) with  $\Delta AIC \leq 2.0$ . The following variables were collinear and not included in the same candidate models: *RSFallCondition* and *JunNovIce*, *WinterAO* and *DaysIce*, and *WinterAO* and *MarMayIce*. K indicates the number of parameters in the model and  $w_i$  is the model weight. Coefficients are reported in the text. A list of models with  $\Delta AIC \leq 7.0$  are provided in Tables S1 and S2.

<b>Model</b>	<b>K</b>	<b><math>\Delta AIC_c</math></b>	<b><math>w_i</math></b>
<b>Female Body Condition (n = 143)</b>			
AgeClass + Coy + JunNovIce + WinterAO	6	0	0.25
AgeClass + Coy + JunNovIce + WinterAO + PriorWinterAO	7	0.6	0.18
AgeClass + Coy + RSFallCondition + WinterAO + DaysIce	7	0.8	0.16
AgeClass + Coy + RSFallCondition + WinterAO + PriorWinterAO + DaysIce	8	1.6	0.11
<b>Male Body Condition (n = 185)</b>			
AgeClass + PriorWinterAO + JunNovIce	5	0	0.26

AgeClass + PriorWinterAO + DaysIce	5	1.5	0.12
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**TABLE 4.** Model selection results for cub recruitment, including the body condition of dependent young (model set 3 from Table 2), yearling litter size (model set 4), and the annual number of yearlings per adult females in the capture sample (model set 5), and percent of females in the annual capture sample with yearlings (model set 6) and their associations with sea ice, ringed seal fall body condition, and winter AO. Dependent young include bears age 1 and 2 accompanying their mother. Models shown are those with  $\Delta AIC_c \leq 2.0$ . Model variables and the type of model used are described in Tables 1 and 2. Collinear variables and the number of candidate models are identified in the text. K indicates the number of parameters in the model and  $w_i$  is the model weight. A list of models with  $\Delta AIC \leq 7.0$  are provided in Tables S3-S6.

Model	K	$\Delta AIC_c$	$w_i$
<b>Dependent Young Body Condition (n = 113 bears)</b>			
Age(Sex) + Cdate + RSFallCondition + WinterAO + PriorWinterAO	7	0	0.40
Age(Sex) + Cdate + WinterAO	5	0.7	0.28
Age(Sex) + Cdate + RSFallCondition + WinterAO	6	2.0	0.15
<b>Yearling litter size (n = 46 females)</b>			
WinterAO	2	0	0.17
PriorWinterAO	2	1.5	0.08
JunNovIce	2	1.6	0.08
DaysIce	2	1.8	0.07
RSFallCondition	2	1.8	0.07
MarMayIce	2	1.8	0.07
<b>Annual yearlings per female (n = 8 years)</b>			
WinterAO	2	0	0.76
<b>% of females per yearling (n = 8 years)</b>			
WinterAO	2	0	0.66

**TABLE 5.** Mean (+/- standard deviation) percent contribution of prey species to the late winter/spring diets of Chukchi Sea polar bears estimated using quantitative fatty acid signature analysis of polar bear fat biopsies and prey blubber. Diets were estimated separately by age class and sex. Potential prey included blubber from bearded seal non-pups, ringed seal non-pups, ringed seal pups, and beluga and bowhead whales.

<b>Age/Sex Class</b>	<b>N</b>	<b>Bearded seal non-pups</b>	<b>Ringed seal non-pups</b>	<b>Ringed seal pups</b>	<b>Beluga whale</b>	<b>Bowhead whale</b>
<b>adult females</b>	66	13.2 (13.3)	57.5 (20.8)	10.0 (7.6)	13.0 (11.0)	6.5 (5.5)
<b>young females</b>	43	11.5 (13.2)	58.5 (23.1)	12.3 (11.0)	12.7 (12.6)	5.1 (5.1)
<b>subadult females</b>	25	8.1 (12.6)	63.2 (17.9)	10.2 (7.2)	15.2 (11.5)	3.4 (3.6)
<b>adult males</b>	67	40.2 (20.6)	17.1 (21.2)	13.4 (7.8)	20.8 (12.6)	8.5 (10.8)
<b>young males</b>	64	26.2 (16.8)	36.4 (26.6)	12.8 (8.9)	17.8 (14.4)	6.7 (8.1)
<b>subadult males</b>	40	10.2 (12.8)	54.6 (26.2)	11.0 (9.4)	18.6 (17.2)	5.6 (6.0)

**TABLE 6.** Summary of relationships between polar bear body condition and recruitment indices (as dependent variables in the columns) and sea ice, seal body condition, winter Arctic Oscillation index (AO), and year (as independent variables in the rows). Relationships between dependent (columns) and independent (rows) variables are based on whether the variable occurred in a model with  $\Delta AIC_c \leq 2.0$  as presented in Tables 3, 4, and S8. The directionality of the relationship between the dependent and independent variables are based on the sign of the coefficient associated with the independent variables in the model and are indicated as “+” for a

positive relationship, “0” for no relationship (i.e. the variable did not occur in a model with  $\Delta AIC_c \leq 2.0$ ), and “-” for a negative relationship.

	<b>Female Condition</b>	<b>Male Condition</b>	<b>Condition of Dependent Young</b>	<b>Yearlings per Female</b>	<b>% of females with yearlings</b>	<b>Yearling litter size</b>	<b>Feeding probability</b>
<b>JunNovIce</b>	-	-	0	0	0	0	0
<b>DaysIce</b>	-	-	0	0	0	0	-
<b>MarMayIce</b>	0	0	0	0	0	0	0
<b>RSFallCondition</b>	+	0	+	0	0	0	+
<b>BSSpringCondition</b>	0	+	0	0	0	0	+
<b>WinterAO</b>	-	0	-	-	-	-	0
<b>PriorWinterAO</b>	-	+	-	0	0	0	+
<b>Year</b>	0	0	0	0	0	0	0

**FIGURE 1.** Capture locations of 469 polar bears immobilized via helicopter darting between mid-March and early May 2008-2017 off the northwestern coast of Alaska in the Chukchi Sea. Inset shows the Chukchi Sea polar bear subpopulation boundary as defined by the International Union for the Conservation of Nature's Polar Bear Specialist Group in 2020.

**FIGURE 2.** Long-term trend in the percent of the Chukchi/Bering Seas continental shelf covered by ice of  $\geq 15\%$  ice concentration averaged daily from March to May (a) and June to November (b) 1985-2019. The box shows the polar bear data collection period (2008-2017).

**FIGURE 3.** Annual patterns in mean daily percent of the Chukchi/Bering Seas continental shelf covered by sea ice of  $\geq 15\%$  concentration between 2008-2017 from the prior June to November (a) and the current March to May (b) and the number of days with sea ice during the prior year (c) based on the estimated day of sea ice retreat and advance from Stern and Laidre (2016).

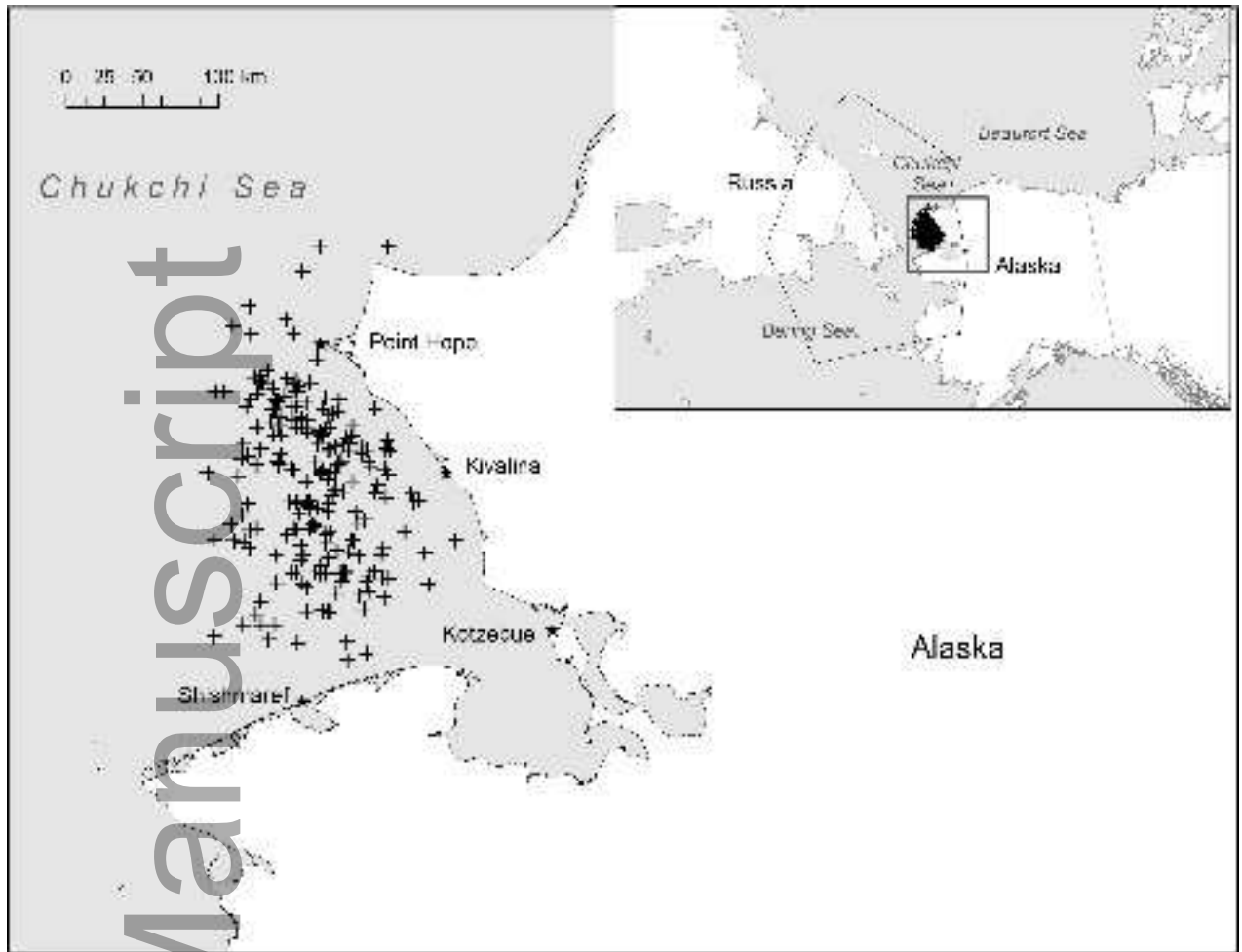
**FIGURE 4.** The inter-relationship of ringed seal body condition mean percent sea ice cover over the Chukchi continental shelf from June to November, and female polar bear body condition. Polar bear body condition is represented as residual body mass such that bears with body condition above zero were in better than average condition and those with condition below zero were in worse than average condition. Similarly, ringed seal body condition is represented as residual blubber thickness. Female polar bear body condition was related to both mean percent sea ice cover over the Chukchi/Bering Seas continental shelf from June to November (b) and ringed seal body condition (c), but these two factors were also collinear (a). Error bars are standard error.

**FIGURE 5.** The inter-relationship of the prior winter Arctic Oscillation (AO), bearded seal body condition and male polar bear body condition. Male polar bear body condition was related to both bearded seal body condition (b) and the prior winter AO (c), but these two factors were also collinear (a). Polar bear body condition is represented as residual body mass such that bears with body condition above zero were in better than average condition and those with condition below zero were in worse than average condition. Similarly, bearded seal body condition is represented as residual blubber thickness. A single low winter AO in 2010 was associated with both low bearded seal and low male polar bear body condition. Error bars are standard error.

**FIGURE 6.** Relationship between the winter Arctic Oscillation index for year  $t$  and (a) the total number of yearlings observed per female and (b) the % of females accompanied by yearlings in the spring of year  $t$ . For both dependent variables, females with cubs-of-the-year were excluded. Results of logistic regressions that use the 110 individual observations of female bears 2008-2017 are provided in the text.

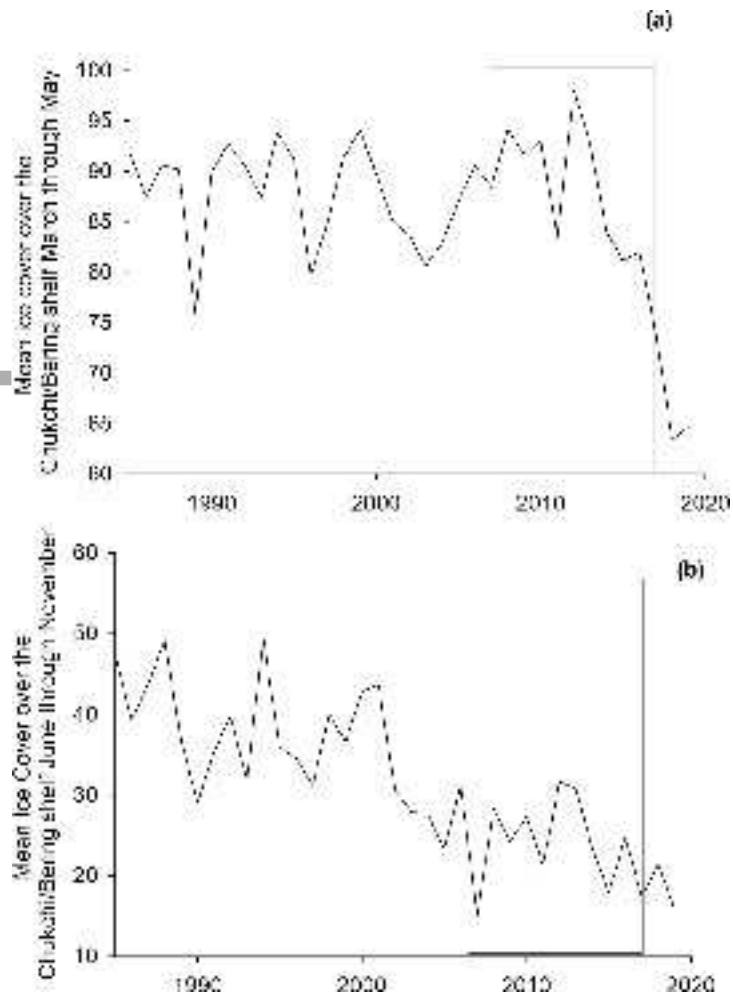
**FIGURE 7.** Results of the first two axes of a redundancy analysis correlation biplot examining relationships between the percent contribution of each prey type in Chukchi Sea polar bear diets (gray arrows) and sea ice (MarMayIce, JunNovIce), prey (RSFallCond), and climatic variables (WinterAO and PriorWinAO)(black dashed arrows) per Model set #7 in Table 2. Where variables and prey percentages align, positive correlations are strongest (e.g., RSFallCondition and RingedNonpup). Where variables and prey percentages align in opposing axes, correlations are strongly negative (e.g., JunNovIce and RingedNonpup proportions). The length of the arrow represents the strength of the association between the variable and the ordination axes shown. Prey type percentages were Hellinger transformed (i.e., the square root of proportions). Prey items included ringed seal pups (RingedPup), beluga, bowhead whale, ringed seal non-pups, and bearded seal pups and non-pups combined.

**FIGURE 8.** The relationship between the probability that a male or female bear fed in the 7-10 days prior to capture per Model Set 8 in Table 2. All bears were subadults or adults and were captured between mid-March and early May, 2008-2017. Model results are provided in Table S8.

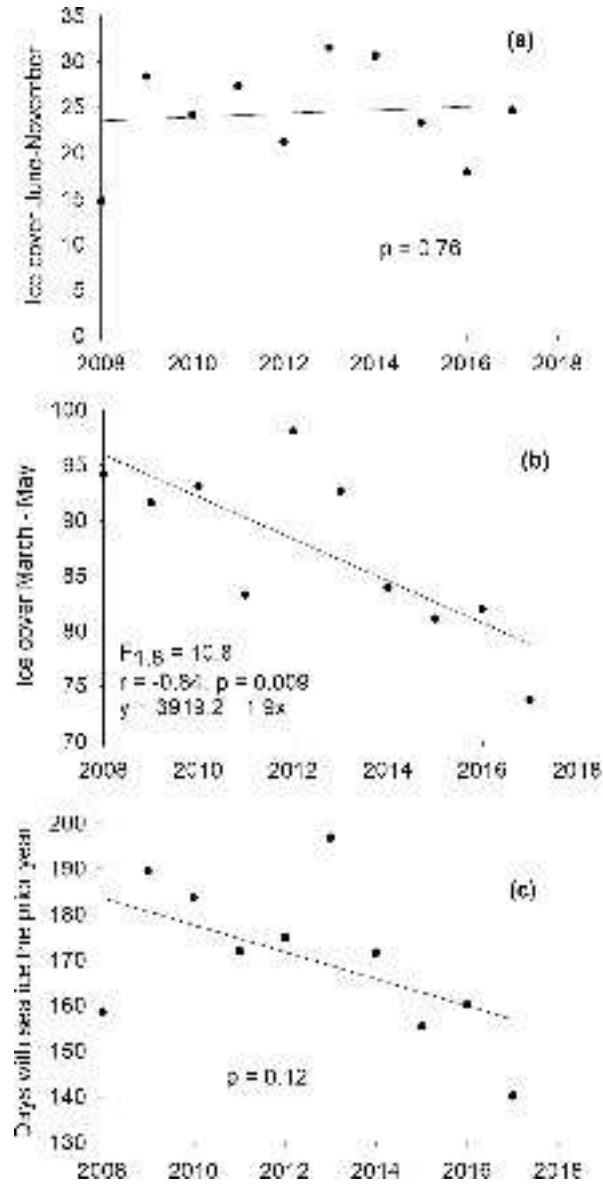


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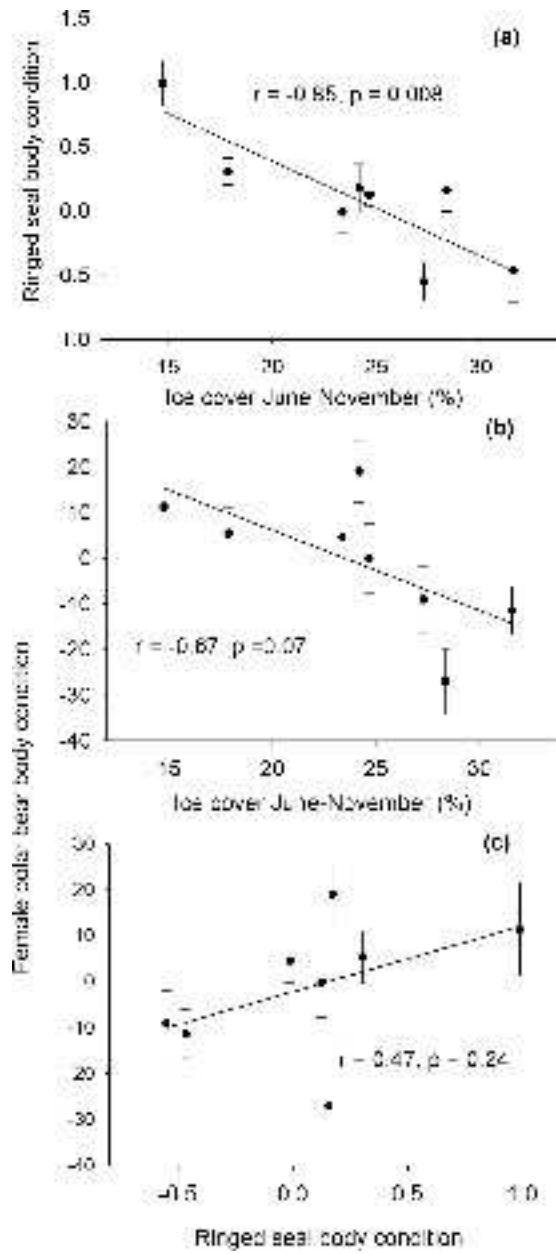




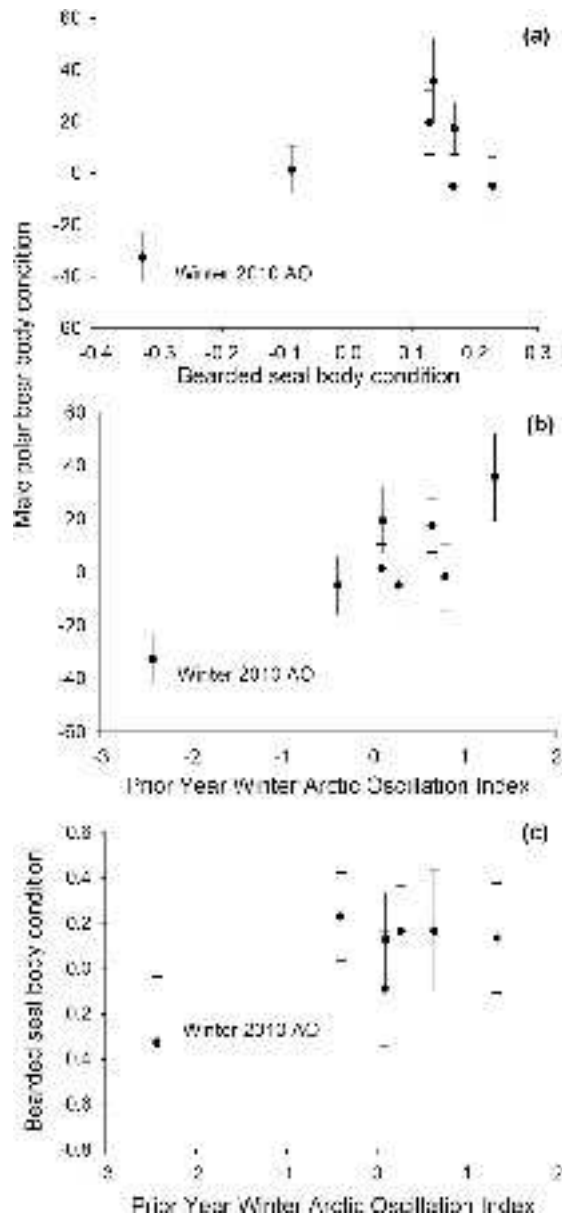
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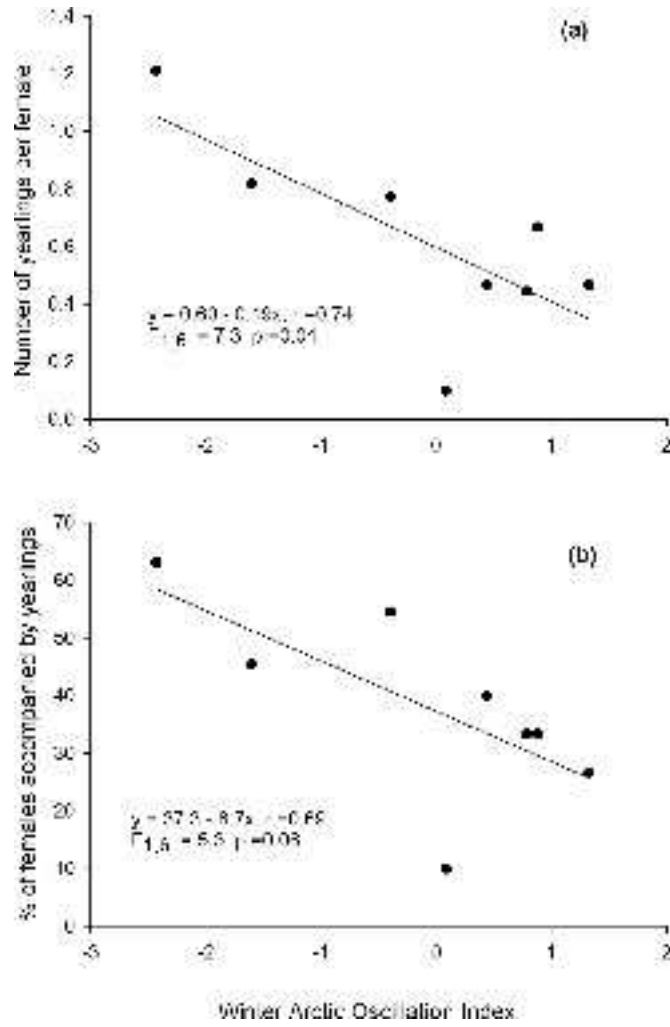
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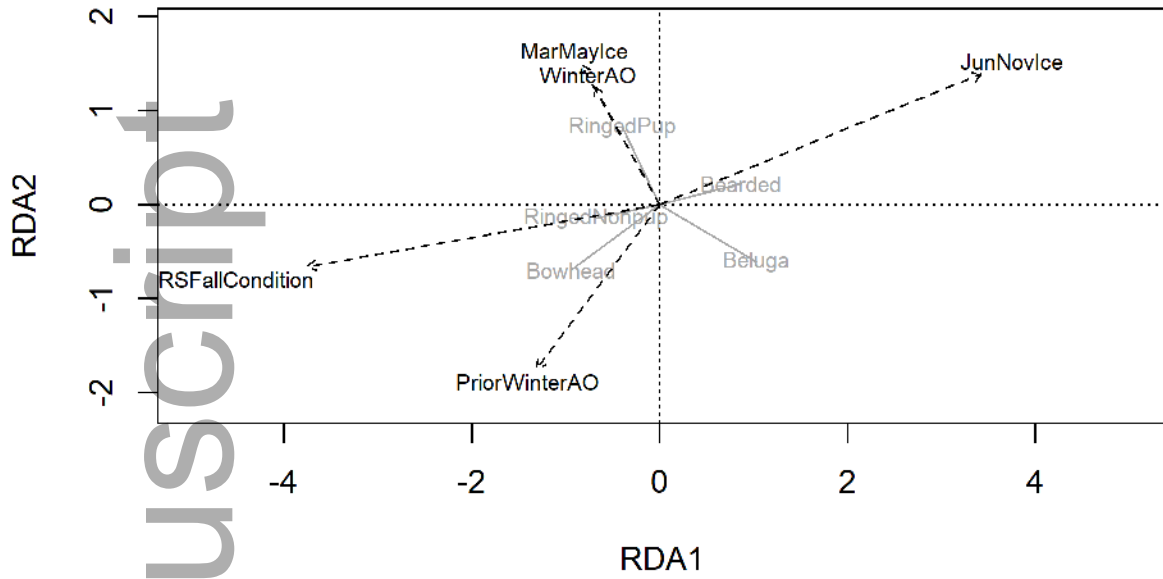
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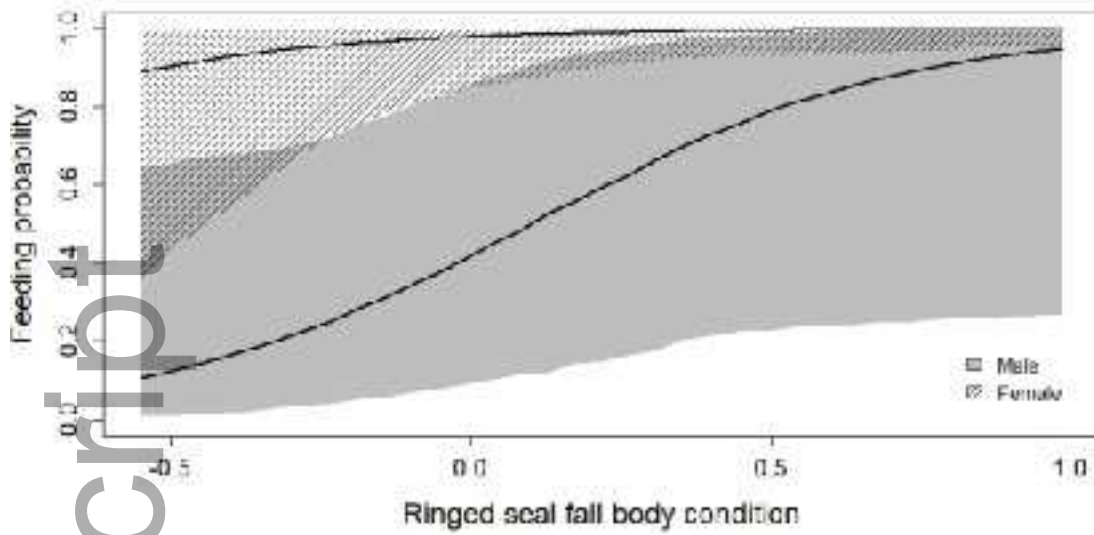
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