


# Dietary ecology of Alaskan polar bears (*Ursus maritimus*) through time and in response to Arctic climate change

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## Funding information

Vanderbilt University; National Science Foundation, Grant/Award Number: 1053839

## Abstract

Arctic climate change poses serious threats to polar bears (*Ursus maritimus*) as reduced sea ice makes seal prey inaccessible and marine ecosystems undergo bottom-up reorganization. Polar bears' elongated skulls and reduced molar dentition, as compared to their sister species the grizzly bear (*Ursus arctos*), are adaptations associated with hunting seals on sea ice and a soft, lipid-rich diet of blubber and meat. With significant declines in sea ice, it is unclear if and how polar bears may be altering their diets. Clarifying polar bear dietary responses to changing climates, both today and in the past, is critical to proper conservation and management of this apex predator. This is particularly important when a dietary strategy may be maladaptive. Here, we test the hypothesis that hard-food consumption (i.e., less preferred foods including bone), inferred from dental microwear texture analysis, increased with Arctic warming. We find that polar bears demonstrate a conserved absence of hard-object feeding in Alaska through time (including approximately 1000 years ago), until the 21st century, consistent with a highly conserved and specialized diet of soft blubber and flesh. Notably, our results also suggest that some 21st-century polar bears may be consuming harder foods (e.g., increased carcass utilization, terrestrial foods including garbage), despite having skulls and metabolisms poorly suited for such a diet. Prior to the 21st century, only polar bears with larger mandibles demonstrated increased hard-object feeding, though to a much lower degree than closely related grizzly bears which regularly consume mechanically challenging foods. Polar bears, being morphologically specialized, have biomechanical constraints which may limit their ability to consume mechanically challenging diets, with dietary shifts occurring only under the most extreme scenarios. Collectively, the highly specialized diets and cranial morphology of polar bears may severely limit their ability to adapt to a warming Arctic.

## KEYWORDS

archaeology, Carnivora, dental microwear, diet, mammal, ursid, *Ursus arctos*

## 1 | INTRODUCTION

Twenty-first-century anthropogenic warming poses major threats to biodiversity across latitudes, with especially pronounced and abrupt effects in the Arctic, such as spatiotemporal loss of ice cover,

lengthened melt seasons, and rapidly rising air and ground temperatures (Stroeve et al., 2014; Yamanouchi, 2011). Most notably, polar bears (*Ursus maritimus*) have captured public attention as a symbol of the costs and consequences that warming poses to wildlife. As receding sea ice habitats have reduced availability and access to their

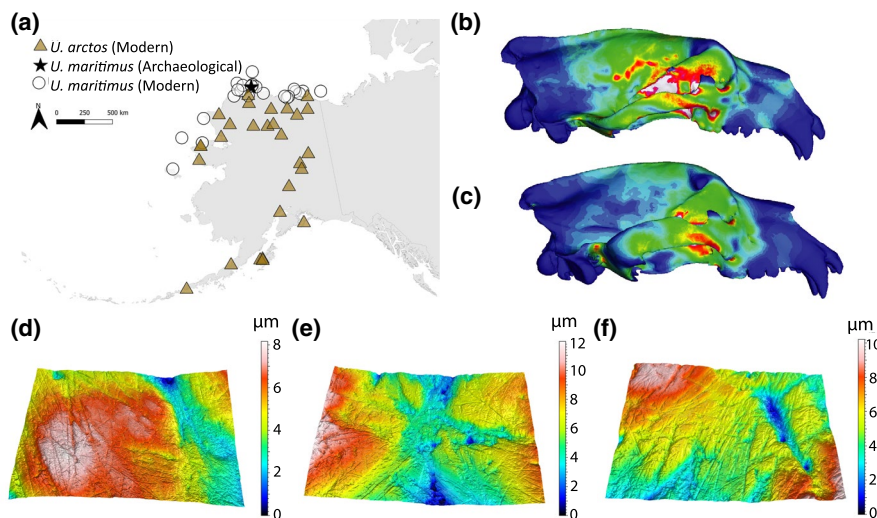
avored prey of Arctic ringed seals (*Pusa hispida*), which haul-out onto land less frequently when faced with inadequate ice and snow conditions, regional polar bear populations have experienced range contraction, geographic isolation, and marked declines in number as well as declines in body condition and overall health (Bromaghin et al., 2015; Hamilton et al., 2014; Laidre et al., 2018; Rode et al., 2012).

Polar bears are unique from other ursids in that they are hypercarnivorous maritime predators, feeding almost exclusively on diets high in flesh and blubber, largely hunted on sea ice (Pagano et al., 2018). Due to the high cost of maintaining their own blubber reserves for essential thermoregulation, polar bears preferentially consume blubber first, with flesh and bone often left behind as a result of increased metabolic costs required to mechanically process and digest tissues that provide lower energy return (Best, 1985; Dyck & Kebreab, 2009). The specialized diet of *U. maritimus* is reflected in their rapid and recent evolution, having diverged from the brown bear, *Ursus arctos*, only about 600,000 years ago during the Middle Pleistocene (Hailer et al., 2012; Hassanin, 2015), resulting in distinct dentition and skull morphology (Slater et al., 2010; Winer et al., 2016; Figure 1b,c). Polar bear canines are enlarged, while their molars are greatly reduced in size and feature prominent cusps. Their cranial morphology, which has evolved to accommodate their role as aquatic predators (e.g., elongated to hunt seals and fish via small holes in ice), is biomechanically weak compared to their omnivorous sister species and is poorly suited to mechanically challenging foods common in many omnivorous or herbivorous diets (Christiansen & Adolfssen, 2005; Slater et al., 2010). Sea ice decline in the 21st century has been shown to have complex effects on dietary composition and foraging success among Alaskan polar bears (Florko et al., 2020). Specialist limitations notwithstanding, polar bears which ordinarily hunt on ice and exploit marine resources of ringed and bearded (*Erignathus barbatus*) seals may be increasing labile land resource use at the subpopulation level with Arctic warming. In particular, the bears may be feeding more frequently on human-killed bowhead whale (*Balaena mysticetus*) carcasses and

other alternative terrestrial diets to compensate for the loss of lipid-dense, high-trophic prey (Bourque et al., 2020; Dyck & Kebreab, 2009; Gormezano & Rockwell, 2013; McKinney et al., 2017). Polar bears might also be expected to utilize their kills more fully when prey are scarce, consuming suboptimal tissues such as bone. In contrast, some bear subpopulations employ adaptive fasts in spring and summer when seal prey productivity is low, a strategy that puts bears at risk for muscle atrophy and can impede hunting activities (Whiteman et al., 2015, 2017, 2018).

Of relevance to polar bears' current and projected dietary responses to Arctic climate change is their behavior during periods of past environmental change. Notably, one such interval, known as the Medieval Warm Period (MWP), took place approximately 1000 years ago (Kinnard et al., 2011; Ljungqvist, 2010; Overpeck et al., 1997). The MWP has generally been referred to as a period between c. 800 AD and 1400 AD when global temperatures, including those in the Northern Hemisphere, were comparable or higher than temperatures in the 20th century (Hughes & Diaz, 1994). However, paleoclimate proxies display sometimes conflicting scenarios for regional atmospheric and sea surface temperature variations, as well as changes in glacial extent and aridity, during the MWP across the North American Arctic (see Jordan, 2009; Mason et al., 2020 for summary of MWP climate proxies in northwestern North America). The northern Alaskan climate during the MWP was no exception, having chaotic weather patterns and dramatic shifts in marine environments. These included heightened storms related to climatic cooling (Mason et al., 2020), development and restriction of beach ridge complexes (Anderson et al., 2020; Mason et al., 2020), and loss of sea ice extent likely associated with warming trends (Clark et al., 2019). The responses of marine and terrestrial faunal communities to these chaotic regional climate shifts remain poorly understood, with only a few exceptions of long-term sampling extending back into the MWP (Clark et al., 2019; Szpak et al., 2018).

As recorded and forecasted declines in seasonal sea ice are likely to cause polar bears to become more mobile and increase energy demands, it is critical to develop a clearer understanding of polar



**FIGURE 1** Map of specimen localities in Alaska (a), finite element models (b, c, from Slater et al., 2010), and 3D surface models showing microwear features of bears (d–f). Finite element models show von Mises stresses in the skull during unilateral M<sup>2</sup> biting for *Ursus maritimus* (b) and *Ursus arctos* (c). Microwear surfaces are representative of archaeological *U. maritimus* (d, ADMR1170), 21st-century *U. maritimus* (e, UAM138279), and modern *U. arctos* (f, UAM134791)

bears' dietary ecology through time—a challenge when examining hypercarnivorous predators that primarily reside in remote regions of the Arctic. In particular, assessing carcass utilization and other hard-food or tissue consumption may give new insights into adaptive strategies available to extant polar bears. In this study, we use dental microwear texture analysis (DMTA) to assess the dietary behavior of Alaskan polar bears in response to Arctic climate change. DMTA is a short-term dietary signal of tooth enamel microwear (acquired through food processing) which can infer soft, hard, and tough food consumption in the weeks to months before an animal's death (DeSantis, 2016). Unlike other dietary proxies which examine bulk diet (e.g., stable isotopes), DMTA is useful in characterizing the textural properties of tissues or materials consumed by a physiologically and morphologically specialized animal (DeSantis, 2016; Prassack et al., 2020; Scott et al., 2005, 2006). Two DMTA attributes are particularly revealing for polar bear diets: complexity (*Asfc*), which corresponds with hard-food consumption (e.g., bone in carnivorous diets); and anisotropy (*epLsar*), which corresponds with tough food consumption (e.g., tough flesh for carnivorous diets; DeSantis et al., 2012, 2015, 2017, 2019; Donohue et al., 2013; Merceron et al., 2017). Specifically, we here tested the hypothesis that polar bear hard-food consumption (e.g., bone, frozen flesh, or hard terrestrial materials) increased over the 20th century and into the 21st century with an inferred decline in prey availability. We also compared the dental microwear of modern bears to that of specimens from the MWP, to test the hypothesis that Alaskan polar bears have maintained similar diets of soft foods (e.g., blubber, flesh) over time—including during another period of pronounced climatic variability and environmental change. Relationships between dental microwear attributes, sex, and body size in polar bears were assessed across space and time, along with dietary comparison to the closely related (and less morphologically specialized) modern Alaskan grizzly bears (*Ursus arctos horribilis*).

## 2 | MATERIALS AND METHODS

### 2.1 | Materials and metadata

All modern Alaskan polar bears ( $n = 49$ , University of Alaska Museum of the North; of these,  $n = 42$  collected 1880–1985,  $n = 7$  collected 2002–2009) were analyzed for antemortem dental microwear textures over time and compared to archaeological polar bear specimens ( $n = 20$ , NIST Associate Director for Management Resources) dated to approximately 1000 years before present (see below; Tables S1 and S2), as well as to modern Alaskan grizzly bears ( $n = 32$ , collected 1949–2005; of these,  $n = 24$ , University of Alaska Museum of the North;  $n = 8$ , Los Angeles County Museum of Natural History, published in Jones & DeSantis, 2016; Table S3). The ursid specimens labeled with a collection date of “1880” ( $n = 3$ ) were assigned to the 19th/20th century; these specimens were collected during several earlier, unknown collection years prior to the 21st century (catalogued as “1880”). For statistical analyses, these were treated

as occurring prior to the 21st century (i.e., “20th century”), but not included in statistical regressions with collection year. Metadata for all modern specimens, including year, month, sex, and associated geographic data, was compiled from respective museum collections using the VertNet database (<http://www.vertnet.org>). When latitude and longitude were not available for a specimen, they were estimated from verbatim descriptive data (e.g., located 40 miles west of the city of “Barrow”) using Google Earth (<https://earth.google.com>). Specimens with estimated localities are noted as such in the supplementary materials.

Archaeological specimens were excavated from the Birnirk site, near Utqiagvik, between 1951 and 1953 by Wilbert K. Carter (Carter, 1966). Twenty polar bear specimens were analyzed: 10 mandibles and 10 skulls (see supplementary information). Sixteen of these specimens were recovered from three archaeological features (Mounds H, L, and Q) associated with the Birnirk and Western Thule cultures, archaeological complexes of the early Iñupiat culture that developed in Northern Alaska after AD 700 (Mason, 2016). Radiocarbon ages on wood, caribou antler, and bone artifacts from these mounds indicate that at least 13 of the Birnirk polar bear remains in our dataset lived, died, and were deposited at the site around 1000 AD (see supplementary materials for radiocarbon data). The other six polar bear specimens from the Birnirk site lack information on the features and artifacts they may have once been associated with, or they were recovered from an archaeological deposit that has yet to be radiocarbon dated; thus, we cannot provide age estimates for the millennium in which these six animals were living.

### 2.2 | Dental microwear texture analysis

For all specimens, microwear textures on the mesial facet of the lower second molar ( $m_2$ ) hyperconulid (an area used for crushing and grinding) were analyzed when possible. DMTA on the upper second molar ( $M^2$ ) was analyzed in specimens when the  $m_2$  was not able to be sampled, as both are functionally equivalent and effective indicators of ursid diets (Donohue et al., 2013).

Wear facets of tooth specimens were cleaned with acetone-soaked swabs before a polyvinyl siloxane dental impression material (President's Jet, Coltène-Whaledent Corp.) was applied to them to create a mold of the grinding surface. The dental impression molds were reinforced with vinylsiloxane dental putty (President, Coltène) before subsequent casting using a high-resolution transparent epoxy appropriate for confocal microscopic imaging (Epotek 301, Epoxy Technologies Corp.). Replica casts were scanned using a Sensofar PLu NEOX white light confocal 3D optical profilometer (Solarius Development, Inc.) under a 100× objective lens. Replicas were scanned as a  $3 \times 3$  grid, then profiles were leveled and converted to a  $2 \times 2$  grid of four rectangular subareas, each leveled a second time, for a total area of  $204 \times 276 \mu\text{m}^2$  in SensoMAP analysis software (per Jones & DeSantis, 2016). Examples of microwear surfaces are represented in Figure 1d–f. Resulting surface files (.sur) were processed through ToothFrax and SFrax (Surfract Corporation)

TABLE 1 Descriptive statistics for each ursid examined, including data from Jones and DeSantis (2016)

| Taxon (time of collection)                 | N  | Attribute           | Min.     | Max.       | Range      | Median     | Mean       | SD (n - 1) | Normality            |
|--|----|---------------------|----------|------------|------------|------------|------------|------------|----------------------|
| <i>Ursus maritimus</i><br>(archaeological) | 20 | Asfc                | 0.896    | 2.545      | 1.649      | 1.562      | 1.606      | 0.424      | 0.663                |
|  |    | epLsar              | 0.00112  | 0.00467    | 0.00355    | 0.00239    | 0.00253    | 0.000935   | 0.704                |
|  |    | Tfv                 | 6533.251 | 17,184.083 | 10,650.832 | 11,952.154 | 11,705.871 | 3096.258   | 0.651                |
|  |    | HAsfc <sub>81</sub> | 0.394    | 1.392      | 0.998      | 0.616      | 0.654      | 0.229      | 0.006 <sup>a</sup>   |
| <i>Ursus maritimus</i> (19th/20th century) | 42 | Asfc                | 0.598    | 3.007      | 2.409      | 1.618      | 1.694      | 0.579      | 0.589                |
|  |    | epLsar              | 0.00155  | 0.00631    | 0.00476    | 0.00314    | 0.00323    | 0.00104    | 0.114                |
|  |    | Tfv                 | 2775.499 | 15,421.056 | 12,645.557 | 10,819.761 | 10,321.901 | 2968.896   | 0.003 <sup>a</sup>   |
|  |    | HAsfc <sub>81</sub> | 0.357    | 2.019      | 1.662      | 0.657      | 0.757      | 0.365      | <0.0001 <sup>a</sup> |
| <i>Ursus maritimus</i> (21st century)      | 7  | Asfc                | 1.368    | 4.81       | 3.442      | 2.481      | 3.054      | 1.537      | 0.082                |
|  |    | epLsar              | 0.00115  | 0.00496    | 0.00381    | 0.00217    | 0.00270    | 0.00146    | 0.195                |
|  |    | Tfv                 | 8038.852 | 15,726.309 | 7687.457   | 13,259.933 | 13,356.473 | 2621.451   | 0.068                |
|  |    | HAsfc <sub>81</sub> | 0.65     | 1.498      | 0.848      | 0.807      | 0.905      | 0.286      | 0.064                |
| <i>Ursus maritimus</i> (modern)            | 49 | Asfc                | 0.598    | 4.81       | 4.212      | 1.687      | 1.888      | 0.899      | <0.0001 <sup>a</sup> |
|  |    | epLsar              | 0.00115  | 0.00631    | 0.00516    | 0.00313    | 0.00315    | 0.00111    | 0.257                |
|  |    | Tfv                 | 2775.499 | 15,726.309 | 12,950.810 | 11,057.221 | 10,755.411 | 3088.527   | 0.008 <sup>a</sup>   |
|  |    | HAsfc <sub>81</sub> | 0.357    | 2.019      | 1.662      | 0.693      | 0.778      | 0.356      | <0.0001 <sup>a</sup> |
| <i>Ursus arctos</i> (modern)               | 32 | Asfc                | 0.833    | 13.152     | 12.319     | 2.685      | 3.507      | 2.872      | <0.0001 <sup>a</sup> |
|  |    | epLsar              | 0.000800 | 0.00613    | 0.00533    | 0.00254    | 0.00296    | 0.00140    | 0.070                |
|  |    | Tfv                 | 83.775   | 16,115.222 | 16,031.447 | 11,265.703 | 10,151.573 | 4170.706   | 0.121                |
|  |    | HAsfc <sub>81</sub> | 0.335    | 2.847      | 2.512      | 0.657      | 0.735      | 0.439      | <0.0001 <sup>a</sup> |

Note: n, sample size; Min., minimum; Max., maximum; Range, total range; SD, standard deviation (n - 1); p < 0.05; Asfc, complexity; epLsar, anisotropy; Tfv, textural fill volume; HAsfc<sub>81</sub>, 9 × 9 heterogeneity.

<sup>a</sup>Denotes  $\alpha < 0.05$ .

software to assess textural properties via scale-sensitive fractal analysis. The median values of the four scans were used to represent a given specimen.

Surface scans were analyzed for complexity ( $Asfc$ ), anisotropy ( $epLsar$ ), textural fill volume ( $Tfv$ ), and heterogeneity ( $HAsfc_{81}$ ). Complexity is a measure of surface roughness that can be used to distinguish soft and hard-feeding behaviors across taxa (DeSantis, 2016; Scott et al., 2005, 2006). In carnivorous taxa, high complexity values generally indicate bone-crunching associated with scavenging carcasses, while hard seed or pit consumption will also produce high complexity values in more omnivorous taxa (e.g., DeSantis, 2016; DeSantis et al., 2012, 2015, 2017, 2019; Donohue et al., 2013; Jones & DeSantis, 2016; Scott et al., 2005, 2006). Anisotropy is a measure of directional uniformity in surface wear features. Parallel scratches observed in taxa whose diets include heavy amounts of shearing tough foods (e.g., shoots, grass, or flesh) produce high anisotropy values (e.g., DeSantis, 2016; DeSantis et al., 2012, 2017; Donohue et al., 2013; Scott et al., 2005, 2006). Textural fill volume is a measure of surface feature depth, calculated as the difference between the surface filled with large (10  $\mu$ m) and small (2  $\mu$ m) cuboids (31). High  $Tfv$  values indicate generally larger and deeper wear features, as is expected with harder food consumption such as carcass-feeding (DeSantis, 2016; DeSantis et al., 2012, 2015, 2017; Donohue et al., 2013). Heterogeneity quantifies the variation in complexity over a given surface area by comparing the complexity of  $9 \times 9$  ( $HAsfc_{81}$ ) subsections relative to the complexity of the larger surface (Scott et al., 2006). While  $HAsfc_{81}$  values are typically indistinguishable in ursids with disparate diets (Donohue et al., 2013; Jones & DeSantis, 2016), it is often useful to distinguishing between grazers and browsers in herbivores (i.e., herbivores eating foods with disparate textures; Merceron et al., 2017) and does provide some insights to extant polar bears diets in this study.

## 2.3 | Body size analysis of polar bears

Lower first molars ( $m_1$ ) are known proxies for mammalian body size; thus, lengths were obtained as outlined by Van Valkenburgh (1990). Molar length is more appropriately an indication of potential body size (as cheek teeth erupt early in life for bears and do not grow thereafter; Miller et al., 2009)—mandibular length (ML) is likely a better indicator of body size at the time of death than  $m_1$  length and was also measured. Photographs of specimens were obtained when dental microwear molding was performed. For a given modern specimen, it was possible to obtain one, both, or neither of the morphological measurements ( $m_1$ ,  $n = 42$ ; ML,  $n = 39$ ; Table S3), depending on preservation. Complete lower mandibles were not widely available for archaeological specimens, so these specimens were excluded from body size analysis. ML and  $m_1$  lengths available for a given specimen were measured in ImageJ software (Schneider et al., 2012) by pixels relative to a centimeter scale standard. Pixel measurements were taken three times using the “Straight” or “Rectangular” tool for

each measurement, and the mean of these measurements was used to calculate a metric length.

## 2.4 | Statistical analysis

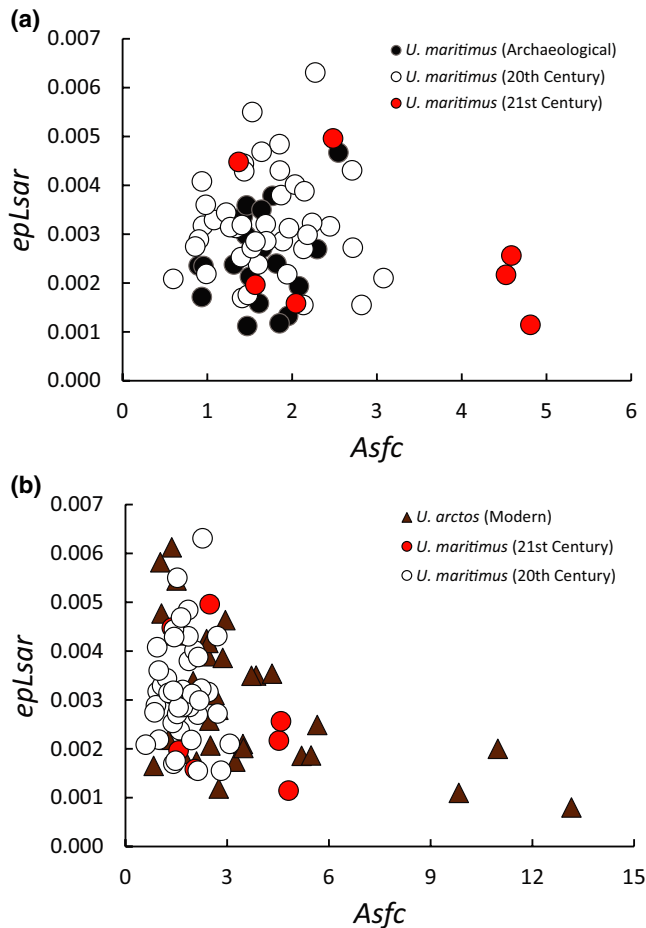
As DMTA data are largely non-normally distributed (Shapiro–Wilk test), nonparametric tests were used to compare DMTA attributes between (Mann–Whitney test,  $\alpha = 0.05$ ) and among groups of specimens (Kruskal–Wallis,  $\alpha = 0.05$ ), with additional parametric tests (Student's  $t$  test) employed when data were normally distributed (Shapiro–Wilk tests; see Table 1). Relationships among microwear, body size, and metadata variables (e.g., collection year, sex, location) were analyzed using nonparametric Spearman's rank order correlations, followed by simple linear regression models of significantly correlated variables.

## 3 | RESULTS

Dental microwear data for all archaeological (approximately 1000 years before present, during the MWP;  $n = 20$ ; Tables S1–S3) and modern (19th/20th and 21st centuries;  $n = 49$ ) polar bear specimens and modern (20th and 21st centuries;  $n = 32$ ) grizzly specimens are summarized in Table 1 and illustrated in Figures 1–3. All data are included in Tables S1–S3, along with morphological measurements and associated metadata. Dental microwear attributes described are  $Asfc$  (complexity),  $epLsar$  (anisotropy),  $Tfv$  (textural fill volume), and  $HAsfc_{81}$  (heterogeneity); high  $Asfc$  and  $Tfv$  values may broadly be interpreted as indicating hard-food consumption, while high  $epLsar$  values are consistent with the consumption of tough foods.  $HAsfc_{81}$  assess heterogeneity of complexity and has not been particularly revealing in carnivorous mammals to date, though it may prove useful in polar bears; we include it here to present a complete dataset (see Section 2 for detailed discussion of DMTA attributes; DeSantis et al., 2012, 2015, 2017, 2019; Donohue et al., 2013; Merceron et al., 2017).

Polar bears from the 20th century ( $n = 42$ , including three specimens which were collected sometime during the 19th and 20th centuries; see Section 2) exhibit  $Asfc$ ,  $Tfv$ , and  $HAsfc_{81}$  values indistinguishable from those of archaeological polar bears ( $p > 0.142$  via all relevant statistical tests). Only  $epLsar$  values are significantly higher in 20th-century polar bears than archaeological specimens ( $p = 0.012$ , Mann–Whitney  $U$ -test;  $p = 0.01$ , Student's  $t$  test). Twenty-first-century polar bears ( $n = 7$ ) have significantly higher  $Asfc$ ,  $Tfv$ , and  $HAsfc_{81}$  values than 20th-century polar bears ( $p = 0.027$ ,  $p = 0.008$ , and  $p = 0.044$ , respectively, Mann–Whitney  $U$ -tests;  $p < 0.0001$  for  $Asfc$ , parametric Student's  $t$  test). Twenty-first-century and 20th-century polar bear  $epLsar$  values are statistically indistinguishable ( $p = 0.184$ , Mann–Whitney  $U$ -test;  $p = 0.244$ , Student's  $t$  test). Twenty-first-century polar bears also have significantly higher  $Asfc$  and  $HAsfc_{81}$  values than archaeological polar bear specimens ( $p = 0.029$  and  $p = 0.019$ ,



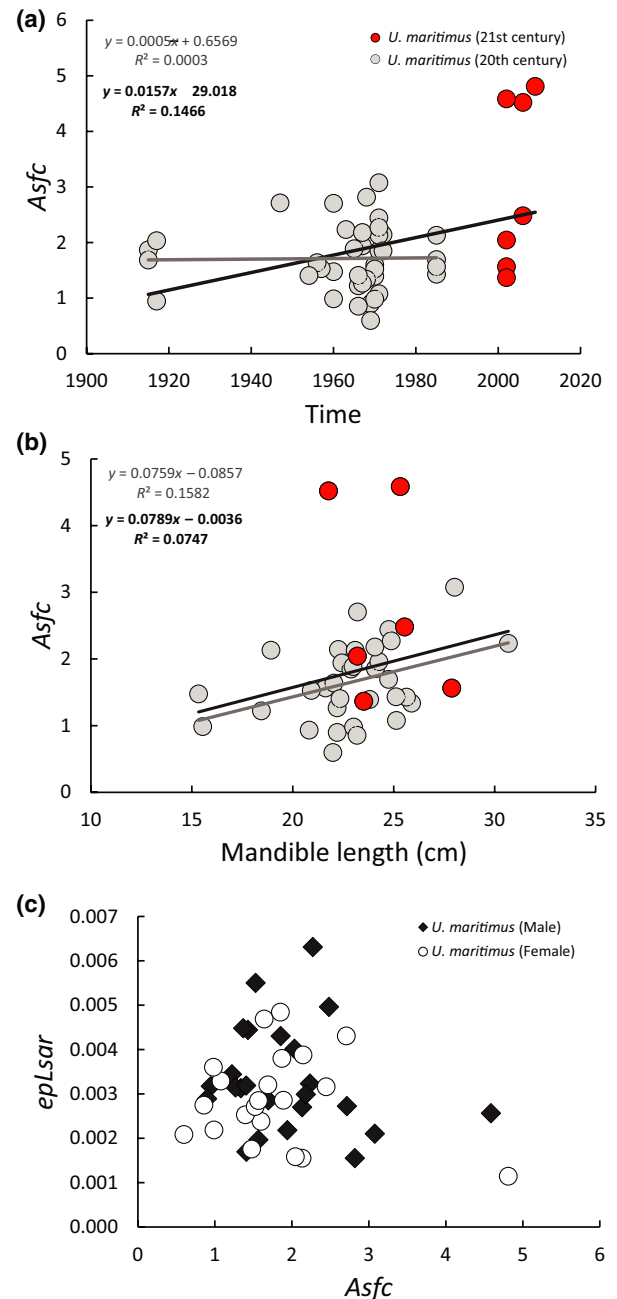


**FIGURE 2** Bivariate plots of *epLsar* (anisotropy) and *Asfc* (complexity) of all *Ursus maritimus* (a), and all modern *U. maritimus* and *Ursus arctos* specimens (b). *U. arctos* microwear includes data from Jones and DeSantis (2016)

respectively, Mann–Whitney *U*-tests;  $p < 0.001$  for *Asfc*, Student's *t* test), while *epLsar* and *Tfv* values are indistinguishable ( $p \geq 0.194$  via all relevant statistical tests).

Twentieth-century polar bear DMTA attribute values (i.e., *Asfc*, *epLsar*, *Tfv*, and *HAsfc<sub>81</sub>*) are not significantly associated with collection year from 1915 to 1985 ( $n = 39$ ,  $p \geq 0.08$ , Spearman rank-correlation test). However, when 21st-century specimens ( $n = 7$ ) are included in this analysis, *Asfc* and *HAsfc<sub>81</sub>* increase significantly over time from 1915 to 2009 ( $p = 0.035$  and  $p = 0.048$  respectively). Additional linear regression analysis for *Asfc* values yielded a significant positive relationship over time (Figure 3a,  $p = 0.009$ ,  $R^2 = 0.147$ ), while there is a nonsignificant relationship between *HAsfc<sub>81</sub>* values and collection year ( $p = 0.095$ ,  $R^2 = 0.062$ ).

Body size (as approximated via ML) is positively correlated with *Asfc* values in 20th-century polar bears ( $p = 0.033$ , Spearman rank-correlation test;  $p = 0.022$ ,  $R^2 = 0.158$ , linear regression analysis); however, this relationship is weaker when 21st-century polar bears, which are of significantly higher *Asfc* values than 20th-century specimens, are included ( $p = 0.031$ , Spearman rank-correlation test;  $p = 0.092$ ,  $R^2 = 0.075$ , linear regression analysis). No other



**FIGURE 3** Modern *Ursus maritimus* dental microwear relationships. *Asfc* (complexity) over time (1915–2012) for modern *U. maritimus* (a); gray line, linear regression from 1915 to 1985 ( $p = 0.508$ ,  $R^2 = 0.0007$ ); black line, linear regression with 21st-century specimens included ( $p = 0.009$ ,  $R^2 = 0.147$ ). *Asfc* (complexity) versus mandibular length in cm for modern *U. maritimus* (b); gray line, linear regression fit for 20th-century specimens only ( $p = 0.022$ ,  $R^2 = 0.158$ ); black line, linear regression with 21st-century specimens included ( $p = 0.092$ ,  $R^2 = 0.075$ ). Bivariate plot of *epLsar* (anisotropy) and *Asfc* (complexity) of *U. maritimus* by sex (c)

DMTA attributes are correlated with ML ( $p \geq 0.116$ , Spearman rank-correlation tests), whether 21st-century specimens are included or excluded from the analysis. While lower first molar ( $m_1$ ) length and lower ML are significantly correlated with one another ( $p = 0.001$

and  $p = 0.008$ , including or excluding 21st-century specimens, respectively, Spearman rank-correlation tests),  $m_1$  length is not significantly correlated with any DMTA attribute values in all analyses ( $p > 0.216$ , Spearman rank-correlation tests). Males do exhibit significantly larger  $m_1$  lengths than females ( $p = 0.001$ , Mann–Whitney  $U$ -test;  $p = 0.002$ , Student's  $t$ -test) and nearly significantly larger MLs ( $p = 0.057$ , Mann–Whitney  $U$ -test) in this dataset, and it is well established that male polar bears are larger than females in body mass (Derocher et al., 2010). However, there are no significant differences in any DMTA attribute values between sexes ( $p \geq 0.237$ , via relevant parametric and nonparametric tests, whether 21st-century specimens are included or excluded from analysis).

Polar bears exhibit significantly lower  $Asfc$  values than grizzly bears ( $p = 0.0006$ , Mann–Whitney  $U$ -test), when comparing all modern bears (including all 21st-century specimens). DMTA attribute values of  $epLsar$ ,  $Tfv$ , and  $HAsfc_{81}$  are indistinguishable ( $p = 0.306$ ,  $p = 0.681$ ,  $p = 0.321$ , respectively, Mann–Whitney  $U$ -tests;  $p = 0.483$  for  $epLsar$ , Student's  $t$ -test).

## 4 | DISCUSSION

The textural properties of Alaskan polar bear diets are largely consistent through time and characteristic of a soft diet from approximately 1000 years before present to and throughout the 20th century (Figures 2 and 3a). Specifically, there are no significant differences in  $Asfc$  or  $Tfv$ , or  $HAsfc_{81}$  values between 20th-century polar bears and those from archaeological sites, and these values remain low, indicating that the degree of hard-food consumption was consistently low during these two time periods. The lack of significant hard-food consumption suggests an absence of widespread carcass-feeding or terrestrial resource use behaviors among polar bears in either period. Twentieth-century polar bears do demonstrate a slight but significant increase in mean  $epLsar$  values relative to those from archaeological sites, signaling a shift toward some tougher food (e.g., more tough flesh) consumption in the modern period (Donohue et al., 2013; Schubert et al., 2010). However, the DMTA of all archaeological and 20th-century polar bear specimens is consistent with a diet of soft foods (i.e., blubber) rather than foods like hard bone, frozen flesh, or harder terrestrial materials such as tubers and seeds (DeSantis, 2016; Donohue et al., 2013).

Although the sample size of 21st-century bears is limited (due to the limited availability of recently collected skeletal polar bear specimens in museum collections), their microwear differs substantially in textural properties from the 20th-century polar bears and archaeological polar bears. Our results suggest that some 21st-century Alaskan polar bears are consuming significantly harder foods than in the preceding century. More durophagous diets produce higher  $Asfc$  and  $Tfv$  values (DeSantis et al., 2012, 2015, 2017, 2019; Schubert et al., 2010), consistent with observed differences between our 20th-century and 21st-century polar bears. The higher hard-food DMTA signal likely indicates increased carcass utilization of seals, scavenging at bowhead whale bone piles,

browsing or hunting on the terrestrial landscape, and/or utilizing human refuse (Bourque et al., 2020; Gormezano & Rockwell, 2013; McKinney et al., 2017). Additionally, the standard deviation of 21st-century polar bear  $Asfc$  values is elevated relative to other polar bear specimens (Table 1; Figure 2a), suggesting increased variability of feeding strategy among individuals of this group, perhaps in response to irregular availability of prey in recent years (Hamilton et al., 2014). The 21st-century polar bear  $Asfc$  values do fragment into two clusters, one being more elevated than the other (Figures 2a and 3a); however, there is no apparent geographic pattern to this distribution, with specimens from both Utqiagvik (formerly known as Barrow) and Prudhoe regions represented in each cluster. Though difficult to draw conclusions about a sample of this size, variability between habitats or other region-specific factors are not satisfactory interpretations for the patterning of 21st-century DMTA data.

There are no significant relationships between polar bear DMTA attribute values and collection year over the course of the 20th century in Alaska (Figure 3a)—thus, no evidence of a dietary shift among polar bears to consume more mechanically challenging foods from 1888 to 1985, as would be expected if the bears had begun to supplement their diets with more carcasses or terrestrial foods toward the latter part of the 20th century. Likewise, archaeological specimens are from the beginning of a period of climatic variability similar to that of the 19th to 20th century, but which took place over a longer period of time—yet also consumed soft foods (Figure 2a; Kinnard et al., 2011; Ljungqvist, 2010; Overpeck et al., 1997). These data suggest that, even during earlier warming periods with potential suboptimal prey access, polar bears generally do not appear to alter their dietary strategy in a significant way or to consume harder tissues or terrestrial food resources to any great extent. The lack of gradual change from typical dietary behaviors (e.g., selective preference for blubbery prey which must be hunted on sea ice) during earlier intervals of climate change, supports the conservation of specialist feeding behavior in this species. The contrast we observe between the diets of the 21st-century polar bears in this study, and those of preceding time periods (Figure 3a), may indicate a potential “tipping point” during the most recent period of accelerated warming—similar to recent dietary shifts in ringed seals (Clark et al., 2019; Szpak et al., 2018). Recent warming also greatly exceeds the temperature and sea ice anomalies of the MWP (Diffenbaugh & Field, 2013; Johannessen, 2008; Kinnard et al., 2011). Dietary changes may also be related to climate-driven regime shifts, which have been documented as occurring around the year 2000 in some Arctic benthic invertebrate communities (Kortsch et al., 2012). Extensive bottom-up reorganizations such as these contribute to the borealization of Arctic marine ecosystems and are highly sensitive to climate transitions (Saros et al., 2019).

Among 20th-century Alaskan polar bears, there is a significant positive relationship between ML and  $Asfc$  values, suggesting that polar bears with larger mandibles consume harder foods (Figure 3b). Therefore, the degree to which polar bears are able to process mechanically challenging food sources (e.g., frozen carcasses, bone,

and/or some terrestrial foods) is presumably mediated, to some extent, by size and physiology. Bears with larger jaws and larger bite forces, as well as an inferred larger body size, may be better able to alter their dietary strategies than smaller bears. However, even larger bears still exhibit low *Asfc* values throughout the 20th century. It is likely that morphological constraints somewhat limit polar bears from successfully utilizing more versatile diets, though conditions may now favor a dietary strategy for which their morphology is not adapted. Not surprisingly, molar size is not significantly related to any DMTA attribute values, in contrast to ML. As molar eruption occurs early in development and is under strong genetic control, polar bear size at the time dental microwear is recorded is better correlated with ML (e.g., an estimate of the actual body size at death, as opposed to potential body size as inferred from molar length). Despite known size differences in male and female polar bears (Derocher et al., 2010; Derocher & Wiig, 2002), and data demonstrating that male polar bears have significantly larger first molars than females (and trend toward larger mandibles, though insignificant), dental microwear textures of male and female specimens were indistinguishable—providing no evidence of divergent dietary strategies between sexes (Figure 3c). Highly variable polar bear body sizes (especially in males, which can range from 300 to 800 kg; Demaster & Stirling, 1981) and the solitary hunting strategies employed by these bears (Derocher et al., 2010; Laidre et al., 2013; Malenfant et al., 2018) are consistent with similar dietary behavior among both sexes.

Metabolic demands also govern much of the dietary preference among polar bears for blubbery, lipid-dense prey. The high energy requirements of polar bears, coupled with reduced intake of fatty seals, produce serious energy deficits which are unlikely to be offset by terrestrial foraging (Derocher et al., 2004; Pagano et al., 2018; Rode, Wilson, et al., 2015). Specialized lipid metabolism may be one of the more important traits associated with polar bears' divergence from other ursids (Liu et al., 2014). While there is some disagreement about the degree to which polar bears are currently utilizing terrestrial food sources like carcasses, berries and vegetation, Arctic char, birds and bird eggs, and garbage, it is clear that this is a strategy for some individuals (Dyck & Kebreab, 2009; Gormezano & Rockwell, 2013; Rogers et al., 2015). Some Hudson Bay polar bear populations have been observed to increase their onshore resource use in recent years, compensating for seal loss with more flexible strategies (Bourque et al., 2020; Gormezano & Rockwell, 2013). Although we observe some polar bears to have increased opportunistic foraging of harder foods in recent decades, as sea ice conditions deteriorate and polar bears experience longer summer fasts, this may not be a physiologically sustainable sustenance strategy. Such foods may offer little nutritional value, and their benefit is not reflected in population demography (Rode, Robbins, et al., 2015).

Compared to grizzlies, their highly omnivorous sister taxon, polar bears consume a much softer and more specialized diet—selecting for blubbery tissues from a kill (Best, 1985; Dyck & Kebreab, 2009). Grizzlies consume a heterogeneous diet of soft and hard foods, including large amounts of salmon, terrestrial ungulates, and some berries and vegetation (including harder tubers/seeds; Belant et al.,

2010; Boertje et al., 1988; Hilderbrand et al., 1999). This is reflected in the microwear differences between species, with much larger and more variable *Asfc* values among grizzlies than polar bears (Table 1; Figure 2b). Grizzlies are more robust than their specialist carnivore cousin, with enlarged grinding molar dentition compared to polar bears and a skull morphology capable of withstanding bite stresses more efficiently than the polar bear's smaller, elongated cranium (Slater et al., 2010; Figure 1b,c). The phenotype of grizzlies is better adapted to process harder foods with a broader range of textural properties than the polar bear, consistent with DMTA data. Polar bear skulls are structurally weak and produce inefficiently high strain energies during biting (Slater et al., 2010). Though polar bears generally have larger bite forces than grizzlies, those forces are poorly distributed, and finite element analysis has indicated that biting on the second molar produces especially high stresses in the polar bear skull compared to the brown bear (Figure 1b,c; Christiansen & Adolphsen, 2005; Slater et al., 2010). Therefore, while larger bite forces may explain some intraspecific variation in hard-food processing in polar bears, under typical conditions, morphology and dentition likely restrict the polar bear from eating harder foods that are regularly consumed by the smaller grizzly. The correlation between polar bear ML and *Asfc* values is much weaker when 21st-century polar bears with high *Asfc* values are included, indicating a departure in recent years from the biomechanical relationship exhibited during preceding decades. Twenty-first-century polar bears observed in this study appear to be consuming harder foods than did polar bears in the recent (i.e., 19–20th centuries) and more distant (~1000 years before present) past—a diet poorly suited to their anatomical abilities.

While further study is needed to make inferences at the population level given the small sample size available for this analysis, if polar bears more widely alter their diets in response to more extreme 21st-century warming, their increased engagement on the terrestrial landscape could be expected to have far-reaching ecological and evolutionary consequences. For example, polar bears may be forced to compete with grizzlies as they move to exploit resources on land, which they are currently known to do for marine-carcass resources like bowhead whale bone piles—common sites of encounter for the two species (Miller et al., 2015; Rode, Wilson, et al., 2015). Additionally, the two species occasionally produce viable, fertile hybrids from opportunistic mating events at carcass sites. These animals, known as pizzlies (or grolar bears), are of intermediate morphological phenotype and more robust than polar bears (Preuß et al., 2009). While it has yet to be seen whether these hybrids will be successful (particularly because they are so few in number and they are often studied in captivity), hybridization with brown bears has been an important part of polar bear evolutionary history, as past admixture occurred during critical phases of glacial oscillation (Edwards et al., 2011). As grizzly and polar bear ranges increasingly converge at higher latitudes in response to changing climates, the prevalence and success of a hybrid lineage may increase, particularly if it is more suited to engage in arctic hunting and terrestrial foraging than polar bears.

Polar bears were successful in Alaska as ice-based maritime hunting specialists during an earlier period of climatic variability and



reduced sea ice (the MWP), and they have maintained a similar dietary strategy through the warming of the early and mid-20th century. The present period of warming, however, is occurring at a scale comparable to the most rapid warming periods of the Cenozoic (i.e., the Paleocene–Eocene Thermal Maximum; Gingerich, 2019), and at a rate which is expected to surpass that of any natural climate variations of that time (Johannessen, 2008). Consequent sea ice decline is producing deleterious effects on polar bear survival and abundance, and it continues to threaten polar bear population sizes and ranges (Bromaghin et al., 2015; Laidre et al., 2018). As melt seasons grow longer, surviving and reproducing through extended periods without access to seals is critical to polar bears' persistence. Recent models predict large-scale declines and extinctions across polar bear sub-populations within the next century if greenhouse gas emissions are not aggressively mitigated (Molnár et al., 2011, 2020). It is likely that polar bear diets are constrained by their specialist morphology and metabolic requirements; nevertheless, a dietary "tipping point" toward harder alternative foods may be occurring in the 21st century, as we observed here in a small number of bears.

## ACKNOWLEDGMENTS

We are grateful to the curators and collection managers of the University of Alaska Museum of the North, most notably Aren Gunderson, Link Olson, Pat Druckenmiller, and Fawn Carter. We also thank Vanderbilt students Autumn Saunders and James Baker for assistance in the collections, Joshua Miller (University of Cincinnati), Matthew Wooller (University of Alaska), and Caitlin Meadows (University of Chicago) for insightful discussions about Arctic ecosystems, and Melissa Pardi (Vanderbilt University) for helpful discussion and composing Figure 1a. Casey Clark, Nicole Misarti, and Anne Jensen of the University of Alaska Fairbanks supplied additional information on radiocarbon ages from the Birnirk site. We would also like to acknowledge that the Birnirk collection was excavated from the traditional lands of the Iñupiat from Utqiaġvik. This work was completed with support from Vanderbilt University and the Littlejohn family (Petherick), a Vanderbilt University Discovery Grant (DeSantis), and equipment funded by the National Science Foundation (1053839, DeSantis).

## AUTHOR CONTRIBUTIONS

Larisa R. G. DeSantis conceptualized the project. Ansley S. Petherick and Larisa R. G. DeSantis sampled museum specimens for DMTA. Ansley S. Petherick performed DMTA, and Larisa R. G. DeSantis performed statistical analysis. Joshua D. Reuther, Scott J. Shirar, and Shelby L. Anderson provided access to and contextual information pertaining to archaeological specimens (including radiocarbon dates). Ansley S. Petherick wrote the manuscript with contributions from Larisa R. G. DeSantis and Joshua D. Reuther. All authors contributed edits.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Petherick AS, Reuther JD, Shirar SJ, Anderson SL, DeSantis LR. Dietary ecology of Alaskan polar bears (*Ursus maritimus*) through time and in response to Arctic climate change. *Glob Change Biol*. 2021;00:1–11. <https://doi.org/10.1111/gcb.15573>