Polar bear's range dynamics and survival in the Holocene

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Highlights

-At the end of the last glacial period, from 15 to 11 ka, polar bears were present in the western coast of Scandinavia (Denmark, Sweden, Norway, Iceland), until this Scandinavian subpopulation went regionally extinct in the early Holocene, about 11.5 ka

-No polar bear remains have been discovered from the period 8 to 6 ka anywhere in the Arctic, but the findings from Svalbard and eastern arctic Siberia 8-9 thousand years ago and from NW Greenland after 6 ka suggest that the likely refugia of the polar bear during the Holocene thermal maximum were in the High Arctic fringes of the Arctic Basin.

-During the last four millennia there has been a significant expansion of the polar bear's range, driven by a cooling trend and associated expansion of the arctic sea ice, until the onset of the current, human-induced warming.

-Our results highlight the dynamism of the polar bear's distribution range in response to changes in high-latitude climate and Arctic sea ice conditions.

Abstract

Polar bear (*Ursus maritimus*) is the apex predator of the Arctic, largely dependent on sea-ice. The expected disappearance of the ice cover of the Arctic seas by the mid 21st century is predicted to cause a dramatic decrease in the global range and population size of the species. To place this scenario against the backdrop of past distribution changes and their causes, we use a fossil dataset to investigate the polar bear's past distribution dynamics during the Late Glacial and the Holocene**.** Fossil results indicate that during the last deglaciation, polar bears were present at the southwestern margin of the Scandinavian Ice Sheet, surviving until the earliest Holocene. There are no Arctic polar bear findings from 8,000-6,000 years ago (8-6 ka), the Holocene's warmest period. However, fossils that date from 8-9 ka and 5-6 ka suggest that the species likely survived this period in cold refugia located near the East Siberian Sea, northern Greenland and the Canadian Archipelago. Polar bear range expansion is documented by an increase in fossils during the last 4,000 years in tandem with cooling climate and expanding Arctic sea ice. The results document changes in polar bear's distribution in response to Late Glacial and Holocene Arctic temperature and sea ice trends.

Key words: polar bear, Holocene, Arctic sea ice, fossils, distribution dynamics

Introduction

Polar bear (*Ursus maritimus*) is distributed throughout the circumpolar Arctic, where its southern range margin is currently determined by the distribution of perennial sea ice (Amstrup, 2003; Stirling and Derocher, 2012). Demographic and distribution models predict a drastic decline of polar bear populations in many regions of the Arctic (Regehr et al., 2016; Stern and Laidre, 2016). To address questions about the future of the polar bear's range, examining the past, which is done here with a combined study of the fossil record, including climate and sea-ice conditions, enables the investigation of species ranges and inferences on the survival strategy of key Arctic mammals during climatic conditions warmer than present. This study is focused on Holocene (present interglacial; the last c. 12,000 years) range dynamics and survival of the polar bear. The relatively abundant Holocene radiocarbon-dated polar bear fossils provide relatively strong evidence of their past presence. Moreover, the climatic conditions of the Holocene are well documented, and the variability of Arctic sea ice can be inferred from marine sediment proxies. During the warmest part of the Holocene, roughly 9-5 ka (Holocene Thermal Maximum, HTM), temperatures in the high latitudes were 1.5-2.5°C higher, and Arctic sea ice area likely smaller than at present (roughly the late 20th century) (Dahl-Jensen et al., 1998; de Vernal et al., 2013a). Comparison between polar bear fossil data and reconstructed sea-ice can illustrate how tightly polar bear range shifts were connected with Arctic sea ice changes, where and how polar bears were able to survive the warmest period of the HTM, and how this information can help predict its future under warmer conditions in the Arctic. The study includes the Late Glacial period, roughly 15-12 ka. This is a period when the temperature in the high latitudes rose from glacial to interglacial levels, causing the large ice sheets in Scandinavia and North America to melt, leading to access to new marine and terrestrial areas in the high latitudes (Heiri et al., 2014; Hughes et al., 2016; Young et al., 2020).

2 Materials and Methods

2.1 Calibration of radiocarbon dates

Late Glacial and Holocene polar bear occurrences based on radiocarbon-dated findings of fossil bones and teeth were obtained from published papers. Some previous studies with data on polar bear fossil evidence are Crockford (2022), Harington (2003) and Ingolfsson and Wiig (2009). Of these, the database collected by Crockford (2022) is the most complete. The database includes many undated archaeological records, which can be associated to relative ages such as “Late Holocene”. Therefore this database is not directly applicable for the purpose of our study.

Most common bone fossils are ulnas, femurs, and skulls and skull fragments (see Supplementary Material). The majority of the fossils have been found in coastal deposits, often buried in beach gravel, shell deposits or marine silt and clay, where they may have been introduced by slumping or ice rafting after the animal’s death. Another common setting of the findings of Holocene polar bear fossils are archaeological sites, which undoubtedly mostly or fully represent polar bears killed by humans (Supporting information Table 1).

The radiocarbon dates of polar bear fossils are usually prepared from the bone collagen instead of the indigenous carbonate of the bone apatite. This is a common procedure with fossil bones (Dunbar et al. 2016), which may be contaminated with older or younger organic material (Taylor 1992). One source of error in dating the fossils buried in earth surface deposits is that they can be contaminated with older or younger organic material, which will lead to biased age estimates (Berglund et al., 1992). For this reason, the most reliable dates are usually achieved when the sample for dating has been obtained by drilling to the center of the bone or teeth.

Radiocarbon dates from marine animal species such as polar bear can be the influenced by the ‘marine reservoir effect’ (Mangerud et al., 1972). In the ocean, carbon-mixing times are ~60 times slower than in the atmosphere, carbon’s residence being ~60 times that of the atmosphere (which amounts to 600 years approximately). As a consequence, marine organisms assimilating oceanic carbon (in the form of bicarbonate) in their hard body tissues (bone and shells) have apparent older radiocarbon ages (Mangerud, 1972). Consequently, residence times of oceanic carbon are highly variable (Toggweiler et al., 1989), ranging from 400 ± 200 years in the well-mixed layer above the thermocline to ~2,000 years in oceans' deep areas and zones of upwelling (e.g., around Antarctica (Stuiver, et al. 1986)). This means that atmospheric ^{14}C values obtained from such fossils need to be corrected considering the carbon reservoir exchange (Reimer et al., 2020). To account consistently for the marine reservoir effect, we recalibrated all uncalibrated polar bear dates collected from literature using CALIB 8.2 program (Stuiver & Reimer 1993), using an isotopic fractionation value $\delta^{13}C = -25‰$, and applying the marine calibration curve Marine20 (Heaton et al. 2020) (Supporting information, Table A.1).

The dataset collected for this study is shown in Supporting information Table 1A. Most of the data are based on direct radiocarbon dating of polar bear fossils. At 15 sites, the chronologies are based on indirect dating, ie. dating of bones other than polar bears or of other material suitable for radiocarbon dating found in the same deposits, for example charcoal or wood samples. In such cases, the dates were calibrated using the atmospheric calibration curve IntCal20 (Reimer et al., 2020). In three cases the age is not based on direct or indirect radiocarbon datings. Of these three cases, one (number 46 in Supporting information Table A1) is from Iceland and the age is based on the stratigraphy of the deposit. Although the estimated age "15 ka" is undeniably approximate, it is normally quite straightforward to identify the late-glacial context in the sedimentary sequences in the glaciated region such as Iceland. Thus, we consider this finding suitable for our study. Findings 17 and 26 in supplement Table A1 are based on the age of archaeological material discovered in the same deposits as the polar bears and deemed adequately reliable to be included in our study.

One relevant fact in studies based on dated fossil bone data is the destruction of fossil bones over time. Such a time-dependent destruction causes a taphonomic bias where the number of findings increases exponentially towards the present (Surovell & Brantingham 2007). Such a bias can have particularly strong influence in studies where the number of fossil findings is used as a surrogate record for the past population size. It is likely that there is a taphonomic bias in the Holocene polar bear data as well, but as we do not aim for estimating the population sizes but rather focus on range shifts, the taphonomic bias does not invalidate the interpretations.

2.2 Sea ice cover

The present-day sea-ice cover is based on data from SMMR and SSM/I passive microwave satellite images. The median April (maximum) and September (minimum) sea-ice extent is averaged over the period 1979-2007 (National Snow and Ice Data Center, USA, https://nsidc.org/).

For the longer-term Holocene period, we base our estimated sea-ice cover in the pan-Arctic region on information from numerous published geological records from the larger Arctic and subarctic region presented by Alsos et al. (2016). These geological sea-ice records are based on the proxy reconstructions from marine sediment cores including biological (diatoms, dinoflagellate cysts, foraminifera, ostracods), sedimentological (ice-rafted debris, IRD), and biogeochemical (IP_{25}, PIP_{25}) sea-ice indicators, each with different strengths and weaknesses/uncertainties. For a detailed overview of these proxies and their strengths and limitations see de Vernal et al. (2013b).

For the Bering Sea region, we show the actual sites (Fig. 1B). Details on Bering Sea sea ice records are provided in the Supplementary Material.

3. Results and Discussion

Late Glacial polar bear findings are from Scandinavia (Fig. 1A). The fossils are concentrated on the Atlantic side near the margin of the Scandinavian Ice Sheet (SIS) and range from 15 ka to 11 ka. The oldest two dates from Sweden are from the Bølling-Allerød interstadial (14.7-12.9 ka) (Berglund et al., 1992), when the estimated summer temperature in the region was 6-10°C (Heiri et al., 2014) and vegetation consisted mostly of dwarf shrubs and herbs (Mortensen et al., 2011). A molar fossil from Iceland has an estimated age of 15 ka. Two fossils from Denmark and Norway date to the Younger Dryas stadial, a roughly 1,000-yr long cold period with glacial conditions from 12.9 ka to 11.7 ka (Rasmussen et al., 2006). Summer temperatures during this period in this region are estimated at 6.0-8.0°C (Heiri et al., 2014).

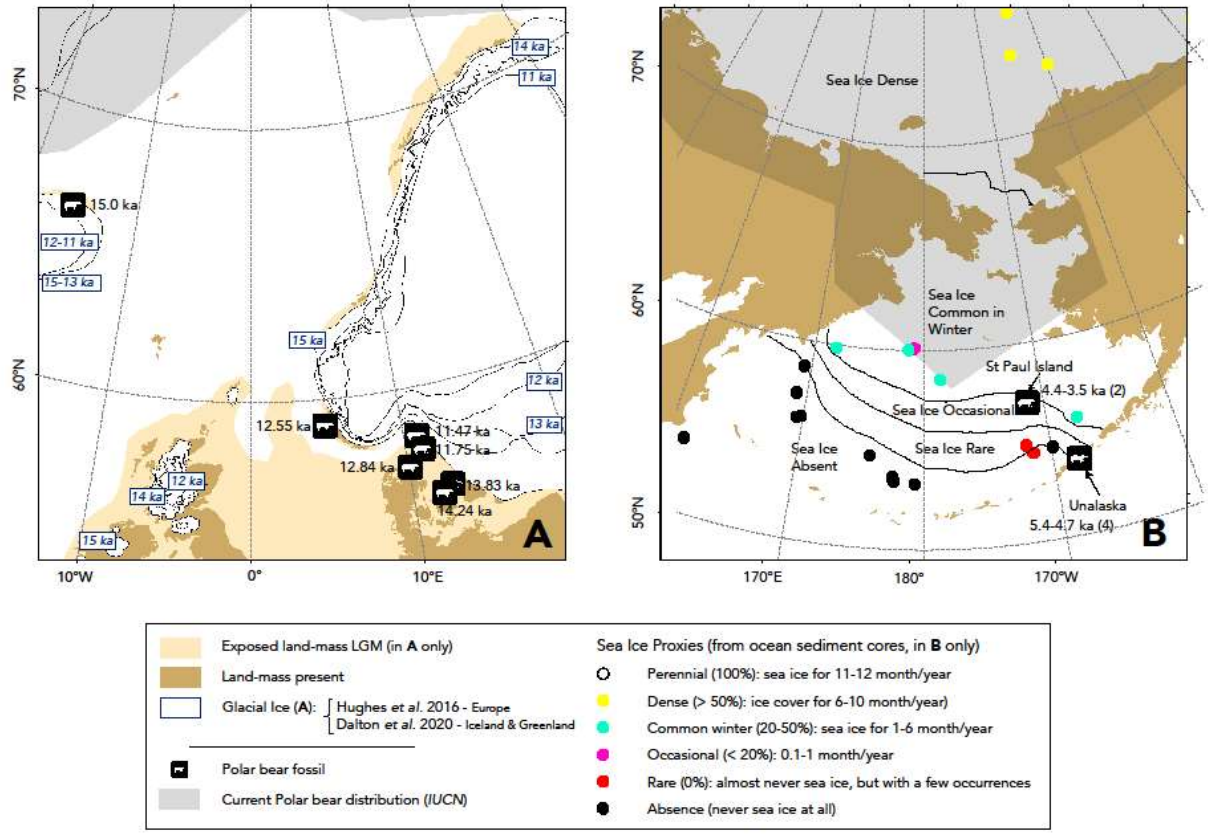

Fig. 1. Polar bear findings from Scandinavia and the Bering Sea. A) Late Glacial polar bear findings in northern Europe and the deglaciation of the Scandinavian ice sheet from 15 to 11 ka (Hughes et al. 2016); B) Polar bear findings in Alaska and Bering sea ice extent between 6 and 4 ka. Sea-ice extent classes according to Alsos et al. (2016). Base maps are the 1:50m "Land" vectorial file and "Graticules" grid obtained from the public domain map dataset Natural Earth: https://www.naturalearthdata.com/. Map projection: WGS 84/IBCAO Polar Stereographic.

The transition from the Younger Dryas to the Holocene 11.7 ka was characterized by summer temperatures rising to over 10°C in southern Scandinavia (Heiri et al., 2014) with a significant reduction in the sea ice (Alsos et al. 2016). This rapid environmental change is correlated with regional extinctions of many glacial and arctic mammals, such as mammoth and reindeer in Scandinavia (Ukkonen et al., 2011). However, the polar bear findings suggest a polar bear population surviving the Younger Dryas-Holocene transition in Kuröd, southern Sweden, eventually disappearing by 11.5 ka (Fig. 1). Overall, fossil data suggest that polar bear disappearance from Scandinavia was probably linked to the climatic and ecosystem change associated with the onset of the Holocene interglacial.

Only two dated polar bear fossil sites exist from the Early Holocene (11-8 ka). These sites are in Zhokhov Island and Svalbard (Fig. 2A). The fossil from Svalbard has been dated to 8.0 ka and represents one individual polar bear (Ingolfsson and Wiig, 2009). The Zhokhov Island site in the East Siberian Sea is an exceptional archaeological site. A collection of polar bear bones represents a minimum number of individuals (MNI) of 130 (Pitulko et al., 2015), with ages ranging generally from 10.0 to 8.0 ka, with a peak at 9-8.6 ka (Fig. S1).

At 10-8 ka, Arctic sea-ice cover is inferred to be roughly comparable with the present (Alsos et al. 2016). The polar bear findings from Svalbard and Zhokhov Island are thus consistent with the inferred limits of perennial sea ice extent, suggesting that the species was present in the Arctic basin (Fig. 2A). Zhokhov Island is an important archaeological site for Holocene polar bear fossils. Up to the Early Holocene, roughly until 8-7.5 ka, the island was connected with the Siberian mainland (Bauch et al., 2001) and the archaeological findings show a hunter-gatherer human population specialized in hunting polar bears and reindeer (Pitulko et al., 2015; Pitulko and Kasparov, 2017). A rich fauna of Arctic mammals, including persistent and abundant polar bear populations, was present 10.0-8.0 ka in the region.

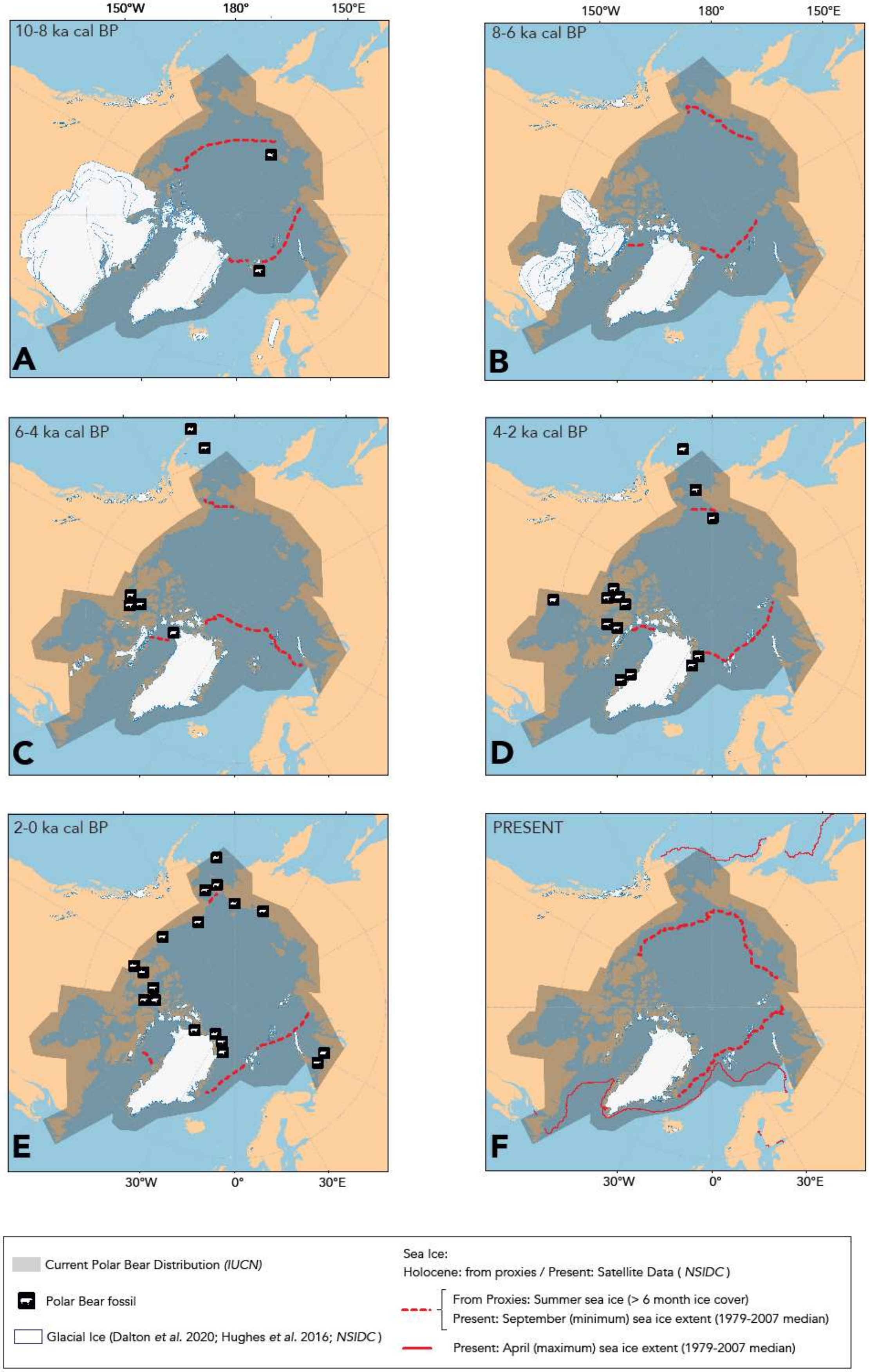
150°W
180°
150°E
10-8 ka cal BP
A
8-6 ka cal BP
B
6-4 ka cal BP
C
4-2 ka cal BP
D
2-0 ka cal BP
E
PRESENT
F
30°W
0°
30°E
Current Polar Bear Distribution (*IUCN*)
Polar Bear fossil
Glacial Ice (Dalton *et al.* 2020; Hughes *et al.* 2016; *NSIDC*)
Sea Ice:
Holocene: from proxies / Present: Satellite Data (*NSIDC*)
From Proxies: Summer sea ice (> 6 month ice cover)
Present: September (minimum) sea ice extent (1979-2007 median)
Present: April (maximum) sea ice extent (1979-2007 median)

Fig. 2. Polar bear fossils and summer sea-ice distribution during the Holocene. A) 10-8 ka, B) 8-6 ka, C) 6-4 ka, D) 4-2 ka, E) 2-0 ka. The extent of the sea ice during summer (> 6 month) is shown as a hatched red line (see also Supplementary Material). In F PRESENT is based on satellite data obtained from https://nsidc.org. The modern polar bear range (based on International Union for Conservation of Nature, IUCN – https://www.iucn.org) is shown as a shaded polygon in all maps. Glacial ice contours were obtained from Dalton et al. (2020) for the North American Ice Sheet complex (NAIS) – including Greenland and Iceland – and Hughes et al. (2016) for Eurasia. Since no timeseries of glacial ice contours was available for Eurasia post 10 ka, the Holocene periods up to 4 ka display inferred glacial ice at 10 ka, and the periods younger than 4 ka display present glacial ice in this region (Svalbard, Franz Joseph Land, and Novaya and Severnaya Zemlya), in line with Solomina et al. (2015), who report lower-than-present glacial extent in the Eurasian High Arctic archipelagoes until ~4-5 ka and a glacial increase thereafter. Contours in NAIS represent glacial ice extents at different times within the 2,000-year periods, with older contours occupying larger extents and vice-versa. For the period 10-8 ka, contours correspond to 9-10.3, 8.5-9.6, and 8-9 ka; for the period 6-8 ka, contours correspond to 7.6-8.5, 7.2-8.1, 7-7.9, 6.5-7.3, and 6-6.8 ka; for the period 4-6 ka, contours correspond to 5.5-6.3, 5-5.71, and 4-4.5 ka; for the period 2-4 ka, contours correspond to 3-3.2, and 2 ka; and for the period 0-2 ka, contour corresponds to 0.91-1 ka. Base maps are the 1:50m "Land" vectorial file and the "Graticules" grid obtained from the public domain map dataset Natural Earth: https://naturalearthdata.com/. Map projection: WGS 84/IBCAO Polar Stereographic.

The period 9-5 ka was the warmest of the Holocene (Holocene Thermal Maximum, HTM) in much of the Arctic, with mean temperatures 1.5-2.5°C higher than at present (Fig. S2) and summer Arctic sea ice significantly reduced (Alsos et al. 2016). No polar bear fossils have yet been found from the period 8-6 ka (Fig. 2B). The oldest polar bear fossil found after this hiatus has an age 5.7 ka. This finding is from Nuulliit, Thule, in northwestern Greenland (Bennike, 1997) (Fig. 2C).

The next oldest findings, dating to roughly 5.4-4.7 ka, are from Unalaska Island, one of the Aleutian Islands, located at 53°57' N, representing a MNI of four at an archaeological site (Fig. 1B) (Knecht et al., 2001). Polar bear was also present 4.4-3.5 ka on St. Paul Island, the largest of the Pribilof Islands, at 57°N (Fig. 1B) in the Bering Sea, where the bone record from Qagnax̂ cave indicates a MNI of seven (Veltre et al. 2008). The findings from St. Paul and Unalaska islands are remarkable because they represent the southernmost polar bear presence in the Holocene and date to the Middle Holocene, when climate was generally warmer than today and sea ice in the Bering Sea was only present in the winter, if at all (Fig. 1B). The climate of Pribilof Islands is influenced by the cold surface waters of the Bering Sea, leading to low summer temperatures and occasional pack ice today (Veltre et al., 2008). Historically, polar bears have occasionally been seen on the Pribilof Islands when pack ice is blown to the southwest from the St. Matthew Island area, the southernmost polar bear population in the Bering Sea, 360 km northeast of St. Paul (Veltre et al., 2008). During the Middle Holocene, sea ice expanded slightly in the Bering Sea ~6-3 ka (Katsuki et al., 2009; Ruan et al. 2017; Jones et al., 2020) occasionally reaching the Pribilof Islands, but it is unlikely that it reached Unalaska Island (Fig 1B). The large MNIs of polar bears on these islands implies that polar bears were able to adapt to living outside of or near the seasonal limits of sea ice when ample resources existed.

Polar bear fossils become more abundant and widespread during the last 4,000 years. Polar bear was present along the Arctic Canadian coast and in the northern coastal Greenland (Figs. 2D, 2E). The 2.5 ka bone deposit from Seahorse Gully, Canada, on the west coast of the Hudson Bay, shows the species in the region where one of the most populous polar bear populations of North America currently exists (Molnár et al, 2012). During the last 2,000 years, polar bear fossils are widespread, occurring at 18 sites which overlap with modern polar bear distribution (Fig. 2E). Important Late

Holocene sites are the Walakpa Site in northernmost Alaska with a MNI of 20 (Stanford, 1976; Murray, 2008), and Vaygach Island in the Novaya Zemlya archipelago and Vhodnoy Cape near the delta of Pechora River, which represent the two westernmost Holocene fossil polar bear sites in Eurasia (Pitulko, 1991; Boeskorov et al., 2018).

Comparison of the results shows that shifts in the polar bear's range over the Holocene have followed Arctic temperature and sea ice trends. This is illustrated by the occurrence of the polar bear as far south as 56°N during the Late Glacial in Scandinavia, when climate there was comparable with modern low Arctic climate (Fig. 1A). Similarly, polar bear's range reduction from the Early Holocene to its minimum during the HTM, and subsequent gradual expansion during the Late Holocene appear related to climate and sea-ice extent. Although it remains unknown where the species survived the warmest millennia of the Holocene, fossils from northern Greenland and Zhokhov Island at 9-8 ka and from Nuulliit in northwestern Greenland at 5.7 ka suggest that the polar bear may have survived on the fringes of the Arctic Basin in northernmost Greenland, the high Arctic Canadian archipelago, Svalbard, and northern Siberian archipelagos, where sea ice was likely widespread, allowing the species to resort to similar sea ice habitats and hunting strategies as at present.

There are Middle Holocene anomalies from this general congruence between climate, sea ice, and polar bear range indicated by fossils from the Aleutian and Pribilof islands. Fossils of ringed seal (*Pusa hispida*), polar bear's main prey, are abundant in the same deposits as the polar bear fossils (Knecht et al., 2001), and polar bears living on the St. Paul Island and Unalaska may not have relied only on the presence of sea ice for hunting but utilized locally exceptionally abundant seal rookeries. Although ringed seals are considered ice-obligate (Moore and Huntington, 2008), terrestrial haul-out behaviour has been observed in the absence of sea ice (Lydersen et al., 2017). Alternatively (or additionally), polar bears in these islands might have preyed on animals other than seals, since behavioural responses towards terrestrial-based hunting and foraging have been observed in several polar bear populations around the Arctic at present (Rode et al., 2014, 2015a; Hamilton et al., 2017; Stempniewicz, 2017; Ware et al., 2017). Although adaptive rewiring has been considered critical for the survival of polar bears in a warmer Arctic (Rode et al., 2014, 2015a), the number of observed bears resorting at present to alternative food sources has so far been low. Also, overall observed negative trends in body mass and population size suggest that terrestrial habitats provide limited or low-quality food resources (Rode et al., 2015b). Moreover, such strategies often lead to overexploitation of resources and eventual extinction cascades (Gilljam et al., 2015). Nevertheless, similar mechanisms may also explain the survival of polar bear during the Eemian interglacial 130-115 ka ago (one fossil in Svalbard (Alexanderson et al., 2013)), when summer temperatures in the Arctic were up to 7-8°C above present (NEEM community members, 2013). Thus, although our study highlights the overall congruence of polar bear range with sea ice and climate, polar bear populations have the ability for prolonged resilience under unusual conditions, as seen through their persistence in certain island settings despite diminished sea-ice extent. The latter calls for a careful consideration of all the mechanisms affecting this species when trying to forecast its future in a warmer Arctic. It also highlights the necessity of protecting special refugia for animals under ecological pressure.

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Supplementary data

1. Polar bear fossils

Late-glacial polar bear fossils

Late-glacial polar bear fossils are currently limited to the Scandinavian region. The eight fossil polar bear findings from Sweden have been described in detail (Berglund et al., 1992). Most of the specimens represent single findings of separated bones or teeth. The five different skeletal parts from Kuröd, Uddevalla are an exception. These pieces seem to come from the same juvenile individual (Berglund et al., 1992). Four of these eight fossils from Sweden have been radiocarbon dated and are included in this study (Supplement Table 1). Of these four dated fossils, one, a thigh bone from Kullaberg, was dated three times by dating the deepest, intermediate and the superficial layers of the bone to test the influence of the dated part of the bone on the results (Berglund et al., 1992). The two oldest of the four radiocarbon dated fossils are dated to 14.2 ka and 13.8 ka, respectively, corresponding to the Bølling-Allerød interstadial period. The two youngest fossils are dated to 11.8 ka and 11.5 ka, which indicate an Early Holocene age. Both dates are from fossil-rich beach deposits from Kuröd, Uddevalla on the Swedish West Coast (Supplement Table 1). In addition, there are four undated fossil findings from southwestern Sweden (Berglund et al., 1992), which were not included in this study, because their ages are uncertain and currently inferred from their sedimentary context. They were discovered in similar sedimentological settings as the dated polar bears, and it is presumed that they represent Late Glacial age, roughly 15-11.7 ka (Berglund et al., 1992).

The polar bear finding from Iceland consists of one molar discovered from marine deposits near Kopasker, northeastern Iceland. There is no direct dating of the molar, but the deposit context suggests an approximate age of 15 ka (Ole Bennike, Geological Survey of Denmark and Greenland, written communication, 2018). The single Late-Glacial polar bear finding from Denmark is a mandible discovered in 1920 from a gravel pit 14 m a.s.l. (Aaris-Sørensen & Petersen, 1984). The radiocarbon age is younger (12.8 ka) than the oldest fossils from the Swedish West Coast (Aaris-Sørensen & Petersen, 1984). Given the proximity of this site to the findings from Sweden, it is likely that the Swedish and Danish fossils represent the same, persistent population of polar bears.

An almost complete polar bear skeleton was discovered in West Norway in 1976 (Blystad et al., 1983), with a radiocarbon age of 12.6 ka, which corresponds to the Younger Dryas stadial (Supplement Table 1). Most of the bones were preserved in a thin layer of sandy-silty marine sediment, 14 m above sea level (a.s.l.), associated with poorly preserved bones of seal and fishbones of shorthorn sculpin (*Myoxocephalus scorpius*). The polar bear was identified as a large, old male (Berglund et al., 1992).

The depositional context of these fossils supports that the Late-glacial polar bears in Scandinavia lived in arctic marine habitats, and using seals as their main source of food. The environments are is usually nearshore gravel, mollusk shell, or carbonate rich marine sediments deposit at an altitude of a few metres or a few tens of metres above the current sea level and thus roughly at the highest Late Pleistocene sea level. The Swedish sites were on the west coast of the continent or on small islands a few kilometres from the continent (Berglund et al., 1992). The find from Kuröd, Uddevalla is from layers rich in fossils of many vertebrate species, including Arctic seals such as ringed (*Pusa hispida*), harp (*Pagophilus groenlandicus*), and bearded seals (*Erignathus barbatus*), and Arctic whales such as bowhead (*Balaena mysticetus*) and beluga (*Delphinapterus leucas*) whales (Fredén, 1988; Berglund et al., 1992). These deposits also include bones of reindeer (*Rangifer tarandus*), showing the sympatry of polar bear and reindeer, as observed currently in Svalbard and the Canadian Arctic Archipelago. Data indicate that it is likely that a polar bear population existed on the Swedish southern coast from about 14 ka to 11 ka.

Holocene polar bear findings

Holocene polar bear fossils are found from Greenland, Svalbard, Canada, Beringia, and the Russian arctic. A few important sites where the Holocene polar bear fossils have been discovered are described here in detail.

Zhokhov findings in the Siberian Arctic

The Zhokhov site, first discovered in the 1980s, is located at 76°N in the Siberian Arctic on the Zhokhov Island, part of the De Long group in the New Siberian Islands. It is one of the northernmost archaeological sites in the world and provides the oldest traces of human occupation at high latitudes, indicating that people explored this region at least as early as the Early Holocene (Makeyev and Pitulko, 1991). The site is located at the southwest end of the Zhokhov Island, stratigraphically associated with the surface of unconsolidated Quaternary sediments, covering the basal bedrock. The size of the excavated area is 71 m^2 and its elevation 20-30 m a.s.l. The cultural assemblage, including stone, bone, ivory and wood artefacts, as well as the large collection of faunal remains, have been investigated since late 1980s and are not confined to a single distinguishable layer (Pitulko et al., 2015). There are 48 radiocarbon dates from the site, obtained from different material (wood, charcoal, plant detritus, reindeer bones, peat) (Fig. S1). No polar bear bones have been directly dated, but one date is from moss found from inside a polar bear skull (Beta-190087, 8.8 ka) (Pitulko et al., 2015). The dates range from 10.0 to 8.0 ka (Fig. S1), suggesting that the site was inhabited for at least two millennia. Some of the dates are from the site are considerably pre-Holocene, 12.6 ka, 14.8 ka, 23.7 ka, 26.5 ka, and 26.7 ka. It is possible that these represent too old dates due to contamination of older organic material, although the persistence of human occupation at the site since the Late Pleistocene cannot be ruled out.

SI Figure 1. The temporal distributions of the calibrated radiocarbon dates from the Zhokhov archaeological site. The outlier dates excluded from the figure are 12.6 ka, 14.8 ka, 23.7 ka, 26.5 ka and 26.7 ka. Data from (Pitulko et al., 2015)

Due to the permafrost, the faunal remains are well preserved both on the surface and in the deposit. The excavations in 2000-2005 show that reindeer and polar bear are by far the most common species, indicated by the number of identified specimen (NISP) for reindeer that was 14,614 and for polar bear 5,915 and the minimum number of individual (MNI) 245 for reindeer and 130 for polar bear (Pitulko et al. 2015). The polar bear MNI was defined on the basis of the most numerous bones from one side of the body. For adult polar bears, this was the left distal humerus. In addition, five sub-adult individuals were defined on the basis of the fragments of the left scapula, and four polar bear cubs by four scattered baby teeth. There is strong evidence to conclude that the Zhokhov site inhabitants earned their livelihood by hunting reindeer and polar bears (Pitulko et al., 2017). This is a unique adaptation model of mobile terrestrial hunters, who hunted reindeer and polar bears in an approximately 2:1 ratio, with polar bear hunting being more important and carried out mainly in wintertime. Polar bear hunting techniques reconstructed from the faunal remains indicate that the animals were hunted in their dens. Evidence that dogs were used for sledging and hunting partly explains the apparent success of finding and killing polar bears in their winter dens (Pitulko et al., 2015; Pitulko and Kasparov, 2017).

Cape Baranov findings

Cape Baranov is an archaeological site 70 km east of the mouth of Kolyma River in Siberia (Oklandinkov, 2008). The landscape is marked by a ridge of flat-topped peaks, several with tors that overlook a series of five small bays along the coast. The remains of four houses were found on the shore of one of these bays. Sixteen polar bear fossils (MNI=4) were found in the strata from three houses. Driftwood from these strata was dated to 1.6 ka. Based on the preservation of bone matter, the polar bear remains were deposited when the houses were occupied. Two complete adult skulls with a full set of teeth were determined to be anatomically identical to modern polar bear skulls. They were reported as the first case of polar bear bones "in a semimineralized condition" in the former Soviet Union (Vereshchagin 2008).

Alaska findings

In the eastern Aleutian Islands, Unalaska, Alaska, is a small community that occupies both Unalaska Island, the largest (2,720 km^2) island in the Fox Islands group and the small (8.5 km^2) Amaknak Island, which is about 60 m north of Unalaska Island in Unalaska Bay. Unalaska is rugged and mountainous, with the higher elevations covered in snow much of the year. However, sea ice does not currently reach this far south.

The polar bear findings from Unalaska are from the Margaret Bay archaeological site on Amaknak Island (53°53’N, 167°33’W) (Davis, 2001). This excavation site lies on a knoll at an elevation of 18 m a.s.l., overlooking both Unalaska and Iliuliuk Bays. The excavation includes several natural stratigraphic layers containing cultural material and one fossil-rich midden, layer 4, sandwiched between two cultural layers. The archaeological evidence shows that the site was semi-permanently inhabited from c. 6.0 to 3 ka. The faunal-rich midden is a 0.1-1 m thick, dense, homogeneous deposit of mammal, fish and bird bones, mixed with abundant shells**.** The preservation of faunal remains in this dense layer is due to abundant shellfish remains (Knecht et al., 2001). All polar bear remains were discovered in layer 4 (Davis, 2001), along with remains of ringed seals, harbour porpoise, Steller sea lion and other typical polar bear prey species. The polar bear remains include a nearly complete adult right mandible with two intact molars, 12 forelimb bones and 11 hind limb bones. The phalanges of polar bears were large and gnarled, with spiky protuberances on the ventral surface, which suggests that the bears were exposed to unusual stress on the feet, possibly from the time spent on the rocky shores of the islands (Davis, 2001). Brown bear (*Ursus arctos*) was also positively identified by three teeth and one thoracic vertebra (Davis, 2001), suggesting overlapping ranges between these two bear species on Unalaska Island in the past.

Four conventional radiocarbon dates have been obtained from charcoal or charred particles from layer 4, with dates ranging from 5.4-4.7 ka. From the descriptions (Davis, 2001; Knecht et al., 2001), it is not clear whether the charred particles represent terrestrial or marine material. Given theconsistency of the four dates, we assume that the dating based on charred remains represents terrestrial material. Before the discovery at Margaret Bay, polar bear fossils were reported from the Chugachik Island at Kachemak Bay, southern Alaska, as early as 1934 (Laguna). However, the finding was later dismissed (Davis, 2001).

St. Paul Island

St. Paul, a 90 km^2 volcanic island, is the largest of the Pribilof Islands in the eastern Bering Sea. St. Paul is the only known Bering Sea island with lava tube caves containing animal bones (Veltre et al., 2008). Unlike in the Aleutians, there are no archaeological sites, suggesting no permanent human occupation prior to the Russian exploration of the islands in 1786. St. Paul's coastline is made up of steep volcanic cliffs, but dunes and tundra cover the uplands. The Pribilof Islands lie near the current maximum limit of sea ice and are only occasionally surrounded by sea ice in the winter (Veltre et al. 2008).

There are two caves on St. Paul with significant polar bear remains. Qagnax̂ Cave was discovered in 1999 (Veltre et al., 2008). A vertical shaft leads to the cave, which acted as a trap for unwitting animals. Below this entrance is a debris cone containing hundreds of bones and teeth, but transport mechanisms such as water and scavengers (primarily foxes) have also spread the bones across the cave. In total, 1,750 bones were collected from Qagnax̂ Cave; 14.3% of these (250) were identified as polar bear bones. The MNI is seven, including at least two adult males and four adult females; 8% of the total bones are from juveniles. Nearly all types of bones were found except for flat (mandible, scapula, innominate) or very fragile bones (ulna, fibula) which were likely destroyed by foxes gnawing on them. The many small, unidentifiable bone fragments make the MNI an underestimate; nonetheless, the polar bear MNI represents at least 18% of the total number of individual animals found in the cave. Two polar bear bones were AMS ^{14}C dated with calibrated ages of 4.4 ka and 3.5 ka (Veltre et al., 2008).

Also on St. Paul and in addition to the Qagnax̂ cave, 15 polar bear bones (MNI = 3, including 2 adults and 1 juvenile) were found in Bogoslof cave. The first skull was found in 1874 by W.L. Hahn and 23 years later R.E. Snodgrass and D.S. Jordan found more polar bear bones along with mammoth teeth.

In 1904, the bones were sent to the Smithsonian Institution. The polar bear bones were analyzed later, but the mammoth teeth were lost (Ray 1971). None of the Bogoslof cave bones have been dated, though the presence of juvenile bones has led to the conclusion that polar bears may have once denned on the island (Ray, 1971).

In light of the findings from Qagnax̂ and Bogoslof caves, it is probable that the polar bear population present on St. Paul Island was roughly coeval with those of Unalaska, that is from approximately 5 ka to 4 ka, or possibly as late as 3.5 ka. Historic records also show that polar bears have been observed sporadically on St. Paul Island in recent centuries. Two were killed in 1848 and 1875; however there have been no confirmed reports of polar bears on the island since the 1920s (Veltre et al., 2008).

St. Matthew Island

St. Matthew Island currently hosts the closest polar bear population to St. Paul Island. Today, polar bears are frequent visitors to St. Matthew Island in winter, when sea ice reaches the island (Klein and Sowls, 2011). However, they were also common in summer until the late 19th century. In 1874, H.W. Elliott visited St. Matthew and reported his findings the following year in a front-page article in *Harper's Weekly*, "*We landed on St. Matthew Island early on a cold gray August morning, and judge our astonishment at finding hundreds of large polar bears….lazily sleeping in grassy hollows, or digging up grass and other roots, browsing like hogs*"(Klein and Sowls 2011). During the summer, hundreds of polar bears grazed on sedges, eating singing voles (*Microtus abbreviatus*), birds and their eggs, as well as walrus, seals, and beached whales. Elliott observed that the St. Matthew bears were healthy and not stranded; their population was large and had been known since the island was explored by Russians in 1764. The last polar bears were killed in the 1890s, possibly by the crew from a Revenue Cutter Service ship that was in the Bering Sea to protect the fur seal from illegal poaching (Klein and Sowls, 2011).

Alaskan Arctic Coastal Plain (The North Slope)

Walakpa is a rich in archaeological and faunal site with remains of many arctic mammalian and bird species, located on a 6.1-m high bluff on the Chukchi Sea, 19.3 km south of the community of Utqiaġvik (Barrow) (Stanford, 1976). Polar bear bones were discovered in a midden, situated at the point of the bluff between the remains of two rows of houses that form the site. The total number of polar bear bones is 34, and these bones are present throughout the whole cultural phase, from about 1.5-1.2 ka to present (Stanford, 1976).

The chronology of the Walakpa site is based primarily on the occurrence in the stratigraphic sequence of certain cultural features. Only two wood-charcoal ^{14}C samples were recovered and dated to 0.9 ka for the upper Birnirk level and 0.8 ka for Early Thule level. These dates fit the archaeological sequence well (Stanford, 1976).

2. Evolutionary history of polar bear

The evolution of the polar bear is generally associated with the development of cold climate and presence of arctic sea ice. The northern hemisphere ice sheets in Greenland and arctic Canada are generally considered to have formed ~14-6 Ma (Zachos et al. 2001), with sea ice appearing in the Arctic Ocean as early as the Eocene (St John 2008). However, there is substantial variability in the inferred appearance of the polar bear as a distinct species, or in the divergence of its lineage from the brown bear. On the basis of morphological comparisons, it was originally estimated that the polar bear is no older than a few hundreds of thousands of years (Kurtén 1964). This estimate concurs with the fact that no Early or Middle Pleistocene fossils of polar bear have been discovered. The oldest dated fossil findings of polar bear are substantially younger, from 130 to 110 ka (Ingolfsson and Wiig 2009; Lindqvist et al. 2010).

The advent of genomic studies on speciation and admixture over the previous decade has placed such approaches at the center of the study of young lineages such as the polar bear. The divergence of polar and brown bears has been estimated using the identity by state (IBS) tracts of DNA and *∂a∂i* (diffusion approximation for demographic inference). These methods can infer changes in population sizes over time, and suggest a divergence time between brown and polar bears at ca. 479–343 ka, with a more likely split around the lower bound of the interval after accounting for genotyping errors (Liu et al., 2014). Although this date is much younger than other genome-based studies, it agrees with fossil evidence.

In contrast, Hailer *et al.* (2012), using nuclear loci from a wide array of polar, brown, and black (*Ursus americanus*) bears, suggest an older divergence time for polar bears from brown bears at ~600 ka (from 338 to 934, well in the Middle Pleistocene). This older age would have allowed the species more time to evolve through various glacial/interglacial periods. Hailer *et al.* (2012) further confirm past, post-divergence hybridization events between polar and brown bears, as well as likely population bottlenecks – possibly during warm interglacials – as seen in the species current low genetic diversity.

Miller *et al.* (2012) hypothesize a very early split between polar, brown, and black bears (~5-4 Ma), followed by a period of complete or near-complete separation, and a more recent increase in gene flow. Their genomic sequence study was also used to estimate the past population structures of the species, suggesting that polar bear numbers might have increased substantially between 800 and 600 ka, which correlates with a Middle Pleistocene cooling. This period was followed by Marine Isotope

Stage 11 (420–360 ka), a very warm (potentially the warmest) and the most protracted interglacial of the past half million years (Miller et al., 2012), which marked the start of a long period with small polar bear numbers. Minor posterior increases (or perhaps changes in polar bears' population structures) were inferred and linked to post-Eemian cooling, followed by a modest late increase interpreted to "reflect cooling during the Last Glacial Maximum although genomic signatures of such recent events are known to have less power" (Miller et al., 2012). The low numbers of polar bears during the past half million years is suggested to explain the much lower genetic diversity of this species in relation to brown bears, and its overall temporal dynamics are interpreted to be in high agreement with polar bears being a highly sensitive species to changes in climate (Miller et al., 2012).

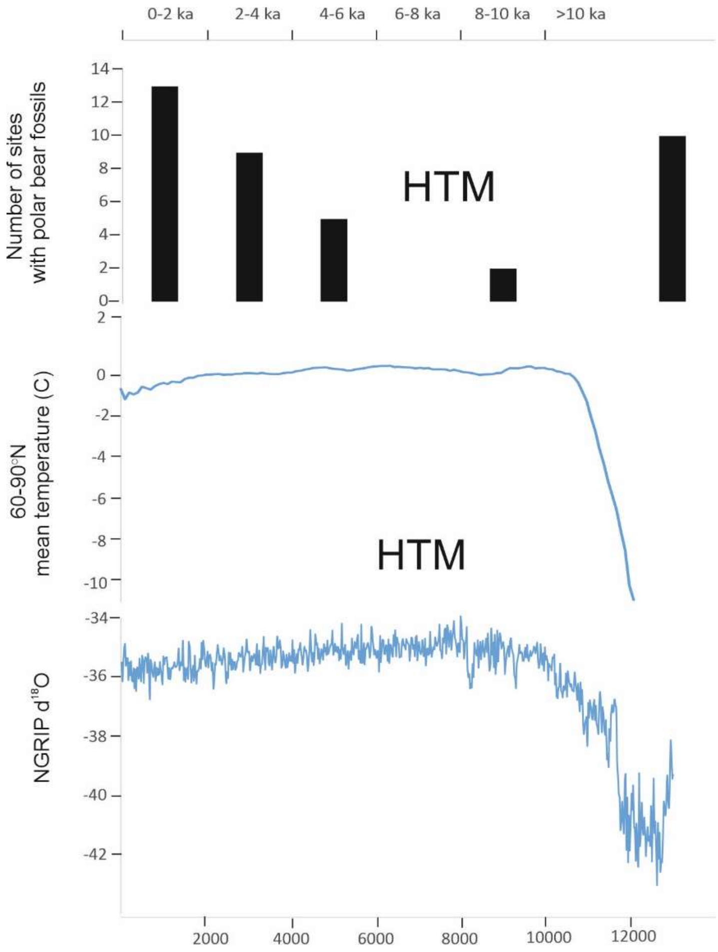
Although they are different species, polar and brown bears can interbreed, as observed both in captivity (Gray, 1972) and, rarely, in the wild (Miller et al., 2012). Further, molecular evidence (mitochondrial DNA) has been used to infer possible past hybridization events after the divergence of the two species (Edwards et al., 2011).

3. Holocene climate

Although the Quaternary is in general a cold climatic period with permanent ice sheets in both hemispheres, it is also characterized by periods when the global temperature has been as high or higher than at present. For example, the last interglacial, the Eemian (130-115 ka), was one of the warmest interglacials of the last 800 ka, with summer temperatures in the Arctic from 3-5°C up to 7-8°C above present (Dahl-Jensen et al., 2013; Yau et al., 2016). This caused the Greenland ice sheet to partially melt, so that during the Eemian interglacial the global sea level was 6-8 m higher than at present (Kopp et al., 2009).

Temperature proxy spanning the Early Holocene (11.7 - 10 ka) indicate cooler conditions than at present, but with a rising trend (Dahl-Jensen, et al., 1998; Briner et al., 2016; Kaufman et al., 2016; Zhang, et al., 2017). Although the highest surface temperature data generally date from 9 to 6 ka, although there exists considerable geographical and seasonal variability, especially in the timing of the onset of this warmest period (Kaufman et al. 2020). Model studies suggest that these differences in timing of the warmest period between sites are linked to their distance from the ice sheets and from the sea as well as to their latitudinal position (Zhang et al., 2017). Before 8 ka, the influence of the Laurentide and Scandinavian ice sheets and the resulting katabatic winds had a direct cooling effect especially on summer climate over the regions surrounding these ice sheets. This was in contrast to conditions in other Northern Hemisphere regions further from the glaciers, where orbital forcing (warm summers and cool winters) dominated climate (Zhang et al., 2017).

This Early to Middle-Holocene warm period is referred to as the Holocene Thermal Maximum (HTM) and is the latest and best-documented consistently warm period in geological history (Kaufman & Broadman, 2023), ideal for studying the impact of warmer arctic summer climate on the polar bear (Fig. S2). Evidence for past temperature can be derived, for example, from ice cores, glacier features, terrestrial and lacustrine sediments, and microfossils and marine microfossil and biomarker evidence, such as alkenones, diatoms, dinocysts, foraminiferal assemblages, Mg/Ca and oxygen isotopes (Kaufman et al. 2020). In general, these proxy methods suggest that HTM summer temperatures were 1.5-2.5°C higher than at present. In response to the HTM, many plant and animal species expanded their ranges northwards, as demonstrated for example by the findings of fossils of pelican (*Pelecanus crispus*), pond turtle (*Emys orbicularis*), and European wild cat (*Felis silvestris*) from Scandinavia where these species are not currently present (Sommer et al., 2011; Nikulina and Schmölcke, 2015), or in the northward and upward expansion of the boreal forest to regions occupied by modern tundra in northern Eurasia and North America (MacDonald et al., 2008). The warming was also associated with a reduction of arctic sea-ice cover in parts of the Arctic (de Vernal et al., 2013).



SI Figure 2. The polar bear fossil sites compared with general Holocene temperature trends in the Arctic. Upper) Number of sites where polar bear fossils have been discovered, presented in 2000-year time bins. Middle) The average temperature anomaly curve for the northern hemisphere extratropics (30-90°N) (Kaufman et al. 2020) Lower) δ^{18}O record from the NGRIP ice core in Greenland (Vinther et al., 2006), where more negative values indicate colder temperatures. X-axis shows the time before present (AD 1950). The approximate timing of the Holocene Thermal Maximum (HTM) is indicated

The Late Holocene (last 4 ka) has been characterized by progressively lower summer temperatures, with the initial cooling starting gradually even earlier (Kaufman et al. 2020). Evidence for this cooling trend are generally observable in all parts of the Arctic. For example, the proxy-based summer temperature reconstructions from northern Scandinavia and the North Atlantic region consistently indicate a steadily decreasing temperature trend until about 200-400 years ago, followed by a moderate to rapid rise over the last century (Sejrup et al., 2016). Similar trends can be seen in records from Alaska, northern Canada and in the Greenland ice core data, with indications of the lowest Holocene temperatures dating to the last millennium (Briner et al., 2016; Kaufman et al., 2016). In a more precise synthesis of lake sediment, glacier, and tree-ring data for the Arctic temperature trend over the last two millennia, a pervasive cooling trend with an average rate of -0.22°C ± 0.06 per 1000-yr was detected from 2 ka through the middle ages and into the Little Ice Age about 500 years ago (Kaufman et al. 2009). The summer cooling is interpreted to be a response to orbitally-induced gradual reduction in summer solar insolation, which especially at high northern latitudes is enhanced by positive feedbacks (arctic amplification), as well as through increased volcanic impact (McGregor et al. 2015). In the mid-20th century, this cooling trend was reversed, with especially strong warming occurring in recent decades (Kaufman et al., 2009; Abram et al., 2016).

4. Bering Sea ice change

With its abundant polar bear fossil records, the Bering Sea is one of the key marine regions to understand the linkages between the polar bear and Holocene sea ice. For the period 6-4 ka BP, we examined sea-ice proxy data from 15 sediment cores (Fig. 1B) with published ice rafted debris (Gorbarenko et al., 2010; Riethdorf et al., 2013), IP_{25} (Meheust et al., 2016; Ruan et al., 2017), or sea-ice diatom records (Sancetta and Robinson 1983, Katsuki and Takahashi 2005, Caissie et al. 2010, Max et al. 2012) and one peat core with a peat cellulose $\delta^{18}O$ record (Jones et al., 2020). In general, for all marine sites in the Bering Sea, age control is relatively poor and based on a variety of methods: radiocarbon dating, $\delta^{18}O$ stratigraphy, or chemostratigraphy correlating to radiocarbon dated cores nearby. Most sites include fewer than five points between 6 and 4 ka, and six sites have only one data point in this age slice. However, three sites have centennial-scale resolution records (Katsuki et al., 2009; Ruan et al., 2017; Jones et al., 2020).

Most sites in the Bering Sea, particularly the western and southern portions of the basin, contain no evidence of sea ice during most of the Holocene (Katsuki and Takahashi 2005; Caissie et al. 2010, Gorbarenko et al., 2010; Max et al. 2012; Riethdorf et al. 2013; Meheust et al., 2016). Two sites on the Umnak Plateau contain evidence of rare sea ice (Sancetta and Robinson 1983; Katsuki and Takahashi 2005), but sites along the shelf slope break contain evidence of winter sea ice (Sancetta and Robinson 1983; Katsuki and Takahashi 2005; Ruan et al. 2017). The peat core from St. Matthew Island extends only to 5.5 ka and reconstructs areal extent of winter sea ice across the Bering Sea (Jones et al., 2020).

On the southeastern Bering Sea shelf (site MC33A), two pulses of sea ice decline occurred at 7.5 ka and 3 ka (Katsuki et al., 2009). Between 6 and 4 ka, open water diatoms decreased suggesting a brief re-advance of sea ice to concentrations greater than today (Katsuki et al., 2009). Further northwest at the shelf-slope break (Site BR07), IP_{25} data indicates a slight re-advance of sea ice between 6 and 2 ka, however there is lack of data between 3 and 4 ka at this site, which makes it unclear how much sea ice fluctuated at this time (Ruan et al., 2017). The peat core from St. Matthew Island shows a decreasing trend in sea ice since 5.5 ka with maxima in sea ice before 5 ka and between 3.2 and 4.5 ka (Jones et al., 2020). The sum of these data indicates that sea ice expanded in the Bering Sea in the 6-4 ka time slice relative to both the early Holocene and today.References

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