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Polar Bear Fossil and Archaeological Records from the Pleistocene and Holocene in Relation to Sea Ice Extent and Open Water Polynyas

REVIEW

SUSAN J. CROCKFORD

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ABSTRACT

The polar bear (*Ursus maritimus*) is the apex predator of the Arctic but its distribution throughout the Pleistocene and Holocene has not previously been reported. Although natural death specimens of this species ('fossils') are rare, archaeological remains are much more common. This historical compilation presents the record of known ancient polar bear remains from fossil and archaeological contexts before AD 1910. Most remains date within the Holocene and derive from human habitation sites within the modern range of the species, with extralimital specimens documented in the north Atlantic during the late Pleistocene and in the southern Bering Sea during the middle Holocene reflecting natural expansions of sea ice during known cold periods. The single largest polar bear assemblage was recovered from an archaeological site on Zhokhov Island, Russia, occupied ca. 8,250–7,800 a BP during the warmer-than-today Holocene Climatic Optimum: 5,915 polar bear bones were recovered, representing 28% of all remains identified. Polar bear fossils and archaeological remains across the Arctic are most often found in proximity to areas where polynyas (recurring areas of thin ice or open water) are known today and which likely occurred in the past, including for the oldest known fossil from Svalbard (ca. 130–115 k a BP) and the oldest known archaeological specimens from Zhokhov Island (ca. 8,000 a BP). This pattern indicates that as they do today, polar bears may have been most commonly found near polynyas throughout their known historical past because of their need for ice-edge habitats at which to hunt seals.

CORRESPONDING AUTHOR:

Susan J. Crockford

Pacific Identifications Inc., CA

sjcrock@shaw.ca

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1. INTRODUCTION

The polar bear (*Ursus maritimus*) personifies the Arctic: it is the quintessential species of the northern sea ice habitat. It is usually classified as a marine mammal because individuals can (and often do) spend their entire lives on sea ice. However, females that make maternity dens on the coast may spend up to 8 months at a time on land and many bears in some regions spend at least a few months on land during the ice-free season (Amstrup 2003; Andersen et al. 2012; Castro de la Guardia et al. 2017; Ramsay & Stirling 1988; Rode et al. 2015; Stirling 1997). The species is currently well distributed across the shallow peripheral seas of the Arctic (Chukchi, Beaufort, Barents, Kara and Laptev) but also occurs in sub-Arctic regions with seasonal sea ice in winter and spring (including Hudson Bay, Labrador Sea, Davis Strait, Denmark Strait, and the Bering Sea) (***Figure 1***).

The most carnivorous and predatory of all bears, the polar bear occupies the top of the Arctic food chain, subsisting primarily on ringed seals (*Phoca hispida*) and to a lesser degree on bearded seals (*Erignathus barbatus*), which have a similar circumpolar distribution (Amstrup 2003). However, polar bears also occasionally hunt other Arctic seal species, walrus (*Odobenus rosmarus*), and small Arctic whales (Heide-Jørgensen et al. 2002; Kochnev 2002; Pereverzev & Kochnev 2012; Thiemann et al. 2007) and will readily scavenge the natural-death or human-hunted carcasses of walrus and large whales (Kavry et al. 2006; Laidre et al. 2018).

Apex predators like polar bears have virtually no natural enemies aside from humans. As a consequence, polar bears are either killed by humans or die a natural death. By far the most common cause of death for polar bears is starvation, which is a natural consequence of injury, illness, old age, lack of hunting experience, and intra-species competition (Amstrup 2003; Calvert et al. 1986; DeMaster, Kingsley & Stirling 1980; Derocher & Stirling 1992; Derocher & Stirling 1995; Ramsay & Stirling 1988; Stirling 1974; Stirling 2002; Stirling & Lunn 1997). These deaths usually occur during the winter when bears are on the sea ice, which means skeletal remains eventually sink to the bottom, never to be found. Very rarely, a polar bear may die of starvation or be killed by another bear on land during the summer/fall ice-free season or a pregnant or post-partum female may die on land in her maternity snow den over the winter, but scavenger activity ensures few skeletal remains survive. For these reasons, skeletal remains of polar bears that have died a natural death are rarely found as paleontological specimens unless they are quickly buried. In this regard, the polar bear stands in marked contrast to its ancestral species, the terrestrial-dwelling brown bear (*Ursus arctos*) which has a rich fossil record (Barnes et al. 2002; Davison et al. 2011; Edwards et al. 2011; Edwards et al. 2014; Kurtén 1968; Kurtén 1988).

However, as polar bears were hunted by humans across the entire Arctic during the Holocene, archaeological remains of polar bears are much more plentiful and provide the primary historical perspective on the distribution and range of the species since the end of the Last Glacial Maximum (LGM, ca. 11,700 a BP) (***Table 1***). A number of archaeologists have pointed out that proximity to polynyas may explain the location of many human settlements in the Eastern Arctic (Andreasen 1997; Gotfredsen 2010; Gotfredsen, Appelt & Hastrup 2018; Grønnow 2016; Grønnow et al. 2011; Hastrup, Mosbech & Grønnow 2018; Henshaw 2003; Jeppesen et al. 2018; Kroon, Jakobsen & Pedersen 2010; Schledermann 1980; Sørensen & Gulløv 2012; Woollett, Henshaw & Wake 2000). Polynyas are recurring areas of thin ice or open water within the pack ice caused by strong prevailing winds or currents that allow concentrations of marine mammals and birds to feed over the winter and/or spring; these include the wide offshore cracks in the ice called 'flaw' polynyas that develop between the edge of shorefast ice and offshore pack ice (Henderson et al. 2021; Stirling 1997; Stirling & Cleator 1981; Stringer & Groves 1991). The major polynyas mentioned in regard to ancient human habitation are the North Water between Ellesmere Island and northwest Greenland, and the Northeast and Sirius Waters off northeast Greenland, although others may have been just as significant in providing human hunters with access to the abundant wildlife they needed to survive (***Figure 2***). Biologists have also noted the importance of both large and small polynyas to polar bear health and survival in the Canadian Arctic and Greenland (Heide-Jørgensen et al. 2016; Henderson et al. 2021; Stirling 1980; Stirling, Cleator & Smith 1981; Vibe 1950; Vibe 1967). Therefore, this analysis explores the historical distribution of ancient polar bear remains across the entire Arctic in relation to expansions of sea ice extent during known cold periods and as it overlaps areas where polynya conditions currently prevail (or may have in the past), as has been suggested for natural-death bowhead whale remains (*Balaena mysticetus*) in the Canadian Arctic during the middle to late Holocene (Dyke & England 2003; Dyke, Hooper & Savelle 1996).

2. MATERIALS & METHODS

This historical compilation presents, with some caveats, the entire record of ancient polar bear remains from fossil, archaeological, and ethnographic contexts prior to

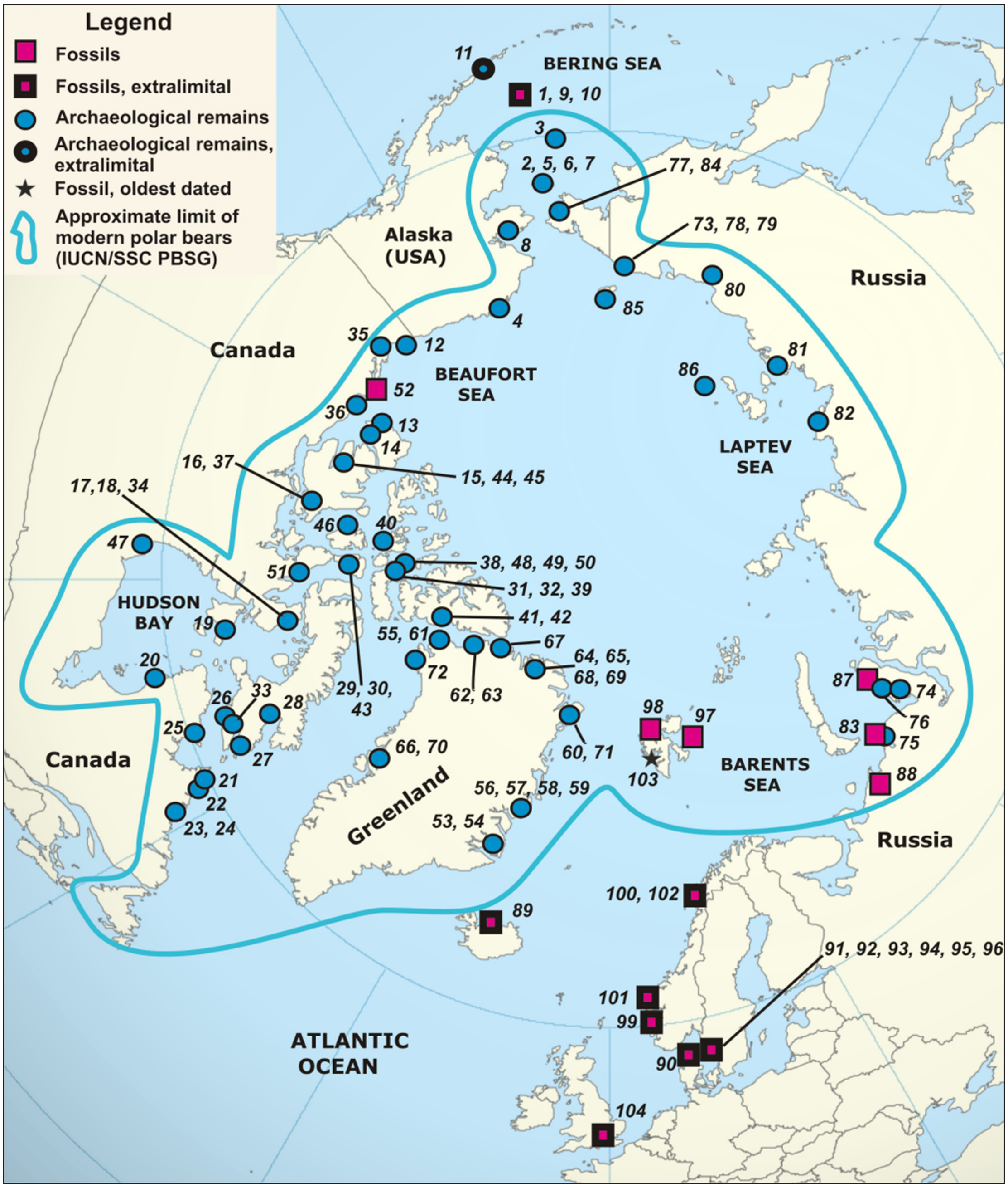

Figure 1 Fossil and archaeological polar bear remains across the Arctic, within the current species range (blue line) vs. extralimital finds as per International Union for the Conservation of Nature, Species Survival Commission, Polar Bear Specialist Group (IUCN/SSC PBSG). See text for explanation of 'fossil' remains. Legend of site numbers (see Table 1 for more details):

1. NE Point, St. Paul Is.; 2. St. Lawrence Is.; 3. Pottery House, St. Matthew Is.; 4. Walakpa; 5. St. Lawrence Is. (3 sites); 6. St. Lawrence Is. (Kukulik); 7. St. Lawrence Is. (Hillside site); 8. Cape Espenberg; 9. Qagnax Cave, St. Paul Is.; 10. Bogoslov Cave, St. Paul Is.; 11. Margaret Bay (UNL-48); 12. Washount (NjVi-2, H3); 13. Agvik (OkRn1); 14. Nelson River site; 15. Co-Op (OdPp-2, H1, H5); 16. Lady Franklin Pt. (NdPd-2); 17. Pingiqqalik (NgHd-1); 18. Naujan (MdHs-1); 19. Sadlermiut (KkHh-1); 20. Qijurittuq (IbGk-31); 21. Staffe Is.; 22. Nachvak Fjord group; 23. Oakes Bay (HeCg-8); 24. Iglosiatik Is.; 25. JfEl-10, Quebec; 26. Talaguak, Baffin Is.; 27. Outer Frobisher Bay (3sites); 28. Cumberland Sound (LlDj-1); 29. Hazard Inlet group (3 sites); 30. Learmonth (PeJr-1); 31. Porden Pt. group (3 sites); 32. Porden Pt. (RbJq-6); 33. Peale Pt. (KkDo-1); 34. Sanirajak (NeHd-1); 35. Kuukpak (NiTs-1, H1); 36. Amundsen Gulf group (4 sites); 37. Bell site (NiNg-2); 38. Port Refuge (Snowdrift); 39. Hornby Head (RbJq-1); 40. Brooman Point; 41. Bache Peninsula, 3 sites; 42. Skraeling Is. (SfFk-4, H 14–16); 43. Cape Garry (PcJq-5); 44. Victoria Is.; 45. Victoria Is.; 46. Cape Richard Collinson; 47. Seahorse Gully (IeKn 6); 48. Port Refuge (upper beach); 49. Port Refuge (Gull Cliff); 50. Port Refuge (Lower Beach); 51. Gulf of Boothia; 52. Baillie Island; 53. Scoresby Sound ('House of Beads'); 54. Scoresby Sound (Skærgårdshalvøen 1); 55. Nugarsuk; 56. Walrus Is.; 57. Clavering Is. (4 sites); 58. Fladstrand; 59. Dødemandsbugten (3 sites); 60. Sephus Müller Næs; 61. Qeqertaaraq; 62. Washington Land; 63. Washington Land; 64. Kolnæs; 65. Vandfeldsnaes; 66. Saqqaq; 67. Solbakken; 68. Adam C. Knuth; 69. Pearylandville; 70. Sønderland; 71. Norde Eskimonæsset; 72. Nuulliit; 73. Cape Schmidt; 74. Yamal Peninsula; 75. Vaygach Is.; 76. Tiutei-Sale 1; 77. Dezhnevo; 78. Cape Schmidt; 79. Cape Schmidt; 80. Cape Baranov; 81. Mainland south of Laptev Strait; 82. Mainland, near Tikai; 83. Vaygach Island; 84. Ekven; 85. Devil's Gorge; 86. Zhokhov Is.; 87. Mordy-Yahk River; 88. Pechora River; 89. Iceland; 90. Asdal DEN; 91. Kuröd Bohuslän; 92. Nedre Kuröd Bohuslän; 93. Hisingen; 94. Kärraberg; 95. Östra Karup; 96. Kullaberg; 97. Svenskøya; 98. Svalbard; 99. Finnøy; 100. Nordcemgrotta; 101. Hamnsundhelleren; 102. Nordcemgrotta; 103. Poolepynten; 104. Kew Bridge.

AD 1910 as recorded in the English scientific literature, presented by country in approximate chronological order (***Table 1***). Some specimens may have been missed because reports were never published, were reported in an inaccessible format (i.e. so-called 'grey literature') or published in a foreign language. Two well-known Russian-language archaeological reports were consulted but there was no attempt to make a comprehensive search of the Russian literature or to access records published in Norwegian, Swedish, Finnish, or Icelandic. However, in many cases, specimens initially reported in a language other than English or in unpublished reports have been cited by other authors in English papers, in which case, I refer to both sources.

The 'fossil' remains reported here are in most cases not actually mineralized and are technically 'subfossils', as is true for the archaeological remains. However, for the purpose of this report, all natural-death remains are referred to as fossils. The table includes information on location, chronological date or dates (if available), approximate geological time period, type of specimen, and abundance information (if available), and sources (references). All geological and climatological time periods used in this paper are defined in ***Table 1*** and the approximate geographical location of the specimen finds are shown in ***Figure 1***.

Some single polar bear finds have been dated directly and where this has been done, the date is reported as given and the lab number for the date provided. However, this level of precision is rare for most archaeological remains except for some specimens from Canada and Greenland (e.g., #51, 71). Specimens from archaeological sites are in most cases given as approximate dates for associated deposits using a range of dating methods (including artifact styles, depth of deposit, and ^{14}C dates on other material, including charcoal) and therefore, lab numbers for dates are not provided. Because they are a marine mammal, direct dates on polar bear bone have been corrected for the carbon reservoir effect, the phenomenon that makes ^{14}C dates on marine material appear older than they actually are by up to about 400 years (depending on the region). Unfortunately for the use of charcoal for dating, the prevalent use of long-dead driftwood by ancient human hunters in the Arctic has a similar effect on accuracy. In addition, charcoal and bone from terrestrial species from Arctic sites may be contaminated *in situ* by oils from marine mammals. With these caveats in mind, modern archaeologists are usually careful in their selection of datable material and choose terrestrial mammal bone such as musk ox or caribou, or fast-growing wood like willow where ever possible (e.g., Friesen, Finkelstein & Medeiros 2020; McGhee 2000), may pre-treat terrestrial mammal bone to test for the presence of sea-mammal lipids (e.g., Desjardins 2018), and/or test terrestrial species together with a marine species to arrive at a local marine-reservoir correction factor (e.g., Dyke et al. 2018). The dating accuracy in the polar bear data presented here therefore varies considerably and makes all but broadly-defined chronological patterns untenable. However, it is considered better to know the true nature of the record than to impose arbitrary limits for inclusion that might discard important records that could, if re-examined, yield more useful information in the future.

In addition to the record of ancient polar bear remains, an Arctic map of the approximate location of known polynyas is provided (***Figure 2***) based on regional studies of this phenomenon (Barber et al. 2001; Grønnow et al. 2011; Jackson et al 2020; Kassens & Thiede 1994; Kern 2008; Morales Maqueda, Willmott & Biggs 2004; Pedersen et al. 2010; Smedsrud et al. 2006; Speer et al. 2017; Stirling & Cleator 1981; Stringer & Groves 1991). Some polynyas are not only important areas of biological productivity and air to breathe for seals, walrus, and whales but contribute extensively to sea ice formation in the Arctic. For example, severe continental weather in Siberia generates cold winds that blow across the shallow Laptev Sea from October to April, which create almost constant upwelling that generates a large flaw polynya about 1,800 km long and 10–15 km wide, called the Great Siberian polynya, which is largely responsible for the almost continuous production of Arctic sea ice every winter (Buckley et al. 1979; de Vernal et al. 2020; Tamura & Ohshima 2011; Wakefield 2020). For polar bears, polynyas offer critical ice-edge hunting opportunities that may otherwise exist only at the periphery of consolidated pack ice. Changes in size and productivity have been documented for a number of polynyas since the end of the LGM that may have influenced polynya availability and thus polar bear distribution during the Holocene: e.g., Northeast Water (Hjort 1997); Kara Sea polynyas (Hörner, Stein & Fahl 2018); North Water (Jackson et al. 2021); and Storfjorden (Rasmussen & Thomsen 2014). Some polynyas may not have existed at all before a certain time: for example, one analysis (Dyke & England 2003) suggested that the polynyas that currently form due to high water flow between the channels that separate Ellesmere and Devon Island in the Central Canadian Arctic (Hell Gate-Cardigan Strait and Penny Strait) probably did not exist before 4,000 BP due to postglacial isostatic uplift. In contrast, some polynyas may have existed in the past that are no longer present today due to sea level and sea ice changes, as I suggest may have existed in the North Atlantic during the LGM and its immediate aftermath.

MAP #	SPECIMEN LOCATION †	AGE (A BP) ‡	TYPE OF DATE	RELATIVE AGE§	SPECIMEN TYPE	REFERENCE
1.	NE Point St. Paul Island Pribilofs USA	ca. 55	[shot 1895]	Late Holocene (LIA)	1 skull (old M)	Ray 1971
2.	St. Lawrence Is. (Kawarin grave) USA	ca. 40	ethnographic	Late Holocene (LIA)	89 skulls (ritual feature)	NPS 2013a
3.	Pottery House St. Matthew Is. USA	ca. 430–350	on deposit	Late Holocene (LIA)	9 assorted elements	Frink et al. 2001
4a.	Walakpa Site (late) USA	ca. 550–0	on deposit	Late Holocene (LIA)	13 assorted elements	Stanford 1976
4b.	Walakpa Site (middle) USA	ca. 1,050–550	on deposit	Late Holocene (MWP)	6 assorted elements	Stanford 1976
4c.	Walakpa Site (early) USA	ca. 1,450–1,150	on deposit	Late Holocene (DAC)	15 assorted elements	Stanford 1976
5.	St. Lawrence Is. (3 sites) USA	ca. 2,000–0	on deposit	Late Holocene (LIA-RWP)	present (not quantified)	Dumond 1998; Collins 1937; Murray 2008
6.	St. Lawrence Is. (Kukulik) USA	ca. 2,000–0	on deposit	Late Holocene (LIA-RWP)	287 skulls (in human burials)	NPS 2013b
7.	St. Lawrence Is. (Hillside site) USA	ca. 1,800–1,550	on deposit	Late Holocene (RWP)	present (not quantified)	Collins 1937; Dumond 1998; Arnold 2000
8.	Cape Espenberg Seward Peninsula USA	ca 2,500	on deposit	Late Holocene (NEO)	1 bone	Saleeby 1994
9a.	Qagnax Cave St. Paul Island USA †	4,830 ± 40	Beta-182978	Middle Holocene (NEO)	1 radius (distal) juvenile	Veltre et al. 2008
9b.	Qagnax Cave USA	4,410 ± 60	SPC-03-76	Middle Holocene (NEO)	1 phalanx adult	Veltre et al. 2008
9c.	Qagnax Cave USA	not dated	n/a	Middle Holocene (NEO)?	248 bones from 6 adult bears (2 M/4 F)	Veltre et al. 2008
10.	Bogoslov Cave St. Paul Island USA †	not dated	on deposit	Middle Holocene (NEO)?	2 adults 1 juvenile (15 bones/fragments total)	Ray 1971
11.	Margaret Bay (UNL-48) Unalaska Is. USA	ca. 4,700–4,100	on deposit	Middle Holocene (NEO)	102 (4 individuals)	Davis 2001; Murray 2008
12.	Washount (NjVi-2, H3) Herschel Is. CAN	ca. 400–260	on deposit	Late Holocene (LIA)	7 assorted elements	Friesen & Hunston 1994
13.	Agvik (OkRn1) Banks Is. CAN	ca. 500–300	on deposit	Late Holocene (LIA)	28 assorted elements	Kotar 2016
14.	Nelson River site Banks Is. CAN	ca. 650–50	on deposit	Late Holocene (LIA)	70 individuals	Arnold 1986; Moody & Hodgetts 2013
15.	Co-Op (OdPp-2, H1, H5) Victoria Is. CAN	ca. 500–50	on deposit	Late Holocene (LIA)	193 assorted elements	Lamy & Spitery 1991; Moody & Hodgetts 2013
16.	Lady Franklin Pt. (NdPd-2) Victoria Is. CAN	ca. 650–50	on deposit	Late Holocene (LIA)	4 assorted elements	Taylor 1972; Desjardins 2018
17.	Pingiqqalik (NgHd-1) Foxe Basin CAN	ca. 600–400	on deposit	Late Holocene (LIA)	55 assorted elements	Desjardins 2018
18.	Naujan (MdHs-1) Foxe Basin CAN	ca. 650–50	on deposit	Late Holocene (LIA)	1 bone	Mathiassen 1927; Desjardins 2018
19.	Sadlermiut (KkHh-1) Southampton Is. CAN	ca. 650–50	on deposit	Late Holocene (LIA)	38 assorted elements	Collins 1956; Collins 1981; Desjardins 2018
20.	Qijurittuq (IbGk-3, H1) Hudson Bay CAN	ca. 200	on deposit	Late Holocene (LIA)	2 assorted elements	Desrosiers et al. 2010
21.	Staffe Is. Labrador CAN	ca. 650–50	on deposit	Late Holocene (LIA)	present (not quantified)	Kaplan & Woollett 2016
22.	Nachvak Fjord group (IgCx-3; IgCv-7) Labrador CAN	ca. 650–50	on deposit	Late Holocene (LIA)	17 assorted elements	Swinarton 2008; Desjardins 2018
23.	Oakes Bay (HeCg-8) Labrador CAN	ca 270–170	on deposit	Late Holocene (LIA)	5 assorted elements	Woollett 2010
24.	Iglosiatik Is. Labrador CAN	ca. 650–50	on deposit	Late Holocene (LIA)	present (not quantified)	Kaplan & Woollett 2016
25.	JfEl-10 Quebec (Hudson Strait) CAN	ca. 650–50	on deposit	Late Holocene (LIA)	31 assorted elements	Lofthouse 2003; Desjardins 2018

(Contd.)

MAP #	SPECIMEN LOCATION †	AGE (A BP) ‡	TYPE OF DATE	RELATIVE AGE§	SPECIMEN TYPE	REFERENCE
26.	Talaguak Baffin Is. on Hudson Strait CAN	ca. 650–50	on deposit	Late Holocene (LIA)	13 assorted elements	Sabo 1981; Desjardins 2018
27.	Outer Frobisher Bay sites (KfDe-5; KfDf-2; KeDe-7) Baffin Is.CAN	ca. 650–50	on deposit	Late Holocene (LIA)	17 assorted elements	Henshaw 1995; Desjardins 2018
28.	Cumberland Sound (LlDj-1) Baffin Is. CAN	ca. 600–100	on deposit	Late Holocene (LIA)	3 assorted elements	Schledermann 1975; Dejardins 2018
29.	Hazard Inlet group (PaJs-3; PaJs-4; PaJs-13) Somerset Is. CAN	ca. 650–50	on deposit	Late Holocene (LIA)	24 assorted elements	Whitridge 1992; Dejardins 2018
30.	Learmonth (PeJr-1) Somerset Is. CAN	ca. 650–50	on deposit	Late Holocene (LIA)	146 assorted elements	Taylor & McGhee 1979; Rick 1980; Dejardins 2018
31.	Porden Pt. group (RbJr-1; RbJr-4; RbJr-5) Devon Is. CAN	ca. 650–50	on deposit	Late Holocene (LIA)	132 assorted elements	Park 1989; Dejardins 2018
32.	Porden Pt. (RbJq-6) Devon Is. CAN	ca. 700–600	on deposit	Late Holocene (LIA/MWP)	3 assorted elements	Howse 2019
33a.	Peale Pt. (KkDo-1) Baffin Is. CAN	ca. 650–100	on deposit	Late Holocene (LIA)	16 assorted elements	Stenton 1987
33b.	Peale Pt. (KkDo-1) Baffin Is. CAN	ca. 850–750	on deposit	Late Holocene (MWP)	3 assorted elements	Stenton 1987
34.	Sanirajak (NeHd-1) Foxe Basin CAN	ca. 750–450	on deposit	Late Holocene (LIA/MWP)	2 assorted elements	Desjardins 2013
35.	Kuukpak (NiTs-1, H1) Mackenzie R. CAN	ca. 750–350	on deposit	Late Holocene (LIA/MWP)	1 bone	Betts & Friesen 2006
36a.	Amundsen Gulf (Tiktalik NkRi-3, H5) CAN	ca. 750–650	on deposit	Late Holocene (MWP)	28 assorted elements	Moody & Hodgetts 2013
36b.	Amundsen Gulf (Pearce Point, Vaughn, Jackson sites)	ca. 650–50	on deposit	Late Holocene (LIA)	at least 4 elements	Morrison 2000; Taylor 1972; Moody & Hodgetts 2013
37.	Bell site (NiNg-2) Victoria Is. CAN	ca. 850–650	on deposit	Late Holocene (MWP)	4 assorted elements	Howse 2019
38.	Port Refuge (Snowdrift) Devon Is. CAN	ca. 1,000	on deposit	Late Holocene (MWP)	present (not quantified)	McGhee 1979; McGhee 1981
39.	Hornby Head (RbJq-1, H2, H3) Devon Is. CAN	ca. 1,100–650	on deposit	Late Holocene (MWP)	17 assorted elements	Howse 2019
40.	Brooman Point Bathurst Is. CAN	ca. 900	on deposit	Late Holocene (MWP)	present (not quantified)	McGhee 1984; Murray 2008
41a.	Skraeling Is. (SfFk-4, H2–12, 17–23) Ellesmere CAN	ca. 850–650	on deposit	Late Holocene (MWP)	235 assorted elements	McCullough 1989
41b.	Eskimobyen (SgFm-4, H25, H26) Ellesmere CAN	ca. 850–650	on deposit	Late Holocene (MWP)	53 assorted elements	McCullough 1989
41c.	Sverdrup Skraeling Is. (SfFk-5, H6) Ellesmere CAN	ca. 850–650	on deposit	Late Holocene (MWP)	13 assorted elements	McCullough 1989
42.	Skraeling Is. (SfFk-4, H 14–16) NE Ellesmere CAN	ca. 850–650	on deposit	Late Holocene (MWP)	66 assorted elements	Howse 2019; McCullough 1989
43.	Cape Garry (PcJq-5) Somerset Is. CAN	ca. 950–750	on deposit	Late Holocene (MWP)	21 assorted elements	Rick 1980; Dejardins 2018
44a.	Co-Op (OdPp-2, H1, H5) Victoria Is. CAN	1,350 ± 40	Gif-8434	Late Holocene (DAC)	1 bone	Harington 2003
44b.	Co-Op (OdPp-2, H1, H5) Victoria Is. CAN	1,310 ± 40	Gif-8178	Late Holocene (DAC)	1 bone	Harington 2003
45a.	Co-Op (OdPp-2, H2) Victoria Is. CAN	1,560 ± 65	Gif-7512	Late Holocene (RWP/DAC)	1 bone	Harington 2003

(Contd.)

MAP #	SPECIMEN LOCATION †	AGE (A BP) ‡	TYPE OF DATE	RELATIVE AGE§	SPECIMEN TYPE	REFERENCE
45b.	Lady Franklin Pt. (NdPd-2) Victoria Is.	1,510 ± 30	CAMS-66368	Late Holocene (RWP/DAC)	1 humerus	Savelle et al. 2012; Ingolfsson & Wiig 2009
46.	Cape Richard Collinson CAN	2,135 ± 120	Beta-18129	Late Holocene (RWP)	canine tooth	Harington 2003
47.	Seahorse Gully (IeKn 6) CAN	ca. 2,600–2,400	on deposit	Late Holocene (NEO)	present (not quantified)	Nash 1976
48.	Port Refuge (upper beach) Devon Is. CAN	ca. 4,000	on deposit	Late Holocene (NEO)	2 assorted elements	McGhee 1979; McGhee 1981
49.	Port Refuge (Gull Cliff) Devon Is. CAN	ca. 4,000–3,000	on deposit	Late Holocene (NEO)	3 assorted elements	McGhee 1979; McGhee 1981
50.	Port Refuge (Lower Beach) Devon Is. CAN	ca. 2,500	on deposit	Late Holocene (NEO)	2 assorted elements	McGhee 1979; McGhee 1981
51a.	Gulf of Boothia central CAN	3,265 ± 15	UCI-42204	Late Holocene (NEO)	1 bone	Dyke et al. 2011
51b.	Gulf of Boothia central CAN	3,515 ± 15	UCI-42211	Late Holocene (NEO)	1 bone	Dyke et al. 2011
51c.	Gulf of Boothia central CAN	3,290 ± 15	UCI-42210	Late Holocene (NEO)	1 bone	Dyke et al. 2011
51d.	Gulf of Boothia central CAN	3,765 ± 15	UCI-2207	Late Holocene (NEO)	1 bone	Dyke et al. 2011
52.	Baillie Island CAN †	not dated	on deposit	Pleistocene	1 bone	Harington 2003; Vincent 1989
53.	Scoresby Sound (House of Beads) GRE	ca. 150–50	on deposit	Late Holocene (LIA)	2 assorted elements	Sandell & Sandell 1991; Sørensen & Gulløv 2012
54.	Scoresby Sound (Skærgårdshalvøen 1) GRE	ca. 150–50	on deposit	Late Holocene (LIA)	a few elements	Degerbøl 1936
55.	Nugarsuk GRE	ca. 300–100	on deposit	Late Holocene (LIA)	5 assorted elements	Møhl 1979
56.	Walrus Is. (caches/shelters) GRE	ca. 550–100	on deposit	Late Holocene (LIA)	16 assorted elements	Gotfredson 2010; Grønnow et al. 2011
57.	Clavering Is. (sites 69, 78, 96, 105) GRE	ca. 550–100	on deposits	Late Holocene (LIA)	25 assorted elements	Gotfredson 2010
58.	Fladstrand (site 41) GRE	ca. 550–100	on deposit	Late Holocene (LIA)	91 assorted elements	Gotfredson 2010
59.	Dødemandsbugten (sites 45–47) GRE	ca. 550–100	on deposit	Late Holocene (LIA)	66 assorted elements	Sørensen et al. 2009; Gotfredson 2010
60.	Sephus Müller Næs (NEWland) GRE	460 ± 60	AAR-1776	Late Holocene (LIA)	1 bone	Andreasen 1997
61.	Qeqertaaraq (H1 + midden) GRE	ca. 850–750	on deposit	Late Holocene (MWP)	19 assorted elements	Howse 2019; Dejardins 2018
62.	Washington Land GRE	960 ± 60	AAR-5775	Late Holocene (MWP)	1 bone	Bennike 2002
63.	Washington Land GRE	1,415 ± 60	AAR-5774	Late Holocene (DAC)	1 bone	Bennike 2002
64.	Kolnæs Peary Land GRE	1,440 ± 45	K-352	Late Holocene (DAC)	R. mandible	Bennike 1991; Harington 2003
65.	Vandfeldsnaes Brønlund Fjord GRE	1,520 ± 110	AAR-1357	Late Holocene (RWP)	1 ulna	Bennike 1997
66.	Saqqaq Disko Bay GRE	ca. 2,900	on deposit	Late Holocene (NEO)	present (not quantified)	Gotfredsen 1992; Bennike 1997
67.	Solbakken (Hall Land) GRE	ca. 4,000–3,500	on deposit	Late Holocene (NEO)	9 assorted elements (mostly one individual)	Darwent 2003; Murray 2008
68.	Adam C. Knuth (Peary Land) GRE	ca. 4,000–3,500	on deposit	Late Holocene (NEO)	3 assorted elements	Darwent 2003; Murray 2008
69.	Pearylandville (Peary Land) GRE	ca. 4,000–3,500	on deposit	Late Holocene (NEO)	2 assorted elements	Darwent 2003; Murray 2008
70a.	Sønderland GRE	3,320 ± 85	K-5928	Late Holocene (NEO)	1 bone	Rasmussen 1996
70b.	Disko Bay GRE	3,470 ± 85	K-5930	Late Holocene (NEO)	1 bone	Rasmussen 1996

(Contd.)

MAP #	SPECIMEN LOCATION †	AGE (A BP) ‡	TYPE OF DATE	RELATIVE AGE§	SPECIMEN TYPE	REFERENCE
71.	Norde Eskimonæsset NEWland GRE	4,076± 90	AAR-1773	Late Holocene (NEO)	1 bone	Andreasen 1997
72.	Nuulliit (Thule) GRE	5,060 ± 95 uncal	K-2560	Middle Holocene (NEO)	1 bone	Knuth 1978; Bennike 1997; Grønnow & Jensen 2003
73.	Cape Schmidt RUS	ca. 100	ethnographic	Late Holocene (LIA)	+50 skulls (2 ritual features)	Kochneva 2007; Vdovin 1977
74.	Yamal Peninsula RUS	ca.250–50	ethnographic	Late Holocene (LIA)	'many skulls' (ritual feature)	Kochneva 2007; Kishchinskiy 1976
75.	Vaygach Island RUS	ca. 250–50	ethnographic	Late Holocene (LIA)	'many' skulls (ritual feature)	Kochneva 2007; Nordenscheldt 1881
76a.	Tiutei-Sale 1 (late) RUS	ca. 850–650	on deposit	Late Holocene (MWP)	89 assorted elements (5 individuals)	Fedorova et al. 1998; Nomokonova et al. 2018
76b.	Tiutei-Sale 1 (early) RUS	ca.1,350–1,150	on deposit	Late Holocene (DAC)	42 assorted elements (6 individuals)	Fedorova et al. 1998; Nomokonova et al. 2018
76c.	Tiutei-Sale 1 (early/late) RUS	ca. 1,350–650	on deposit	Late Holocene DAC/MWP)	164 assorted elements (10 individuals)	Fedorova et al. 1998; Nomokonova et al. 2018
77.	Dezhnevo Bering St. RUS	ca. 1,500–900	on deposit	Late Holocene (DAC)	33 assorted elements	Gusev et al. 1999; Savinetsky et al. 2004
78.	Cape Schmidt RUS	ca. 1,250–1,150	on deposit	Late Holocene (DAC)	skulls from human burials	Dikov 1988
79.	Cape Schmidt RUS	ca. 1,950–1,350	on deposit	Late Holocene (RWP)	'many' skulls (ritual feature)	Dikov 1988
80.	Cape Baranov Kolyma R. mouth RUS	ca. 1,855–1,525	on deposit	Late Holocene (RWP)	16 assorted elements	Bland 2008; Vereshchagin 1969
81.	Mainland south of Laptev Strait RUS	not dated	on deposit	Late Holocene?	present (not quantified)	Vereshchagin 1969
82.	Tikai (Laptev Sea) RUS	not dated	on deposit	Late Holocene?	present (not quantified)	Vereshchagin 1969
83.	Vaygach Island RUS †	1,971 ± 25	OxA-23631	Late Holocene (RWP)	R. ulna	Boeskorov et al. 2018
84.	Ekven Bering St. RUS	<2,700 BP uncal	on deposit	Late Holocene (NEO)	10 assorted elements	Savinetsky et al. 2004
85.	Devil's Gorge Wrangel Is. RUS	ca. 3,620–2,950	on deposit	Late Holocene (NEO)	1 skull fragment; 1 claw	Dikov 1988; Tein 1977; Tein 1978
86.	Zhokhov Island RUS	ca. 8,250–7,800	on deposit	Middle Holocene (HCO)	5,915 assorted elements (130 individuals)	Pitulko et al. 2015
87.	Mordy-Yahk River mouth RUS †	not dated	on deposit	Pleistocene?	1 R. ulna (M)	Vereshchagin 1969; Harington 2008
88.	Pechora River mouth RUS †	not dated	on deposit	Pleistocene?	1 molar tooth	Harington 2008
89.	Iceland ICE †	ca. 13000	on deposit	Late Pleistocene (YD)	present (not quantified)	Áskelsson 1938; Petersen 2010
90.	Asdal DEN †	12,900–12,400	K-3741	Late Pleistocene (YD)	1 L. mandible (M)	Aaris-Sørensen 2009; Berglund et al. 1992
91.	Kuröd Bohuslän SWE †	10,170 ± 125 uncal	Lu-1075	Late Pleistocene (YD)	1 dist. femur + 4 other elements	Kurtén 1988; Berglund et al. 1992
92.	Nedre Kuröd Bohuslän SWE †	10,360 ± 130 uncal	Lu-1074	Late Pleistocene (YD)	1 rib fragment + 2 other elements	Kurtén 1988; Berglund et al. 1992
93.	Hisingen SWE †	not dated	on deposit	Late Pleistocene (YD)?	1 L. maxilla (M)	Kurtén 1988; Berglund et al. 1992
94.	Kärraberg Vekkinge parish SWE †	not dated	on deposit	Late Pleistocene (YD)?	1 skull (F?)	Kurtén 1988; Berglund et al. 1992
95.	Östra Karup Bastad SWE †	12,230 ± 130 uncal	Lu-1076	Late Pleistocene	1 R. ulna (F)	Berglund et al. 1992; Aaris-Sørensen 2009

(Contd.)

MAP #	SPECIMEN LOCATION †	AGE (A BP) ‡	TYPE OF DATE	RELATIVE AGE§	SPECIMEN TYPE	REFERENCE
96.	Kullaberg Scania SWE †	12,320 ± 125 uncal	Lu-602	Late Pleistocene	1 R. femur	Berglund et al. 1992; Aaris-Sørensen 2009
97.	Svenskøya Svalbard NO †	7,760 ± 50	T-4167	Middle Holocene (HCO)	1 bone	Harington 2008; Ingolfsson & Wiig 2009
98.	Svalbard NO †	ca. 8,200	on deposit	Middle Holocene (HCO)	>1 bone	Harington 2008
99.	Finnøy NOR †	10,925 ± 110 uncal	T-4724	Late Pleistocene (YD)	1 almost complete skeleton (M)	Blystad et al. 1983; Berglund et al. 1992
100.	Nordcemgrotta Kjæpsvik NOR †	ca. 22,000 uncal	direct date	Late Pleistocene [1]	ulna + others	Lauritzen et al. 1996; Hufthammer 2001
101.	Hamnsundhelleren NOR †	36,000–28,000 uncal	direct date	Late Weichselian (MIS 3) [2]	>1 bones	Valen et al. 1996; Hufthammer 2001
102.	Nordcemgrotta Kjæpsvik NOR †	ca. 115,000	on deposit	Early Weichselian	1 rib (mtDNA) + 2 other elements	Lauritzen et al. 1996; Davison et al. 2011
103.	Poolepynten Svalbard NOR †	ca. 130,000–110,000	LuS-6155	Eemian Interglacial/MIS 5e	1 L. mandible (M)(mtDNA)	Ingolfsson & Wiig 2009; Lindqvist et al. 2010
104.	Kew Bridge, Thames River UK †[3]	ca. 70,000	on deposit	Early Weichselian	1 R. ulna (M)	Kurtén 1988; Harington 2008

Table 1 Fossil and archaeological polar bear remains by approximate chronological date, by country; site numbers as in Figure 1. Abbreviations: USA, United States of America; CAN, Canada; GRE, Greenland; RUS, Russia; ICE, Iceland; DEN, Denmark; SWE, Sweden; NOR, Norway; UK, United Kingdom; F, female; M, male; R, right, L, left; H, house; Is., Island; Pt., Point; ca., approximately; LIA, Little Ice Age; MWP, Medieval Warm Period; DAC, Dark Age Cold; RWP, Roman Warm Period; HCO, Holocene Climatic Optimum; NEO, Neoglacial; YD, Younger Dryas. † indicates fossil specimens, see text for explanation.

† Indicates 'fossil' specimens, see text.

‡ These are calibrated radiocarbon years BP unless indicated otherwise. Carbon 14 dates on polar bear bone are corrected for marine reservoir effect unless indicated otherwise; one historic specimen (#1) is a calendar date (e.g., AD 1875) and one (#103) is an IRSL ('infrared-stimulated luminescence') date on sediments.

§ Relative geological and climatological time periods (a BP) defined as: Pleistocene 2,500,000–11,700; MIS 5e/Eemian Interglacial 130,000–115,000; Last Glacial Maximum (LGM) 30,000–19,700; Holocene 11,700–1950; Younger Dryas (YD) 12,900–11,700; Early Holocene 11,700–8,200; Middle Holocene 8,300–4,200; Holocene Climatic Optimum (HCO) 9,000–5,500; Neoglacial 5,500–2,000; Roman Warm Period (RWP) 2,000–1,500; Dark Ages Cold (DAC) 1,500–1,050; Medieval Warm Period (MWP) 1,050–650; Little Ice Age (LIA) 650–50 (Alley 2000; Cohen et al. 2013; Kaufman et al. 2004; Lamb 1982; Marcott et al. 2009; Polyak et al. 2010; Soon & Baliunas 2004).

1. The 'Hamnsund Interstadial' was a short-lived ice retreat originally dated to 22–19k uncal a BP in W. Norway. See text for discussion.

2. The Ålesund Interstadial was a short- lived ice treat dated to 30k a BP in W. Norway (Hufhammer 2001).

3. The species identification of this specimen has been disputed but not resolved, see text for details.

Figure 2 Known recurrent major and flaw polynyas across the Arctic (after Barber et al. 2001; Grønnow et al. 2011; Jackson et al 2020; Kern 2008; Morales Maqueda et al. 2004; Pedersen et al. 2010; Smedsrud et al. 2006; Speer et al. 2017; Stirling and Cleator 1981; Stringer and Groves 1991). The 'Wandel Water' (Z) is a proposed polynya that forms under certain climatic conditions in the Wandel Sea (e.g., Schweiger et al. 2021).

3. RESULTS

Most ancient remains of polar bears come from archaeological sites and ethnographic locations within the modern range of the species that date within the Holocene. Extralimital polar bear specimens have been documented in the north Atlantic during the late Pleistocene and in the Bering Sea during the middle Holocene (***Figure 1***, ***Table 1***). These extralimital records indicate that sea ice extended beyond the present maximum extent (currently reached in March every year) at two particular points in time: in the Bering Sea during the mid-Holocene Neoglacial cold period (Crockford 2008; Crockford & Frederick 2007; Caissie et al. 2010;

Davis 2001) and in the North Atlantic during the Younger Dryas (YD) cold period. The YD was a rapid return to cold conditions that briefly interrupted the warming that began ca. 19,700 a BP and which eventually brought the LGM to an end ca. 11,700 a BP (Alley 2000; Bradley & England 2008; Cheng et al. 2020).

3.1 EXTRALIMITAL FOSSIL RECORDS

In the Bering Sea, there are both fossil and historic era records that date to the mid-to-late Holocene: an old bear shot on St. Paul Island in the Pribilof Islands in 1875 (#1) dates to the Little Ice Age (Ray 1971), and two assemblages on the same island found in vertical caves (Qagnax and Bogoslov), which functioned as lethal 'death traps' (#9 and 10), date to the early part of the Neoglacial. The 250 polar bear bones from Qagnax Cave constitute the largest fossil assemblage found in the Arctic and represent at least eight bears, two of which were dated directly (Veltre et al. 2008). The material from nearby Bogoslov Cave (n = 15, three individuals) has not been dated but presumably comes from a similar period (Ray 1971).

Iceland, southern Norway, southern Sweden, and Denmark have generated nine fossil polar bear remains (#89–99), seven of which date within the brief YD cold period and two (#93, 96) date to a slightly earlier time when the region was undergoing active deglaciation (Aaris-Sorensen 2009; Aaris-Sorensen & Petersen 1984; Áskelsson 1938; Berglund et al. 1992; Bylstad et al. 1983; Harington 2008; Ingolfsson & Wiig 2009; Petersen 2010). During both periods, the Skagerrak Strait between Norway and Denmark was essentially a dead-end fjord of the North Sea with ice cover in winter and spring which probably had an associated polynya due to cold winds blowing off the thick ice sheet that still covered Norway and Sweden (Berglund et al. 1992; Gyllencreutz 2005; Stroeven et al. 2016). Most of these extralimital fossil remains are isolated bones or a small cluster of bones that have been dated directly, although there is also one almost complete skeleton of an old male approximately 28 years old (#99) (Berglund et al. 1992; Næss 2018). The complete mandible from an adult male recovered in Denmark (#90) is shown in ***Figure 3***.

The sheer number of natural death remains of polar bears recovered in Scandinavia that date within a narrow time frame is unique. It suggests strongly that the climatic conditions during the late LGM that created suitable habitat for polar bears so far south of their modern range were associated with unusual circumstances that have not existed elsewhere in time or space. Either death rates from starvation or bone survival rates—or both—were unusually high. It is possible that polar bears existed at high densities due to limited suitable habitat in the region, resulting in greater competition and higher overall death rates, and/or that abrupt sea level changes and rapid sediment accumulation during deglaciation preserved a greater number of bones than usual. I suggest the clustering of remains along that ancient shoreline indicate that polynya formation was likely a feature of the sea ice in the region at that time, similar to those that develop in Frobisher Bay and Cumberland Sound on Baffin Island today (***Figure 2***) (Gyllencreutz 2005), although no geophysical evidence of such a phenomenon has been reported.

Three additional Scandinavian specimens pre-date the end of the LGM and also lie outside the current range of the species on the Norwegian coast. The specimen from Nordcemgrotta (#102), on a small island on the northwest coast, has been dated to the beginning of the Early Weichselian glacial period (ca. 115k cal a BP) and has had mitochondrial DNA (mtDNA) extracted and reported (Davison et al. 2011; Hufthmammer 2001; Lauritzen et

Figure 3 Left mandible of polar bear found at Kjul Å near Asdal in northern Jylland (Denmark). Age: ca. 12.4–12.9k cal a BP (Photo by Geert Brovad, courtesy Natural History Museum of Denmark).

al. 1996). Specimen #101 was found in a coastal cave farther south and dates to the Late Weichselian ('Ålesund Interstadial', aka MIS 3 interstadial 3.1, ca. 36,000–28,000 cal a BP), an LGM ice retreat documented in this region (Hufthammer 2001; Lambeck et al. 2010; Valen et al. 1996). Another specimen found at the Nordcemgrotta site (#100) has a date of 22,000 ^{14}C a BP (Hufthammer 2001; Lauritzen et al. 1996) and is associated with the so-called 'Hamnsund Interstadial' which was another, but short-lived ice retreat dated to 22,000–19,000 ^{14}C a BP in western Norway (Winguth et al. 2005: 181). All three specimens are associated with ice sheet formation and expansion over Svalbard and Scandinavia during the last Glacial period. Ice sheet formation pushed Barents Sea polar bears and other Arctic marine mammals to the southern North Sea (Post 2005), except during short periods when suitable habitat existed along the Norwegian coast during temporary ice retreat.

A fourth pre-LGM polar bear specimen (#104, ca. 70k cal a BP) also lies outside the current range of the species but its taxonomic identity has been disputed. It was originally identified as polar bear several decades ago (Kurtén 1988), with a note it was large even for that species. However, while C.R Harington (2008: S25) argued that the identification of polar bear is plausible based on sea level changes and ice conditions in the North Sea during that time (e.g., Bennike et al. 2014; Post 2005), he also stated:

> 'Andy Currant of the Natural History Museum – London (*personal communication*) believes that the Kew Bridge bear ulna represents a huge brown bear rather than a polar bear, based on faunas similar to that at Kew Bridge from many British sites containing dominant steppe bison (*Bison priscus*) and reindeer (*Rangifer tarandus*) with wolves (*Canis lupus*) and gigantic brown bears moderately represented'.

This opinion that the Kew Bridge specimen is not polar bear, also expressed in an interview with the BBC in 2007 (Amos 2007) and a note in a 2009 scientific paper (Ingolfsson & Wiig 2009), awaits the official verification of a published note by Currant that corrects the record.

A small third lower molar tooth (not included in ***Table 1***), reported to resemble polar bear in size and shape, was recovered amongst remains of black bear (*Ursus americanus*) from an archaeological site in coastal New England called Crouch's Cove, apparently of Late Holocene age (perhaps LIA), that was excavated in the mid-1800s (Packard 1886; Wyman 1868). The tentative nature of the original identification precluded its inclusion in this record, although if confirmed it would represent an extralimital record. Similarly, the report of a cluster of bones (right humerus, left femur, right fibula, some ribs, plus vertebrae 1 and 2) of undetermined chronological age from Lough Gur near Limerick, Ireland in 1858 identified as polar bear (Denny 1859) would also be an extralimital occurrence but do not appear in any other record and is therefore considered an identification error.

3.2 FOSSIL RECORDS WITHIN MODERN RANGE

Only seven polar bear fossils have been found within the current range of the species and all were found in proximity to modern polynyas. Four are from the Barents Sea (#88, 97, 98, 103): three from Svalbard (#97, 98, 103), a short distance from the central Storfjorden Bay polynya, and one from the southern Barents Sea coast of Russia (#88) where small coastal flaw polynyas routinely form (not shown in ***Figure 2***) (Harington 2008; Ingolfsson & Wiig 2009). One Pleistocene-aged specimen was found in the Kara Sea (#87) where coastal polynyas are also common (Harington 2008; Vereshchagin 1969). A right ulna from an adult bear dated to 1,971 ± 25 BP, recovered from Vaygach Island (#83) in the same area, is presumed to be from a natural deposit as it predates the known occupation of the region by Nenets people (Boeskorov et al. 2018). Another Pleistocene-aged specimen was recovered from the eastern Beaufort Sea (#52) at the edge of the modern Bathurst polynya (Harington 2003; Vincent 1989).

Aside from the Vaygach Island bone, only three of these specimens have been dated more precisely than 'Pleistocene'. One is the oldest dated fossil (#103), a complete mandible with canine tooth from a male bear with a chronological age that falls within the warm Eemian Interglacial, ca. 130–110 ka BP. This specimen has also yielded a complete mtDNA sequence that has been critical for inferring polar bear evolutionary history (Ingolfsson & Wiig 2009; Lan et al. 2022; Lindqvist et al. 2010). The other two specimens from Svalbard (#97, 98) date to the Holocene, ca. 8,000 a BP (Harington 2008; Ingolfsson & Wiig 2009) and are the earliest reported polar bear remains from the Eastern Arctic after the end of the LGM and the melting of the Svalbard ice sheet, ca. 10,000–8,200 a BP (Rasmussen & Thomsen 2014).

3.3 EXTRALIMITAL ARCHAEOLOGICAL RECORDS

In the Aleutian Islands, archaeological remains of polar bear (n = 102, 24 confidently identified as polar bear, plus an additional 78 presumed to be polar bear rather than brown bear as both species were confidently identified) were recovered from Margaret Bay on Unalaska Island near Dutch Harbour (#11) (Davis 2001). The dates of the deposits (based on charcoal) have a similar range to the Pribilof fossil specimens (#9, 10) mentioned above (ca. 4,700–4,100 a BP). The slightly younger but still Neoglacial-aged deposit at the Amaknak Bridge site (UNL-50), lies adjacent to Margaret Bay, and while it lacks polar bear remains it does have faunal indicators (especially foetal and newborn ringed and bearded seal remains) used as evidence that late spring sea ice extended much farther south than it does today (Crockford & Frederick 2007; Crockford & Frederick 2011). The historic era specimen shot on the Pribilofs indicates that sea ice expanded that far south during the LIA (as it has done occasionally in recent times), but as far as is known, not as far south as the eastern Aleutians as it did during the Neoglacial (Brown, van Dijken & Arrigo 2011; Crockford & Frederick 2007; Frey et al. 2015).

3.4 ARCHAEOLOGICAL RECORDS WITHIN RANGE

One unique archaeological assemblage stands out from all others with regards to polar bear remains: the faunal material from the Zhokhov Island site (record #86), at 76⁰N where the Laptev Sea meets the East Siberian Sea. The site was excavated in 1989–1990 (Pitulko 2003; Pitulko 1993; Pitulko & Kasparov 1996) and again in 2000–2005 (Pitulko et al. 2015). It is not only the oldest archaeological site in the Arctic with polar bear bones but also contains by far the most polar bear remains of any human occupation (n = 5,915). In contrast to most sites, where they represent at most 3.5% (usually less) of the total mammalian remains recovered (***Table 2***), polar bear bones at the Zhokhov Island site comprised 28.4% of the total and represent at least 130 individuals. Domestic dogs were also recovered and were assumed to have chewed many of the damaged polar bear bones (Pitulko & Kasparov 2017). The site was inhabited for at most 450 years between ca. 8,250 and 7,800 a BP (Pitulko et al. 2019), although most of the deposits date to a brief period ca. 8,000–7,900 a BP. It is known that the initial flooding of Beringia by rising sea levels at the end of the LGM began before 10,000 a BP, which made the Arctic

MAP REF. & SPECIMEN LOCATION	COUNT	NISP	PERCENTAGE
11. Margaret Bay (UNL-48) Unalaska Is. AK	102	12,548	<1
36. Tiktalik (NkRi-3, H5) CAN	28	6216	<1
14. Nelson River CAN	?	70†	3.5
15. Co-Op (OdPp-2, H1, H5) Victoria Is. CAN	193	22,200	<1
37. Bell site (NiNg-2) Victoria Is. CAN	4	5,791	<1
17. Pingiqqalik (NgHd-1) Foxe Basin CAN	55	10,753	<1
19. Sadlermiut (KkHh-1), CAN	38	2,818	1.3
29. Hazard Inlet group, Somerset Is. CAN	24	10,235	<1
43. Cape Garry (PcJq-5) Somerset Is. CAN	21	2,658	<1
30. Learmonth (PeJr-1) Somerset Is. CAN	146	4,892	3.0
39. Hornby Head (RbJq-1, H2, H3) CAN	17	1,820	<1
41a. Skraeling (SfFk-4, H2–12, 17–23) CAN	235	9625	2.4
41b. Eskimobyen (SgFm-4, H25–26) CAN	53	3185	1.7
41c. Sverdrup (SfFk-5, H6) CAN	13	391	3.3
42. Skraeling Is. (SfFk-4, H14–16) CAN	66	2,810	2.3
61. Qeqertaaraq, (H1 + midden) GRE	19	2,249	<1
56. Walrus Is. (caches/shelters) GRE	16	1,044	1.5
58. Fladstrand (site 41) GRE	91	4,642	2.0
59. Dødemandsbugten (sites 45–47) GRE	66	2,625	2.5
53. Scoresby Sound (House of Beads) GRE	2	522	<1
67. Solbakken, GRE	9	60	15.0
76c. Tiutei-Sale 1 Early-Late RUS (total sample)	295	3,423	8.6
76b. Tiutei-Sale 1 Early only (DAC) RUS	42	159	26.4
76a. Tiutei-Sale 1 Late only (MWP) RUS	89	1,931	4.6
86. Zhokhov Island RUS	5,915	20,855	28.4

Table 2 Select archaeological assemblages with polar bear remains expressed as the relative proportion of the total number of identified specimens (NISP) of all mammals not including whale. † indicates percentage based on minimum number of individuals rather than bone count. Map reference information as in Table 1.

accessible again to marine mammals that had taken refuge in the North Pacific during the LGM (Crockford, Frederick & Wigen 2002; Dyke, Hooper & Savelle 1996; Dyke et al. 1999; de Vernal et al. 2020; Guthrie 2004; Heaton & Grady 2003; Polyak et al. 2010). Therefore, the large assemblage of skeletal remains recovered from Zhokhov Island marks the first evidence known of the return of polar bears to the western Arctic after being driven out by extraordinarily thick ice cover during LGM.

The Zhokhov site occupants were primarily reindeer hunters and apparently treated polar bears as a terrestrial resource, as there were few other marine mammals remains present (e.g., only six seal bones, no walrus, no whale). This is a pattern not seen elsewhere in the Arctic, regardless of time period. The bears appear to have been primarily females (some with newborn young) taken on land in winter or early spring with spears from their winter maternity dens although mixed sexes were perhaps taken in traps on land during the ice-free season (Pitulko et al. 2015). The range of total length of intact mandibles recovered (n = 37, sex/age unknown; mean 223.1 mm, range 206–268 mm) indicates at least a few adult males as well as females were taken, based on measurements of modern adult bears from Svalbard and East Greenland (female, n = 47: mean 217.8 ± 6.6, range 203.1–232.9 mm; male, n = 58: 243.2 ± 11.2, range 216.1–265.9 mm) (Bechshøft et al. 2008).

Approximately 8,300 years ago, the slightly elevated terrain of Zhokhov Island was part of a low coastal plain that extended ca. 100 km north of the present coastline. It remained above sea level after Beringia was inundated. Today few areas of the eastern Laptev Sea and the East Siberian Sea are deeper than 50 m (Pitulko et al. 2019). However, as sea levels continued to rise, the region was transformed ca 7,800 a BP into an archipelago—the New Siberian Islands—which put an end to the human occupation. The Great Siberian flaw polynya first developed after the end of the LGM at about 14–16 cal ka BP (Taldenkova et al. 2008). Today, it extends as far east as the New Siberian Islands (Kassens & Thiede 1994; Speer et al. 2017). Given that Siberian winters 8,000 a BP were cold (Kokorowski et al. 2008; Nazarova et al. 2013) but with reduced summer sea ice cover offshore compared to today (Taldenkova et al. 2008), it seems likely that polynya formation documented since the 20th century also occurred to some degree at the time of the site's occupation (Andreev et al. 2009; Hörner et al. 2018; Kassens & Thiede 1994; Timokhov 1994). Since Zhokhov Islanders were not marine mammal hunters, the faunal remains from this site are unhelpful in determining whether the Pacific walrus, which currently over-winter in the Great Siberian polynya, were present at that time (Fay 1982; Lindqvist et al. 2009). However, the presence of polar bear is consistent with ecological conditions similar to today, including the reliable off-shore presence of breeding ringed seals in spring which make land-based denning by females possible (Amstrup & Gardner 1994; Pitulko et al., 2015; Ramsay & Stirling 1988; Stirling 1997; Stirling 2002).

All other Holocene-aged archaeological sites are within the modern range of polar bears. Archaeological sites with more than ten polar bear elements are primarily near modern major open-water polynyas, including the one south of St. Lawrence Island, and in Peard Bay (off Utqiaġvik, Alaska – formerly known as Barrow), the Cape Bathurst polynya, the North Water, the Sirius Water, as well as those in the Kara, Laptev Sea and East Siberian Seas, Frobisher Bay, Bellot Strait, and Hell Gate/Cardigan Strait (between Ellesemere and Devon Islands) (***Table 3***). As ***Table 2*** indicates, sample sizes for virtually all of these are so much smaller than Zhokhov Island that they are best compared to each other. Of these, the Tiutei-Sale 1 site on the Yamal Peninsula (#76), where polar bear bones comprised 42 of 159 bones (i.e., n = 42/159) or 26.4% of the early occupation during the Dark Ages Cold period (DAC) component, had the highest relative abundance after Zhokhov Island. However, for all periods combined bear remains at Tiutei-Sale 1 represent only 8.6% of the sample (and 21 individuals). In only one other site did polar bear remains comprise more than 5% of the sample: the Neoglacial-aged site of Solbakken in Greenland opposite the northeastern end of Ellesmere Island (#67), where polar bear remains made up 15.0% of the mammalian sample (n = 9/60). However, this metric is skewed because most of the polar bear remains appear to be from one individual (Darwent 2003) and the total sample size is small. Sites with the next highest abundance of polar bear remains were in the Canadian Arctic Archipelago: at Sverdrup (#41) on Ellesmere Island at 3.3% (n = 13/391) (adjacent to the North Water) and Learmonth (#30) on Somerset Island, at 3.0% (n = 146/4,892) (near the Bellot Strait polynya). At the Nelson River site (#14) adjacent to the Cape Bathurst polynya, the material was reported only as minimum number of individuals (MNI) rather than bone count but a minimum of 70 individuals accounted for 3.5% of the mammalian MNI remains reported (Moody & Hodgetts 2013).

Four sites with fewer than four polar bear bones each were found in northeast Greenland at Peary Land that date to several periods (#64, 65, 68, 69) (Bennike 1991; Bennike 1997; Darwent 2003; Grønnow & Jensen 2003). Sites here are closest to the geographic North Pole (ca. 82^0 N) of any archaeological sites with faunal remains (from both terrestrial and marine species). The large polynya that developed in that region in 2018 and again in 2020 (Ludwig et al. 2018; Moore et al. 2018; Schweiger et al. 2021) (called here the 'Wandel Water', ***Figure 2***) may not be an entirely new phenomenon but a recurrent feature that has formed historically to some degree under particular climatic conditions. Alternatively, it may also be that this area is close enough to the NE Water for both people and polar bears to access seals. Polar bears are rare in this area because the thick offshore ice

SITE #	POLYNYA CODE	POLYNYA NAME	POLAR BEAR COUNT
97, 98, 103	A	Storfjorden Bay	1 each
74, 75?, 76	C	Kara Sea group	>10 each
83, 87	C	Kara Sea group	1 each
86	D	Great Siberian flaw	>10 each
81, 82	D	Great Siberian flaw	P (at least 1 each)
85	E	Wrangel Island	1
3	G	St. Matthew Island	9
2, 6	H	St. Lawrence Island	>10 each
5, 7	H	St. Lawrence Island	P (at least 1 each)
4a, 4c	L	Peard Bay	>10
13, 14, 36a	M	Cape Bathurst	>10 each
36b, 52	M	Cape Bathurst	1–4 each
29, 30, 43	N	Bellot Strait	>10 each
40	O	Penny Strait/Queens Channel	1
31, 39	P	Hell Gate/Cardigan Strait	>10 each
32, 38, 49, 50	P	Hell Gate/Cardigan Strait	1–3 each
17	Q	Fury and Hecla Strait	>10
18, 34	Q	Fury and Hecla Strait	1–2 each
20	S	Hudson Bay flaw	2
27, 33a, 33b	T	Frobisher Bay	>10 each
28	U	Cumberland Sound	3
41a-41c, 42, 61	V	North Water	>10 each
62, 63, 72	V	North Water	1 each
60, 71	W	NE Water	1each
56, 57, 58, 59	X	Sirius Water	>10 each
53, 54	Y	Scoresby Sound Water	2 each
64, 65, 68, 69	Z	Wandel Water (proposed)	<4 each

Table 3 Fossil and archaeological sites near polynyas, by site number (as per Table 1) and polynya code (as per Figure 2) according to count of polar bear remains (those with 1–9 vs. >10 bones). P indicates 'present'.

precludes the survival of the seals they need to survive (Bennike 1991), but they do occur. In 1992, a female bear with a satellite collar travelled from the Beaufort Sea, across the Arctic Ocean to an area off the northeast coast of Greenland, then moved west across the Peary Land coast of northern Greenland, and eventually made her way into Kane Basin at the North Water (***Figure 2***) (Durner & Amstrup 1995). Such transient occurrences may be more common than has been documented. In addition, in 2018 and 2019, three polar bear maternity dens made in snow banks around icebergs grounded in land-fast ice were observed in the Peary Land area and females with cubs were also sighted (Laidre & Stirling 2020). These records indicate a small resident population of polar bears and therefore, a reliable source of breeding ringed seals nearby.

Despite polar bears being abundant in Hudson Bay today because of the flaw polynya that develops every winter between the shorefast ice and the central pack ice (Henderson et al. 2021; Stirling 1997), only two archaeological sites in the region have bear remains (Desrosiers et al. 2010; Nash 1976) and no polar bear fossil remains at all have been recovered (Harington 2003). The area was covered by remnants of the Laurentide Ice Sheet until about 8,000 a BP (Condron and Winsor 2012) and Hudson Bay as we know it today did not exist until about 7,800 a BP. At that time sea level was about 165 m above present sea level at Churchill (Dredge 1992). Due to changes in the shoreline and currents, it may not have been suitable ringed seal and polar bear habitat until about 6,500 a BP (Bilodeau et al. 1990; Harington 1988; Harington 2008). By about 2,000 a BP, sea level was still about 25m above present levels and the shoreline several kilometers inland from its present position. This means any coastal sites occupied by ancient people (and any terrestrial maternity dens of polar bears) would be of recent age and well inland from the present coastline unless they were located on elevated terrain (Murray 2008; Nash 1976).

The relative dearth of archaeological sites reporting polar bear remains from across the huge expanse of the Russian Arctic coast is almost certainly a reflection of my inability to read or access the Russian literature and because some regions may be better surveyed than others. The Yamal Peninsula and the coast of Chukotka, in particular, appear to have been relatively well surveyed and reported by archaeologists and ethnologists. Work by ethnologists in the 1800s, for example, indicate the Nenets people considered polar bears to have strong spiritual qualities and polar bear 'monuments' discovered during the 1800s and early 1900s (#73–76) are evidence of this belief system (Kishchinskiy 1976; Kochneva 2007; Vdoving 1977). Such features are composed of large numbers of polar bear skulls that appear to have accumulated over centuries and span the Russian Arctic from Chukotka to the Barents Sea. Similar finds, but with no other details provided, have been reported from Wrangel Island and adjacent to the villages of Vankarem, Inchoun, Enormino, Akkani and others in Chukotka (Kochneva 2007). Archaeological reports of polar bear skulls associated with human burials (#78) and a prehistoric ritual feature (#79) involving multiple polar bear skulls associated with a shaman, come from much older time periods at Cape Schmidt (opposite Wrangel Island on the Chukotka coast), support the suggestion that this spiritual role for polar bears was long-standing (Dikov 1988).

This belief seems to have travelled with ancient peoples of Siberia east to St. Lawrence Island in the Bering Sea. There is little detail available on the polar bear remains from sites on this prominent island (e.g., #5, 7), which were excavated in the early 20th century when faunal remains were of little interest to archaeologists (e.g., Rainey 1941). In the reports that are available (e.g., Collins 1937), species are listed only as 'present' and could be almost 2,000 years old or only a few centuries. However, two caches of polar bear skulls excavated by Dr. Otto Geist in the 1930s eventually made their way to the American Museum of Natural History along with his field notes and were later catalogued for repatriation to their ancestral communities (NPS 2013a; NPS 2013b). These consisted of 89 skulls collected at Cape Chibulak (near Gambell) from the grave of a hunter named Kowarin who died in 1910 (#2) and another 287 skulls from prehistoric human burials near Kukilik (near Savoonga), some of which may be almost 2,000 years old (#6). These finds extend the Russian pattern of a strong and long-standing spiritual role for polar bears into the Bering Sea at St. Lawrence Island.

There is only one archaeological site with polar bear remains recorded on St. Matthew Island in the southern Bering Sea (#3) (***Table 3***) (Frink et al. 2001), but this is the only prehistoric site ever excavated (Griffin 2008). However, it is known from historic records that as late as 1875, hundreds of polar bears used the island as a summer refuge and winter denning area but were exterminated by the 1890s by indiscriminate hunting (Elliott 1875; Elliott & Coues 1875; Klein & Sowls 2011). Bears have not recolonized the island since, but as illustrated (***Figure 2***), St. Matthew Island develops a prominent polynya on its south coast in spring similar to St. Lawrence Island, which almost certainly made it as suitable a denning area as Wrangel Island in the Chukchi Sea is today (Garner et al. 1994; Voorhees et al. 2014).

3.5 CHANGE THROUGH TIME

Only the Tiutei-Sale 1 site on the Yamal Peninsula provided data adequate to addressing whether relative polar bear abundance might have changed between distinct short-term climatic changes at the same location over time (***Table 2***) (e.g., Briffa et al. 2013; Connolly & Connolly 2014). At Tiutei-Sale 1, the Medieval Warm Period (MWP) deposits yielded relatively fewer polar bear bones (4.6% of the sample) than the preceding DAC (26.4%). Although the DAC results may be skewed by the much smaller sample size compared to the MWP sample (159 vs. 1,931), it does suggest the possibility that polar bears may have been hunted more frequently during the DAC period at this location but cannot tell us unequivocally that this was because the animals were more abundant.

3.6 ABSENCE OF DATA

As far as it has been possible to determine, there are no fossil polar bear remains reported from Ireland, although it has been suggested polar bears evolved nearby and abundant brown bear remains have been recovered (Edwards et al. 2011; Edwards et al. 2014). In addition, although there are fossil remains reported, no archaeological remains of polar bears have been found anywhere in the UK or Scandinavia. No archaeological or fossil remains have been recovered from the Barents Sea coasts of northern Norway or Finland (Rankama 2003). Similarly, there were no ancient polar bear remains of any kind found in the Sea of Okhotsk or the Gulf of Alaska in the western Arctic although the presence of ringed seal bones dated to the LGM on Prince of Wales Island, Southeast Alaska suggest there was almost certainly suitable ice-edge habitat for polar bears in the region (Heaton & Grady 2003). Furthermore, although bowhead whales apparently returned to the western Canadian Arctic via Bering Strait soon after it was physically possible to do so (Atkinson 2009; Dyke & England 2003; Fisher et al. 2006), I was informed by geologist Art Dyke (pers. comm., 2007) that no natural-death assemblages of polar bears were found during the shoreline surveys of both eastern and western portions of the Canadian Arctic Archipelago that recovered early to mid-Holocene bowhead and walrus fossil remains (Dyke, Hooper & Savelle 1996; Dyke et al. 1999; Dyke et al. 2011; Dyke & Savelle 2001).

4. DISCUSSION

Within the past 130 ka, sea ice conditions have at times been very different than they are today and this has affected where polar bears have been able to live. The thick perennial ice that developed during the LGM pushed polar bears south and out of the Arctic entirely. They returned when warmer conditions prevailed during the HCO. The Eemian Interglacial and the HCO, although both were warmer than today with less summer ice, apparently provided adequate habitat for polar bears to survive around Svalbard and in the East Siberian Sea. During the Neoglacial cold period of the Middle and Late Holocene, sea ice extended farther south into the Bering Sea than it does today, which allowed polar bears to temporarily reach the Pribilof Islands and the Eastern Aleutians.

The oldest dated polar bear fossil (ca. 130–110k a BP) was found within the modern range of the species, which is also true for virtually all Holocene-age archaeological sites with polar bear remains (one exception). Extralimital polar bear fossil specimens have been documented in the north Atlantic from the late Pleistocene (13 records) and in the southern Bering Sea during the mid-Holocene (three records). Prevailing sea level, ice sheet, and sea ice conditions surrounding the ancient Skagerrak fjord between Norway and Denmark during the YD support a suggestion that the region probably had an associated polynya, although this has not been confirmed by geophysical evidence.

The enormous assemblage of polar bear bones found at the Zhokhov Island archaeological site in the East Siberian Sea (ca. 8.2–7.8k a BP) and two fossil specimens recovered from Svalbard, Norway (also ca. 8.2–7.8k a BP) are so far the earliest evidence of the return of polar bears to the Arctic after the end of the LGM and all date to the same period of the HCO. The Zhokhov assemblage is the only archaeological site dating to the HCO and has by far the highest proportion of polar bear remains, as well as the greatest number of remains, recovered from any time period across the Arctic. Prevailing climatic conditions in the East Siberian Sea region during the HCO indicate that a polynya in some form probably existed about 8,000 years ago as it does today.

Except for the Zhokhov site and one Neoglacial-aged site in the southern Bering Sea, archaeological sites older than 2,000 years have relatively few polar bear remains. Only one archaeological site with deposits that span a complete climatic shift within the last 2,000 years (Tiutei-Sale 1 site on the Yamal Peninsula) has data that are indicative of a shift from hunting more bears during a cold period (DAC) to fewer during a subsequent warm period (MWP), but no broad conclusions can be drawn from this example. Except for two Neoglacial-aged natural-trap sites in the Bering Sea and one almost-complete late Pleistocene skeleton from southern Norway, fossil remains are predominantly single element finds.

Archaeological sites with more than ten polar bear elements are primarily near modern open-water polynyas, as are most of the isolated fossil remains. Polar bear remains from sites near the Hell Gate-Cardigan Strait and Penny Strait polynyas all date well after the postglacial uplift 4,000 years ago that created the polynyas. On St. Lawrence Island in the Bering Sea, evidence from historic- and prehistoric-era ritual burials of polar bears indicate that polar bears have been relatively abundant there for at least the last 2,000 years, as expected due to the prominent polynya that today forms along the southern coast. It is also possible that at times during the past 4,000 years, a polynya of some size formed off northern Greenland in the Wandel Sea, making it possible for humans living in Peary Land to add seals and polar bears to their usual diet of terrestrial species such as Arctic hare (*Lepus arcticus*), Arctic fox (*Vulpes lagopus*), and muskox (*Ovibos moschatus*) (Darwent 2003). However, it is also possible that historically, both bears and people in northern Greenland travelled to the nearby NE Water to hunt seals.

In contrast, there are few archaeological bones and no fossil remains of polar bears found in Hudson Bay but this dearth of records is consistent with the dynamic geological and sea level history of the region.

5. CONCLUSION

Most ancient polar bear remains from fossil and archaeological contexts before A.D. 1910 date within the Holocene and derive from human habitation sites within the current range of the species. Extralimital specimens have been documented in the north Atlantic during the late Pleistocene and in the southern Bering Sea during the middle Holocene, both of which were cold periods when Arctic sea ice expanded to the south of modern limits in winter. The earliest evidence for the return of polar bears to the Arctic after the end of the LGM dates to the early HCO (ca. 8,000 a BP) in both the Atlantic and Pacific sectors, even though bowhead whales in the Pacific returned almost 2,000 years earlier. Unfortunately, none of the skeletal evidence is adequate for determing if changes occurred in abundance of polar bears in response to short-term climatic changes. However, the geographic distribution of ancient remains, from both fossil and archaeological contexts, indicates that polynyas have been important ice-edge habitats for polar bears since the last Interglacial period, as they are today.

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The author has no competing interests to declare.

AUTHOR AFFILIATION

Susan J. Crockford *orcid.org/0000-0002-6340-7962*
Pacific Identifications Inc., CA

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