Holocene climate changes in eastern Beringia (NW North America) —

A systematic review of multi-proxy evidence

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Abstract — Reconstructing climates of the past relies on a variety of evidence from a large

number of sites to capture the varied features of climate and the spatial heterogeneity of climate change. This review summarizes available information from diverse Holocene

paleoenvironmental records across eastern Beringia (Alaska, westernmost Canada and adjacent seas), and it quantifies the primary trends of temperature- and moisture-sensitive records based in

part on midges, pollen, and biogeochemical indicators (compiled in the recently published Arctic Holocene database, and updated here to v2.1). The composite time series from these proxy

records are compared with new summaries of mountain-glacier and lake-level fluctuations, terrestrial water-isotope records, sea-ice and sea-surface-temperature analyses, and peatland and

thaw-lake initiation frequencies to clarify multi-centennial- to millennial-scale trends in

Holocene climate change. To focus the synthesis, the paleo data are used to frame specific

questions that can be addressed with simulations by Earth system models to investigate the causes and dynamics of past and future climate change. This systematic review shows that,

during the early Holocene (11.7-8.2 ka), rather than a prominent thermal maximum as suggested previously, temperatures were highly variable, at times both higher and lower than present

(approximate mid-20th-century average), with no clear spatial pattern. Composited pollen, midge and other proxy records average out the variability and show the overall lowest summer and

mean-annual temperatures across the study region during the earliest Holocene, followed by

warming over the early Holocene. The sparse data available on early Holocene glaciation show

that glaciers in southern Alaska were as extensive then as they were during the late Holocene.

Early Holocene lake levels were low in interior Alaska, but moisture indicators show pronounced

differences across the region. The highest frequency of both peatland and thaw-lake initiation

ages also occurred during the early Holocene. During the middle Holocene (8.2-4.2 ka), glaciers

retreated as the regional average temperature increased to a maximum between 7 and 5 ka, as reflected in most proxy types. Following the middle Holocene thermal maximum, temperatures decreased starting between 4 and 3 ka, signaling the onset of Neoglacial cooling. Glaciers in the Brooks and Alaska Ranges advanced to their maximum Holocene extent as lakes generally rose to modern levels. Temperature differences for averaged 500-year time steps typically ranged by 1-2°C for individual records in the Arctic Holocene database, with a transition to a cooler late Holocene that was neither abrupt nor spatially coherent. The longest and highest-resolution terrestrial water isotope records previously interpreted to represent changes in the Aleutian low-pressure system around this time are here shown to be largely contradictory. Furthermore, there are too few records with sufficient resolution to identify sub-centennial-scale climate anomalies, such as the 8.2 ka event. The review concludes by suggesting some priorities for future paleoclimate research in the region.

Keywords: Holocene, Paleoclimate, Beringia, Alaska, Yukon, synthesis, multi-proxy, climate change

1. Introduction

As sea level rose during the transition from the Pleistocene to the Holocene, the vast non-glaciated landmass extending from northeastern Siberia to northwestern Canada (Beringia) was transformed. The dry, treeless landscape was replaced by the present-day mosaic of boreal forest, peatlands and thaw lakes bordered by epicontinental seas – an environment dramatically different than any during the preceding 100,000 years. Compared to the dramatic transformation that preceded it, the environmental changes of the Holocene, and the climate changes that drove them, were relatively minor. Nonetheless, these changes reveal how the climate system behaves when boundary conditions are similar to present. This similarity adds confidence to interpretations of Holocene paleoclimate archives, many of which are based on knowledge of the relation between modern climate and environmental conditions. On the other hand, the relatively small climate signal challenges our paleoclimate indicators. All paleoclimate archives are influenced to some extent by factors other than climate, and they often represent a combination of climate variables, including their seasonality. In addition, the sub-millennial-scale features of Holocene climate are likely to be overlooked in natural archives without extraordinarily high sample resolution (generally sub-centimeter scale), and accurate century-scale geochronology.

Considering the substantial challenges involved in reconstructing Holocene climate change, we must explore all available evidence from a wide variety of sources. And considering the diversity of the climatologies encompassed by the vast area of eastern Beringia (about 5×10^6 km²), we must consider evidence from as many sites as possible in order to capture the spatial heterogeneity of climate change and to discern real variability from uncertainties. Fortunately, the Holocene environmental and climate history of eastern Beringia has received extensive research attention over the past five decades. The enormity of this previous work, however, and

the evolving scientific understanding that it represents, challenges us to organize, extract and apply the most reliable information it holds. To address this goal, this systematic review builds on the recent comprehensive compilation of Arctic Holocene proxy climate records (Sundqvist et al., 2014) by revealing the prominent trends represented by the records within the database alongside paleoclimate evidence from archive types that cannot be adapted to fit a database of continuous time series. After summarizing evidence from multiple sources, we find that no single archive type provides a superior proxy for past climate, but that, by comparing evidence from diverse indicators, we can investigate proxy biases while revealing any common signals.

1.1. Research questions

This review focuses on the observational evidence for Holocene climate changes in eastern Beringia, but to understand the *causes* of the changes, and how they relate to the global climate system, requires an investigation of climate-forcing mechanisms and climate-feedback processes. One fruitful approach to investigating the causes of climate change involves simulations by Earth system models. This review does not consider the output of climate models, but rather addresses research questions that should help inform future investigations using Earth system models to elucidate the causes and dynamics of past and future climate change. Addressing these questions requires that we qualify the most robust features of the full range of proxy records over the large region of eastern Beringia – a scale that is commensurate with the resolution of global models:

- What are the primary differences between the climate of the early and late Holocene?
- Is there evidence for a mid-Holocene thermal maximum around 6 ka? If so, how much warmer was it?

- What was the magnitude of temperature variability at the site level during the middle and late Holocene?
- Is there evidence for a widespread and rapid climate transition during the Holocene that might represent a step-wise shift in the mode of ocean-atmospheric circulation?
- Is there evidence in the region for an abrupt climate reversal at 8.2 ka, as has been observed elsewhere?

1.2. Scope

This review summarizes the available evidence for Holocene climate change across eastern Beringia (Fig. 1) as expressed through a variety of proxy types, including physical, chemical and biological, from marine and terrestrial archives. It includes the first quantitative synthesis of the proxy records within the Arctic Holocene database (Sundqvist et al., 2014), focusing on Alaska (north of 58° N latitude), Yukon and western Northwest Territories (west of 125° W longitude). We herein update the Arctic Holocene database from version 2 (Sundqvist et al., 2014) to version 2.1 by including the recently published records from Corser Bog (Nichols et al., 2014) and the midge-based paleoclimate reconstruction from Upper Fly Lake (Bunbury and Gajewski, 2009), which was previously overlooked. In addition, we include the new record from Kurupa Lake (Boldt et al., 2015), a highly resolved temperature reconstruction from northern Alaska that fills a large gap in spatial coverage, although it extends back to only 5.7 ka. All other records from eastern Beringia in the Arctic Holocene database extend back to at least 6 ka; most (75%) extend to at least 9 ka, and half (47%) extend back to 11.5 ka. Of the 105 study sites from both marine and terrestrial settings that were considered from the region, only 32 (Table 1) met the criteria for resolution (at least one data point every 400 years on average), duration (at least 6-2 ka), and geochronology (at least one control point every 3000 years). A comprehensive and

systematic approach to selecting the time series is fundamental to an unbiased and reproducible
146 synthesis of available information. The data and metadata for all versions of the Arctic Holocene
database are available at NOAA Paleoclimatology (<http://ncdc.noaa.gov/paleo/study/15444>).

148 In addition to a synthesis of the records that meet the criteria for the Arctic Holocene
database, this review compares the primary patterns of climate change from those continuous
150 time series to other evidence of paleoclimate change from the region. Specifically, this review
expands on a recently published summary of mountain glacier fluctuations (Solomina et al.,
152 2015); distills evidence for changes in lake levels and the duration of sea-ice cover; summarizes
all available water-isotope records and places them in the context of a new spatial analysis of
154 isotopes in modern precipitation; presents temperature reconstructions based on previously
published pollen, midge, and other proxy types; updates the inventory of ages for the initiation of
156 peatlands (Jones and Yu, 2010) and highlights the initiation ages for thaw lakes from the region
(Walter Anthony et al., 2014); and finally, analyzes the primary trends in the time series of proxy
158 temperature- and moisture-sensitive records contained in the recently published Arctic Holocene
database and systematically searches for the 8.2 ka event.

160 This review summarizes more evidence of Holocene climate change in eastern Beringia
than any previously. Rather than discussing the strengths and weaknesses of the various proxy
162 types or individual records, this systematic review reveals similarities and differences among
proxy types and records. The extent to which they present a coherent signal is a key indication of
164 their credibility, arguably more informative than the error bars chosen to characterize a subset of
quantifiable uncertainties. Most of the discussion concerns climate changes on time scales of
166 multiple centuries to millennia and does not consider the multi-decadal changes that are known
from annually resolved records. More detailed information about climate changes over the last

1000-2000 years, including the instrumental period, is available outside of this review, and is the focus of an ongoing international effort (PAGES Arctic 2k; <http://www.pages-igbp.org/ini/wg/arctic2k/intro>), and an overview of climate change during the past 6 ka globally is provided by Wanner et al. (2008).

In this review, we adopt the age of the onset of the Holocene as represented in Greenland ice at 11.7 ka (1 ka = 1000 cal yr BP, where BP = before 1950 AD) (Walker et al., 2009) as well as the ages of the proposed subdivision of the Holocene Epoch at 8.2 and 4.2 ka for the early-middle and the middle-late boundaries, respectively (Walker et al., 2012). When summarizing multiple time series using 500-year bins, we round the ages of the boundaries to 11.5, 8.0 and 4.0 ka. On the basis of this review, records from eastern Beringia do not show marked changes that coincide with the times of these boundaries; nevertheless, the three-part subdivision of the Holocene serves as a useful construct for this review. Unless noted otherwise, the terms “present” and “modern” are used to indicate approximately average mid-20th-century conditions.

2. Glacier fluctuations

Mountain ranges located across eastern Beringia contain evidence for Holocene glacier fluctuations, most of which was recently summarized by Solomina et al. (2015). In our review (Fig. 2; Table 2), we update and expand on this summary by: (1) providing a more comprehensive compilation of the extent of glaciers during the Holocene, prior to 2000 years ago, including: moraine ages based on (a) ¹⁰Be surface-exposure dating in the central Brooks Range (Pendleton, 2013), (b) lichen ages from project reports and unpublished theses on Holocene glacier fluctuations in the northwest Alaska Range (Denali Park); (c) other published results not included in the review of Solomina et al. (2015), including those with information on the extent

of glaciers during the early Holocene; (2) omitting the two records that are based on tidewater glaciers (Icy Bay and Glacier Bay) because tidewater glaciers around the Gulf of Alaska are known to fluctuate in response to non-climate-related dynamics (Mann, 1986; Post and Motyka, 1995); and (3) specifying the relation between the geochronological control and the position of the glacier (e.g., moraines stabilize after glaciers retreat).

2.1. Early Holocene

Glaciers across eastern Beringia had mostly retreated well into the mountain tributary valleys prior to the Holocene (Hamilton et al., 1986, and references therein). Evidence for late-glacial or early Holocene glacier advances represented by moraines are known from three places: (1) Fish Lake valley, north-central Alaska Range, where surface-exposure dating of moraine boulders shows that glaciers had paused or re-advanced around 11.6 ka (Young et al., 2009); (2) Denali Park area, northwest Alaska Range, where the MP4 moraines are thought to be younger than an interval of widespread peat growth down-valley beginning around 10.4 ^{14}C ka (= 12.5 ka), and older than peat that grew on top of MP4 drift around 9.6 ^{14}C ka (= 11.0 ka) (TenBrink and Waythomas, 1985); and (3) Mt. Waskey, southwest Alaska, where surface-exposure ages of boulders on a remarkably prominent moraine range from 12.4-11.0 ka (Briner et al., 2002). In all three cases, the moraines could represent advances that culminated during the Younger Dryas (YD; 12.8- 11.5 ka) and stabilized after.

Additional constraints on the position of glaciers during the early Holocene are provided by the age of glacial rockflour deposited in lakes. Re-advances are known from sedimentary sequences at two sites. The sparse data available show that some glaciers in southern Alaska were as extensive during the early Holocene as they were during the late Holocene. In the

southern Kenai Mountains, sediment in Emerald Lake near Homer contains an on-off signal of the thickness of the Grewingk Glacier (LaBrecque, 2014; LaBrecque and Kaufman, in review). A sharp transition from the basal inorganic mud to organic-rich mud around 11.4 ka marks the initial retreat of the Grewingk Glacier below the divide of Emerald Lake, and up-valley of its late Holocene maximum extent. The overlaying organic-rich sediment is interrupted by stony mud that records a brief re-advance as ice overtopped the divide again between 10.7 and 9.8 ka. In the eastern Prince William Sound, Cabin Lake near Cordova, contains evidence for a brief interval of meltwater input from Sheridan Glacier that occurred 11.2-11.0 ka (Zander et al., 2013).

2.2. Middle Holocene

Evidence for glaciers retreating up-valley of their subsequent late Holocene extents has been reported from southern Alaska where sedimentary sequences captured in downstream lakes have been interpreted in terms of the up-valley glacier extent. The most convincing evidence in the region is from Waskey Lake, where glaciers disappeared entirely between 9.1 and 3.2 ka around Mt. Waskey, the highest massif of the Ahklun Mountains (southwest Alaska; Levy et al., 2004). In the northern Kenai Mountains, North Goat Glacier retreated from the drainage divide that now separates it from the Goat Lake drainage around 9.5 ka (Daigle and Kaufman, 2009). In a similar setting in the southern Kenai Mountains, the Grewingk Glacier retreated below the drainage divide of Emerald Lake at 9.8 ka (LaBrecque, 2014). The Grewingk Glacier did not spill meltwater into the lake again until the Little Ice Age, beginning around AD 1350 (0.6 ka).

Evidence from outcrops has also been used to infer the extent to which glaciers retracted during the early to middle Holocene. Several authors have suggested that glaciers retreated

behind their modern extent, including Calkin (1988) for the central Brooks Range and TenBrink and Waythomas (1985) for the northern Alaska Range.

2.3. Late Holocene (Neoglacial)

Following a protracted interval with little evidence for glacier activity, when mountain glaciers were probably no larger than their 20th century extent, glaciers around Alaska expanded to positions comparable to their Little Ice Age extents beginning between around 4.5 and 3.0 ka. Neoglacial advances are known from several mountain ranges, including the Ahklun, St. Elias, Chugach and Coast Mountains, and the Alaska and Brooks Ranges, most of which were included in the recent summary of Solomina et al. (2015). Their interpretation of three intervals of expanded mountain glaciers in Alaska (4.5-4.0, 3.3-2.9 and 2.2-2.0 ka) is consistent with the additional evidence of moraine ages compiled for this review, including from the central Brooks Range (Pendleton, 2013) and the northwestern Alaska Range (Denali Park; summarized in Table 2) where glaciers apparently reached their Holocene maximum early during the late Holocene. In addition, one study reported early Neoglacial moraines beyond the limit of Little Ice Age moraines in The Chugach Mountains (McKay and Kaufman, 2009). Following a series of Neoglacial fluctuations, many glacier margins, especially in southern Alaska, registered an advance during the first millennium AD (between 600 and 900 AD; Reyes et al., 2006). This was followed by glacier growth throughout the region during the Little Ice Age, which can generally be subdivided into three parts as described in more detail by Barclay et al. (2009), Wiles et al. (2004), and Solomina et al. (in review). Recent studies of the timing of glacial-isostatic relative-sea-level changes in the eastern Gulf of Alaska area support the history of glacier fluctuations determined from moraines (Mann and Streveler, 2008; Garrett et al., 2015).

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262 2.4. *Limitations and uncertainties*

Interpretations of past climate from glacier records involve several important caveats. Glaciers
264 fluctuate in response to both changes in accumulation, due to snowfall, as well summer ablation,
which is a function of summer temperature, among other variables. The response time of glaciers
266 to climate forcing varies, depending on a variety of factors. Many Holocene moraines have been
dated using lichenometry, which must be applied with caution (e.g., Webber and Andrews, 1973;
268 Osborn et al., 2015). While we recognize that all geochronological tools have important
limitations, our compilation includes ages based on ^{14}C and ^{10}Be isotopes that together show a
270 pattern generally consistent with that based on lichenometry.

Little is known about the extent of glaciers during the Holocene prior to Neoglaciation.
272 Scattered evidence for early Holocene advances in Alaska was reviewed by Calkin (1988) and
Barclay et al. (2009). The interpretations rely on probable-distant minimum- *or* maximum-
274 limiting ages, none of which afford conclusive evidence for the age and extent of glaciers. The
recently discovered early Holocene (10.7-9.8 ka) advance at Grewingk Glacier (LaBrecque and
276 Kaufman, in review) has not been described from elsewhere in the region. If reproducible at
other sites, it suggests that conditions were conducive to glacier growth despite summer
278 insolation that was higher than during the late Holocene. Likewise, during the middle Holocene,
evidence for the extent to which glaciers retreated prior to the Neoglacial expansion is limited.

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3. Sea-ice cover and sea-surface temperature

Alaska is surrounded on three sides by ocean, including the marginal seas of the Arctic (Chukchi and Beaufort Seas) and the Pacific (Bering Sea and the Gulf of Alaska) Oceans. Changes in the duration and extent of sea-ice cover are known to have a major effect on air surface temperatures onshore (e.g., Walsh et al. (2001) for the Arctic Ocean). The extent of sea-ice cover also responds to climate, including changes in ocean-atmospheric circulation. Here, we summarize evidence for sea-ice extent during the Holocene from the marginal seas, as well as information about sea-surface temperature (SST) from the highest-resolution sediment cores available from the region.

3.1. Arctic Ocean

One indicator of the history of sea-ice cover is the distribution of ^{14}C -dated remains of animals preserved in raised marine deposits. Pacific bowhead whales reached their maximum abundance in the Beaufort Sea between around 11.5 and 8.5 ka, and then retreated abruptly indicating that sea-cover decreased then increased (Dyke and Savelle, 2001). Two boreal-subarctic thermophilic mollusks, *Mytilus edulis* and *Macoma balthica*, spread from Bering Strait along the Beaufort Sea coast at least as far as the modern limit of *M. edulis*, coincident with the entry of Pacific bowheads around 11.5 ka (Kaufman et al., 2004). These thermophilous mollusks require summer SST above 0°C for successful dispersion of larvae, indicating reduced summer sea ice. Thus, summer SST rose above current values immediately following 11.5 ka. Around the same time, isotopes in ice wedges near Barrow indicate a shift in sea-ice extent and wintertime moisture source (Meyer et al., 2010). The abundance of dated thermophilous mollusks from the Canadian Arctic Archipelago reached a maximum during the interval 11.5–8.5 ka. *M. balthica* then withdrew from the western Arctic during the late Holocene.

Sea-ice reconstructions from marine sediment cores derive primarily from dinocyst assemblages and, to a lesser degree from a biomarker synthesized by sea-ice-dwelling diatoms (IP₂₅) (de Vernal et al., 2013). Three Holocene-long reconstructions of sea-ice duration based on dinocyst assemblages are available from approximately the same region in the Chukchi Sea. They show no strong agreement (Fig. 3), other than a general lack of an overall trend during the Holocene.

3.2. *Pacific Ocean*

Sedimentary records from the Bering Sea suggest cool conditions with expanded sea ice during the YD, and it became warmer and more ice-free during the early Holocene (e.g., Sancetta and Robinson, 1983). At 11.3 ka, diatom assemblages in the southern Bering Sea (around 54°N latitude on the Umnak Plateau) shifted from one dominated by sea-ice-adapted species to one dominated by warmer-water, North Pacific species indicative of seasonally ice-free conditions (Caissie et al., 2010). Alkenone data from the same study indicate that this assemblage shift was coincident with a SST increase of more than 3°C. Similarly, estimates of alkenone-based SST and IP₂₅-based sea-ice extent from the western Bering Sea (Max et al., 2012) suggest that warming from the YD to the early Holocene was accompanied by a drastic reduction in sea ice to less-than-modern levels. This transition may reflect a shift from increased flow of cold Arctic waters to the Bering Sea during the YD to greater north Pacific flow during the warm, low-sea-ice early Holocene (Caissie et al., 2010). A similar YD-to-early-Holocene temperature evolution in the high-latitude north Atlantic suggests strong teleconnections between the regions, potentially linked to the strength of the Atlantic Meridional Overturning Circulation (Max et al., 2012, and references therein).

The evolution of Holocene SST and sea ice in the Bering Sea is nuanced and regionally heterogeneous. In the western Bering Sea an early Holocene thermal maximum is evident between 11 and 9 ka, and gradually decreases throughout the Holocene (Max et al., 2012). Both dinocyst assemblages and IP₂₅ proxies point to ice-free conditions during the thermal maximum and variable conditions during the middle and late Holocene that suggest periods of both open water and modest sea-ice concentrations. In the southern Bering Sea, Holocene temperatures show no strong trends after the 11.3 ka thermal optimum, oscillating between 6.5° and 8.5°C with a hint of a minimum near ~4.5 ka (Caissie et al., 2010). The region appears to have been relatively ice-free during the Holocene, with no seasonal re-advance of sea ice over the Umnak Plateau. A recently published alkenone-based SST record from core GC-33 (about 55°N) at a nearby southern Bering Shelf site extends back to 9.4 ka (Harada et al., 2014) and also suggests Holocene temperature variations between about 6.5° and 8.5°C. Temperatures in the earliest portion of the record were as high as anytime subsequently, but equally warm conditions also occurred at around 6.0 and 2.6 ka. Relatively cool conditions existed at about 8 and 4 ka. The same study found that the proportion of sea-ice-related diatoms was highest during the earliest part of the record and decreased toward the present; this was attributed to the gradual increase in winter insolation at 50° N (Harada et al., 2014). The apparent contradiction between warm early Holocene SST and greater sea ice may at least partially be explained by seasonal discrepancies, given that alkenone-based SST estimates are likely biased toward the warm season (Harada et al., 2014).

3.3. Limitations and uncertainties

Evidence for the extent and timing of Holocene sea-ice and SST changes in eastern Beringia is based on few studies. Low sedimentation rates and geochronological issues in the Arctic Ocean generally hamper interpretations of Holocene sequences. Furthermore, the potential seasonal bias of each proxy type is relatively poorly constrained. The divergent results from the Chukchi Sea do not allow for a consistent regional interpretation of the history of sea-ice cover.

4. Permafrost and peatland initiation ages

4.1. Permafrost and thaw lakes

Permafrost forms and degrades in response to climate change. Kaufman et al. (2004) summarized scattered evidence for pronounced permafrost thaw in eastern Beringia during the early Holocene. For example, ice wedges thawed between 11.6 and 6.5 ka on the Seward Peninsula (Hopkins et al., 1960) and the active layer (the seasonally thawed upper portion of a permafrost) deepened between 10.3 and 9.1 ka along the Arctic coast of northwest Canada (Burn, 1997) and in the central Yukon (Burn et al., 1986). Warmer and wetter early Holocene conditions on the North Slope are also indicated by enhanced hillslope erosion and increased active-layer-detachment slides, which resulted in rapid aggradation of alluvial valleys (Mann et al., 2010). More recently, Walter Anthony et al. (2014) compiled information on the timing of the formation of thaw lakes from across Beringia. They showed that thaw lakes became widespread across Beringia between 14 and 9 ka, with thaw activity accelerating between 11.5 and 9.0 ka. For this review, we extracted from their database the initiation ages of thaw lakes from the eastern Beringian sites. On the basis of ages at 22 sites where basal ages are younger than 12 ka, the highest initiation rate of thaw lakes occurred between 11 and 10 ka (Fig. 4b), suggesting that high temperatures caused massive ground ice to thaw immediately following the

YD. The lowest rate of thaw-lake development occurred between 6 and 4 ka, suggesting that
temperatures decreased to prevent further permafrost degradation. Permafrost expanded in the
region during the middle Holocene when many thaw lakes show evidence of partial or full lake
drainage. For example, near the Mackenzie Delta, lakes drained after 4.5 ka (Mackay, 1992).
This allowed benthic aquatic mosses and littoral peat to accumulate rapidly (Walter Anthony et
al., 2014).

4.2. Peatlands

The vast peatlands in eastern Beringia developed in response to climate changes that followed
the last glacial maximum. Jones and Yu (2010) suggested that the high rate of peatland initiation
in Alaska during the early Holocene was related to warmer postglacial climate and attributed
high rates of peat accumulation to increased seasonality in temperature (Jones and Yu, 2010) and
likely precipitation (Jones et al., 2014). In this review, we update the database of peatland-
initiation ages in Jones and Yu (2010) with additional 19 previously unpublished ages from
eastern Beringia, while focusing on the Holocene (Fig. 4a; Table S1). On the basis of this
evidence, the highest rate of peatland initiation occurred around 11-10 ka, concurrent with the
peak in thaw-lake initiation ages. Most of the peatland-initiation dates come from south-central
Alaska and north of the Brooks Range, where the age-frequency patterns are similar. In addition
to high rates of peatland initiation, high rates of vertical accumulation of well-preserved peat
occurred between 11.5 and 9.0 ka in four peatlands on the Kenai Peninsula, indicating that
conditions were optimal for their growth (Jones and Yu, 2010). Gajewski et al. (2001) found that
the relative abundance of *Sphagnum* spores, as represented in the North American Pollen
Database, peaked around 9 ka in eastern Beringia. However, some peatlands did not contain

Sphagnum in early initiation stages, and the presence of *Sphagnum* spores does not correlate well with changes in *Sphagnum* abundance (LaCourse and Davies, 2015). The pace of peatland formation decreased rapidly around 9 ka, after which the rate of initiation was roughly 50-25% of the early Holocene rate. The lowest initiation of new peatlands occurred between 5.5 and 4.0 ka, coincident with a cessation in new thaw-lake initiation (Fig. 4), suggesting cooler conditions.

In peatlands affected by permafrost, the available records show early Holocene degradation as indicated by thaw lake formation and drainage (Hunt et al., 2013; O'Donnell et al., 2012), with aggradation beginning around 6.5 ka in the Koyukuk lowlands (O'Donnell et al., 2012) and around 4.5 ka on the southern Seward Peninsula (Hunt et al., 2013). In the McKenzie River Delta, permafrost aggradation in peatlands began around 8 ka (Tarnocai and Zoltai, 1988) and at 6.2 ka in the Northwest Territories (Vardy et al., 2000). On the Seward Peninsula, a transition to low carbon-accumulation rates after 4.5 ka suggests the onset of permafrost aggradation (Hunt et al., 2013). Most recent permafrost aggradation in peatlands occurred in the last 1 ka (Meyers-Smith et al., 2008; O'Donnell et al., 2012; Jones et al., 2012, 2013).

4.3. Limitations and uncertainties

In addition to climate, the initiation of peat accumulation also depends on local topography and hydrological settings, and substrate permeability biogeography, among other factors (Charman, 2002). Peatland initiation through paludification (peat expansion onto non-wetland terrain) may be triggered by an increase in moisture, whereas peatland initiation by terrestrialization (lake infilling) may be caused by a decrease in moisture. Distinguishing between these two processes is often not possible with published basal date information. Similarly, permafrost aggradation and degradation may be influenced by landscape processes that may not be directly associated

with temperature (e.g., Mann et al., 2002), especially over short spatial-temporal scales.

5. Lake-level fluctuations

Lake-level fluctuations in eastern Beringia have been investigated using a variety of sedimentary, micro- and macro-fossil indicators. We compiled much of the available information from the region, but did not complete a comprehensive review. Water-level changes at each lake were simplified by assigning each millennium to one of four lake-level-status categories (Fig. 5).

During the early Holocene, lake levels were generally low, indicating dryer-than-present conditions, with moisture increasing to near-modern levels by the middle Holocene. At the sub-regional level, we find differences between the lakes of northern and interior Alaska versus those of southern Alaska and southern Yukon. In northern and interior Alaska, lake level was

consistently low during the early Holocene and then rose beginning around 9 ka. Among these are: (1) Birch Lake, which has overflowed since 6 ka (Abbott et al., 2000); (2) Jan Lake, which rose from 9.0 ka to the present (Barber and Finney, 2000); and (3) Harding Lake, which rose rapidly around 9.4 ka and remained high and stable thereafter (Finkenbinder et al., 2014).

Hydrologic modeling at Jan Lake indicates that precipitation during the early Holocene was about 25 to 40% less than modern values (Barber and Finney 2000). In northern Alaska, the level of Nikivlik Lake rose immediately following the YD (Mann et al., 2002), and then decreased between around 10 and 8 ka (Gaglioti et al., 2014). In the northern Yukon, Trout Lake was at least 6.5 m shallower prior to about 10 ka (Irvine et al., 2012).

In southern Alaska and southern Yukon, the signal is less uniform among lakes compared with interior Alaska, with some evidence of high lake levels during the earliest Holocene, followed by low lake levels that persisted into the middle Holocene. Multiple lakes on the Kenai

Peninsula record water levels lower than present during the early Holocene, including: (1) Discovery Pond, which was low around 11.7 to 9.2 ka (Kaufman et al., 2010); (2) Arrow Lake, which was low from prior to 9.5 ka (the basal age) to 9.0 ka (R. Anderson et al., 2006); (3) Portage Lake, which was also low prior to 9.5 ka (the basal age) to about 8.0 ka (R. Anderson et al., 2006); and (4) a series of lakes and fens studied by E. Berg (unpub. data) that all show low levels between about 10 and 8 ka. In the western Prince William Sound, the sedimentary sequence at Cabin Lake is marked by an unconformity between 8.8 and 3.4 ka, indicating that lake level was lower some time during this interval (Zander et al., 2013). In southern Yukon, the level of Upper Fly Lake inferred from chironomid assemblages was high prior to around 10 ka, low between 10 and 7 ka and increased to the present-day levels between 7-4 ka (Bunbury and Gajewski, 2009).

6. Water ($\delta^{18}\text{O}$ and δD) isotope records

Most of the terrestrial isotope ($\delta^{18}\text{O}$ or δD) records available in eastern Beringia are from lake sediments, but archives also include glacier ice (Zdanowicz et al., 2014) and ice wedges (Meyer et al., 2010), plant-derived cellulose (Epstein, 1995) and more recently the bulk organic matter (Jones et al., 2014) and leaf waxes in peat (Nichols et al., 2014). Published interpretations of the paleo-climatic controls influencing isotope changes at these sites include precipitation minus evaporation (effective moisture), source and seasonality of precipitation, temperature, orographic uplift, and glacial meltwater input (Table 3). Only four isotope records in the region meet the criteria for the Arctic Holocene database: Jellybean, Mica and Takahula Lakes and Mt. Logan ice. Here, we add the recent analyses from Corser Bog (Nichols et al., 2014) and consider records from several other sites that do not meet the selection criteria.

6.1. Oxygen isotopes in modern precipitation

Interpretations of paleo-isotope records are guided by an understanding of the controls on the oxygen isotope composition of modern precipitation ($\delta^{18}\text{O}_\text{P}$). The spatial coverage of $\delta^{18}\text{O}_\text{P}$ data in the Global Network of Isotopes in Precipitation (GNIP; <http://www.iaea.org/water>) is limited to six sites in eastern Beringia (Fig. 6), although efforts are ongoing to improve the regional coverage (e.g., Delavau et al., 2015). Despite the sparse coverage, most stations include at least 36 months of temporally synchronous isotope data (1962–1965), and collectively provide valuable information on spatial-temporal patterns of $\delta^{18}\text{O}_\text{P}$. Interpolation of mean weighted summer (JJA) and winter (DJF) $\delta^{18}\text{O}_\text{P}$ values from all available GNIP data (1962–1989) (Fig. 6) show decreasing $\delta^{18}\text{O}_\text{P}$ with increasing latitude and continentality. Winter $\delta^{18}\text{O}_\text{P}$ values are lower than summer values, and these seasonal differences become more pronounced with increasing latitude and continentality, which can be ascribed to the effects of temperature, moisture source and moisture transport trajectories, orographic uplift of air masses and possibly winter sea-ice to the north.

6.2. Paleo-isotope records ($\delta^{18}\text{O}$ and δD)

Comparison of the available isotope records from eastern Beringia (Fig. 7) highlights the spatio-temporal heterogeneity of Holocene hydroclimate in this region, combined with the individualistic controls on water isotope values in different lakes. Nonetheless, several records share some common features. For example, of the sites that have been interpreted to reflect effective moisture, Takahula Lake in northern Alaska is the most highly resolved; it exhibits a ~6‰ increase in $\delta^{18}\text{O}$ values from 5.5 to 4.0 ka, suggesting a major decrease in effective

moisture (Clegg and Hu, 2010). The $\delta^{18}\text{O}$ pattern at Qalluuraq Lake in northern Alaska shows a shift of similar magnitude, although the resolution of the record is lower (Wooller et al., 2012a). Changes in δD of *n*-alkanes from Corser Bog, supported by paleobotanical evidence of a transition of sedge-dominated wetland to a *Sphagnum* bog, imply dry conditions between around 8.5 and 3.5 ka (Nichols et al., 2014). The timing of this dry interval precisely matches the duration of the unconformity interpreted as desiccation of nearby Cabin Lake (Zander et al., 2013). In contrast, other lakes from the Brooks Range, interior Alaska, and the Yukon (Meli, Quartz and Marcella Lakes) lack such a shift and instead suggest little change in effective moisture over this interval (L. Anderson et al., 2001, 2007; Wooller et al., 2012b). During the late Holocene, Quartz and Marcella Lakes show a $\sim 4\text{‰}$ increase in $\delta^{18}\text{O}$ values, implying a decrease in effective moisture, but this could alternatively suggest enhanced meridional flow delivered isotopically enriched precipitation to these lakes.

At other sites including Tangled Up, Hundred Mile, Mica and Jellybean Lakes, and Horse Trail Fen, $\delta^{18}\text{O}$ values of modern lake and bog water reflect the local $\delta^{18}\text{O}_\text{P}$, suggesting that proxies at these sites also reflect $\delta^{18}\text{O}_\text{P}$ (L. Anderson et al., 2001, 2005; Yu et al., 2008; Schiff et al., 2009; Jones et al., 2014). However, these paleo-isotope records show little coherence during the Holocene (Fig. 7), suggesting that variations in $\delta^{18}\text{O}_\text{P}$ are influenced by multiple, site-specific mechanisms, such as atmospheric temperature, moisture source and Raleigh distillation, or by proxy-record-specific kinetic or vital effects (e.g., Leng and Marshall, 2004). Variations in $\delta^{18}\text{O}$ values of *Chara* stem encrustations and *Pisidium* shells at Tangled Up and Hundred Mile Lakes, respectively include shifts that are too large to be caused by a change in temperature alone. The isotopes at both lakes are likely influenced by evaporation (effective moisture) and/or poorly constrained vital effects, in addition to temperature-dependent fractionation (Table 3).

The changes in a number of eastern Beringia paleo-isotope records have been attributed
512 to the prevailing atmospheric circulation pattern, particularly the North Pacific winter surface
pressure field (Aleutian Low). In addition to modulating the amount, seasonality and temperature
514 of precipitation events, the Aleutian Low also influences the source, transport, and rain out
history of moisture across the region (Rodionov et al., 2007). However, different authors have
516 invoked different mechanisms to explain the relation between the pressure field and the isotope
values. Fisher et al. (2004) proposed that isotope fluctuations in Mt. Logan ice reflect changes in
518 moisture source, whereby under enhanced meridional flow (stronger Aleutian Low), moisture is
transported to Mt. Logan from low-latitude air masses. Similarly, Schiff et al. (2009) interpreted
520 higher $\delta^{18}\text{O}$ values in diatoms from Mica Lake as indicating storms that track from the south,
which is associated with meridional flow driven by a strong Aleutian Low. Likewise, a recent
522 analysis of instrumental pressure fields and storm-track trajectories demonstrated a strong
positive relation between moisture source area and isotope values at Adak in the central Aleutian
524 Islands (Bailey et al., 2015). In contrast, L. Anderson et al. (2005) interpreted lower $\delta^{18}\text{O}$ values
in carbonate of Jellybean Lake as indicating a stronger Aleutian Low through enhanced
526 orographic uplift of air masses. This contradicts the $\delta^{18}\text{O}$ data from carbonate formed in
Jellybean Lake during the instrumental period (<http://www.ncdc.noaa.gov>; ID 5445), which
528 correlate positively with the strength of the winter Aleutian Low (inverse correlation with the
North Pacific Index; $r = -0.48$, $p < 0.02$ (the sign of the correlation was incorrectly reported by L.
530 Anderson et al., 2005). This is consistent with the output of an isotope-enabled general-
circulation model (Field et al., 2010), which simulates higher $\delta^{18}\text{O}_p$ around the Gulf of Alaska
532 during a strengthened Aleutian Low. Jones et al. (2014) also invoked orographic uplift associated

with the Aleutian Low to explain the $\delta^{18}\text{O}$ variation in a peat core taken from Horse Trail Fen,
534 although peat is likely to be less sensitive to winter than to summer conditions.

536 6.3. *Limitations and uncertainties*

Only three isotope records from eastern Beringia extend back through the full Holocene epoch
538 (Mt. Logan, Horse Trail Fen, Qalluuraq Lake), limiting our ability to evaluate long-term trends.
Interpretation of paleo- $\delta^{18}\text{O}$ values is not only complicated by the complex processes that drive
540 $\delta^{18}\text{O}_\text{P}$ (e.g., Leng and Marshall, 2004), but also by the fractionations that occur between water
and the various compounds employed as paleo-archives (ice, carbonate, opal, insect chitin, bulk
542 organic matter and cellulose). Furthermore, each of these archives could reflect seasonal
differences between the timing of mineral formation and their source water input. The records
544 may represent summer or winter conditions, or an integration of both, which is, in turn,
influenced by site-specific hydrologic processes, which are typically discussed in the original
546 publication of the records. For example the vascular plants in peat reflect water isotopes in
precipitation that falls during the summer growth season, while the lake and ice core isotope
548 records have been predominantly interpreted to reflect winter precipitation inputs. These
disparities and limitations may partly explain why this review of available Holocene isotope
550 records finds no consistent patterns in $\delta^{18}\text{O}$ values through time or space.

552 7. **Midge-based temperature reconstructions**

Species distributions and abundances of midges (Chironomidae, Ceratopogodinae and
554 Chaoboridae) show strong relations to summer temperature in many regions, and subfossil midge
assemblages have become a common quantitative proxy for paleotemperatures (Walker and

Cwynar, 2006). Here we summarize major trends in Holocene midge-based temperature reconstructions from eastern Beringia, including seven that were included in the Arctic Holocene database plus an additional five published records from eastern Beringia that do not meet the criteria for the Arctic Holocene database. The records provide fairly broad geographic coverage, albeit with a small concentration of sites in south-central Alaska and the nearby southwest Yukon. A composite temperature reconstruction was generated by binning each record into 500-year intervals, with standardized temperature anomalies calculated relative to the average values over the four time steps represented in all records. For consistency, temperatures modeled using weighted averaging partial least squares (WAPLS) approach were used for all records, including those for which multiple models were used in the original studies (Table 4). For Trout Lake, where reconstructions are available from two core sites, all original values were merged to provide maximum time coverage.

7.1. Primary trends

Overall, the composite of midge records from eastern Beringia show some evidence for highest summer temperatures during the early Holocene (10.0-9.5 ka), with minor cooling over the late Holocene (Fig. 8). Seven of the 12 records register the lowest summer temperatures of the Holocene between 4 and 2 ka. Among the midge-based temperature records extending back to 11.5 ka, more than half register the highest reconstructed temperatures of the Holocene at times prior to 10 ka. In contrast with midge-based temperature reconstructions from British Columbia to the south (Rosenberg et al., 2004; Chase et al., 2008) and parts of northeastern Canada (Briner et al., this volume), however, midge records from this region show little evidence for persistent warmth throughout the early Holocene, perhaps apart from a brief interval of peak temperatures

~10-9 ka, as reflected in the composite reconstruction (Fig. 8). Two sites in this synthesis of 12

580 sites were significantly warmer through the first half than the second half of the Holocene

(Upper Fly Lake in the southwest Yukon and Qaluuraq Lake on the Alaskan North Slope;

582 Bunbury and Gajewski 2009; Wooller et al., 2012a). At several sites, reconstructed temperatures

rose through the early Holocene to a mid-Holocene maximum (e.g., Clegg et al., 2011), and at

584 the remaining sites, Holocene temperatures exhibit no clear multi-millennial trends. There is no

clear regional pattern to the trends. Six additional midge records from Alaska and the Yukon not

586 published in peer-reviewed journals but presented in theses support this overall picture, with only

one of the six showing strong evidence that the first half of the Holocene was overall

588 significantly warmer than the second half (MacIsaac, 2003; Barley, 2004; Stepanovic, 2006;

Clegg, 2011).

590 *7.2. Limitations and uncertainties*

592 Although in many settings this proxy appears to perform well in reconstructing summer

temperature changes (Brooks et al., 2012), other environmental variables including water depth,

594 vegetation, water chemistry and nutrient availability also affect modern midge distributions in

eastern Beringia (Walker and MacDonald, 1995; Walker et al., 2003; Wilson and Gajewski,

596 2004; Barley et al., 2006; Kurek and Cwynar, 2009). Two potential confounding factors are of

particular concern in interpreting the temperature reconstructions from midge records in this

598 region: vegetation change (with many sites having experienced shrub and forest migrations

during the Holocene), which may have influenced lake sediment organic content among many

600 other factors, and hydroclimatic changes and resulting lake-level variability. For example,

Kaufman et al. (2012) concluded that vegetation change (especially establishment of *Alnus*, and

resulting changes in local nitrogen cycling), likely had confounding effects on midge-inferred temperatures at Lone Spruce Pond in southwest Alaska. Nonetheless, where validation strategies have been employed to assess the robustness of midge-inferred temperature reconstructions in Alaska and the Yukon, the results are often encouraging. At Trout Lake, for example, Irvine et al. (2012) performed reconstructions on two parallel cores recovered from contrasting water depths. The two cores agree very well in both absolute values and millennial-scale trends. Clegg et al. (2010) compared high-resolution midge-inferred temperatures at Moose Lake with a tree-ring derived temperature reconstruction and with other proxy records, and found strong agreement.

8. Pollen-based climate inferences

8.1. Vegetation history

Fossil pollen records from numerous lakes and bogs across eastern Beringia reveal a series of major vegetation changes during the Holocene (e.g., Anderson and Brubaker, 1993, 1994; Gavin and Hu, 2013; Gajewski et al., 2014) (Fig. 9). In this review, we combine evidence from the three major biomes represented in the region: tundra, boreal forest and cool-temperate forest. In coastal southern Alaska, conifers moved up the coast and replaced the *Alnus* shrubland that had developed shortly after deglaciation. *Picea sitchensis* established in southeast Alaska between 11 and 10 ka (Mann, 1983; Cwynar, 1990; Hansen and Engstrom, 1996), then spread northward to eastern Prince William Sound by 8.4 ka (Peteet, 1986), and reached the southern Kenai Peninsula by 4 ka (Ager, 2000). *Tsuga* moved into the region somewhat later; *T. mertensiana* and *T. heterophylla* expanded in southeast Alaska between 10 and 8 ka, then spread north to reach eastern Prince William Sound by 4 ka (Mann, 1983; Peteet, 1986; Cwynar, 1990; Kautz et al., 2012), and arrived on the Kenai Peninsula 4-2 ka (Heusser, 1983; Ager et al., 2010).

In other parts of eastern Beringia, the Holocene began with the expansion of *Populus*
626 *balsamifera* and possibly tree birches (*Betula papyrifera*) into the shrub-birch (e.g., *Betula nana*,
B. glandulosa) tundra that prevailed during the late glacial (e.g., Anderson and Brubaker, 1994;
628 Edwards et al., 2005). This deciduous woodland was present from 11.5 to 10-9 ka, at which point
different sequences of vegetation change occurred in different parts of the region. *Picea glauca*
630 appears to have expanded from east to west, beginning at 10 ka in southern Yukon (e.g., Cwynar,
1988; Cwynar and Spear, 1995) and in eastern and southern Alaska, where it reached modern
632 values within a few centuries of initial appearance (e.g., R. Anderson et al., 2006; Tinner et al.,
2006). In west-central Alaska, however, *P. glauca* abundance remained below its modern levels
634 until 6-5 ka (e.g., Brubaker et al., 1983; Hu et al., 1996), and in southwestern Alaska it reached
its current values only after 4-2 ka (e.g., Hu et al., 1995; Brubaker et al., 2001; Kaltenrieder et al.,
636 2011). *Picea mariana* expanded across eastern and central Alaska between 10 and 5.5 ka, and
thus arrived after *P. glauca* at most sites (e.g., Tinner et al., 2006; Higuera et al., 2009). *Alnus*
638 spread across the region from 9 to 6 ka, apparently from west to east, such that it followed the
arrival of *P. glauca* in the eastern part of the region and preceded *P. glauca* expansion in
640 southwestern Alaska (e.g., Brubaker et al., 2001; Tinner et al., 2006). Analyses of the fossil
pollen and stomata of *Pinus contorta* at sites in southern Yukon and Northwest Territories
642 suggest that, as with *P. glauca* in west-central Alaska, its expansion might have been delayed
after its initial arrival. Stomata are common in lake sediments beginning at 6 ka, indicating its
644 local presence (Edwards et al., 2015). Pollen data, however, suggest that the main population
expansion of *P. contorta* was asynchronous across the region, taking place 2000-4000 years later
646 (e.g., Cwynar, 1988; MacDonald and Cwynar, 1991; Cwynar and Spear, 1995).

In northern and higher-elevation parts of the region, different vegetation types developed following the deciduous woodland of the early Holocene. In northern Alaska, *Populus* declined at 10-9 ka, leaving shrub-birch tundra as the prevailing vegetation type (e.g., Mann et al., 2002, 2010). *Alnus* then expanded at 8-7 ka (e.g., Oswald et al., 1999, 2003). Further east, on the Tuktoyaktuk Peninsula of northern Northwest Territories, northward range extensions of *Myrica* and *Typha* coincided with the early Holocene interval of elevated *Populus* (Cwynar, 1982; Ritchie et al., 1983). On the nearby Mackenzie Delta, *Picea* was present between 10 and 7 ka at sites up to 70 km north of its modern treeline (Ritchie and Hare, 1971). Similarly, pollen and plant macrofossil evidence from sites above the present-day alpine treeline in central Yukon suggest that *Picea* forest occurred beyond its modern altitudinal limit from 11.6 to 5.6 ka (Cwynar and Spear, 1991; Szeicz et al., 1995). Further south, *Picea* treeline appears to have been higher than present between 3.6 and 3 ka in the northern St. Elias Range (Denton and Karlen, 1977), although a pollen record from the nearby Kluane Lake region suggests little change in alpine treeline during the Holocene (Bunbury and Gajewski, 2009).

8.2. Climate interpretations

Pollen data from eastern Beringia have been used to infer Holocene climate in a variety of ways. Generalized reconstructions have been based on the modern ecological preferences and geographic distributions of the key taxa and the sequence of their arrivals across the region (e.g., Anderson and Brubaker, 1993). Specifically, the early Holocene expansion of *Populus* was thought to reflect rising temperatures, with summers possibly warmer than at present (e.g., Hopkins et al., 1981; Kaufman and Hopkins, 1985; Brubaker et al., 2001; Mann et al., 2002, 2010; Peros et al., 2008). Ritchie (1984) interpreted the northward range extensions of *Populus*,

Morella, and *Typha* on the Tuktoyaktuk Peninsula as reflecting July and mean annual temperatures 3°C higher than today. Similarly, Mann et al. (2010) suggested that *Populus* expansion in northern Alaska indicated July temperatures above 10°C. The subsequent arrivals of *P. glauca*, *P. mariana*, and *Alnus* in Alaska have been interpreted to reflect increasing moisture during the middle and late Holocene (e.g., Anderson and Brubaker, 1993). The synchronous increase in *Picea* at 10 ka across a large area of southern Yukon is interpreted as a response to a warming climate (Gajewski et al., 2014).

Specific climate variables have also been reconstructed from pollen data using more quantitative approaches applied to networks of fossil pollen records, including (1) a pollen-climate transfer function (Heusser et al., 1980), (2) a rule-based biomization approach (e.g., Prentice et al., 1996), and (3) the modern analogue technique (e.g., Overpeck et al., 1985). These analyses yield considerable site-to-site variability, but averaging across sites has been used to generate regional climate reconstructions (Fig. 10). The transfer function (quantitative analyses of pollen-vegetation-climate relations) was developed to quantify glacial-interglacial-scale shifts for coastal northwest North America using reference sites from across the region (Heusser et al., 1980) and was subsequently applied to late glacial and Holocene pollen assemblages from around the Gulf of Alaska (Heusser et al., 1985). It is based on a linear combination of the relative proportions of three taxa for temperature (*Poaceae*, *Tsuga heterophylla*, and *Pinus*) and two for annual precipitation (*Tsuga heterophylla* and *Pinus*). The results indicate warmer-than-present conditions from 11 to 10 ka, followed by nearly 2°C additional warming between 10 and 8 ka, after which temperatures declined steadily until 5 ka.

Biomization reconstructs biomes on the basis of plant functional types (PFT). The method involves assigning palynological taxa to one or more PFTs, which are combined to

define biomes following a specific set of rules. In the Arctic, CAPE (2001) distinguished six
694 tundra biomes of increasing summer temperature requirements based on regionally coherent
pollen assemblages. The approach is described further in the Paleoenvironmental Atlas of
696 Beringia (PALE Beringian Working Group, 1999). Their time-slice analysis (Fig. 10) showed
that temperatures were lower than present nearly everywhere in eastern Beringia at 10 ka. At 6
698 ka, temperatures were mixed between colder and similar to present.

Temperature and precipitation estimates based on the modern analogue technique (MAT)
700 have received considerable attention, and of the available MAT-derived climate reconstructions
from the region, nine meet the criteria for inclusion in the Arctic Holocene database. For this
702 approach, fossil pollen assemblages are matched to modern pollen samples and, in turn, a
modern vegetation type and/or present-day climate values. Viau et al. (2008) applied the MAT to
704 pollen records in eastern Beringia, with modern pollen samples from across North America
available as analogues. Averaging the reconstructions from 45 sites suggests that the early
706 Holocene summer (Jul) was colder than at present and winter (Jan) was warmer, yielding mean
annual temperatures similar to today. Precipitation was higher than at present until 7 ka, while
708 winter and summer temperatures remained above and below those of today, respectively, until 8-
7 ka. The MAT analysis yields relatively warm and wet conditions between 10 and 7 ka due to
710 high *Picea* pollen percentages, followed by cooler, drier conditions after the expansion of *Alnus*
at 8-7 ka, as fossil-pollen spectra that contain abundant *Alnus* tend to find analogues in shrub-
712 tundra areas, which feature cold, dry climate. The discrepancy between qualitative interpretations
and MAT results for early Holocene climate is discussed in Viau et al. (2008) and may be due to
714 the MAT methodology, which reconstructs the modern seasonal cycle even for the early
Holocene when the orbital configuration differed. It may also be partly attributable to the high

716 abundance of *Populus* in the pollen assemblages, which lack modern analogues (e.g., Peros et al.,
2008). The closest MAT matches for the early Holocene, however, are shrub tundra sites with
718 high *Betula* and low *Picea* and *Alnus* abundances, which yield climate analogue with relatively
high precipitation, cool summers, and warm winters (Viau et al., 2008). Some interpretations
720 suggest that high *Populus* abundance during the early Holocene may have been directly
influenced by ecological and edaphic factors (e.g., Cwynar, 1982; Ritchie, 1984; Hu et al., 1993;
722 Peros et al., 2008), with climate as the possible ultimate control. A tree-ring analysis (Edwards
and Dunwiddie, 1985) together with the decline of *Populus* in northern Alaska during the YD
724 (Mann et al., 2002, 2010) further indicates that elevated *Populus* reflects warm conditions. It is
difficult to resolve these contrasting interpretations of early Holocene pollen records in the
726 absence of modern analogues for *Populus*-dominated pollen spectra.

728 8.3. Limitations and uncertainties

Several methodological and ecological considerations should be taken into account when
730 interpreting pollen-derived climate reconstructions. The lack of strong modern analogues is
potentially problematic, especially during the early Holocene (Peros et al., 2008), although Viau
732 et al. (2008) found good modern analogues for most Holocene pollen assemblages. Quantitative
reconstructions may also be limited when key taxa have broad ecological tolerances and climatic
734 ranges (e.g., Birks and Birks, 2000), although this has been questioned (Gajewski, 2006, 2015).
In addition, vegetation composition can be influenced by shifts in soil conditions, disturbance,
736 and other ecological factors, all of which may interact with climate change (e.g., Hu et al., 1993,
1996; Mann et al., 2002; Oswald et al., 2003; Edwards et al., 2015). Lastly, migrational lags may
738 have created disequilibrium between climate and vegetation (e.g., Bennett, 1985), although

Webb (1986) and Gajewski (1993) suggest this is not a significant problem when deriving
740 paleoclimate estimates from networks of pollen records. In the case of *P. glauca*, however, a
study of modern population genetics provided unambiguous evidence that this species existed in
742 Alaska during the last glaciation (L.L. Anderson et al., 2006), and a recent re-evaluation of fossil
pollen data reached the same conclusion for *P. glauca* and other woody taxa (Brubaker et al.,
744 2005). Thus, the Holocene expansion of *P. glauca* in particular, and possibly other taxa more
generally, may be interpretable in terms of climate in eastern Beringia.

9. Synthesis stream I — Records in the Arctic Holocene database

9.1. Approach

To systematically investigate the spatial-temporal pattern of past climate changes and to
750 quantitatively characterize any prominent patterns that might be revealed requires a spatially
distributed network of relevant paleoclimate time series. Here we present the first quantitative
752 synthesis of records from eastern Beringia compiled in the Arctic Holocene database (Sundqvist
et al., 2014; updated here to version 2.1). The records include all available continuous time series
754 that extend back to at least 6 ka and are supported by an average of at least one analysis every
400 years. The average resolution of the 32 records is 148 ± 103 (± 1 SD) years during the
756 interval of common overlap, 6-2 ka. The geochronology of each record is supported by at least
one age control point every 3000 years. Their paleoclimate interpretations have previously been
758 described in peer-reviewed publications (cited in Sundqvist et al., 2014). Trends extracted from
these records are compared with information from other paleoclimate indicators in section 10
760 where the two streams are integrated and focused on addressing questions that can be
investigated using the output of Earth system models.

762

9.2. Temperature

764 We focus first on the temperature-sensitive records from the Arctic Holocene database (Table 1).
Composite reconstructions were generated based separately on pollen (n = 9) and midges (n = 7).
766 The only available pollen-based reconstructions rely on MAT and include both summer and
annual (average of summer and winter) temperature; the midge-based reconstruction is for July
768 air temperature based on WAPLS. For these composites, time series for each record were binned
in 500-year intervals. Temperature anomalies for each time step were then calculated relative to
770 the average values over just the time steps represented across all records. In addition, a third
composite was generated based on other proxy types, namely indicators of production, carbonate
772 geochemistry, and MBT (n = 7). A separate composite was calculated for the SST records from
the Chukchi Sea (n = 3). The other proxy records were normalized to have zero mean and unit
774 variance over the period of common overlap (6-0 ka), and the composite is reported in standard
deviation (SD) units. Prior to the normalization period, a few records show untenably high
776 variability, which dominates the mean of the records. Therefore, time steps with values that
exceeded ± 3 SD were excluded from this composite.

778 The three composites exhibit generally similar trends (Fig. 11). During the early
Holocene, all three composites contain both the coldest and warmest 500-year intervals, although
780 they occur at different times based on the different proxies. The composite midge-based curve of
July air temperature based on just the records selected for the Arctic Holocene database (n = 7)
782 generally conforms to the composite that includes additional records (n = 12), except over the
early Holocene when the former shows warming and the later does not. Although the midge-
784 based mean composite temperature increases during the early Holocene, site-level records

indicate either cold or warm conditions. A clearer warming trend during the early Holocene
786 might be indicated by the pollen reconstruction (especially for summer) and in the other proxies.
During the middle Holocene all three composites reach a maximum between 7.0 and 5.5 ka.
788 During the late Holocene, temperatures generally decrease, although the trend over the past 1 ka
differs among proxy types, with warming indicated by the midges and other proxies, and
790 especially in the SST of Chukchi Sea.

We then considered all temperature-sensitive records in the Arctic Holocene database
792 collectively rather than by proxy type (Fig. 12). For the pollen-based reconstructions, we used
the mean annual temperature (average of July and January) because it is known to be less
794 sensitive to evolving seasonality over the Holocene (Viau et al., 2008). Hierarchical cluster
analysis (HCA) was used to subdivide the records into groups with similar trends. For this
796 analysis, the 500-year-binned time series were standardized to have zero mean and unit variance
over the full duration of each individual record. The HCA of the standardized records was
798 performed with the Euclidean distance and Ward's linkage clustering. Missing values in records
shorter than 11.5 ka were removed prior to the computation of each pairwise distance in the data
800 set, and the distances were scaled up to account for the larger dimension of the full sample.
Composites were constructed by averaging the individual binned proxy records from each cluster.
802 The results show that clusters are not subdivided according to proxy type. The primary split
separates series with highest mean standardized temperature prior to 10 ka against those with
804 lowest mean standardized temperatures during this interval. The mean values of all clusters show
at least a secondary peak in mean temperature between 6.5 and 4.5 ka. The spatial pattern of the
806 three clusters shows little coherence, although sites that lack an early Holocene thermal

maximum are most common in the southern part of the region. Records that do not extend back
808 the full duration of the Holocene complicate this assessment.

The timing of temperature changes represented in the Arctic Holocene database was
810 further assessed using the significance of zero crossings of the derivative (SiZer) method, which
detects significant non-zero slopes in time series across a range of smoothing timescales
812 (Chaudhuri and Marron, 1999). Figure 13 shows SiZer results for 1000-year time slices for the
same records used for cluster analysis across 700- to 2000-year smoothing windows. Early
814 Holocene time slices show mixed trends before ~8 ka, with little spatial coherence between sites
with significant cooling (dark blue) and warming (dark red) trends. Furthermore, the trends at
816 many sites are not significant at all smoothing timescales (light red/blue) indicating little or no
trend. Between 6-8 ka there is some evidence for interior warming in continental portions of
818 eastern Alaska and the Yukon that may be opposed by cooling at more western and coastal sites.
Although many interior and coastal sites exhibit a shift to significant cooling trends between 4-5
820 ka, there are an equal number of exceptions that show little trend or, in one (Lily Lake),
significant warming. Late Holocene trends are generally weak and incoherent, although some
822 coastal site do exhibit continued significant cooling from 2-3 ka.

824 9.3. *Moisture*

The Arctic Holocene database includes 17 records from eastern Beringia that have been
826 interpreted in terms of moisture changes. They include pollen-inferred annual precipitation based
on MAT (n = 9), other moisture-sensitive proxy records (n = 3; sand flux, midges, $\delta^{13}\text{C}$) and
828 isotope records that are sensitive to various aspects of hydroclimate change (n = 5) (Table 1).
Each record was binned and standardized according to the procedure specified for the

temperature-sensitive records, and cluster analysis was used to subdivide the records (other than $\delta^{18}\text{O}$) into two groups (Fig. 14). Similar to the temperature-sensitive records, the resulting two groups differ depending on whether they indicate wet or dry conditions (predominantly pollen-based mean annual precipitation) during the early Holocene. Following around 7 ka, both groups show little change in inferred moisture. The five $\delta^{18}\text{O}$ records were treated separately because the isotope values cannot be interpreted as simply wetter versus drier; however, they can be used to evaluate the timing of changes, regardless of the mechanism. All records show their highest 500-year-average isotope values between 6.5 and 4.0 ka, although three of the records do not extend back beyond 9 ka, and each has been interpreted differently in terms of moisture.

9.4. Limitations and uncertainties

Factors that can undermine climate reconstructions based on proxy evidence have been described in previous sections. In addition to the climate interpretation itself, age uncertainty in proxy time series is a fundamental limitation in reconstructions of past climate. All of the records considered here are from sedimentary sequences with age models supported by at least one radiocarbon age every 3000 years. Because the sediment in lacustrine and marine environments has accumulated relatively continuously over the Holocene, the ages of samples between dated horizons can be interpolated with reasonable certainty based on age-modeling procedures. Nonetheless, the accuracy of the age models varies among sites, and is related to a variety of factors involving the type of material that is analyzed (e.g., bulk sediment or macrofossils), the origin of its carbon, and sediment reworking, among others. Additional information about the age models for each of the time-series, including a “geochronology accuracy score”, is provided by Sundqvist et al.

(2014). To minimize these complications, we emphasize trends in stacked records at multi-centennial (500 year) to millennial time scales.

10. Synthesis stream II – Questions for future data-model comparisons

10.1. Approach

This section integrates the evidence from composited proxy-specific and multi-proxy time series from the Arctic Holocene database with evidence from paleo records presented in previous sections that cannot be adapted to fit a database of continuous time series. To structure the synthesis, we focus on five research questions that can be investigated by future studies using paleoclimate models, with the goal of understanding climate-forcing mechanisms and the dynamics of climate change.

10.2. What are the primary differences between the climate of the early and late Holocene?

The contrasting climate of the early and late the Holocene (pre-industrial) is generally stronger than between more closely spaced intervals of time. This large difference in both climate forcing and its environmental impact should stand out more clearly within the proxy datasets and within the response of Earth system models compared with differences over shorter timespans. During the early Holocene in eastern Beringia, insolation forcing (including enhanced seasonality) was likely modulated strongly by regional factors, including flooding of continental shelves (causing changes in continentality) and changes in ocean and atmospheric circulation that accompanied ice-sheet retreat, and albedo-induced climate feedbacks associated with the post-glacial expansion of forests and thaw lakes (Bartlein et al., 2015). These influences are reflected in

874 proxy indicators of all types, which show that multi-centennial to millennial-scale trends
diverged more among sites during the early Holocene than during the late Holocene (Fig. 11).

876 Previous compilations of proxy data have focused on specific time slices. Quantitative
reconstructions based on MAT (Viau et al., 2008) and the biome analysis used by CAPE (2001)

878 both indicate generally lower-than-modern summer temperatures at 10 ka. In contrast, qualitative
approaches (e.g., Anderson and Brubaker, 1993) indicate higher temperatures at 10 ka. This

880 agrees with dendroclimatological inferences (Edwards and Dunwiddie, 1985) and evidence for
range extensions suggesting that temperature on the Tuktoyaktuk Peninsula was as much as 3°C

882 higher than modern during the early Holocene (Ritchie, 1984). Similarly, beetle fauna from the
Ikpikpuk River indicate July temperatures were 2-3°C higher around 10.6 ka (Nelson and Carter,

884 1987; reported for this site as 3.5°C higher by Elias, 2001). Beetles from four other Holocene
sites analyzed using the mutual climatic range method (Elias, 2001) indicate July temperatures

886 ranging from 2.2°C higher than present (Blow River; 10.6 ka) to -2.3°C lower (Old Crow; 9.5
and 9.0 ka). Trace-element analysis of ostracode shells from Farewell Lake (Alaska Range)

888 suggests that temperatures peaked between 9.7 and 9.1 ka (Hu et al., 1998). Alkenone-derived
SST reconstructions from the northwest Pacific region show a pronounced temperature

890 maximum during the early Holocene between 11 and 9 ka (Max et al., 2012). The frequency of
thaw-lake and peatland initiation was highest during the early Holocene, suggesting moister and

892 warmer summers. During the early Holocene, lake levels in eastern Beringia were in generally
lower compared with the late Holocene, although lakes in southern Alaska fluctuated more than

894 in interior Alaska. Evidence from southern Alaska indicates that mountain glaciers paused
sometime during the earliest Holocene, and a re-advance is registered at one site between 10.7

896 and 9.8 ka (Emerald Lake; LaBrecque and Kaufman, in review), suggesting lower summer

temperature or higher winter accumulation. In contrast, glaciers advanced everywhere during the
late Holocene, consistent with other proxy temperature records that show overall cooling during
the late Holocene.

Temperature-sensitive proxy records exhibit more variability during the early Holocene
than the late Holocene. Early Holocene variability is represented by diverse proxy types that
show evidence for intervals that were both colder and warmer than present, both at the site-level
and by proxy type. The contrast between early and late Holocene variability is clearly exhibited
by the results of the cluster analysis, which subdivides both the temperature- and moisture-
sensitive records in the Arctic Holocene database primarily according to their differences during
the early Holocene (Figs. 12, 14).

*10.3. Is there evidence for a middle Holocene thermal maximum around 6 ka? If so, how much
warmer was it?*

Paleoclimate models commonly simulate the climate under benchmark boundary conditions at 6
ka (Otto-Bliesner et al., 2009). We evaluate the average temperature for this interval based on the
records within the Arctic Holocene database from across eastern Beringia. The interval between
7 and 5 ka was more uniformly warm in eastern Beringia than during the early Holocene (Fig.
11). The composite for the midge records shows July air temperature between 7 and 5 ka was
about 0.2°C higher on average than the most recent millennium. Similarly, the composite for the
pollen records shows the two millennia were on average about 0.3 and 0.2°C warmer for summer
and annual, respectively. The standardized values for the other proxy records (not including
Chukchi Sea SST) average 0.8 SD higher.

To evaluate whether the middle Holocene was significantly warmer in the three temperature composites (Fig. 11), we used a series of one-tailed t-tests to test whether the mean of a 500-year time interval was greater than that of the population mean. A Monte Carlo approach allowed us to account for the uncertainty around the mean value for each bin. A value was drawn at random from the distribution for each bin (based on the mean ± 1 SD and assuming normal distribution) and the t-test routine was repeated 10,000 times. Bins with a median p-value < 0.05 were considered to be significantly warmer. The results show that the bin spanning 5.5-5.0 ka is significantly warmer in all three composites, and more generally, a concentration of significantly warmer-than-average bins between 5 and 7 ka.

The composite of all temperature-sensitive records standardized over the length of each record (Fig. 12b; $n = 26$) shows the single highest mean SD value interval between 6.5 and 6.0 ka, consistent with other analyses that highlight a mid-Holocene thermal maximum. For example, glaciers were also more retracted during the middle Holocene compared to their early and late Holocene extents. On the other hand, some individual records show maximum temperatures some time during the early Holocene, although there is thus far no clear spatial pattern to this heterogeneity. In the full ($n = 26$) composite, the period between 10.5 and 9.0 ka has consistently high values, representing warmth registered for different proxies at different times, perhaps reflecting differences in their response to seasonal forcings or to the relative importance of changes in temperature versus moisture, or possibly to errors in some age models.

10.4. What was the magnitude of temperature variability at the site level during the middle and late Holocene?

Quantifying the range of natural climate variability over centuries is fundamental to

understanding the climate system, and must be factored into projections of future climate.

Natural climate variability is expected to be large when averaged over timescales longer than

centuries. However, climate models run to simulate long periods, both in control runs and with realistic Holocene forcings, consistently underestimate the variability compared with those

observed in the paleorecord (e.g., Ault et al., 2013; Laepple and Huybers, 2014). Paleoclimate records are vulnerable to both underestimating (e.g., tree ring records) and overestimating (e.g.,

aliased sampling in sediment records) low-frequency climate variability, whereas climate models are likely missing feedback processes over multi-centennial time scales. The range of

temperature variability on centennial timescales is emerging as a critical target for paleodata-climate model comparisons.

Here we report the maximum to minimum range of mean temperature estimates averaged over 500-year time steps for all temperature records in the Arctic Holocene database for which

temperatures are reported in degrees ($n = 21$). We considered only the middle and late Holocene, the period represented by all records, and that followed the more variable early Holocene. Most

records show a range of 1-2°C (Fig. 15). July temperature ranges tend to be lower for individual midge records than for annual temperature ranges inferred from pollen; pollen-based summer

temperature ranges are similar to those of the midge-based records (not shown in Fig. 15). The midge- and pollen-based temperature ranges are lower than the two most recently published

temperature reconstructions from the region, including productivity-inferred summer

temperature at Kurupa Lake, in the Brooks Range (Boldt et al., 2015), and MBT/CBT-derived

mean annual temperature from Corser Bog near Cordova (Nichols et al., 2014). In both cases, we choose the more conservative of the alternative temperature reconstructions published by the

original authors to calculate the temperature ranges. Whether these two new reconstructions overestimate the true temperature range by a factor of two or more requires further investigation.

10.5. Is there evidence for a widespread and rapid climate transition during the Holocene that might represent a step-wise shift in the mode of ocean-atmospheric circulation?

If the Arctic system exhibited abrupt, non-linear transitions during the Holocene in response to gradual insolation changes, then this may portend abrupt future changes in the arctic system and global climate. Major millennial-scale trends in Holocene climate at northern high latitudes are often simply attributed to the long-term decline in summer insolation. Feedback mechanisms no doubt leverage the relatively small radiative forcing by influencing atmosphere-ocean circulation patterns and sea-ice extent, both of which have been known to shift rapidly. These mechanisms may have contributed to the pronounced ecological shifts during the Holocene (e.g., Clegg et al., 2011), such as the transition from shrub tundra to boreal forests, and activation of fire regimes (e.g., Higuera et al., 2009; Kelly et al., 2013).

Following the generally warm conditions of the middle Holocene, many sites and types of proxy records across eastern Beringia show evidence for cooler conditions over the late Holocene. Among the most consistent indications of the cooling is the expansion of mountain glaciers, some of which reached their maximum Holocene extent at around 4.5 and 3.0 ka. Elsewhere, however, the early Neoglacial extent was similar to or exceeded by the advance(s) of the Little Ice Age. Glacier growth during the late Holocene is consistent with other proxy records of long-term cooling since around 6 ka, but does not necessarily imply a marked, step-wise transition in ocean-atmospheric circulation. The results of the SiZer analysis likewise show no stepped transitions and instead highlight the incoherent trends among the records in the Arctic

Holocene database. We summarize that, if any thresholds were crossed during the middle to late
988 Holocene, they were likely local geomorphic or ecological thresholds rather than a rapid shift in
the mean state of climate.

990 Shifts in large-scale patterns of ocean-atmospheric circulation around 4 ka have been
described from the eastern North Pacific (e.g., Barron and Anderson, 2011). Similarly, a shift in
992 the Pacific North American Pattern, a prominent mode of atmospheric variability across North
America, is implicated at around 4 ka (Liu et al., 2014). Evidence for this shift is based on
994 oxygen-isotope records, including from Jellybean Lake in southern Yukon (L. Anderson et al.,
2005). Of the four long and highly resolved isotope records from the northern Gulf of Alaska
996 area that have been interpreted to represent changes in atmospheric circulation (Mt. Logan ice,
Horse Trail Fen, Jellybean and Mica Lakes) three show a significant ($p < 0.05$) shift in mean
998 $\delta^{18}\text{O}$ values after 3.9 ka. The most convincing shift is exhibited at Horse Trail Fen ($p = 0.001$),
which together with nearby Mica Lake, shows a transition to overall lower $\delta^{18}\text{O}$ values after 3.9
1000 ka. In contrast, $\delta^{18}\text{O}$ values at Jellybean Lake – the record selected to represent the area by Liu et
al. (2014) – shifted to higher mean values, and Mt. Logan glacier ice does not show a significant
1002 mid-Holocene shift ($p = 0.12$). Considering the divergence in these isotope records, all of which
have been interpreted to represent changes in ocean-atmospheric circulation, selecting one record
1004 over another to characterize the region is presently untenable. Instead, we stacked the four Gulf
of Alaska records by binning at 500-year intervals and normalizing their $\delta^{18}\text{O}$ values to a mean
1006 of zero over the intervals in common (Fig. 16i; standardizing the variance of the records has little
effect; not shown). Although possibly more representative of the northern Gulf, the composite is
1008 based on records that are too variable and too few to identify a step that can be confidently
interpreted as a shift in ocean-atmospheric circulation.

1010
1012 *10.6. Is there evidence in the region for an abrupt climate reversal at 8.2 ka, as has been
observed elsewhere?*

The 8.2 ka event was one of the largest climate anomalies of the Holocene (Morrill and Jacobsen,
1014 2005). It is well documented in proxy records from around the North Atlantic region as a sudden
cooling lasting for 100-150 years. It has been linked to the final abrupt drainage of proglacial
1016 Lake Agassiz into the North Atlantic (e.g., Hofmann et al., 2012), which is thought to have
decreased Atlantic Meridional Overturning Circulation, and reduced northward oceanic heat
1018 transport (Morrill et al., 2013a). There is evidence that the 8.2 ka climate anomaly reached
beyond the North Atlantic (Morrill et al., 2013b), but little is known about its expression in
1020 eastern Beringia. Here we assess the evidence for the 8.2 ka event in the region as represented by
the proxy records in the Arctic Holocene database.

1022 To detect the 8.2 ka event in the proxy records, we applied a similar methodology as
described in Morrill et al. (2013b). All records in the Arctic Holocene database were first
1024 screened for their resolution over the broad window of 9.7 to 6.7 ka, and the time series were
analyzed at their original resolution. Only one record (Mt. Logan ice core) from eastern Beringia
1026 met the rigorous 50-year-average resolution prescribed by Morrill et al. (2013b). The resolution
criterion was therefore relaxed to 100-year-average minimum; three records from eastern
1028 Beringia met this criterion, including the ^{18}O record from Mt. Logan ice (Fisher et al., 2008), and
biogenic silica records from Kusawa Lake (Chakraborty et al., 2010) and Lone Spruce Pond
1030 (Kaufman et al., 2012). Linear trends were removed and the mean (μ) and variance (σ) of the
background climate were calculated for two 1000-year-long windows on either side of 8.2 ka
1032 (7.7-6.7 and 9.7-8.7 ka). To qualify as an event, a proxy value must exceed $\mu \pm 2\sigma$ sometime

during the period between 8.7 and 7.7 ka. An event around 8.2 ka was detected in only one (Lone Spruce Pond) of the three records. In contrast, the event was not detected in the biogenic silica record from Arolik Lake, also located in southwestern Alaska, which was sampled at about 50-year resolution (Hu et al., 2003), but was excluded from the Arctic Holocene database because its youngest age is > 2 ka. Although not meeting the criterion above, chironomids were sampled at high resolution for the period around 8.2 ka in Fly Lake, and a decrease in water level as well as July temperatures were reconstructed at this time (Bunbury and Gajewski, 2009). For comparison, we also tested records from the Canadian Islands and Greenland portion of the Arctic Holocene database using the same event-detection procedure. In this region, 27 records met the 100-year-resolution criterion, of which 20 passed the anomaly test for an event. This analysis highlights the need for more finely resolved records from Beringia.

11. Conclusions

11.1. Overview

A systematic review of multiple proxy indicators has clarified the primary trends in Holocene climate change in eastern Beringia (Fig. 16). Rather than a uniform thermal maximum during the early Holocene (11.0-9.5 ka) as suggested by Kaufman et al. (2004), temperature and moisture appear to have been more variable during the early Holocene than anytime subsequently. The large-magnitude climate changes that accompanied the deglacial interval continued to a lesser degree into the early Holocene as the climate system approached its modern condition. Different proxy types show evidence for temperatures that were both higher and lower than present during the early Holocene. No clear spatial pattern has emerged. Composites based on pollen, midge and other records from eastern Beringia in the Arctic Holocene database average out the

1056 variability and show that the lowest temperatures overall across the study region occurred during
the first millennium of the Holocene, and that temperatures generally increased during the early
1058 Holocene. Peatland initiation and thaw-lake formation both peaked simultaneously between 11
and 10 ka, then decreased over the early Holocene, implying a response to changing seasonality
1060 rather than summer temperature alone. Early Holocene lake levels were generally lower than
present, although the signal is strongest in interior Alaska. The apparent discrepancy between
1062 low lake levels and high peatland initiation suggests that the seasonal distribution of precipitation
during the early Holocene played a major role. That is, increased summer precipitation benefited
1064 peatlands, while decreased winter precipitation reduced lake levels and promoted peatland
development through terrestrialization.

1066 During the middle Holocene, the regional average temperature increased to a maximum
for all proxy types between 7 and 5 ka, strong evidence for a middle Holocene thermal maximum.
1068 The composite of pollen and midge-inferred temperatures show that on average for the region,
the millennium centered on 6 ka was between 0.5 and 0.2°C warmer than the most recent
1070 millennium. Glaciers were more retracted than during either the early or late Holocene.
Following the middle Holocene thermal maximum, temperatures decreased and sometime
1072 between around 4 and 3 ka, glaciers in the Brooks and Alaska Ranges advanced to their
maximum Holocene extent, although the timing of the glacier maxima do not coincide with
1074 pronounced cold intervals as represented by the pollen, midge or other-proxy composites.
Permafrost also began to aggrade at this time, and the active layer became thinner. We do not
1076 find evidence that the transition to a cooler late Holocene climate necessarily was caused by an
abrupt region-wide climate shift, and the longest and highest resolution isotope records that have
1078 previously been interpreted to represent changes in ocean-atmospheric circulation over the North

Pacific are largely contradictory. There are too few records with sufficient resolution to identify sub-centennial-scale events in the region, including at 8.2 ka.

11.2. Comparisons with other reviews of Holocene climate

The zonally averaged Holocene mean-annual temperature reconstruction for 30-90° N latitude by Marcott et al. (2013; hereafter, “M13”) resembles the pollen, midge and other proxy composites for records in the Arctic Holocene database, in terms of their timing and trends (Fig. 16). The M13 reconstruction includes only two records from eastern Beringian, but like our proxy composites, it shows that temperatures increased during the early Holocene, peaked during the middle Holocene, and then decreased to the present (pre-industrial). The magnitude of the mean-annual temperature changes indicated by the M13 reconstruction (herein binned at 500-year resolution for comparison with our composites) is considerably higher, however, by about 1°C compared with the midge- or pollen-based (summer and annual temperatures, respectively) records in eastern Beringia, with temperatures in M13 averaging 1.4°C higher during the millennium centered on 7 ka than during the most recent millennium. This highlights the differences between the Atlantic region, which dominates the M13 reconstruction, and eastern Beringia. Alternatively, the pollen- and midge-based reconstructions from eastern Beringia underestimate the Holocene temperature changes that occurred there, which is consistent with the most recent temperature reconstructions (Boldt et al., 2015; Nichols et al., 2014) that show a larger range of summer-temperature fluctuations (section 10.4). A divergence between the aggregated proxy records from eastern Beringia and the zonal mean is further indicated by the lack of overall cooling in the three composites over the last 2000 years, a prominent feature of both M13 and the Arctic-wide average temperature reconstructed from high-resolution proxy

records, which is likely representative of mean-annual temperature (McKay and Kaufman, 2014) (Fig. 16c). Furthermore, other than the Little Ice Age, none of the global cold periods identified by Wanner et al. (2011), including the 8.2 ka event, nor the broader rapid climate change intervals identified by Mayewski et al. (2004), are obvious in eastern Beringia (Fig. 16g). Like our composite proxy time series, the global-cold and rapid-change intervals were identified based on the consensus of individual records, with each interval spanning 300 to 1000 years in duration. Visual inspection of individual proxy records in our dataset at their original resolution does not reveal a coherent pattern of cooling or change during these intervals.

11.3. Future research priorities

This systematic review has clarified the major features of Holocene climate in eastern Beringia and has helped to sharpen research questions for the future. Among these are questions related to the proxy records themselves, the spatial patterns of climate variability, and the drivers of climate and ecological changes.

- How well do proxy indicators reflect climate, and what non-climatic variables influence their interpretations? What aspects of seasonality and combination of climate variables are represented, and does variation in seasonality of proxies explain some of the apparent spatial variability documented in this synthesis? How can these influences be investigated using a multi-proxy approach? More specifically, can emerging tools like water isotope tracers combined with climate models be used to further elucidate the controls on past and future hydroclimate around the region?

1126 • What was the spatial pattern of Holocene climate changes in eastern Beringia? Does the lack
of spatial coherence documented in this review reflect problems with the proxy records that
obscure any coherent patterns, or is it a real feature of regional climate change in this region
1128 of diverse geography and climatology? Did the centennial-scale climate events that have
been documented elsewhere influence eastern Beringia? Few records in eastern Beringia
1130 have the resolution necessary to detect abrupt climate anomalies, highlighting the need for
greater spatial coverage of highly resolved and accurately dated paleoclimate datasets than is
1132 currently available.

1134 • What is the role of external forcing (e.g., insolation) versus internal modulating factors (e.g.,
ocean-atmosphere dynamics, sea-ice cover, vegetation feedbacks) in driving Holocene
1136 climate evolution in eastern Beringia? How sensitive is this region to ocean-atmospheric
circulation changes in the North Pacific and sea-ice changes in the coastal areas?
1138 Comparisons between paleoclimate data and model simulations at varying spatial scales are
needed to elucidate the influence of different climate forcings, feedbacks, and other
1140 modulating effects, and therefore to better foresee what their influences may be in the future
(e.g., of predicted vegetation changes or changes in ocean circulation).

1142 • Can we tease apart the effect of climate and ecological changes on vegetation during the
1144 Holocene? The pronounced biome and disturbance-regime (fire and insect) shifts over the
Holocene contrast sharply with the relatively small changes in reconstructed temperature at
1146 many sites. What were the feedback processes that may have interacted with climate change

to induce major ecological changes, and were there threshold effects? Is there a climate
1148 explanation for the asynchronous pattern of *Picea* expansion across the region?

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1158 **Dedication**

“The many threads of evidence, inquiry, and hypothesis in the preceding pages pattern
1160 themselves into a tapestry of history — the history of the landscape of Beringia, at one time
dominated by the sea, at another by a great plain; once covered with forest, then with treeless
1162 tundra; once populated by mammoth, horse, and bison, hunted by Paleolithic man; now the home
of seal, walrus, and polar bear, sought by the world’s most skillful sea-mammal hunters.”

1164 — David M. Hopkins, *The Cenozoic History of Beringia—A Synthesis*, 1967

1166 **Author contributions**

DK lead the review of Holocene climate change in the region and the development of the Arctic
1168 Holocene database. He wrote a large portion of the manuscript and managed the substantial input
from co-authors, whose primary contributions include (section #: author initials): 2: AW; 3: CS;

1170 4: MJ, ZY; 5: RSA; 6: AH, MW, HB; 7: YA; 8: WO, KG, RSA, BC; 9: CM, NM, CS; 10: YA,
CR, NM, BC; 11: FSH, YA. The authorship order is divided into two alphabetical groups: the
1172 first group comprises the five primary co-authors who generated original quantitative analyses,
figures and/or considerable text. All co-authors contributed extensively to this review.

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Tables

- 1972 **Table 1** Sites included in this review from the Arctic Holocene database arranged from north to south.
- 1974
- 1976 **Table 2** Age of Holocene moraines and glacial deposits older than 2000 years included in this review arranged from north to south.
- 1978 **Table 3** Terrestrial water isotope records included in this review arranged from north to south.
- 1980
- 1982 **Table 4** Midge-based temperature reconstructions included in this review arranged from north to south.

1994 **Figure Captions**

Fig. 1. Eastern Beringia with locations of sites included in this review. Numbers increase

1996 from east to west. Symbols and color represent the type of paleoclimate indicator.

Bathymetric contour at –50 m below present approximates the shoreline at 11 ka. Land

1998 DEM base map from GTOPO30 (data available from the US Geological Survey,
<https://lta.cr.usgs.gov/GTOPO30>); bathymetric map from Manley (2002).

2000

Fig. 2. Summary of Holocene glacier advance and stabilization ages arranged by latitude

2002 across Alaska. Five categories of ages are: (1) “Stabilization” ages are based on

lichenometry and surface exposure (^{10}Be) on moraine boulders, which date the time of

2004 landform stabilization (i.e., minimum-limiting age on period of glacier expansion). (2)

“Maximum” ages are based on ^{14}C ages on wood from below or within till from at or near

2006 the ice limit for a period of expansion. (3) “Initiation” ages are also based on ^{14}C on wood,
but from sites near the modern glacier margin and therefore represent a more distant

2008 maximum age on the culmination of the advance. (4) “Expanded” position ages are based on
continuous or nearly continuous records that document the length of time the glacier was at

2010 its maximum position. (5) “Minimum” ages are based on ^{14}C ages that postdate ice retreat.

Length of horizontal lines on plot symbols is suggestive, except for “expanded” ages, which

2012 reflect the duration of maximum glaciation. Gray and black vertical bands show the

“advances” summarized for Alaska by Solomina et al. (2015). Only ages younger than 2 ka

2014 are included in this review. Details for each age are listed in Table 2.

2016 **Fig. 3.** Reconstruction of the sea-ice duration (months per year with > 50% concentration) in
the Chukchi Sea based on three dinocyst-based records (GGC-19, P1/B3, and HLY0501, as
2018 summarized by de Vernal et al., 2013). Colder* = longer sea-ice duration is generally related
to lower sea-surface temperature, although ocean-atmospheric circulation also influences ice
2020 cover.

2022 **Fig. 4.** Frequency of basal (initiation) ages on (a) peatlands and (b) thaw lakes in eastern
Beringia binned at 500-year intervals. “Warmer*” = frequent thaw-lake and peatland
2024 initiations ages are generally interpreted as summer warmth, although local factors and
precipitation also influence these systems. Peatland ages updated from Jones and Yu (2010;
2026 supplement); thaw-lake ages from Walter Anthony et al. (2014).

2028 **Fig. 5.** Figure 5. Lake-level status for lakes in eastern Beringia arranged from north to south.
Categories are qualitative and simplified into 1000-year intervals. White areas indicate no
2030 information (base or top of recovered record, or unconformity (dashed line)).

2032 **Fig. 6.** Mean weighted (a) summer and (b) winter oxygen isotopes in modern precipitation
($\delta^{18}\text{O}_{\text{precip}}$) collected at sites (black diamonds) in the Global Network of Isotopes in
2034 Precipitation (<http://www-naweb.iaea.org>).

2036 **Fig. 7.** All available Holocene isotope (terrestrial oxygen and hydrogen) records from
eastern Beringia. Upper half of diagram shows records interpreted by their original authors
2038 to represent effective moisture and lower half are records that represent atmospheric

circulation, most notably, the Aleutian low-pressure system. Gulf of Alaska composite
shown in Fig. 16 is an average of Mica Lake, Horse Trail Fen, Jellybean Lake, and Mt.
Logan ice. Information about each record is in Table 3.

Fig. 8. Midge-inferred July air temperatures at 12 sites in Alaska and the Yukon, and a
composite of all records at 500-year time steps. Temperature axes are all in °C and scaled
equally, except for the composite. Data from two core sites with contrasting water depths are
shown for Trout Lake (Irvine et al., 2012), and temperatures from Lone Spruce Pond are
means of reconstructions from three models (Kaufman et al., 2012). See Table 4 for sources
and site information.

Fig. 9. Spatial-temporal patterns of Holocene vegetation change in eastern Beringia based
on fossil-pollen analysis. Representative studies for each of the subregions include: (A)
northern Alaska = Oswald et al., 1999, 2003; (B) Mackenzie Delta = Ritchie and Hare,
1971; Ritchie et al., 1983; (C) central Yukon = Cwynar and Spear, 1991; Szeicz et al., 1995;
(D) east-central Alaska = Carlson and Finney, 2004; Tinner et al., 2006; (E) southern Yukon
= Cwynar, 1988; Cwynar and Spear, 1995); (F) southeast Alaska = Hansen and Engstrom,
1996; (G) southern Alaska = Peteet, 1986; Cwynar, 1990; (H) Kenai Peninsula = Heusser,
1983; Anderson et al., 2006; Ager et al., 2010); (I) southwest Alaska = Hu et al., 1995;
Kaltenrieder et al., 2011; (J) west-central Alaska (Brubaker et al., 1983; Hu et al., 1996).
Horizontal bars illustrate changes in biomes; names of plant taxa indicate timing of
expansion in each subregion. Dates are approximate given variability within the subregions.

Green and purple areas on the location map are modern distributions of boreal and temperate
forests, respectively, from Little (1971) available at <http://esp.cr.usgs.gov/data/little/>

Fig. 10. Previously published pollen-inferred reconstructions for (a) mean annual and (b) summer temperature. Top row shows anomalies (6 ka minus present-day, °C) of individual site reconstructions aggregated (without interpolation) onto a 2° grid (Bartlein et al., 2011 as replotted in 2014). Middle row in (a) shows anomalies (°C) for 10 and 6 ka fitted to a polynomial surface, with classed values (colder/negative versus warmer/positive) at individual sites (Viau et al., 2008). Middle row in (b) shows mean summer temperature for 10 and 6 ka scaled based on the qualitative growing-season temperature index derived from the CAPE tundra biome classification scheme (colors of sites indicate the direction and magnitude of change from present); background colors are output from a model simulation (CAPE, 2001). Lower row are composite temperature reconstructions based on 45 sites using the single best analogue (Viau et al., 2008).

Fig. 11. Holocene temperature history of eastern Beringia based on multiple proxy types: (a) midges and (b) pollen assemblages, and (c) other temperature-sensitive indicators from lake and marine sediment. Records are from the Arctic Holocene database and are listed in Table 1. Data were binned at 500-year intervals. Temperatures are anomalies relative to a mean of zero for the intervals represented by all records for each of the three composites. (a) Midges represent July air temperature (black line and data points); red-dashed line composite includes an additional five records as shown in Fig. 8. (b) Pollen represents annual mean temperature (black line, with associated data points); red-dashed line composite is summer

2084 temperature (no data points are shown and record is truncated below -2°C). (c) “Other”
2086 proxy records include geochemical and production indicators; standardized values are
2088 normalized to ± 1 SD variance over the last 6 ka; time steps with values $>$ or < 3 SD were
2090 excluded, affecting the composite beyond 6 ka (red-dashed line). Chukchi Sea average sea-
surface temperature shown separately (blue line; $n = 3$; no data points shown). Vertical light-
red bar highlights the middle Holocene warm interval between 7 and 5 ka. X’s mark bins
with mean values significantly ($p < 0.05$) higher than the Holocene mean.

2092 **Fig. 12.** Standardized time series and hierarchical clustering of temperature-sensitive proxy
records from eastern Beringia. Values are 500-year means standardized relative to the last
2094 11.5 ka, and scale bars show values in standard deviation (SD) units. (a) Records are ordered
according to their cluster determined by using Euclidean distance and complete linkage
2096 grouping; “+” and “-“ indicate the maximum and minimum 500-year-average temperatures
for the record, respectively. (b) Alaska-wide composite of the 26 temperature records, and
2098 composites (c, d, e) based on the tree clusters. Composites were constructed by averaging
the individual standardized records from each cluster. Vertical gray bars correspond to the
2100 standard deviation of the mean. Heatmap and dendrogram were produced using built-in
plotting and statistical functions in R (R Core Team, 2015). Records compiled in the Arctic
2102 Holocene database and are listed in Table 1.

2104 **Fig. 13.** SiZer-based trend analysis of annual average or warm season paleotemperature data
using smoothing windows of 700 to 2000 years. Scale reflects fraction of filter windows

with significant warming (positive) or cooling (negative) trends. Records compiled in the Arctic Holocene database and are listed in Table 1.

Fig. 14. Standardized time series and hierarchical clustering of moisture-sensitive proxy records from eastern Beringia within the Arctic Holocene database. Values are 500-year means standardized relative to the last 11.5 ka, and scale bars show values in standard deviation (SD) units; “+” and “-“ indicate the maximum and minimum 500-year-average values for the record, respectively. (a) $\delta^{18}\text{O}$ records. (b) Other moisture-sensitive proxy records (pollen, sand flux, midges, $\delta^{13}\text{C}$) ordered according to their cluster determined by using Euclidean distance and Ward’s linkage grouping. The horizontal side bar identifies the two main clusters. (c) Composite of all 12 proxy records shown in (b). (d, e) Composites based on the two clusters determined by the hierarchical cluster analysis. Composites were constructed by averaging the individual standardized records from each cluster. Vertical gray bars correspond to the standard deviation of the mean. Heatmap and dendrogram were produced using built-in plotting and statistical functions in R (R Core Team, 2015). Records compiled in the Arctic Holocene database and are listed in Table 1.

Fig. 15. Site-level temperature ranges (difference between minimum and maximum) for average 500-year binned proxy records in the Arctic Holocene database. Only the middle and late Holocene are included (since 8 ka). Pollen-based temperatures are for annual mean; midge and others are for summer. Records compiled in the Arctic Holocene database and are listed in Table 1.

Fig. 16. Holocene proxy climate records from eastern Beringia summarized in this review in

2130 relation to other paleoclimate data. (a) Insolation anomalies for summer (JJA), winter (DJF)
and annual monthly averages at 65° N latitude. (b) Mean-annual temperature reconstructions
2132 for (black line) 90-30° N latitude zonal mean (Marcott et al., 2013) and (red line) Arctic-
wide mean (v.1.1.1, McKay and Kaufman, 2014); both reconstructions reduced to 500-year-
2134 mean time steps; values are anomalies relative to 1961-1990; temperature scale is
compressed relative to panels c-d. (c) Midge-inferred July air temperature (n = 7). (d)
2136 Pollen-inferred mean-annual temperature (n = 9). (e) Other temperature-sensitive proxy
records (n = 7). Panels c-f are composites of records compiled in the Arctic Holocene
2138 database and updated in this review to v2.1; see Fig. 11 for details. (f) Standardized
composite of all temperature-sensitive proxy records (n = 26); see Fig. 12 for details. (g)
2140 Blue bars are global rapid climate change events identified by Mayewski et al. (2004).
Black bars are global cold events of Wanner et al. (2011). Red bars are periods of expanded
2142 mountain glaciers the eastern Beringia, including the interval prior to about 9.5 ka (double-
line arrow) when some glaciers in southern Alaska were as large as during the late Holocene
2144 (this study and Solomina et al., 2015); see Fig. 2 for details. (h) Frequency of initiation ages
for (black line) peatlands (this study and Jones and Yu, 2010) and (red line) thaw lakes (data
2146 selected from Walter Anthony et al., 2014); see Fig. 4 for details. (i) Composite of isotope
records from around the Gulf of Alaska that were interpreted to represent atmospheric
2148 circulation changes (n = 4); see Fig. 7 for details. (j) Proportion of lake-level records
interpreted as high or overflowing for lakes in (red) interior Alaska and (black) southern
2150 Alaska and Yukon; see Fig. 5 for details. (k) Standardized composite of all moisture-

sensitive proxy records subdivided into two clusters (red: $n = 5$; black: $n = 7$); see Fig. 14 for

2152 details. Gold dashed lines highlight the general trends described in the text.

Figure 1. Eastern Beringia with locations of sites included in this review. Numbers increase from east to west. Symbols and color represent the type of paleoclimate indicator. Bathymetric contour at -50 m below present approximates the shoreline at 11 ka. Land DEM base map from GTOPO30 (data available from the US Geological Survey, <https://lta.cr.usgs.gov/GTOPO30>); bathymetric map from Manley (2002).

Figure 2. Summary of Holocene glacier advance and stabilization ages arranged by latitude across Alaska. Five categories of ages are : (1) “Stabilization” ages are based on lichenometry and surface exposure (^{10}Be) on moraine boulders, which date the time of landform stabilization (i.e., minimum-limiting age on period of glacier expansion). (2) “Maximum” ages are based on ^{14}C ages on wood from below or within till from at or near the ice limit for a period of expansion. (3) “Initiation” ages are also based on ^{14}C on wood, but from sites near the modern glacier margin and therefore represent a more distant maximum age on the culmination of the advance. (4) “Expanded” position ages are based on continuous or nearly continuous records that document the length of time the glacier was at its maximum position. (5) “Minimum” ages are based on ^{14}C ages that postdate ice retreat. Length of horizontal lines on plot symbols is suggestive, except for “expanded” ages, which reflect the duration of maximum glaciation. Gray and black vertical bands show the “advances” summarized for Alaska by Solomina et al. (2015). Only ages older than 2 ka are included. Details for each age are listed in Table 2.

Figure 3. Reconstruction of the sea-ice duration (months per year with > 50% concentration) in the Chukchi Sea based on three dinocyst-based records (GGC-19, P1/B3, and HLY0501, as summarized by de Vernal et al., 2013). Colder* = longer sea-ice duration is generally related to lower sea-surface temperature, although ocean-atmospheric circulation also influences ice cover.

Figure 4. Frequency of basal (initiation) ages on (a) peatlands and (b) thaw lakes in eastern Beringia binned at 500 year intervals. Warmer* = frequent thaw-lake and peatland initiation age are generally interpreted as summer warmth, although local factors and precipitation also influence these systems. Peatland ages updated from Jones and Yu (2010; supplement); thaw lake ages from Walter Anthony et al. (2014).

Figure 5. Lake-level status for lakes in eastern Beringia arranged from north to south. Categories are qualitative and simplified into 1000-year intervals. White areas indicate no information (base or top of recovered record, or unconformity (dashed line)).

Figure 6. Mean weighted (a) summer and (b) winter oxygen isotopes in modern precipitation ($\delta^{18}\text{O}_{\text{precip}}$) collected at sites (black diamonds) in the Global Network of Isotopes in Precipitation (<http://www-naweb.iaea.org>).

Figure 7. All available Holocene isotope (terrestrial oxygen and hydrogen) records from eastern Beringia. Upper half of diagram shows records interpreted by their original authors to represent effective moisture and lower half are records that represent atmospheric circulation, most notably, the Aleutian low-pressure system. Gulf of Alaska composite shown in Fig. 16 is an average of Mica Lake, Horse Trail Fen, Jellybean Lake, and Mt. Logan ice. Information about each record is in Table 3.

Figure 8. Midge-inferred July air temperatures at 12 sites in Alaska and the Yukon, and a composite of all records at 500-year time steps. Temperature axes are all in °C and scaled equally, except for the composite. Data from two core sites with contrasting water depths are shown for Trout Lake (Irvine et al., 2012), and temperatures from Lone Spruce Pond are means of reconstructions from three models (Kaufman et al., 2012). See Table 4 for sources and site information.

Figure 9. Spatial-temporal patterns of Holocene vegetation change in eastern Beringia based on fossil-pollen analysis. Representative studies for each of the subregions include: (A) northern Alaska = Oswald et al., 1999, 2003; (B) Mackenzie Delta = Ritchie and Hare, 1971; Ritchie et al., 1983; (C) central Yukon = Cwynar and Spear, 1991; Szeicz et al., 1995; (D) east-central Alaska = Carlson and Finney, 2004; Tinner et al., 2006; (E) southern Yukon = Cwynar, 1988; Cwynar and Spear, 1995; (F) southeast Alaska = Hansen and Engstrom, 1996; (G) southern Alaska = Peteet, 1986; Cwynar, 1990; (H) Kenai Peninsula = Heusser, 1983; Anderson et al., 2006; Ager et al., 2010; (I) southwest Alaska = Hu et al., 1995; Kaltenrieder et al., 2011; (J) west-central Alaska (Brubaker et al., 1983; Hu et al., 1996). Horizontal bars illustrate changes in biomes; names of plant taxa indicate timing of expansion in each subregion. Dates are approximate given variability within the subregions. Green and purple areas on the location map are modern distributions of boreal and temperate forests, respectively, from Little (1971) available at <http://esp.cr.usgs.gov/data/little/>.

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Table 1 Sites included in this review from the Arctic Holocene database.

Site # (Fig 1)	Site	Lat (N°)	Lon (W°)	Elev (m)	Oldest (yr BP)	Youngest (yr BP)	Resolution (yr)	Proxy	Citation	other (Fig 11c)	temp (Fig 12)	moist (Fig 14)	v2.1 updates
1	P1/B3	73.68	162.66	-201	9626	126	145	dinocysts	de Vernal et al. 2005		x		
8	HLV0501-05	72.69	157.52	-415	8209	225	116	dinocysts	de Vernal et al. 2013		x		
12	GGC-19	72.16	155.51	-369	6660	52	76	d18O.forams; dinocysts	Farmer et al. 2011		x		
60	Trout Lake - combined	68.83	138.75	150	15425	1784	207	midges	Irvine et al. 2012		x		
13	Kurupa Lake	68.35	154.61	920	5698	-53	2	chlro	Boldt et al. 2015	x	x		new
16	Takahula Lake	67.35	153.67	275	8132	-51	65	d18O.calcite	Clegg & Hu 2010				
17	Ranger Lake	67.14	153.36	820	35525	0	369	pollen	Viau et al. 2008; Brubaker et al. 1983		x	x	change refs V&G 2009 to V et al. 2008
7	Wolverine Lake - April Core	67.10	158.91	60	7407	24	33	MAR	Mann et al. 2002			x	
51	Screaming Lynx Lake	66.07	145.40	223	10611	-43	72	midges	Clegg et al. 2011		x		
77	Lac Meleze	65.22	126.12	650	13699	-32	299	pollen	Viau & Gajewski 2009; MacDonald 1987		x	x	
76	Bell's Lake	65.02	127.48	580	13299	0	256	pollen	Viau & Gajewski 2009; Szeicz et al. 1995		x	x	
75	Andy Lake	64.65	128.08	1360	13192	0	236	pollen	Viau & Gajewski 2009; Szeicz et al. 1995		x	x	
61	Honeymoon Pond	64.63	138.40	1160	10795	17	154	pollen	Viau & Gajewski 2009; Cwynar & Spear 1991		x	x	
31a	Dune Lake	64.42	149.90	134	11326	-43	31	d13C.bulk_organics	Finney et al. 2012			x	
44a	Quartz Lake	64.21	145.81	293	10949	777	212	midges	Wooller et al. 2012b		x		
18	Farewell Lake	62.55	153.63	230	12517	-50	242	MgCa.ostracodes	Hu et al. 1998	x	x		
46	Hudson Lake	61.90	145.67	657	9574	-28	117	midges	Clegg et al. 2011		x		
72	Candelabra Lake	61.68	130.65	1040	12567	352	222	pollen	Viau & Gajewski 2009; Cwynar & Spear 1995		x	x	
41	Hallet Lake	61.49	146.24	1128	7913	-52	35	BSi	McKay & Kaufman 2009	x	x		log-transform BSi
45	Greyling Lake	61.39	145.74	1015	18127	-29	162	OM	McKay & Kaufman 2009				
55	Moose Lake	61.37	143.60	437	6008	-20	47	midges	Clegg et al. 2011		x		
63a,b	Upper Fly Lake	61.07	138.09	1326	13417	0	206	pollen; midges	Bunbury & Gajewski 2009		xx	xx	add midges (temp & moisture)
24	Rainbow Lake	60.72	150.80	63	13506	-54	301	midges	Clegg et al. 2011		x		
37	Mica Lake	60.92	147.87	3	9504	-44	212	d18O.diatom	Schiff et al. 2009				corrected coordinates
59	Mt Logan	60.58	140.50	5300	12950	-40	10	d18O.ice	Fisher et al. 2008				
50a,b	Corser Bog	60.53	145.45	60	11116	103	343	dD.water_inferred; MBT	Nichols et al. 2014	x	x		new
66	Jellybean Lake	60.35	134.80	730	7556	-52	22	d18O.calcite	L. Anderson et al. 2005				
64	Kusawa Lake	60.28	136.18	671	12298	77	87	BSi	Chakraborty et al. 2010	x	x		
74	Hall Lake	60.03	129.02	690	11334	67	136	pollen	Viau & Gajewski 2009; Cwynar & Spear 1995		x	x	
6b	Lone Spruce Pond	60.01	159.15	135	14524	-5	40	BSi	Kaufman et al. 2012	x	x		
4	Waskey Lake	59.86	159.21	150	10979	71	85	OM	Levy et al. 2004	x	x		
65	Lily Lake	59.20	135.40	230	12740	54	208	pollen	Viau & Gajewski 2009; Cwynar 1990		x	x	add ref V&G 2009

Notes:

Site short name = title of tab in excel spreadsheet - database with proxy and geochronology data

Punctuation for list of proxy types connotes the following: a.b — a = general type of analysis and b = specific type of analysis or material (e.g. "d18O.foram" = oxygen-isotope analysis of foraminifera);

a a;b — a and b = records from different physical sequences collected at the same site

Proxy type abbreviations as follows: BSi = biogenic-silica content; MAR = mass accumulation rate; OM = organic-matter content; MBT = methylation of branched tetraether

Table 2 Age of Holocene moraines and glacial deposits older than 2000 years included in this review.

Site # (Fig 1)	Site name	Mountains	Approx lat (°N)	Approx long (°W)	Age (cal ka) ±	Relation to period of expansion	Evidence	Reference
29	Atigun Pass area - 8 moraines	Central Brooks Range	68.3	150.0	4.1	Stabilization	Lichen cluster 143 mm	Calkin 1988; adjusted growth curve by Solomina & Calkin 2003
29	Atigun Pass area - 9 moraines	Central Brooks Range	68.3	150.0	3.3	Stabilization	Lichen cluster 115 mm	Calkin 1988
29	Atigun Pass area - 8 moraines	Central Brooks Range	68.3	150.0	2.7	Stabilization	Lichen cluster 95 mm	Calkin 1988
32	Atigun River valley	Central Brooks Range	68.3	149.8	2.6	Stabilization	10Be on 1 moraine boulder	Badding et al. 2013
32	Atigun River valley	Central Brooks Range	68.3	149.8	4.6	Stabilization	10Be on 3 moraine boulders	Badding et al. 2013
25	East Erratic cirque	Central Brooks Range	68.3	150.8	2.9	Stabilization	10Be on 2 moraine boulders	Pendleton 2013
25	East Erratic cirque	Central Brooks Range	68.3	150.8	2.6	Stabilization	10Be on 2 moraine boulders	Pendleton 2013
14	Kurupa River valley	Central Brooks Range	68.2	154.5	2.7	Stabilization	10Be on 3 moraine boulders	Badding et al. 2013
15	Arrigetch Peaks (Arr-1)	Central Brooks Range	67.4	154.2	3.4	Stabilization	10Be on 4 moraine boulders	Pendleton 2013
15	Arrigetch Peaks (Arr-2)	Central Brooks Range	67.4	154.2	2.3	Stabilization	10Be on 1 moraine boulder	Pendleton 2013
36	Yanert Glacier	West Alaska Range	63.6	148.0	3.6	Stabilization	Lichenometry	Waythomas & Werner unpub; growth curve of Denton & Karlen 1977
42	Black Rapids Glacier	East Alaska Range	63.5	146.2	3.4	Max age	Youngest organic material below till (Falls Cr)	Reger et al. 1993
53	Fish Lake valley	East Alaska Range	63.5	144.5	11.6	Stabilization	10Be on moraine boulders (oldest of cluster)	Young et al. 2009
53	Fish Lake valley	East Alaska Range	63.5	144.5	3.2	Stabilization	10Be on moraine boulders (oldest of cluster)	Young et al. 2009
47	Canwell Glacier	East Alaska Range	63.3	145.6	3.3	Stabilization	Mean lichen diameter of 144 mm on south lateral	Reger & Pewe 1991
21	Peters Glacier	West Alaska Range	63.3	151.0	3.1	Stabilization	Lichenometry	Werner 1982
48	Gulkana Glacier	East Alaska Range	63.2	145.5	4.8	Stabilization	Max lichen on lateral (M1) 198 mm	Pewe & Reger 1983; adjusted to cal yr by Beget 1994
48	Gulkana Glacier	East Alaska Range	63.2	145.5	4	Max age	14C-dated Jarvis Cr Ash immediately below M2 moraine	Beget 1994; age of Jarvis = Hayes as per Riehle et al. 1990
19	McKinley Park MP4 moraines	West Alaska Range	63.2	152.0	12.5	Max age	14C age (oldest age on peat in front of moraines)	TenBrink & Waytomas 1985; adjusted to cal yr by this study
19	McKinley Park MP4 moraines	West Alaska Range	63.2	152.0	11.0	Min age	14C age (oldest age on peat on top of moraines)	TenBrink & Waytomas 1985; adjusted to cal yr by this study
19	Foraker Glacier - 2 moraines	West Alaska Range	63.2	151.6	3.7	Stabilization	14C ages and lichenometry	TenBrink & Waytomas 1985; growth curve of Denton & Karlen 1977
19	Foraker Glacier - 3 moraines	West Alaska Range	63.2	151.6	0.3	Stabilization	Lichenometry	TenBrink & Waytomas 1985; growth curve of Denton & Karlen 1977
19	Foraker Glacier	West Alaska Range	63.2	151.6	2.0	Stabilization	Lichenometry	TenBrink & Waytomas 1985; growth curve of Denton & Karlen 1977
56	Nebesna Glacier	Wrangell Mountains	62.3	142.8	2	Expanded	Youngest of 3 14C ages on wood below ice-marginal delta	Wiles et al. 2002
57	Barnard Glacier	Wrangell Mountains	62.0	141.8	2.4	Max age	Youngest of 2 14C ages on wood in till (loc 4)	Wiles et al. 2002
58	Seven Sisters Glacier	North St Elias Range	61.6	141.5	2.9	Expanded	14C on vegetation below till of outer moraine	Denton & Karlen 1977; adjusted to cal yr by Barclay et al. 2009
43	Greyling River valley cirques	East Chugach Mountains	61.5	146.2	2.9	Stabilization	Lichenometry	McKay & Kaufman 2009; growth curve of Denton & Karlen 1977
45	Greyling Lake	East Chugach Mountains	61.4	145.7	4.3	Initiation age	OM decrease; DBD increase; sed rate increase	McKay & Kaufman 2009
34	Bartlett Glacier	Northern Kenai Mountains	60.7	149.0	2.4	Max age	14C age on log beneath till - Tustumena III advance	Karlstrom 1964; adjusted to cal yr by Reger et al. 2007
49a	Cabin Lake	East Chugach Mountains	60.5	145.5	11.1	Expanded	Rockflour deposition from Sheridan Glacier	Zander et al. 2013
52	Sheridan Glacier	East Chugach Mountains	60.5	145.3	3	Max age	14C on log in lake sediment overlain by till	Tuthill et al. 1968; adjusted to cal yr by Barclay et al. 2009
30	Goat Lake	Kenai Mountains	60.3	149.9	9.5	Min age	Top of glacial-lacustrine mud	Daigle & Kaufman 2009
4	Waskey Lake	Ahklun Mountains	59.8	159.1	11.7	Stabilization	10Be on moraine boulders	Briner et al. 2002
4	Waskey Lake	Ahklun Mountains	59.8	159.1	9.1	Min age	Cessation of glacier-erosional input to lake sediment	Levy et al. 2004
4	Waskey Lake	Ahklun Mountains	59.8	159.1	3.2	Initiation age	Re-establishment based on 14C from lake sediment	Levy et al. 2004
20	Emerald Lake	Kenai Mountains	59.6	151.1	11.4	Min age	Top of glacial-lacustrine mud	LaBrecque 2014
20	Emerald Lake	Kenai Mountains	59.6	151.1	10.3	Expanded	Rockflour deposition from Grewingk Glacier	LaBrecque 2014
67	Battle Glacier	Coast Mountains	58.7	134.6	2.2	Max age	14C on sump in lateral moraine	Röthlisberger 1986 (cited in Barclay et al. 2009)
67	Herbert Glacier	Coast Mountains	58.6	134.6	3.1	Max age	14C age on in situ stump	De Simone personal comm. (cited in Barclay et al. 2009)
68	Herbert Glacier	Coast Mountains	58.6	134.6	2.1	Max age	14C age on log in till	Röthlisberger 1986 (cited in Barclay et al. 2009)
69	Mendenhall Glacier	Coast Mountains	58.5	134.5	3.0	Max age	14C age on log in till - average of 2 ages	Röthlisberger 1986 (cited in Barclay et al. 2009)
69	Mendenhall Glacier	Coast Mountains	58.5	134.5	2.1	Max age	14C age on in situ stump - average of 2 ages	Röthlisberger 1986 (cited in Barclay et al. 2009)
71	Paterson Glacier	Coast Mountains	56.9	132.7	3.3	Max age	14C age on log in till	Viens 2005 (cited in Barclay et al. 2009)

Table 3 Terrestrial water isotope records included in this review.

Site # (Fig 1)	Site name	Lat (°N)	Long (°W)	Elev (m asl)	Material	Site hydrology	Primary interpretation	Additional considerations	Included in Arctic Holocene database	Citation
9b	Qalluuraq	70.4	157.4	14	Chitin (chironomid head capsules)	Thermokarst, shallow	Evaporation, effective moisture	Lake may have been intermittently connected to the River Meade. Changes in site hydrology evidenced by paleoecological transformations (fen-lake-fen-lake).	no - < 400 yr sample resolution	Wooller et al. 2012a
35	Meli	68.7	148.5	741	α -cellulose	Closed, deep	Effective moisture	Trends in the $\delta^{18}\text{O}$ do not correlate with bulk geochemical or sediment lithology. The large range in $\delta^{18}\text{O}$ (6‰) indicates a temperature change of 17°C, which is untenable. Evaporative enrichment is likely.	no - does not span 6-2 ka	L. Anderson et al. 2001
33	Tangled Up	67.5	149.4	440	Calcite (<i>Chara</i>)	Open, shallow	Atmospheric temperature	A lowering of lake level by 0.5 m would change the lake to a closed basin, which could explain shifts to higher isotope values and covariance between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$. The lake is dammed by a large alluvial fan over which the primary inflow avulses. Freshly abandoned inflow channels and shorelines attest to major surface hydrological changes.	no - does not span 6-2 ka	L. Anderson et al. 2001
16	Takahula	67.4	153.7	275	Calcite (<i>Chara</i>)	Effectively closed	Effective moisture, seasonality and other factors	Prior to 3 ka, $\delta^{18}\text{O}$ is interpreted changes in the seasonality of precipitation. Two very	yes	Clegg & Hu 2010
44b	Quartz	64.2	145.8	293	Aragonite (<i>Pisidium</i>)	Closed	Evaporation and other factors	negative $\delta^{18}\text{O}$ values around 3 ka could indicate the input of Tanana River water.	no - < 400 yr sample resolution	Wooller et al. 2012b
38	Hundred Mile	61.8	147.8	506	Aragonite (<i>Pisidium</i>)	Closed, shallow, groundwater-fed	Atmospheric temperature or seasonality	Carbonate content increases as isotope values decrease. Evaporation might be an important control.	no - does not span 6-2 ka	Yu et al. 2008
37	Mica	60.7	147.9	3	Opal (diatoms)	Open, deep	Moisture-source trajectories linked to the Aleutian Low	Major shift toward higher variability during the late Holocene.	yes	Schiff et al. 2009
59	Mt. Logan	60.6	140.5	5300	Ice	n/a	Moisture-source trajectories linked to the tropical Pacific and ENSO	High-elevation site	yes	Fisher et al. 2004, 2008
50a	Corser	60.5	145.5	60	n-alkanes (C_{25} , C_{26})	Bog, peat	Evaporation during growing season or changes in precipitation source and seasonality	The δD of n-alkanes reflects both the δD of peat water, which is complicated by variable fractionation factors among different plant species.	yes - v2.1	Nichols et al. 2014
22	Jellybean	60.4	134.8	730	Calcite (authigenic)	Closed, spring-fed	Extent of rain-out related to the Aleutian Low	$\delta^{18}\text{O}$ data from carbonate formed during the instrumental period correlates positively with the strength of the winter Aleutian Low	yes	L. Anderson et al. 2005
66	Horse Trail	60.4	150.9	45	Total organic matter	Fen, peat	Extent of rain-out related to the Aleutian Low and seasonality	Summer moisture is likely more important in controlling $\delta^{18}\text{O}$ of fen surface than winter precipitation. Primary vegetation type evolved from bryophyte to sedge to Sphagnum. Accumulation rate between about 8.6 and 1.6 ka is very low, suggesting a possible hiatus.	no - > 3000 yr between ages	Jones et al. 2014
70a	Marcella	60.1	133.8	750	Calcite (<i>Chara</i>)	Closed, spring-fed	Evaporation, effective moisture	Modern <i>Chara</i> encrustations reflect water isotopes, indicating that they precipitate in approximate equilibrium.	no - does not span 6-2 ka	L. Anderson et al. 2007

Table 4 Midge-based temperature reconstructions included in this review.

Site # (Fig 1)	Site name	Lat (°N)	Lon (°W)	Elev (m asl)	Training set & model (RMSEP)*	Additional factors	Included in Arctic Holocene database	Citation
9a	Qalluuraq	70.4	157.3	14	WA-PLS-2 (1.46°C)	assemblage shifts correspond with major lithologic/hydrologic changes	yes	Wooller et al. 2012b
60	Trout	68.8	138.8	150	WA-PLS-1 (1.58°C)	assemblage shifts with arrival of <i>Alnus</i> , but no corresponding modeled temperature change	yes - combined records from 2 cores	Irvine et al. 2012
5	Burial	68.4	159.2	460	WA-PLS-1 (1.58°C)		no - sample resolution > 400 yr	Kurek et al. 2009a
62	Hanging	68.4	138.4	500	WA-PLS-1 (1.58°C)	evidence for Holocene lake-level change	no - > 3000 yr between ages	Kurek et al. 2009b
51	Screaming Lynx	66.1	145.4	223	WA-PLS-2 (1.46°C)		yes	Clegg et al. 2011
44a	Quartz	64.2	145.8	293	WA-PLS-2 (1.46°C)	geomorphically complex site with history of hydrologic change	yes	Wooller et al. 2012a
2	Zagoskin	63.4	162.1	7	WA-PLS-1 (1.58°C)	sea level rise in early Holocene may have dampened seasonality and altered lake levels	no - sample resolution > 400 yr	Kurek et al. 2009a
46	Hudson	61.9	145.7	657	WA-PLS-2 (1.46°C)		yes	Clegg et al. 2011
55	Moose	61.4	143.6	437	WA-PLS-2 (1.46°C)		yes	Clegg et al. 2010
63a	Upper Fly	61.0	138.1	1326	MAT, WA-PLS-3**	reconstruction differs from pollen-inferred; authors note climate gap in midge training set	yes	Bunbury & Gajewski 2009
24	Rainbow	60.6	150.7	63	WA-PLS-2 (1.46°C)		yes	Clegg et al. 2011
6a	Lone Spruce	60.0	159.1	135	WA-PLS-2 (1.46°C), WA (1.57°C), WAtol (1.55°C)	authors speculate vegetation and resulting nutrient changes drove major Holocene assemblage shifts	no - sample resolution > 400 yr	Kaufman et al. 2012

* All training sets from Barley et al. (2006), except Upper Fly Lake.

** Training set from Bunbury & Gajewski (2009); RMSEP is not reported, but sample-specific standard errors are 1.66-2.10°C for WA-PLS and 1.56-2.51°C for MAT.