Late Quaternary paleoclimate of western Alaska inferred from fossil chironomids and its relation to vegetation histories

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ABSTRACT

Fossil Chironomidae assemblages (with a few Chaoboridae and Ceratopogonidae) from Zagoskin and Burial Lakes in western Alaska provide quantitative reconstructions of mean July air temperatures for periods of the late-middle Wisconsin (~39,000–34,000 cal yr B.P.) to the present. Inferred temperatures are compared with previously analyzed pollen data from each site summarized here by indirect ordination. Paleotemperature trends reveal substantial differences in the timing of climatic warming following the late Wisconsin at each site, although chronological uncertainty exists. Zagoskin Lake shows early warming beginning at about 21,000 cal yr B.P., whereas warming at Burial Lake begins ~4000 years later. Summer climates during the last glacial maximum (LGM) were on average ~3.5 °C below the modern temperatures at each site. Major shifts in vegetation occurred from ~19,000 to 10,000 cal yr B.P. at Zagoskin Lake and from ~17,000 to 10,000 cal yr B.P. at Burial Lake. Vegetation shifts followed climatic warming, when temperatures neared modern values. Both sites provide evidence of an early postglacial thermal maximum at ~12,300 cal yr B.P. These chironomid records, combined with other insect-based climatic reconstructions from Beringia, indicate that during the LGM: (1) greater continentality likely influenced regions adjacent to the Bering Land Bridge and (2) summer climates were, at times, not dominated by severe cold.

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1. Introduction

Much of eastern Beringia (Alaska and Yukon) remained unglaciated during the last glacial maximum (LGM: ~25,000–17,000 calibrated years before present [cal yr B.P.]), except in mountainous regions and lowlands south of the Alaska Range (Hamilton, 1986; Kaufman and Manley, 2004; Briner et al., 2005). Continuous and well-dated paleoenvironmental records that span the LGM to the present are extremely rare (Anderson and Brubaker, 1994; Ager, 2003; Kaufman et al., 2003), and fossil pollen samples from the LGM often have little or no relation to modern vegetation communities (Anderson et al., 1989). Furthermore, conflicting interpretations of Beringian LGM environments exist (Schweger et al., 1982) because of evidence for great abundance and variety of

megafauna grazers (bison, horse, and woolly mammoth) on the one hand, but pollen-based interpretations of a tundra vegetation of low productivity on the other (e.g. Cwynar, 1982; Anderson et al., 1994). Establishing records to investigate regional paleoclimate and its influence on sub-Arctic environments is therefore warranted.

Most investigators agree that during the LGM, Beringia was arid and cold, and that there was a pronounced west-to-east environmental gradient in eastern Beringia, with significantly colder and drier conditions than present within interior Alaska and Yukon (Ager and Brubaker, 1985; Barnosky et al., 1987; Anderson, 1988; Lozhkin et al., 1993; Anderson and Brubaker, 1994; Elias et al., 1997; Guthrie, 2001). These generalizations are often based on or supported by pollen-derived vegetation records. While vegetation histories have been the primary basis of our understanding of Beringian environments (see Ager and Brubaker, 1985; Anderson et al., 1994; Anderson and Brubaker, 1994), they nevertheless have limitations. Pollen can be dispersed to great distances, wind-pollinated taxa may be overrepresented, some key taxa are distinguishable only at the family level, thereby limiting environmental inference, and plant communities may respond to changing

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soil characteristics irrespective of changing climate. Providing independent paleoclimatic reconstructions at adequate temporal resolution may greatly enhance interpretations of Beringian environments.

In this context, few insect-based paleoclimate reconstructions exist from Beringia. Some fossil beetle evidence indicates relatively mild climatic conditions in eastern Beringia during the LGM, with summer temperatures 1–4 °C cooler than modern and mean January temperatures above modern (Elias, 2001). Insect-based paleoclimate reconstructions from western Beringia (northeastern Siberia) demonstrate that during the LGM, inferred temperatures of sites located ~600–800 km south of the LGM Arctic coastline were similar to modern temperatures of sites situated ~700–800 km from the modern Arctic coastline (Alfimov and Berman, 2001). Due to lower sea levels and reduced regional moisture during the LGM, Alfimov and Berman (2001) propose that summer temperatures at sites currently at the Arctic coast were twice those of modern. They also conclude that the fundamental distinction between late Pleistocene and modern climates in northeastern Siberia is not simply a decrease in temperature, but an increase in continentality. This assertion is supported by paleobotanical evidence demonstrating that north Siberian LGM summers were warmer than present and climate was more continental (Kienast et al., 2005). Furthermore, if summer temperatures were milder than presumed, then the likelihood increases that Beringia was a glacial refugium for boreal tree species such as *Picea* during the late Pleistocene (Brubaker et al., 2005; Anderson et al., 2006; Zazula et al., 2006), at least in localities where adequate moisture was available.

Here, we present chironomid-inferred temperature reconstructions spanning portions of the late-middle Wisconsin to the present from two lakes located in western Alaska. Chironomidae are non-biting insects (Insecta: Diptera) with aquatic larval and winged adult life stages. Their head capsules are generally the most abundant insect fossils in lake sediments and chironomid distributional abundance is strongly correlated with summer temperatures (Walker et al., 1991; Olander et al., 1997; Lotter et al., 1997; Barley et al., 2006). The above attributes of chironomids facilitate their informative value in paleotemperature reconstructions. We examine inferred summer temperature trends and make comparisons with vegetation histories from the same lake cores. This study addresses the following questions: (1) How do summer temperatures during the late-middle Wisconsin compare to other periods in the records? (2) Were summer temperatures during the LGM severely cold? (3) What is the magnitude and timing of the postglacial thermal maximum in western Alaska? (4) Are major shifts in vegetation coincident with inferred temperature changes? Answering these questions provides insight into the paleoclimate development of eastern Beringia and the response of sub-Arctic landscapes to environmental change within a region vital as a: (1) glacial refugium, (2) a potential human migration route, (3) an intercontinental link for biota, and (4) influential component of the global climate system.

2. Study sites

St. Michael Island is located ~100 km northeast of the Yukon Delta on the south shore of Norton Sound, Alaska. Numerous maar lakes, including Zagoskin Lake (63°26.9′N, 162°06.3′W, 7 m asl), occur on the landscape (Fig. 1). Zagoskin Lake has a maximum water depth of 19.7 m and a surface area of 16 ha. In July 2004, the surface-water temperature at Zagoskin Lake was approximately 20 °C and the profundal temperature was 6 °C. The catchment is relatively small and steep-sided. There is no outlet and a small, possibly seasonal, inflowing stream occurs at the north end. The present vegetation of St. Michael Island is mainly mesic shrub tundra,
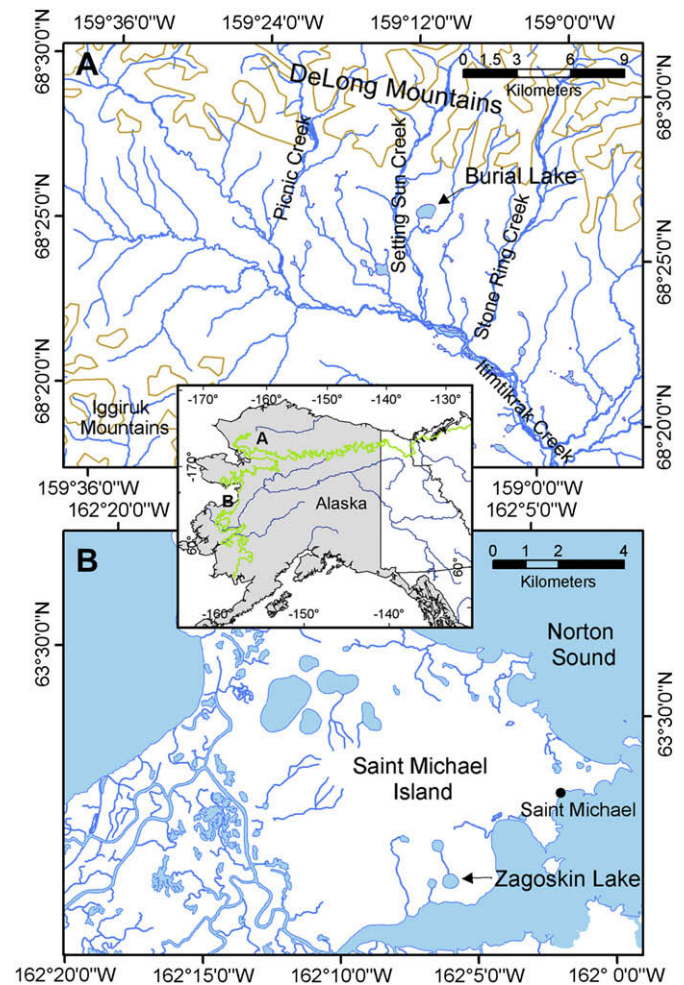

Fig. 1. Map of eastern Beringia (Alaska and Yukon) showing the locations of (A) Burial Lake and (B) Zagoskin Lake, as well as study site maps denoting hydrological features.

whereas the maar catchments are vegetated with large shrub willows (*Salix* spp.) and alders (*Alnus crispa*) (Ager, 2003). The modern climate of St. Michael Island is moderated by the proximity of the Bering Sea and lies within a transitional climate zone between the Arctic, continental, and maritime zones (Joint Federal-State Land Use Planning Commission for Alaska, 1973). Mean monthly temperatures in the region are above 0 °C from May through September, with July as the warmest month, having an observed (1970–2000) mean temperature of 13.1 °C at nearby Unalakleet The Alaska Climate Research Center, 2008 (http://climate.gi.alaska.edu).

Burial Lake (68°26.6′N, 159°10.12′W, 460 m asl) is flanked by the DeLong Mountains to the north and Baird Mountains to the south in the western Brooks Range, Alaska (Fig. 1). The site is ~100 km north of the modern treeline zone and is situated in the headwaters of the Anisak River within the northwestern limit of the Noatak Basin. During the mid and late Pleistocene, mountain glaciers repeatedly blocked the Noatak River and formed a series of large proglacial lakes (Hamilton, 2001), collectively known as Glacial Lake Noatak (Hamilton and Van Etten, 1984). Glacial Lake Noatak likely never reached the headwaters of the Anisak River (Hamilton, 2001), nor did it inundate Burial Lake. Burial Lake is approximately circular with a maximum water depth of 19.8 m. The lake surface area is ~80 ha with a small and gently sloping catchment. There are no inflowing streams. One shallow outlet exists at the southwest end. The mean July air temperature in the western Noatak Basin

Table 1
Zagoskin Lake radiocarbon ages (Muhs et al., 2003) and associated calibrated ages (this paper).

Lab #	Depth (cm) range of bulk sediment, midpoint (cm) used in age model	^{14}C yrs B.P. Radiocarbon age	Calibrated ages (cal yr B.P.) 2σ estimate (range)
W-4929	129–140, 134.5	4830 ± 80	5550 (5325–5727)
W-4625	166–181, 173.5	6430 ± 90	7350 (7169–7499)
W-4931	230–244, 237	8120 ± 110	9060 (8652–9402)
W-4915	374–389, 381.5	11,060 ± 100	12,990 (12,852–13,155)
W-4928	490–500, 495	14,970 ± 170	18,250 (17,696–18,714)
W-4918	591–605, 598	15,110 ± 120	18,420 (18,050–18,723)
W-4642	781–804, 792.5	21,500 ± 250	25,820 (25,100–26,540)[a]
W-4640	955–980, 967.5	23,900 ± 240	28,620 (28,022–29,218)[a]
W-4930	1108–1119, 1113.5	25,800 ± 400	31,010 (37,076–31,944)[a]
W-4630	1191–1215, 1203	25,690 ± 420	30,880 (29,882–31,878)[a]
W-4925	1335–1350, 1342.5	27,750 ± 550	33,100 (31,898–34,302)[a]
W-4379	1490–1520	>39,000	Infinite age

Other ages calibrated using CALIB v 5.0.1 (Stuiver and Reimer, 1993; Reimer et al., 2004).
[a] Denotes age estimate using Fairbanks0107 calibration curve (Fairbanks et al., 2005).

(~300 m asl) is estimated at 11 °C (Edwards et al., 2003). Assuming a normal lapse rate, July air temperatures at Burial Lake are likely to be about 10 °C.

3. Methods

3.1. Chronologies and age-depth models

A 15.2-m core was obtained near the center of Zagoskin Lake at a water depth of 18 m using a modified Livingstone piston corer. Geochemical analyses (Muhs et al., 2003) and a vegetation history (Ager, 2003) are discussed in detail elsewhere. The estimated age of the sediment was determined by conventional radiocarbon dating of bulk sediment samples (Muhs et al., 2003). Two tephras (1.6–1.4 m and 5.15–5.1 m) were identified by Ager (2003), with the uppermost tephra attributed to the ~3600 ^{14}C yrs B.P. Aniakchak eruption (Begét et al., 1992). The accepted age of this tephra is younger by ~1200 ^{14}C yrs than the nearest radiocarbon age at Zagoskin Lake (1.4–1.29 m; 4830 ± 30 ^{14}C yrs B.P.) and suggests uncertainties in the chronology at this core depth. Ages <20,000 ^{14}C yrs B.P. were calibrated (Table 1) to calendar years using CALIB v 5.0.1 (Stuiver and Reimer, 1993; Reimer et al., 2004). The midpoint of the cumulative probability of the calibration curve was used. Five ages >20,000 ^{14}C yrs B.P. were calibrated using the Fairbanks0107 calibration curve (Fairbanks et al., 2005). The basal age of >39,000 ^{14}C yrs B.P. is infinite and not used in the age-depth model. The age-depth model was constructed using a second order polynomial forced through zero (Fig. 2A).

A 4.61-m core was obtained from the littoral sediments at 8 m water depth in Burial Lake. A detailed lithology of the sediments and a vegetation history will be reported elsewhere (Abbott et al., in preparation). Age estimates of the chironomid samples in this study were assigned following the age-depth model of Abbott et al. (in preparation). Fourteen AMS (accelerator mass spectrometry) ^{14}C dates were obtained from unidentified aquatic macrophytes, wood fragments, and humic acids from bulk sediments (Table 2) using pretreatment methods given in Abbott and Stafford (1996). Four AMS ^{14}C dates were rejected for use in the age-depth model due to: (1) small sample weight and possible contamination with modern carbon (AA-35195 and AA-35198), (2) a humic acid extraction resulting in a considerably older date (OS-18369) than the closest adjacent date, and (3) proximity to an identified unconformity at ~340 cm (AA-35199). Abbott et al. (in preparation) identify the unconformity based on a gravel lag layer in the sediment profile that is barren of pollen and on abrupt changes in pollen values above and below this level. The rejected date is on wood below the unconformity, but is likely derived from vegetation growing during

the depositional hiatus. All ages <20,000 ^{14}C yrs B.P. were calibrated using CALIB v 5.0.2 (Stuiver and Reimer, 1993; Reimer et al., 2004). Ages >20,000 ^{14}C yrs B.P. were calibrated using the Fairbanks0107 calibration curve (Fairbanks et al., 2005). The age-depth model for Burial Lake (Fig. 2B) was constructed in two parts: (1) a linear regression through the basal four calibrated ages and (2) an interpolation between calibrated ages younger than the unconformity at ~340–330 cm (Abbott et al., in preparation).
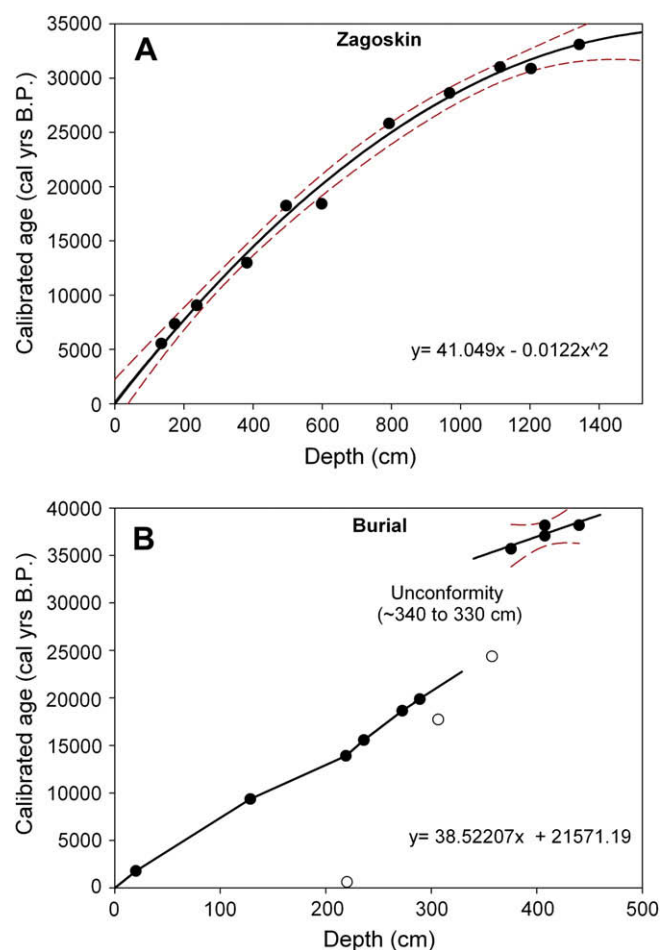
Fig. 2. Age-depth model for the (A) Zagoskin Lake and (B) Burial Lake cores. Rejected ages from Burial Lake are represented by open circles. The dashed lines indicate 95% confidence intervals.

Table 2
Burial Lake radiocarbon ages and associated calibrated ages.

Lab #	Material dated	Sediment depth (cm) used in age model	^{14}C yrs B.P. Radiocarbon age	Calibrated ages (cal yr B.P.) 2σ estimate (range)
OS-18365	Aquatic macrophytes	20	1850 ± 55	1785 (1625–1921)
AA-35197	Aquatic macrophytes	128.5	8390 ± 140	9360 (9011–9606)
CAMS-73172	Wood fragments	219	12,020 ± 190	13,900 (13,416–14,572)
AA-35195	Aquatic macrophytes	220	640 ± 85[a]	N/A
OS-17700	Wood fragments	236	13,150 ± 65	15,560 (15,221–15,930)
OS-18367	Wood fragments	272.5	15,300 ± 180	18,650 (18,094–18,913)
CAMS-73173	Aquatic macrophytes	289	16,740 ± 260	19,880 (19,403–20,421)
AA-35198	Aquatic macrophytes	306.5	14,660 ± 250[a]	N/A
AA-35199	Aquatic macrophytes	357.5	20,330 ± 280[a]	N/A
OS-18368	Wood fragments	375.5	30,300 ± 300	35,690 (35,072–36,308)[b]
CAMS-73174	Aquatic macrophytes	407.5	31,680 ± 360	37,060 (36,264–37,856)[b]
CAMS-73175	Wood fragments	407.5	32,770 ± 470	38,165 (37,175–39,155)[b]
OS-27279	Aquatic macrophytes	440	32,780 ± 280	38,180 (37,548–38,812)[b]
OS-18369	Humic acid extraction	447.5	42,600 ± 2800[a]	N/A

Other ages calibrated with CALIB v 5.0.2 (Stuiver and Reimer, 1993; Reimer et al., 2004).

[a] Identifies rejected radiocarbon ages.
[b] Denotes age estimate using Fairbanks0107 calibration curve (Fairbanks et al., 2005).

3.2. Chironomid sampling and identification

Head capsules of Chironomidae and Ceratopogonidae, along with mandibles of Chaoboridae, were processed from sediments following methods given in Walker (2001). Dried sediments from Zagoskin Lake were weighed, rehydrated overnight in distilled water, and heated in 5% KOH for ∼20 min. Moist sediments from Burial Lake were volumetrically sampled and otherwise followed similar KOH treatments. Sediments were rinsed with distilled water on a 95-μm mesh sieve and the remaining material was backwashed into a beaker. Aliquots from each sample were poured into a Bogorov tray. Using a dissecting microscope, head capsules and Chaoboridae mandibles were hand-picked with forceps from successive aliquots for the entire sample. Picked remains were then placed on a cover glass, spread out, and mounted on a slide using Entellan®. Chironomids were identified with a compound microscope at 400× magnification, primarily with reference to Wiederholm (1983), Oliver and Roussel (1983), and Walker (2007). For consistency, Appendix 1 in Barley (2004) was also used for taxonomic groupings distinct to the transfer function applied; such as *Zalutschia*-types, *Parakiefferiella*-sp B, Tanypodinae, and members of Tanytarsini.

A minimum count of 50 head capsules was targeted for reliable quantitative inferences (Heiri and Lotter, 2001; Larocque, 2001; Quinlan and Smol, 2001). A total of 74 out of 78 samples from Zagoskin Lake met this criterion (summary head capsule count of all samples: min. = 43, max. = 254, mean = 94). The four samples with <50 head capsules were still included as their counts were all >40 whole mentum equivalents. All 86 samples from Burial Lake

had head capsule counts >50 (min. = 53, max. = 440.5, mean = 142.5). Rarefaction analysis was performed using PRIMER v5 (Clarke and Gorley, 2001) to estimate taxon richness from standardized sample sizes. The minimum head capsule count from each site was selected as the standard sample size.

3.3. Chironomid zonation and pollen-inferred vegetation community patterns

Chironomid zones (Figs. 3 and 4) were delimited using the optimal-splitting-by-information-content technique in PSIMPOLL v 4.25 (Bennett, 2005). Percentage data were square-root transformed, taxa never reaching >2% abundance were excluded, and proportions were then recalculated prior to zoning. Significant zones were identified using variance reduction as a percent of the total variance with comparison to a broken-stick model (Jackson, 1993; Bennett, 1996).

Timing of major shifts of pollen-inferred vegetation communities at Zagoskin Lake (Ager, 2003) and Burial Lake (Abbott et al., in preparation) were summarized as the Axis 1 sample scores of a detrended correspondence analysis (DCA) (Fig. 5B). The relative abundance of all pollen taxa (Zagoskin: 72 taxa from 151 samples, Burial: 59 taxa from 45 samples) was square-root transformed and rare species downweighted prior to analysis. DCA was performed with detrending by segments in CANOCO v 4.5 (ter Braak and Šmilauer, 2002).

3.4. Paleotemperature inference model and analog assessments

All identifiable midges (mainly Chironomidae, with a few Chaoboridae and Ceratopogonidae) were included as a percentage of the total count. Inferred temperatures were estimated using a model developed by Barley et al. (2006). Mean July air temperature explains 48% of all explainable variance (12% of the total variance) in chironomid assemblages composing the 136 lake training set. A weighted averaging-partial least squares (WA-PLS) 1-component model was selected as the strongest inference model (r^2_{boot} = 0.77, RMSEP = 1.58 °C) for our study sites. The 1-component model is the most parsimonious and attains the lowest maximum bias (2.4 °C) of all WA-PLS models considered (1- or 2-component); despite only a marginally lower r^2_{boot} and slightly larger RMSEP than the comparable 2-component model (r^2_{boot} = 0.81, RMSEP = 1.46 °C).

More credible inferences are expected from fossil data if their taxonomic composition approximates that of modern communities (Birks et al., 1990; Jackson and Williams, 2004). To assess whether fossil assemblages are comparable to modern assemblages within the western North American training set (Barley et al., 2006), analog matching with squared chord distance (SCD) was undertaken using the modern analog technique (MAT) in C2 (Juggins, 2003). SCD was selected as the dissimilarity measure as it has a robust signal-to-noise metric (modestly increasing the weighting of rare taxa) for use with the MAT in pollen-based studies (Overpeck et al., 1985; Gavin et al., 2003; Jackson and Williams, 2004). Fossil assemblages with minimum dissimilarity coefficients (min DC) less than the upper 95% confidence interval of the mean min DC (analog cutoff value) of the 136 lake training set were accepted as reasonable analogs. Fossil assemblages with min DC exceeding the analog cutoff value were considered poor analogs. Prior to analog matching, all percentage data were transformed to proportions out of one. Rare taxa (those with less than 7 occurrences out of 136 lakes) were removed from the training set. All fossil taxa were included in this analysis.

Fig. 3. Chironomid stratigraphy of Zagoskin Lake illustrating assemblage trends of selected taxa. Taxa are ordered according to their weighted average location in time (oldest to youngest). Temperature optima (in parentheses) are estimated by Barley et al. (2006) for those taxa within the training set. Average rarified taxon richness is listed for each zone.
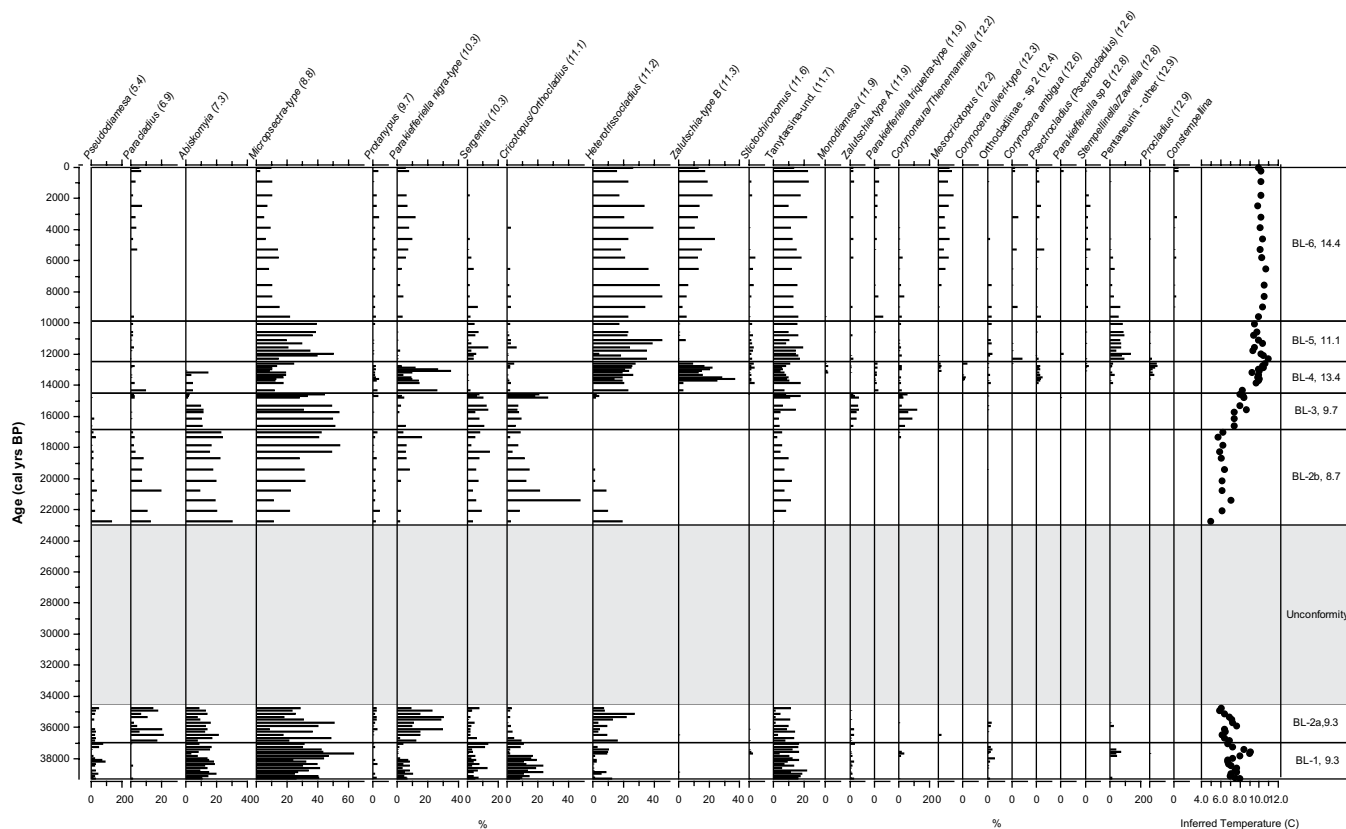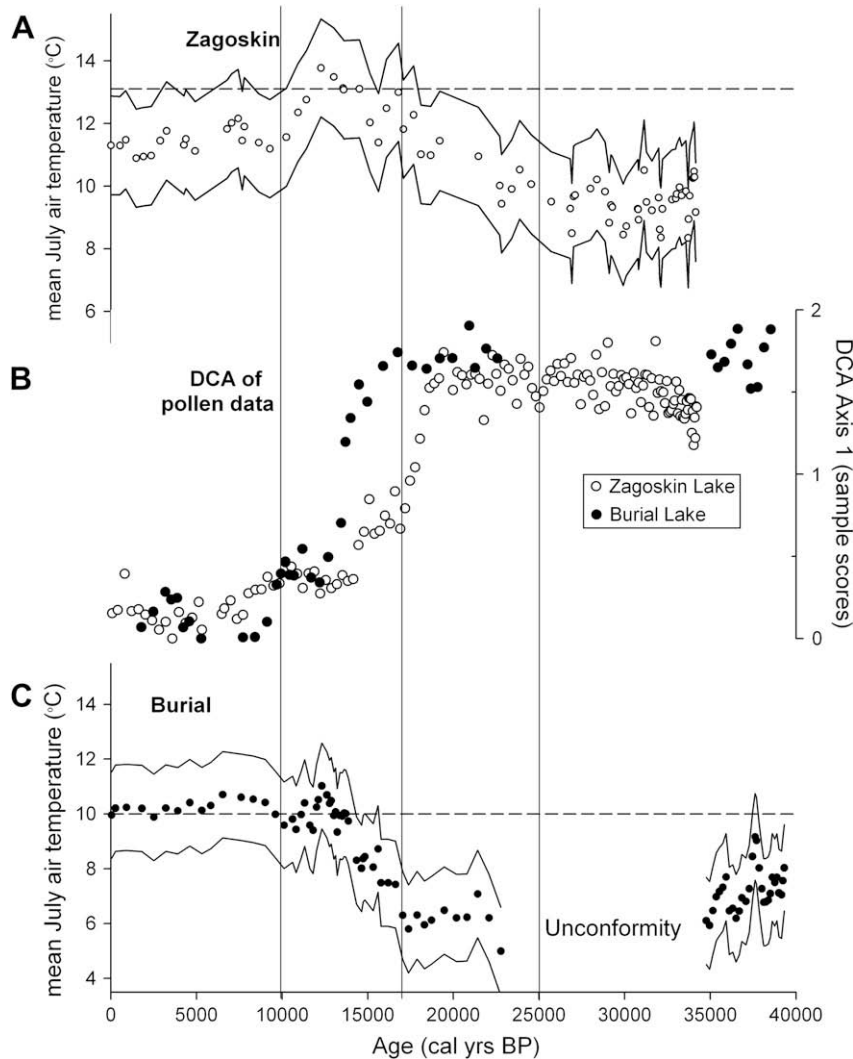

Fig. 4. Chironomid stratigraphy of Burial Lake illustrating assemblage trends of selected taxa. Taxa are ordered cold to warm according to their temperature optima (in parentheses) estimated by Barley et al. (2006). The unconformity from ∼34,500 to 23,000 cal yr B.P. is highlighted with grey fill. Average rarified taxon richness is listed for each zone.

Fig. 5. Inferred temperatures with sample-specific prediction errors (1.56–1.63 °C) from (A) Zagoskin Lake and (C) Burial Lake, in addition to (B) pollen-inferred vegetation community changes (DCA Axis 1 sample scores). Dashed lines represent the modern, observed mean July air temperature of each site. Vertical lines at 25,000, 17,000, and 10,000 cal yr B.P. follow the temporal divisions within the discussion section.

4. Results

4.1. Zagoskin Lake chironomid zones

Fifty-nine taxa (including Chironomidae, Chaoboridae, and Ceratopogonidae) are identified from five zones (Fig. 3). *Cricotopus/Orthocladius* and Tanytarsini undeterminable (und.) are the most common taxa and occur in ~95% of samples.

Zone ZL-1 (34,000–30,000 cal yr B.P.) – The dominant taxa include *Abiskomyia, Constempellina, Paracladius, Cricotopus/Orthocladius, Micropsectra*-type, and Tanytarsini (und.). Other taxa that attain moderate abundances are *Zalutschia*-type B, *Sergentia, Pseudosmittia/Smittia, Mesocricotopus,* and *Corynoneura/Thienemanniella*.

Zone ZL-2 (30,000–25,000 cal yr B.P.) – The most abundant taxa are *Constempellina, Pseudosmittia/Smittia, Paracladius,* and *Cricotopus/Orthocladius*. Taxa that show a trend of decreased abundance compared to the previous zone include *Zalutschia*-type B, *Sergentia, Micropsectra*-type, Tanytarsini (und.), and *Corynoneura/Thienemanniella*.

Zone ZL-3 (25,000–18,400 cal yr B.P.) – Tanytarsini (und.) and *Chironomus* dominate this zone. Taxa that decrease in abundance in

ZL-3 compared to ZL-2 include *Constempellina, Sergentia, Pseudosmittia/Smittia, Paracladius,* and *Cricotopus/Orthocladius. Hydrobaenus/Oliverdia* is absent from the remainder of the record after ~23,000 cal yr B.P.

Zone ZL-4 (18,400–11,200 cal yr B.P.) – This zone shows the greatest taxa richness (14.7) of all zones and includes abundance maxima of five taxa: *Cladotanytarsus mancus*-type, *Endochironomus, Stempellinella/Zavrelia, Polypedilum,* and *Dicrotendipes*. Chaoboridae and Ceratopogonidae only occur in ZL-4 (not shown), as well as, *Corynocera ambigua, Pagastiella, Pseudochironomus,* and *Microtendipes. Micropsectra*-type and *Mesocricotopus* show variable abundances in this zone.

Zone ZL-5 (11,200 cal yr B.P.–modern) – *Stictochironomus* and *Corynoneura/Thienemanniella* increase in abundance toward the present. *Corynoneura/Thienemanniella, Heterotrissocladius, Zalutschia*-type A, Pentaneurini, and *Zalutschia zalutschicola* are all common and reach maxima post mid-Holocene.

4.2. Burial Lake chironomid zones

Thirty-nine taxa (only Chironomidae) occur within six zones (Fig. 4). *Micropsectra*-type and Tanytarsini (und.) are present in

every sample and only seven Chironomini taxa occur throughout the entire record.

Zone BL-1 (39,000–37,000 cal yr B.P.) – This zone includes four taxa that attain abundances near 20%: *Abiskomyia*, *Micropsectra*-type, *Cricotopus/Orthocladius*, and Tanytarsini (und.). Additional taxa reaching ∼10% abundance includes *Pseudodiamesa*, *Parakiefferiella nigra*-type, and *Heterotrissocladius*. Only two Chironomini taxa, *Sergentia* and *Stictochironomus*, occur in BL-1.

Zone BL-2 (37,000–16,800 cal yr B.P.) – This zone is divided into BL-2a and BL-2b because of an erosional unconformity (Abbott et al., in preparation). However, zoning methods did not distinguish between assemblages from BL-2a and BL-2b. Assemblage compositions are generally similar to BL-1, except for increasing abundances of *Paracladius*, *P. nigra*-type, and *Heterotrissocladius*.

Zone BL-3 (16,800–14,500 cal yr B.P.) – The only taxa exceeding 20% are *Micropsectra*-type and *Cricotopus/Orthocladius*. Taxa that decrease in abundance compared to the previous zone (BL-2) include *Pseudodiamesa*, *Paracladius*, *Abiskomyia*, *P. nigra*-type, and *Heterotrissocladius*. *Zalutschia*-type A and *Corynoneura/Thienemanniella* attain their maximum values of the entire record here.

Zone BL-4 (14,500–12,500 cal yr B.P.) – This zone shows greater taxa richness (13.4) compared to all previous zones. Nine taxa absent from BL-3 occur in BL-4. Five taxa (*Monodiamesa*, *Parakiefferiella triquetra*-type, *Corynocera oliveri*-type, *C. ambigua*, and *Stempellinella/Zavrelia*) register their first occurrence in BL-4. *Micropsectra*-type, *Sergentia*, and *Cricotopus/Orthocladius* all decrease in abundance in BL-4, whereas *Heterotrissocladius*, *P. nigra*-type, and *Zalutschia*-type B increase in abundance. *C. oliveri*-type is restricted to this zone.

Zone BL-5 (12,500–9900 cal yr B.P.) – The principal taxa include *Micropsectra*-type, *Heterotrissocladius*, and Pentaneurini. *Pseudodiamesa* and *Abiskomyia* are absent from later samples in this zone. Both *P. nigra*-type and *Zalutschia*-type B decrease by ∼20–30% abundance. Pentaneurini attains its maximum abundance in the entire record in BL-5.

Zone BL-6 (9900 cal yr B.P.–modern) – This zone shows the greatest taxa richness (14.4) of all zones. The main trends include decreasing abundance of *Micropsectra*-type and increasing abundances of *Paracladius*, *P. nigra*-type, *Zalutschia*-type B, and *Mesocricotopus*. *Heterotrissocladius* and Tanytarsini (und.) are common within BL-6.

4.3. Inferred temperatures

The Zagoskin Lake temperature reconstruction begins at ∼34,000 cal yr B.P. with inferences for ZL-1 ranging from 8.3 to 10.5 °C (Fig. 3). Temperatures in ZL-1 are variable and show no clear trend. Zone ZL-2 (∼30,000–25,000 cal yr B.P.) records the lowest mean temperature of all zones (9.4 °C), as 11 of 12 inferences are <10 °C. Temperatures in ZL-3 (∼25,000–18,400 cal yr B.P.) are on average 1.0 °C greater than temperatures from the previous zones. The overall trend within ZL-4 is a ∼2.5 °C increase in temperature from ∼18,400 to 11,200 cal yr B.P. Zone ZL-4 records the highest inferred temperature of the entire record (13.8 °C) at 12,300 cal yr B.P. The general temperature trend during the Holocene (ZL-5) is a ∼1.0 °C decrease toward present. Temperatures in ZL-5 range between 10.9 and 12.3 °C.

Burial Lake temperatures within BL-1 (∼39,000–37,000 cal yr B.P.) average 7.5 °C (Fig. 4). At ∼37,600 cal yr B.P. temperatures are ∼9.0 °C; the highest inferred temperatures prior to ∼14,000 cal yr B.P. The mean temperature of BL-2 (∼37,000–16,800 cal yr B.P.) is 6.4 °C, the lowest mean of all zones, and temperatures range between 5.0 and 7.7 °C. Temperatures within BL-2 are generally stable at ∼6.0 °C from ∼22,000 to 17,000 cal yr B.P. Temperatures in BL-3 increase by ∼1.0 °C from

∼16,600 to 14,600 cal yr B.P. In BL-4, temperatures increase rapidly from 8.3 °C at 14,300 cal yr B.P. to 10.7 °C near the end of the zone at 12,600 cal yr B.P. In BL-5, the maximum temperature (11.0 °C) of the entire record occurs at 12,300 cal yr B.P. This maximum is followed by a general decrease in temperatures by about ∼1.5 °C until ∼10,000 cal yr B.P. In BL-6 (∼9900 cal yr B.P. to modern), temperatures are nearly constant and range from 9.9 to 10.7 °C. Reconstructions indicate a slight cooling trend toward modern beginning at ∼6500 cal yr B.P. The mean inferred temperature of BL-6 is 10.2 °C, the highest mean of all zones.

4.4. Analog matching by SCD

An analog cutoff value of 0.278 was established using the upper 95% confidence interval of the mean min DC of the modern training set (Fig. 6). Only 3 of 78 fossil assemblages from Zagoskin Lake are considered reasonable analogs. The mean min DC from Zagoskin Lake is 0.55, much greater than the mean min DC of the training set (0.258). Sixty-five percent or 56 of 86 fossil assemblages from Burial Lake are considered reasonable analogs. The mean min DC from Burial Lake is 0.24, which is less than the mean min DC of the training set. Of the 30 poor-analog assemblages from Burial Lake, all have min DC that are within 2 standard deviations of the mean min DC of the training set.

4.5. Pollen data summarized by DCA

Combined, DCA Axis 1 and Axis 2 represent 39% and 46% of the variance in pollen-derived vegetation community data from Zagoskin Lake ($\lambda_1 = 0.29$, $\lambda_2 = 0.04$, total inertia = 0.86) and Burial Lake ($\lambda_1 = 0.36$, $\lambda_2 = 0.04$, total inertia = 0.89), respectively. The gradient lengths (degree of taxa turnover) of DCA Axis 1 for Zagoskin Lake are 1.8 SD (standard deviation units) and 1.9 SD for Burial Lake. Only DCA Axis 1 scores (Fig. 5B) are further considered as the eigenvalue of Axis 1 (λ_1) are an order of magnitude greater than the eigenvalue of Axis 2 (λ_2) at both sites. Zagoskin Lake DCA Axis 1 shows high values from ∼34,000 to 19,000 cal yr B.P. and a period of rapidly decreasing values from ∼19,000 cal yr B.P. to the start of the Holocene. Holocene DCA Axis 1 values gradually decrease toward present. Burial Lake DCA Axis 1 shows high values from ∼39,000 to 35,000 cal yr B.P. and ∼23,000 to 17,000 cal yr B.P., followed by a brief period of rapidly decreasing values to the early Holocene. Overall, Holocene DCA Axis 1 values indicate a decreasing trend toward the present.

5. Discussion

5.1. Regional paleoclimate significance and analogs

This study represents the first chironomid-inferred temperature reconstructions from the region adjacent to the former Bering Land Bridge. These records capture aquatic responses to broad-scale summer climate patterns from the LGM to the present and also permit estimates of late-middle Wisconsin summer climates. Caution in accepting the absolute inferred temperatures is warranted because the majority of samples is poor analogs at Zagoskin Lake and ∼35% of samples are poor analogs at Burial Lake (Fig. 6). Additionally, sample-specific prediction errors range between 1.56 and 1.63 °C. Zagoskin Lake has few modern analogs (only 3 of 78) with the training set and the min DC of most fossil samples are 2.5 standard deviations greater than the analog cutoff. A majority of fossil samples (65%) from Burial Lake are considered reasonable modern analogs (Fig. 6).

The numerous poor analogs generally arise from moderate differences in abundances of common down-core taxa that are all
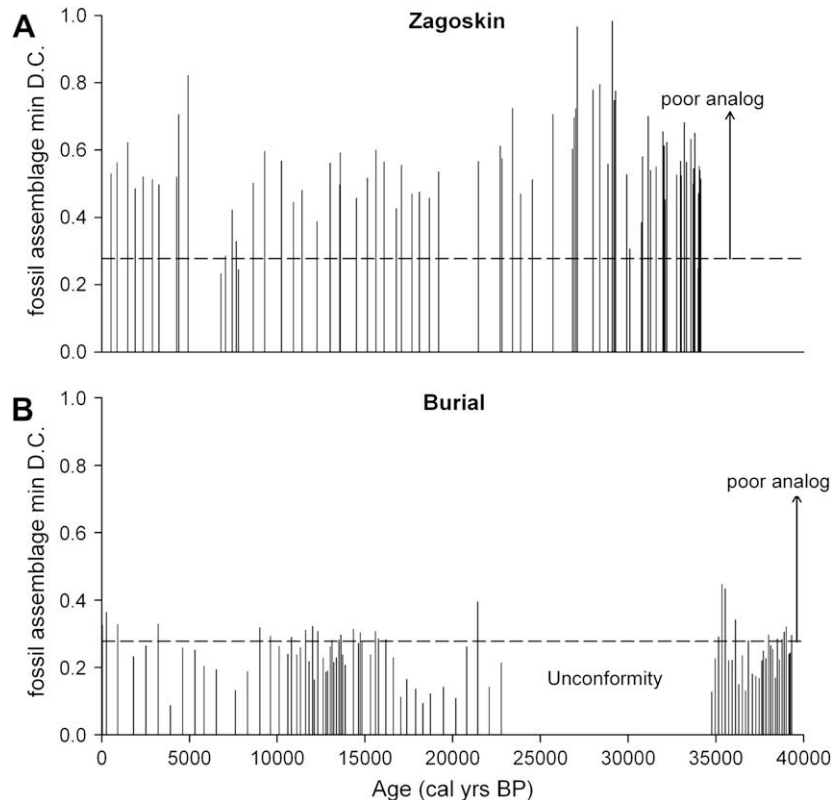
Fig. 6. Analog comparison between the (A) Zagoskin Lake or (B) Burial Lake fossil assemblages and the modern assemblages within the training set (Barley et al., 2006). Fossil samples with minimum dissimilarity coefficients (min DC) greater than the upper 95% confidence interval of the mean min DC of the training set are considered poor analogs. The analog cutoff is denoted by a dashed line.

present in the training set. The transfer function applied uses weighted averaging of temperature optima estimated for each taxon (although taxa are not totally independent as relative abundances are calculated). Therefore, high fossil sample dissimilarities when compared with the modern training set may not necessarily hinder the validity of the inferred temperature trends. Most fossil samples contain a substantial proportion of taxa well represented in the modern training set, often >90%. The fossil samples identified as poor analogs are merely a product of a training set with many sites having similar assemblages, especially near the warm end of the climate gradient sampled. This results in a stringent analog cutoff value. Furthermore, poor or no-analog situations encountered from Lateglacial and Holocene chironomid records may nevertheless provide reasonable inferences of climatic trends (Rosenberg et al., 2004; Whitney et al., 2005). Lotter et al. (1999) demonstrate that WA-PLS models are able to predict accurately observed temperatures even when analogs are poor or non-existent.

### 5.2. Middle to late Wisconsin (>25,000 cal yr B.P.)

Continuous paleoenvironmental records >25,000 cal yr B.P. in Beringia are extremely sparse and exhibit a considerable degree of chronological uncertainty (Hopkins, 1982; Anderson and Lozhkin, 2001). This makes interpretations of regional environmental change challenging. Pollen records from several Alaskan sites during the middle to late Wisconsin are broadly indicative of herb-dominated (Cyperaceae, Poaceae, and *Artemisia*) tundra landscape with a minor *Betula* shrub component (Anderson and Lozhkin, 2001; Ager, 2003). It is generally assumed that temperatures in western Alaska prior to ~25,000 cal yr B.P. were not as cold as the LGM (Anderson et al., 1994; Anderson and Lozhkin, 2001; Ager,

2003). Regional evidence of enhanced peat growth, ice-wedge collapse, and relative soil warmth imply a milder and moister climate than climates during the LGM (Anderson and Lozhkin, 2001).

Palynological evidence at Zagoskin Lake (Fig. 7) shows a slight increase in shrubs (*Betula* and Ericales) and sedges (Cyperaceae) and implies, at least, a slightly more mesic climate compared to the LGM (Ager, 2003). Pollen-based evidence from Burial Lake (Fig. 8) also suggests comparatively more shrubs (*Betula* and *Salix*) and Cyperaceae prior to ~35,000 cal yr B.P. than during the LGM around 20,000 cal yr B.P. (Abbott et al., in preparation). Other sediment records from western Alaska suggest relative warmth prior to ~25,000 cal yr B.P. (Hopkins, 1982; Elias, 2000; Kaufman et al., 2003). Fossil beetle assemblages from northern Alaska and Yukon Territory suggest that summer temperatures are near or above modern values, especially around ~35,000 cal yr B.P. (Elias, 2000). Biogenic silica values (a proxy of aquatic primary productivity) from Arolik Lake, southwestern Alaska, are substantially higher between ~33,000 and 30,000 cal yr B.P. than during the LGM (Kaufman et al., 2003) and imply greater summer temperatures. Hopkins (1982) proposes this period as a Beringian-wide interstadial named the Boutellier Interval.

Overall, chironomid-inferred temperatures and assemblage compositions at Zagoskin Lake do not suggest a well-defined interstadial during the late-middle Wisconsin. At Burial Lake, an unconformity hinders the interpretation of this part of the record. However, a relatively warm period occurred at ~37,600 cal yr B.P. with temperatures from four samples ranging from ~8.0 to 9.0 °C, the warmest inferences before 16,000 cal yr B.P. Prior to ~25,000 cal yr B.P. at Zagoskin Lake and ~35,000 cal yr B.P. at Burial Lake, estimated mean July air temperatures were on average ~3.5 °C colder than the modern temperature at each site (Fig. 5A
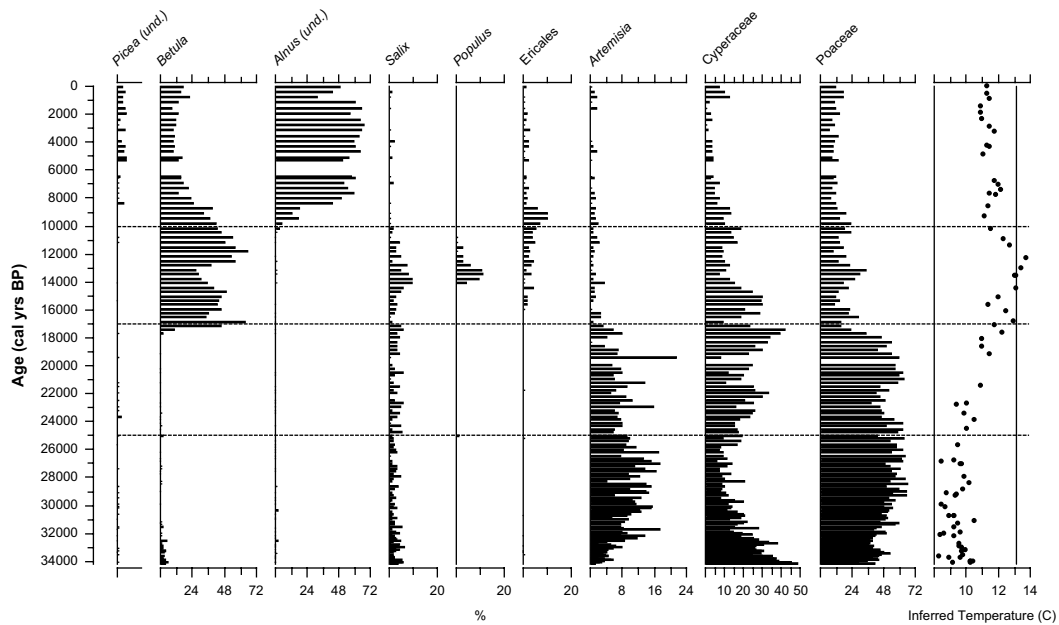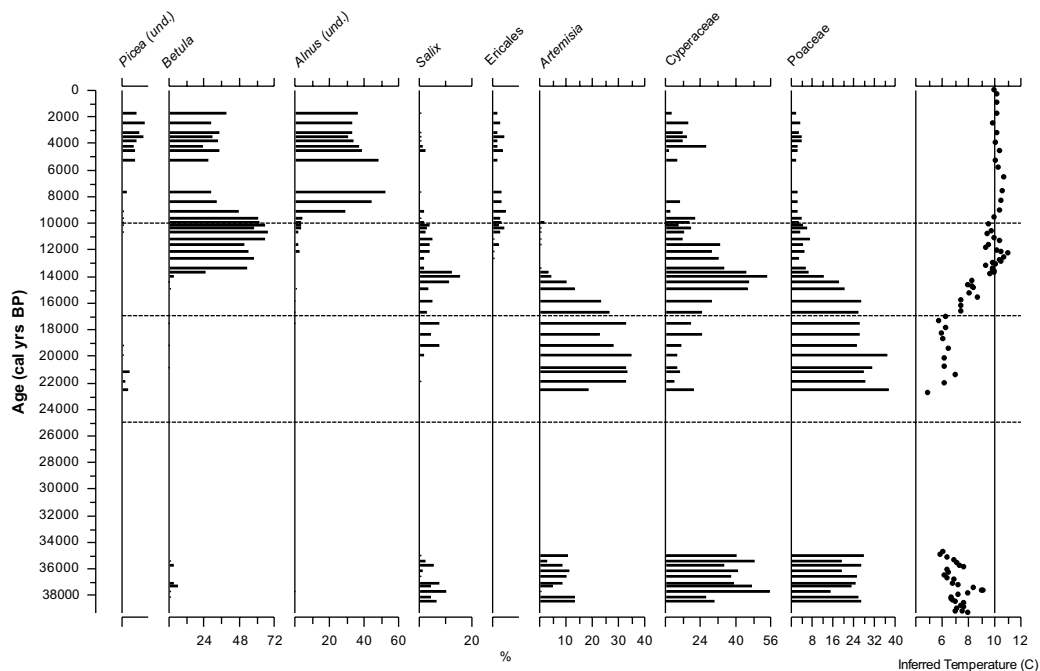
Fig. 7. Summary pollen percentage diagram from Zagoskin Lake modified after Ager (2003). Chironomid-inferred mean July air temperatures (°C) with the modern observed temperature also plotted. Horizontal lines at 25,000, 17,000, and 10,000 cal yr B.P. follow the temporal divisions within the discussion section.

and C). Abundant cold-indicator taxa (e.g. *Abiskomyia* and *Paracladius*) and few Chironomini were also observed from both sites (Figs. 3 and 4).

5.3. Last glacial maximum (~25,000–17,000 cal yr B.P.)

Climatic conditions in Beringia were influenced by a combination of factors, including the Laurentide Ice Sheet to the east, lower sea level, and vegetation that differed greatly from modern

(Bartlein et al., 1991; Edwards and Barker, 1994; Bigelow et al., 2003). Early climate simulation models suggest that during the LGM, Alaska experienced warmer winters, slightly colder July temperatures, and significantly lower July precipitation than at present (Barnosky et al., 1987). More recent outputs from global coupled ocean-atmosphere-sea ice-land surface climate models (e.g. NCAR's CSM1 and CCSM3) show contrasting results (Shin et al., 2003; Otto-Bliesner et al., 2006). For example, CCSM3 simulated annual surface temperatures at LGM suggest substantial warming

Fig. 8. Summary pollen percentage diagram from Burial Lake modified after Abbott et al. (in preparation). Chironomid-inferred mean July air temperatures (°C) with the modern temperature also plotted. Horizontal lines at 25,000, 17,000, and 10,000 cal yr B.P. follow the temporal divisions within the discussion section. An unconformity exists between ~34,500 and 23,000 cal yr B.P.

occurred in Alaska (>4 °C compared to pre-industrial conditions), whereas CSM1 indicates cooling in the region of 2 °C. A LGM sensitivity simulation with CCSM3 indicates that changes in surface temperatures are sensitive to the height of the ice sheet over Canada, thus using lower ice sheet height yields a cooling of 0.5–1.5 °C over Alaska compared to pre-industrial conditions (Otto-Bliesner et al., 2006). Palynological studies from Alaska provide substantive consensus that LGM summer climates were considerably colder and more arid than those of the Holocene (Colinvaux, 1964; Hopkins, 1982; Ager and Brubaker, 1985; Anderson, 1985; Anderson et al., 1994; Edwards and Barker, 1994; Anderson and Lozhkin, 2001; Ager, 2003). Cryoturbated paleosols located on the Seward Peninsula dated to 21,500 cal yr B.P. suggest mean annual temperatures were −6 to −8 °C (Höfle et al., 2000), at least as cold, if not colder, than modern for the Seward Peninsula.

In contrast, some quantitative evidence, derived from fossil beetle assemblages, suggests rather mild climatic conditions compared to the fossil pollen data. Elias (2001) infers LGM mean July temperatures (TMAX) from one site on the Seward Peninsula as slightly warmer than modern by 0.9 °C, although he acknowledges that this estimate is based on a large range (5.5–9.5 °C). Several beetle assemblages from eastern Beringia suggest that mean summer temperatures were cooler (1–4 °C) than modern (Elias, 2001), which is in general agreement with climate simulations for the LGM in Alaska (Barnosky et al., 1987; Shin et al., 2003; Otto-Bliesner et al., 2006). Alfimov and Berman (2001), using beetle assemblages as a climate proxy, infer LGM mean July temperatures warmer than modern for northeastern Siberia and suggest that continentality was far greater in the region than it is today. Greater continentality experienced by many Beringian environments during the LGM certainly may explain large differences between LGM and Holocene climates (Guthrie, 2001).

From ~25,000 to 17,000 cal yr B.P., mean July temperatures from Zagoskin Lake and Burial Lake average 2.3 and 3.8 °C colder than modern, respectively (Fig. 5A and C). By ~21,000 cal yr B.P., inferred temperatures at Zagoskin Lake were 2.0 °C below modern and gradual warming is observed much earlier compared to at Burial Lake. At Burial Lake, inferred temperatures began to increase at ~17,000 cal yr B.P. from values of 6–7 °C for the previous ~6000 cal yr. Pollen-derived vegetation change summarized by DCA Axis 1 for Zagoskin Lake changes substantially around 19,000 cal yr B.P. (Fig. 5B), whereas at Burial Lake, significant vegetation change occurs at 17,000 cal yr B.P. (Fig. 5B). In general, both chironomid and pollen data indicate that environmental change began early in the late Wisconsin at Zagoskin Lake (Figs. 5B and 7). However, dating uncertainties cannot be ruled out as an explanation for the difference between sites. The Zagoskin Lake age-depth model (Fig. 2A) is based on dates from bulk sediment, possibly making the sediments older than the true age of deposition (Abbott and Stafford, 1996). This may explain the ~2000 year offset in broad-scale vegetation change (DCA Axis 1 sample scores) between sites (Fig. 5B). Clearly, discrepancies exist between regionally inferred LGM paleoenvironmental patterns from Zagoskin and Burial Lakes and are difficult to reconcile from these records alone. Possible explanations may include Burial Lake's greater elevation and proximity to the Anisak glacier and Glacial Lake Noatak (Hamilton, 2001).

High loess mass accumulation rates at Zagoskin Lake during the LGM (Muhs et al., 2003) likely influenced aquatic communities and imply that aridity was a major environmental factor. Presumably, substantial inputs of eolian silt would have altered lake water chemistry, habitat availability, and primary productivity within the lake, possibly overriding the importance of temperature on chironomid communities. Greater continentality experienced during the LGM also likely reduced lake levels to well below

modern. Shallow lakes have lower thermal inertia and therefore warm faster after lake ice thaws, attain higher temperatures during summer, and experience reduced thermal stratification. If lake levels were substantially lower during the LGM because of greater continentality, then it is likely that warm summer temperatures were attained even though winters may have been severe.

5.4. Lateglacial to early Holocene (~17,000–10,000 cal yr B.P.)

The transition from the Wisconsin glacial interval to the Holocene is defined by rapid, large-magnitude shifts in abiotic factors (Edwards et al., 2001; Mann et al., 2002) that greatly influenced community composition across a range of environments (Elias et al., 1996; Elias, 2000; Bigelow and Edwards, 2001). In general, increases in relative abundances of Betula, Salix, Populus, and Ericales occurred across western Alaska during deglaciation (Ager and Brubaker, 1985) and are generally presumed to be related to broad-scale climate change (i.e. greater temperatures and effective moisture). Evidence of boreal beetle taxa rarely found today beyond the treeline zone were identified from sediments of the now inundated Bering Land Bridge and suggest slightly warmer than modern summers (~1–2 °C) and more extreme winters during the Lateglacial (Elias et al., 1996; Elias, 2001).

Summer temperatures from Zagoskin Lake were near modern throughout this period, while those at Burial Lake were ~2 °C below modern values from ~17,000 to 14,000 cal yr B.P. At Burial Lake, summer temperatures were near modern values between ~14,000 and 10,000 cal yr B.P. (Fig. 5A and C). Zagoskin Lake assemblages were also relatively rich in taxa (Fig. 3), especially more warm-adapted Chironomini. Vegetation community dynamics at Zagoskin Lake and Burial Lake suggest major changes in community composition during this period (Fig. 5B). Additionally, well-dated ocean sediment records from the northwestern Pacific demonstrate that between 18,500 and 15,000 cal yr B.P. pronounced sea-surface temperature increases of ~5 °C occurred (Sarnthein et al., 2006).

Chironomid-inferred mean July temperatures from both sites reached their maximum for the entire record at ~12,300 cal yr B.P., as modern (observed) values were slightly exceeded, although within the prediction error of the inference model applied when comparing adjacent inferences. The timing of the thermal maximum at each site is in general agreement with other records from western Alaska (Elias, 2000; Kaufman et al., 2004). The thermal maximum also correlates with the maximum relative abundance of Populus pollen (~11%) attained at Zagoskin Lake (Fig. 7). Today, Populus is not present on St. Michael Island. Thus, environmental conditions during the thermal maximum must have been more favorable for Populus than today. Burial Lake records no substantial Populus peak (Abbott et al., in preparation) during the thermal maximum, suggesting that Populus in the study region was limited by local, not regional factors (Anderson, 1988).

Increased Populus on the postglacial landscape is a widespread, although asynchronous, phenomenon recorded at many sites in eastern Beringia (Anderson and Brubaker, 1994; Edwards and Barker, 1994). It has been explained by increasing (Bartlein et al., 1995) or maximum summer insolation (Ritchie et al., 1983). Ager (2003) proposes that summer climate during this time may have been dry and not necessarily cold, irrespective of some evidence for Younger Dryas cooling in the region, primarily in south and west coastal areas (Elias, 2000; Hu et al., 2002; Kaufman et al., 2003; Hu et al., 2003). High summer insolation values and potentially lower lake levels resulting in warmer lake water temperatures could explain the thermal maximum at Zagoskin Lake. However, coeval evidence of Populus expansion indicates that the inferred thermal

maximum impacted terrestrial and aquatic ecosystems, and that the chironomid-inferred high temperatures are not simply an artifact related to specific within-lake factors. Interestingly, this shift to Chironomini-dominated assemblages and greater richness, indicative of warmer temperatures, began nearly 7000 years prior to the thermal maximum at 12,300 cal yr B.P. at Zagoskin Lake. Subtle increases in *C. mancus*-type, Pentaneurini, and five additional Chironomini taxa are noted (Fig. 3). All of these taxa are indicative of moderate or warm temperatures, as evidenced from their temperature optima (>12.8 °C) in the training set (Barley et al., 2006) and ranked temperature optima in other northern high-latitude studies (Bennike et al., 2004).

5.5. Early Holocene to the present (~10,000 cal yr B.P. to the present)

At both sites, inferred temperatures decrease toward modern values following the postglacial thermal maximum (Fig. 5A and C). This trend may be in part a response to the inundation of the Bering Land Bridge by rising sea levels, with the area of the present Norton Sound being mostly submerged by ~8000 cal yr B.P. (Manley, 2002). After the glacial–interglacial transition, Zagoskin Lake and Burial Lake may have experienced a climate with less seasonality due to decreased summer insolation and a greater maritime influence. Closer proximity to the ocean likely increased effective moisture and dampened seasonal and daily temperature ranges at each site.

Similar changes in *Picea*, *Betula*, and *Alnus* pollen-inferred abundances during the Holocene are also evident from both sites (Figs. 7 and 8) and are a general characteristic of western Alaskan vegetation histories (Anderson et al., 1994). Ager (2003) proposes that early Holocene pollen assemblages at Zagoskin Lake suggest regional moisture increases, with increasing Ericales and *Alnus* on the landscape. Our sites likely experienced a more continental climate during the middle to late Wisconsin glacial interval than at ~10,000 cal yr B.P., when effective moisture was greater due to the proximity of the Bering Sea. Greater effective moisture may have increased lake levels, as evidenced by the reduction in Chironomini richness at Zagoskin Lake. Minor variability in Holocene temperatures is also apparent; however, sampling resolution is too sparse to recognize specific Holocene climate events. DCA Axis 1 sample scores summarizing vegetation compositional changes at Zagoskin Lake and Burial Lake also imply relative environmental stability during the Holocene (Fig. 5B).

6. Conclusions

Chironomid-based temperature estimates indicate that summer climates during the middle to late Wisconsin in western Alaska were not dominated by severe cold; rather, our reconstructions suggest that mean July temperatures during the LGM were on average ~3.5 °C below modern for Zagoskin Lake and Burial Lake. An explanation for these findings is that greater continentality significantly influenced the climate of regions east of the Bering Land Bridge prior to its inundation by rising sea levels. Consistent warming trends are observed beginning just prior to ~21,000 cal yr B.P. at Zagoskin Lake and at ~17,000 cal yr B.P. at Burial Lake. Major vegetation community changes assessed by indirect ordination analyses are also recorded, beginning at ~19,000 cal yr B.P. at Zagoskin Lake and at ~17,000 cal yr B.P. at Burial Lake. These broadly coincide with inferred summer temperatures, approaching modern values for each site. Inferred temperatures also provide evidence of an early thermal maximum at each site, at ~12,300 cal yr B.P. During the postglacial thermal maximum, mean July air temperatures were slightly above modern,

and warm-adapted Chironomini were moderately abundant at Zagoskin Lake. This relative warmth occurred nearly synchronously with an increase in *Populus* pollen at Zagoskin Lake. After ~10,000 cal yr B.P., inferred temperatures, as well as vegetation changes, indicate relative environmental stability at both sites. The combination of chironomid-inferred mean July temperatures and vegetation reconstructions allows us to distinguish the response of aquatic and terrestrial systems to major climate changes of the late Quaternary.

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