1	A continental-scale chironomid training set for reconstructing Arctic temperatures
2	
3	Andrew S. Medeiros ^{1*} , Melissa L. Chipman ^{2,3} , Donna R. Francis ⁴ , Ladislav Hamerlík ^{5,6} , Peter
4	Langdon ⁷ , Peter J. K. Puleo ² , Grace Schellinger ² , Regan Steigleder ² , Ian R. Walker ⁸ , Sarah
5	Woodroffe ⁹ , and Yarrow Axford ²
6	1. Dalhousie University, School for Resource and Environmental Studies, College of
7	Sustainability, Halifax, Nova Scotia, Canada
8	2. Northwestern University, Department of Earth and Planetary Sciences, Northwestern
9	University, Evanston, IL, USA
10	3. Syracuse University, Department of Earth and Environmental Sciences, Syracuse, NY,
11	USA
12	4. University of Massachusetts, Department of Geoscience, Amherst, Massachusetts, USA
13	5. Matej Bel University, Faculty of Natural Sciences, Banska Bystrica, Slovakia
14	6. Institute of Zoology, Slovak Academy of Sciences, Bratislava, Slovakia
15	7. University of Southampton, School of Geography and Environmental Science,
16	Southampton, UK
17	8. University of British Columbia Okanagan, Departments of Biology, and Earth,
18	Environmental and Geographic Sciences, Kelowna, British Columbia, Canada
19	9. Durham University, Department of Geography, Durham, UK
20	
21	* Author for correspondence: Andrew S. Medeiros; <u>andrew.medeiros@dal.ca</u>

22 Key words: Arctic, midges, Greenland, Chironomidae, paleotemperature models,

23 paleolimnology, training set

24 Paper type: Primary Research Article

25

26 Abstract

27 We present chironomid species assemblage data from 402 lakes across northern North America, Greenland, Iceland, and Svalbard to inform interpretations of Holocene subfossil chironomid 28 29 assemblages used in paleolimnological reconstruction. This calibration-set was developed by reidentifying and taxonomically harmonizing chironomids in previously described surface 30 sediment samples, with identifications made at finer taxonomic resolution than in original 31 publications. The large geographic coverage of this dataset is intended to provide climatic 32 analogs for a wide range of Holocene climates in the northwest North Atlantic region and North 33 American Arctic, including Greenland. For many of these regions, modern calibration data are 34 sparse despite keen interest in paleoclimate reconstructions from high latitudes. A suite of 35 chironomid-based temperature models based upon this training set are evaluated here and the 36 37 best statistical model is used to reconstruct late glacial (Allerød and Younger Dryas) and 38 Holocene paleotemperatures at five non-glacial lakes representing a wide range of climate zones across Greenland. The new continent-scale training set offers more analogs for the majority of 39 40 Greenland subfossil assemblages than existing smaller training sets, with many analogs in Iceland and northern Canada. We find strong agreement between chironomid-based 41 reconstructions derived from the new model and independent glacier-based evidence for multi-42 43 millennial Holocene temperature trends. Some of the new Holocene reconstructions are very

similar to published reconstructions, but at a subset of sites and time periods we find improved 44 paleotemperature reconstructions attributable both to the new model's finer taxonomic resolution 45 and to its expanded geographic/climatic coverage, which resulted in increased characterization of 46 species optima. In the late glacial, the new model's finer taxonomic resolution yields unique 47 ability to resolve temperatures of the Allerød from colder temperatures of the Younger Dryas, 48 although the magnitude of that temperature difference may be underestimated. This study 49 demonstrates the value of geographically and climatically broad paleoecological training sets. 50 51 The large, taxonomically harmonized dataset presented here should be useful for a wide range of future investigations, including but not limited to paleotemperature reconstructions across the 52 Arctic. 53

54

55 Introduction

Understanding environmental change in the past can facilitate a better understanding of current 56 and future climate, but reliable proxies for the past are needed in order to achieve this goal. 57 Subfossil assemblages of chironomids (Diptera: Chironomidae) have well-demonstrated utility 58 59 for reconstructing paleotemperatures (Hofmann 1988; Walker et al. 1991; Walker 1995; Engels 60 et al. 2020). Insects are known to be especially responsive to temperature-dependent processes that govern growth, reproduction, feeding behavior, and emergence (Danks 2007; Lee and 61 62 Denlinger 2012). The indirect effect of temperature on the physical and chemical characteristics of lakes is known to be a principle mechanism for determining the distribution chironomid larvae 63 (Eggermont and Heiri 2011). For Arctic regions, a dominance of cold-stenothermal taxa that lack 64 65 a plurimodal response (Rossaro 2008) strengthen the temperature-assemblage relationship.

66	Spatial surveys of surface sediments across multiple bioregions in adjacent northern Canada and
67	Alaska (e.g. Walker 1990; Gajewski et al. 2005; Barley et al. 2006; Francis et al. 2006; Medeiros
68	and Quinlan 2011) and Iceland (Langdon et al. 2008) have identified temperature as the primary
69	control on modern chironomid species distributions, facilitating a calibration approach to
70	paleotemperature reconstructions (Smol 1992). Accordingly, chironomid assemblages now
71	provide a large fraction of the quantitative Holocene paleotemperature reconstructions available
72	from the Arctic (e.g., Kaufman et al. 2016; 2020), although large spatial gaps remain.
73	In recent years chironomid records have added substantially to the sparse database of
74	summer paleotemperature reconstructions from Greenland, where ice cores provide high-
75	resolution but annually integrated temperature reconstructions (e.g., see review by Axford et al.
76	2021). Past summer temperatures are a key factor in understanding the Greenland Ice Sheet's
77	past sensitivity to temperature change, thus a high priority for paleoclimate reconstruction. While
78	some studies have shown that chironomid assemblages from Greenland are primarily responsive
79	to temperature (Millet et al. 2014), published chironomid-based paleoclimate inferences from
80	Greenland have either taken a qualitative approach or have relied upon calibration data (training
81	sets) from adjacent regions of Canada and Iceland due to very limited availability of data from
82	across most of Greenland's climate zones (Brodersen and Bennike 2003; Wooller et al. 2004;
83	Schmidt et al. 2011; Axford et al. 2013, 2017, 2019; Millet et al. 2014; McFarlin et al. 2018).
84	Dense networks of training set collections from Greenland have only been accomplished in two
85	logistically accessible regions near Kangerlussuaq and Nuuk (Brodersen and Anderson 2002;
86	Medeiros et al. 2021; Figure 1). These two study sites are separated by < 300 km and experience
87	relatively warm summer temperatures compared with most of Greenland, which spans ~1500 km

north to south and a wide range of climates from the high Arctic to the subarctic. Published 88 reconstructions from chironomids agree well with a broad range of independent evidence for 89 Holocene climate (e.g., from ice core proxies and glacier extents; Axford et al. 2021), but 90 91 reliance on training sets and models developed outside Greenland adds uncertainty to those 92 reconstructions as these are principally different biogeographic regions that are known to have 93 unique assemblages (Medeiros et al. 2021). In addition, Fortin et al. (2015) demonstrated that increasing the number of modern analogues in the calibration approach using chironomid 94 95 assemblages allowed for improved interpretation of past climate. Thus, there is strong incentive to develop training sets that include as many analogous modern assemblages and comparable 96 climate zones as possible. 97

Here, we assemble taxonomically harmonized chironomid assemblage data from the 98 surface sediments of 402 lakes spanning northern North America, parts of Greenland, Svalbard, 99 and Iceland, creating a climatically and geographically broad calibration set. We evaluate the 100 applicability of a broad-based regional chironomid transfer function for reconstructing 101 quantitative temperatures in Greenland, an assessment that may be relevant to other under-102 103 sampled regions as well. Furthermore, we aim to present a climatically and geographically broad, 104 taxonomically harmonized training set that may be useful to paleoecologists for reconstructions across the Arctic. 105

106

107 Materials and methods

108 Training set sites and data sources

109	We present a large dataset of chironomid assemblages collected from the surficial sediments of
110	402 lakes from northern North America, southwest and east Greenland, Iceland, and Svalbard
111	(Figure 1; Supplemental Table S1). Most of these samples (except 12 new sites from east
112	Greenland and Svalbard, see the paragraph below) have been previously used in local and
113	regional training sets and studies of chironomid distributions (Walker et al. 1991; Brodersen and
114	Anderson 2002; Gajewski et al. 2005; Francis et al. 2006; Langdon et al. 2008; Porinchu et al.
115	2009; Medeiros and Quinlan 2011; Medeiros et al. 2014; Fortin et al. 2015; Medeiros et al.
116	2021). We re-identified the chironomids used in these studies in order to harmonize taxonomy
117	across this broad region and among our international collaborations. We note that not all samples
118	from previously published datasets were available for renumeration due to loss of the original
119	sample since the time of publication (Supplementary Table S1). The re-identified samples from
120	northeast Canada, southwest Greenland, and Iceland were previously combined in an
121	investigation of biogeography, which found that within each region air temperature explained the
122	largest amount of variation in chironomid assemblages, but spatial (i.e., biogeographic) controls
123	were also important between regions (Medeiros et al. 2021). Since existing published chironomid
124	training sets offer few climatic and biogeographic analogues for the sparsely populated, under-
125	sampled, Mid to High Arctic regions of Greenland, and especially for eastern Greenland, we also
126	publish here for the first time surface assemblages collected from 6 additional lakes in eastern
127	Greenland, and 6 lakes from Svalbard (Figure 1). For these new sites, the uppermost 0–1 cm of
128	sediment was collected from the deepest part of the lakes in the summer of 2010.

1.

• 1



Figure 1. The 402 sites in the full calibration-set (●) for North America, Greenland, Svalbard
and Iceland. Locations of downcore records from Greenland (Last Chance Lake [LCL], Fishtote
Lake, North Lake, Lake N14, and Deltasø), to which the temperature-inference model presented
here is applied, are shown as triangles (▲). The extent of the North American Boreal Zone is

outlined (Brandt 2009) and the settlements of Narsarsuaq, Nuuk, and Kangerlussuaq are shown(•).

136

137 The calibration set (Figure 1) includes sites that span from \sim 51.4 to 80.8 °N and \sim 16 to -165° W, covering a gradient in annual mean temperatures from 4.4 to -22.9 °C, summer (mean 138 of the warmest quarter) temperatures from -1.2 to 12.8 °C, and altitude from 0 to 855 m a.s.l., 139 and spanning from boreal forest to High Arctic tundra. Each of the original regional training sets 140 141 were collected as part of their own separate study (Supplemental Table S1) with associated field collection protocols. As the original study design of each dataset differed slightly in the manner 142 in which environmental data were collected, we used a standardized estimate of mean annual 143 temperature and mean summer temperature of the warmest quarter, extracted for each lake across 144 all training sets using the WorldClim 2.1 gridded bioclimatic dataset at 2.5 minute resolution 145 (Fick and Hijmans 2017). This provides a uniform estimate of temperature (based on an average 146 temperature from 1970-2000 CE) for all sites in our study despite the paucity of weather stations 147 across most of the study area. The WorldClim gridded climate dataset does not provide single-148 149 month inferences, so instead of using July air temperature (the variable mostly used for 150 reconstructions in chironomid-based transfer function models) in our model, we used the bioclimatic variable 'mean annual air temperature of the warmest quarter' (June, July, and 151 152 August [JJA] for northern North America) to represent summer air temperatures. The WorldClim dataset uses an elevation model to generate temperature normals and does not fully account for 153 small-scale local topography, so conceivably WorldClim-estimated site temperatures in high-154 155 relief or coastal areas could be less accurate. However, temperature gradients within the high-

156 relief Iceland and southwest Greenland training sets in the WorldClim temperature estimates are not notably smaller than in the original estimates, suggesting that local topography is quite well 157 represented in WorldClim modeling. Overall, the WorldClim temperature estimates for the 158 159 training set sites are in good agreement with the previously published temperature estimates for 160 the sites (which utilized differing, locally determined best-available methods for estimating temperatures; see Supplemental Figure S1). The WorldClim JJA mean temperature estimates are, 161 as expected, overall slightly lower than the published July mean temperature estimates, with a 162 163 mean difference of 1.1 °C (±0.9 °C). High-resolution chironomid assemblage data and summer temperatures from all sites are archived at the US NSF Arctic Data Center 164 https://doi.org/10.18739/A27H1DN9Q. 165

166

167 Downcore subfossil data

To assess analogues for late Pleistocene and Holocene subfossil assemblages in Greenland, and 168 169 to evaluate temperature reconstructions based upon the new calibration dataset, we utilized new late glacial and Holocene subfossil assemblage data from Lake N14 in southernmost Greenland 170 171 (Figure 1) and published Holocene subfossil assemblage data from four lakes representing three 172 additional geographically and climatically distinct regions of Greenland: Fishtote Lake and North Lake in the west near Disko Bugt (Figure 1; Axford et al. 2013), Deltasø in the northwest 173 174 near Qaanaaq and Pituffik/Thule Air Base (Axford et al. 2019), and Last Chance Lake in the east inboard of Scoresby Sund (Axford et al. 2017). For the four published sites, detailed site 175 geography and sediment chronologies are presented in the respective original publications. The 176 original publications report the following modern (late 20th/early 21st century instrumental) mean 177

July temperature estimates for each of the sites or nearest weather stations: 7.7 °C at North and
Fishtote lakes, 6.1 °C at Deltasø, and 7.1 °C at Last Chance Lake (the latter likely being an
overestimate, from a weather station 600 m lower in elevation and 140 km away). All four lakes
are small (< 0.5 km² and < 20 m deep) and three have been isolated from glacier meltwater since
regional deglaciation in the early Holocene. Deltasø has been influenced by meltwater since a
local glacier advance ~1850 CE.

Lake N14 is a small lake ($< 0.1 \text{ km}^2$, $Z_{max} = 8 \text{ m}$) on Angissoq Island off the coast of 184 185 southernmost Greenland (Figure 1; 59°58.85'N, 45°10.80'W; 33 m a.s.l.). Lake N14 is an isolation basin that was among the earliest in Greenland to deglaciate and isolate from the sea 186 after the last glacial maximum, and is known to contain a lacustrine record of the late Allerød, 187 the Younger Dryas and the entire Holocene (Björck et al. 2002). Modern (1981-2010 CE) mean 188 JJA air temperature is 7.1 °C (and 7.6 °C for July) recorded at the Qagortog coastal weather 189 station ~85 km northwest of Lake N14. WorldClim 2.1 estimates of the mean temperature of the 190 warmest quarter (JJA, 1970-2000 CE) is 7.8 °C at this site. Bedrock throughout and surrounding 191 the watershed is Paleoproterozoic granite and granodioritic gneiss (Steenfelt et al. 2016). The 192 193 sediment core used here (19-N14-N7) was collected in summer 2019 from the central region of 194 the lake at 4.2 m water depth using a percussion piston corer. Surface sediments (from 0-1 and 1-2 cm depths combined) were collected nearby with an Ekman sampler to assess modern 195 196 chironomid assemblages. The core is ~380 cm long and contains 345.5 cm of laminated, banded or very moss-rich lacustrine sediment underlain by a basal unit of glaciomarine clay. We 197 examine subfossil chironomid assemblages from the bottom lacustrine section to reconstruct the 198 199 relatively large temperature changes that occurred over Greenland in the late glacial period and

200	earliest Holocene, especially across the Allerød-Younger Dryas and Younger Dryas-early
201	Holocene transitions at 12,900 and 11,700 cal yr BP respectively (Björck et al. 2002; Rasmussen
202	et al. 2006; Buizert et al. 2014; 2018).
203	The age model for Lake N14 sediments is based upon AMS ¹⁴ C ages of aquatic mosses (n
204	= 18) supplemented with ages of organic matter in 1-cm-thick bulk sediment samples for
205	intervals where plant macrofossils were absent ($n = 6$; see Supplementary Table S2). Ages were
206	calibrated using Calib version 8.2 (Stuiver et al. 2022) and the IntCal20 calibration curve
207	(Reimer et al. 2020). Age modeling utilized the R package Bacon (Blaauw and Christen 2011;
208	see Supplemental Figure S2). Lacustrine sedimentation began prior to the oldest ¹⁴ C age of
209	13,605 (13,480-13770 2σ ; Table S2), at ~13,700 cal yr BP according to our age model.
210	

211 Data Analysis

All chironomid analyses were performed using R v4.0.2 (R Core Team 2013). The gradient 212 lengths of chironomid assemblages from the 402-lake dataset were determined through a 213 Detrended Correspondence Analysis (DCA) using the vegan package (Oksanen et al. 2013). As 214 distinct clusters of sites were observed in DCA, we tested for overlap between sediment core 215 samples and the modern samples using multivariate homogeneity of group dispersions (Figure 2; 216 Supplemental Figure S3). In order to compare the sediment cores to the modern dataset, 217 218 chironomid assemblages were coded by region and statistically compared using 9999 219 permutations of an ANOVA of Bray-Curtis distances between samples using the betadisper function of the vegan package, which is a multivariate analogue of Levene's test for homogeneity 220 221 of variance (Anderson et al. 2006).

Summer air temperature inference models were developed using partial least squares 222 (PLS), weighted average (WA), and weighted average partial least squares regressions 223 (WAPLS). Models were developed using identifications merged to the taxonomic resolution that 224 225 aligns to the downcore datasets. The downcore record from Lake N14 was identified with 226 relatively high taxonomic resolution using the new training set, whereas models used with the 227 published downcore records required merging of training set taxa to match the lower taxonomic resolution of older published data. Most notably, to harmonize with published downcore data 228 229 Heterotrissocladius, Micropsectra, and Oliveridia/Hydrobaenus morphotypes were each lumped as groups in the model rather than split into their respective species-level morphotypes (see 230 complete harmonization in Supplemental Table S3). Thus, the new reconstructions from 231 published data did not leverage the full taxonomic resolution of the new training set. See 232 Supplemental Information for full details. 233

Species data were square-root transformed, and models were cross-validated with a 9999 234 bootstrap process. Model selection followed the criteria outlined in Fortin et al. (2015), where 235 r_{iack}^2 was maximized and the maximum bias and root mean squared error of prediction (RMSEP) 236 237 were minimized. To apply the new model to published downcore chironomid records from each 238 core, we merged taxa as needed to match the taxonomic resolution of the downcore assemblage 239 data and calculated anomalies versus the uppermost sample in each record. The new chironomid-240 based calibration-set was used to reconstruct Holocene summer air temperatures based upon published assemblage data from Last Chance Lake, Deltasø, Fishtote Lake, and North Lake 241 (using a taxonomically "coarse model") and late glacial and early Holocene temperatures based 242 243 upon new assemblage data from Lake N14 (using a "high resolution model"). In both cases, the

WA-PLS2 model was found to be significant, and had a higher r^{2}_{iack} and lower bias and RMSEP 244 than other models (Supplementary Table 4). We applied the WA-PLS2 models to the assemblage 245 data for each core. For the previously published downcore records, we also compared the new 246 247 reconstructions to published temperature anomalies for each lake. We analyzed goodness-of-fit 248 of reconstructions of each core, as well as the squared chord distance of analogues between the 249 downcore intervals and training set (see supplemental information). To further assess how late Pleistocene and Holocene downcore samples from Greenland compare with the calibration-set, 250 251 the trajectory of subfossil data from each core was passively plotted within the modern calibration space constrained to summer air temperature using timetrack analysis within the 252 package 'analogue' (Simpson 2007; Supplemental Figure S6). 253

254

255 **Results**

A DCA of all sampling locations indicated strong regional spatial gradients, with some regions
appearing highly dissimilar to lakes in Greenland (Figure 2a). An analysis of multivariate
homogeneity of variances conducted on a Bray-Curtis distance matrix (Anderson 2006) showed
that modern chironomid assemblages from Greenland (the majority of which were from low
Arctic sites in southwest Greenland) were most similar to those of Iceland; however, some sites
were more similar to regions of northern Canada. Samples from Svalbard were more similar to
both northern North America and Greenland (Figure 2b).



Figure 2 Analysis of applicability of regions covered in the 402 calibration-set for
reconstructions of lakes in Greenland demonstrated by a) Detrended Correspondence Analysis
(DCA) of chironomid assemblages, and b) multivariate homogeneity of variances with noneuclidean distances between sites. Group centroids shown as ellipsoids based on 95 %
confidence intervals where original distances to principal coordinates are calculated (Anderson
2006).

Based on the results shown in Figure 2, we included Icelandic sites in our analysis due to the high probability of assemblage analogues for Greenland lakes. This is supported by reported similarities between aquatic invertebrate faunas (e.g., Gislason 2021). Ultimately, several samples in our downcore reconstructions had good analogs in Iceland (Supplementary Figure S3).



276

Figure 3 Chironomid-based paleotemperature model using 402 lakes in northern Canada and
Alaska, southwest and east Greenland, Iceland and Svalbard. a) Modeled mean summer
temperatures versus observed (WorldClim climate mean of the three warmest months), b)
residuals from the model.

281

For northwest and east Greenland, the new Holocene temperature reconstructions are 282 similar to the original published reconstructions that used smaller training sets from North 283 America (Francis et al. 2006; Fortin et al. 2015; Figs. 4b and 4c). In west Greenland, Axford et 284 al. (2013) reported somewhat divergent temperature reconstructions utilizing two different 285 training sets, one from Iceland and one from northeast North America. For those sites, situated 286 ~250 km north of the nearest Greenland calibration sites in our training set, the strongest analogs 287 in the new training set were found in Iceland (Supplemental Figure S3). Accordingly, the new 288 289 reconstructions more closely resemble the published reconstructions that were based on the

Icelandic training set, although the new reconstructions diverge significantly from the Iceland-290 291 based reconstructions in the early Holocene at Fishtote Lake and from 6000 to 4000 cal yr BP at North Lake (Figure 4d). Downcore assemblages from all four lakes and three regions of 292 293 Greenland had good analogues within the training-set (Supplemental Figure S4); however, Last Chance Lake had a number of intervals that showed a poor fit to the model (Supplemental Figure 294 S5). This was primarily due to the large number of *Psectrocladius* nr. *barbimanus*-type, a taxon 295 that is primarily represented in the mid-late Holocene and thus far rarely found in modern 296 297 sediments.



Figure 4. New chironomid-based reconstructions of mean summer temperatures in three regions
of Greenland compared with published chironomid-based July temperature reconstructions and
independent evidence for summer climate. (a) July insolation forcing at 65 °N (Berger and

Loutre 1991); (b, c, d) summer paleotemperature records from east, northwest and west 302 Greenland, respectively. New reconstructions (in black) use the region-wide WAPLS model 303 304 presented here. Anomalies were calculated versus the uppermost sample in each record. Original published July air temperature reconstructions (from Axford et al. 2013; 2017; 2019) are shown 305 306 in colors (blue lines are reconstructions based upon the northern North American WAPLS model of Fortin et al. (2015) with RMSEP 1.9 °C; solid (dashed) red lines are based upon the northeast 307 North American WA model with (without) tolerance down-weighting of Francis et al. (2006) 308 309 with RMSEP 1.5 °C (1.6 °C); green lines are based upon the Icelandic WAPLS model of Langdon et al. (2008) with RMSEP 1.1 °C). Where the original publication indicated a preferred 310 reconstruction model, only that model is shown here. For each site, sample-specific errors are 311 shown for the new model and one older model for comparison. Vertical orange bars mark 312 periods when ice caps near each lake were smaller than their current extents, suggesting summer 313 temperatures warmer than those of the mid-20th century (ice cap/glacier names are given in the 314 figure; results from Lowell et al. 2013; Levy et al. 2014; Schweinsberg et al. 2017; 2019; Axford 315 et al. 2019). 316

Subfossil species assemblages from Lake N14 in southernmost Greenland reflect major
climate changes of the Allerød, Younger Dryas, and early Holocene, as do the corresponding
temperature reconstructions (Figure 5; Supplemental Figure S7). Assemblages in the lowest part
of the core, i.e., the early Allerød, were dominated by several morphotypes of the cold
stenotherm *Hydrobaenus* (Supplemental Figure S7). The extreme cold stenotherm *Oliveridia*rose to >50 % abundance in the later part of the Allerød and dominated Younger Dryas
assemblages at abundances up to 92 %. Overall head capsule concentrations dropped within the

Younger Dryas. In the uppermost Younger Dryas sample and bottom two Holocene samples, concentrations were so low that statistically representative count sums (\geq 50) could not be obtained, even after combining adjacent samples (Supplemental Figure S7). Allerød and Younger Dryas samples had closest analogs in Arctic Canada, but the goodness-of-fit to the WAPLS2 model was poor (Supplemental Figure S8).

Oliveridia and *Hydrobaenus* declined abruptly at the start of the Holocene 11,700 cal yr 329 330 BP. These cold stenotherms remained but in low abundances and were largely replaced by 331 morphotypes of *Micropsectra* and *Psectrocladius*, plus low abundances of *Einfeldia pagana*-type and Corynocera oliveri-type (Supplemental Figure S4), yielding an inferred rapid warming to 332 interglacial temperatures at the start of the Holocene (Figure 5). Head capsule concentrations 333 were extremely low in the first few centuries of the Holocene, due to high concentrations of 334 aquatic moss remains, but chironomid assemblages were nonetheless clearly distinct from those 335 of the Younger Dryas. Overall head capsule abundances rose ~11,100 cal yr BP, and for several 336 hundred years chironomids shifted back to Allerød-like assemblages dominated by Hydrobaenus 337 and to a lesser extent Oliveridia. By 10,600 cal yr BP, Einfeldia and C. oliveri-type returned to 338 339 the lake. At ~10,500 cal yr BP, Hydrobaenus and Oliveridia completely disappeared and 340 assemblages were dominated by *Psectrocladius* and *C. oliveri-type*. Holocene assemblages since 10,500 cal yr BP were represented by analogues from Greenland; only these? most recent 341 342 intervals had a 'good' goodness-of-fit to the WAPLS2 model (Supplemental Figure S5). The new transfer function modeled an accurate estimate of modern temperatures based upon recent 343 assemblages at Lake N14; chironomids in a surface sediment sample (0-2 cm depth) collected in 344 345 2019 yielded a modeled JJA temperature of 7.0 °C, compared with meteorological JJA

temperature of 7.1 °C at nearby Qaqortoq. Sample-specific errors of downcore reconstructions



347 were slightly smaller using the new temperature-inference model (Figure 5).

Figure 5. Late glacial and early Holocene air temperature reconstructions from southernmost
Greenland. Chironomid-based (a) absolute summer air temperature reconstructions and (b) air
temperature anomalies at Lake N14 compared with summer and winter temperature
reconstructions for the nearby town of Narsarsuaq, Greenland (c). New reconstructions of JJA
temperatures (in black) use the region-wide WAPLS model presented here. Anomalies in panel
(b) were calculated versus a reconstruction from modern Lake N14 surface sediments. July air
temperature reconstructions shown in blue are based upon the northern North American WAPLS

356	model of Fortin et al. (2015) and in green and red are based upon the northeast North American
357	WA model of Francis et al. (2006) (with and without tolerance down-weighting, respectively).
358	Sample-specific errors are shown for both WAPLS models (but for figure clarity, not for all
359	models). Estimates of winter (pink) and summer (violet) temperatures at Narsarsuaq are from
360	Buizert et al. (2018) and are based upon Summit ice core $\delta^{15}N$ combined with estimates of past
361	seasonality and spatial patterns in climate derived from climate model simulations. The Younger
362	Dryas is shaded light blue and a cryptic interval of cold indicator taxa and low chironomid-
363	inferred early Holocene temperatures is shaded light gray. See Figure 1 for site locations.
364	
365	Discussion
366 367	Greenland analogs in the continent-scale training set
368	Our results show that modern chironomid assemblages from non-glacial lakes in multiple climate
369	zones of Greenland, enumerated with relatively detailed taxonomic resolution, are well
370	represented by analogues in Arctic Canada and Iceland (Supplemental Figure S3). A basic
371	premise of models built from calibration data of chironomid-temperature relationships is that the
372	primary relationship is significant and comparable between different regions and in different
373	temporal settings (Juggins 2013). Although there are known differences in within-region
374	chironomid-environment relationships between Iceland and Greenland (Medeiros et al. 2021),
375	the overlap between chironomid assemblages of these two regions (Figure 2b) in our analysis
376	strongly suggests analogues from Iceland could improve interpretations of downcore assemblage
377	shifts. Some assemblages in Greenland, especially those dominated by morphotypes of
378	Hydrobaenus and Oliveridia, were also similar to Arctic Canada. Calibration data from

379	Greenland itself remain limited to a few small areas, albeit with the substantial altitudinal
380	differences among sites in southwest Greenland providing a more extensive climate gradient than
381	implied by the narrow geographic spatial coverage. Given the challenges of acquiring an
382	extensive calibration dataset from sparsely settled mid to high Arctic parts of Greenland, it is
383	encouraging that analogues for both current and past assemblages across Greenland's broad
384	climate footprint are reasonably well-represented by available data elsewhere.
385	
386	Species optima in the continent-scale vs. regional training sets
387	
388	Chironomids have a non-linear response to temperature (Rossaro 1991; Danks 2007), and if we
389	know this relationship we can accurately predict the underlying optima and tolerance of

temperature estimated from the mode and standard deviation of the Gaussian curve (Battarbee 390

2000). The expansion of calibration space, as well as increased precision in the chironomid-391

temperature relationship, should increase the ability of models to accurately reflect the Gaussian 392 distribution of a taxon relative to environmental variables. This, in turn, should improve the 393

394 accuracy of paleoenvironmental reconstructions.

In our dataset, we differentiate taxa commonly merged, including morphotypes of 395 Psectrocladius, Cricotopus/Orthocladius, Tanytarsini, and several taxa from the Tribe 396 397 Pentaneurini. In particular, lakes in Greenland have chironomid assemblages with several different Psectrocladius morphotypes and/or Tanytarsini taxa, which Axford et al. (2013; 2017) 398 noted had notable shifts throughout the early-mid Holocene. For example, the optima of different 399 400 Psectrocladius morphotypes were found to be up to 4 °C different from one another in our new

401	model, consistent with the merged group's broad tolerance in older datasets (e.g., tolerance of
402	3.6 °C in Francis et al. 2006). Whereas the broad, lumped subfamily Tanytarsini had an air
403	temperature optimum of 9.9 °C and tolerance of 4.3 °C in the North American training set of
404	Francis et al. (2006), the new training set distinguishes between different morphotypes within the
405	subfamily, which have optima ranging from 6.1 to 9.5 °C. The optimum of <i>Dicrotendipes</i> ,
406	important in Holocene assemblages from North Lake, was found to be lower in our high-
407	resolution dataset (Supplemental Table S3; 6.9 °C vs. 11.3 °C in Fortin et al. 2015 and 15.1 °C in
408	Francis et al. 2006). This most likely reflects different species (formerly lumped at the genus
409	level) being represented in the various training sets. In our high-resolution dataset, we
410	differentiate Dicrotendipes notatus-type (optima 8.1 °C in our high-resolution model) from
411	Dicrotendipes nervosus-type (optima 6.9 °C). Previous work has documented Dicrotendipes in
412	shallow littoral areas of high-Arctic lakes associated with macrophytes (Brooks et al. 2007;
413	Medeiros and Quinlan 2011). Since the new model includes additional shallow cold lakes
414	hosting abundant Dicrotendipes nervosus-type, our larger dataset likely captures a better
415	representation of this taxon's true temperature optimum (Supplemental Table S3).

416

417 Evaluating paleotemperature reconstructions in Greenland

418

Downcore chironomid assemblages from Lake N14 provide a unique opportunity to test how the
continent-scale midge training set performs compared with previously published training
sets/transfer functions, throughout major climate shifts of the latest Pleistocene (Allerød,
Younger Dryas) and early Holocene (Figure 5). Unlike for the previously published sites

423	discussed below, subfossil chironomids from Lake N14 in south Greenland were identified here
424	at the same fine taxonomic resolution as the training set, allowing us to explore the effects of
425	finer taxonomic resolution in the new model. We compared Lake N14 reconstructions using the
426	high-resolution new model versus the more coarsely resolved published models (the Fortin et al.
427	(2015) WA-PLS model, and the Francis et al. (2006) WA model with and without tolerance
428	downweighting). We also compared chironomid-based temperature reconstructions with
429	independent estimates of annual and summer temperature shifts in nearby Narsarsuaq (135 km
430	north of Lake N14). Buizert et al. (2018) derived their Narsarsuaq estimates from a combination
431	of ice core-based temperature inferences at Summit on the central Greenland Ice Sheet, and
432	climate model-derived estimates of past spatial patterns and seasonality of temperatures. The
433	Narsarsuaq temperature estimates have the advantage of being fully independent of our
434	chironomid-based inferences, but the disadvantage of presuming that climate shifts on
435	Greenland's south coast paralleled those at Summit ~1300 km away and far inland. That
436	assumption means large uncertainty in the Narsarsuaq temperature estimates.
437	A structure in the residuals reveals model overestimation of the lowest summer
438	temperatures and underestimation of highest summer temperatures in our dataset (Figure 3). This
439	is common for large calibration datasets as the samples encompass both a large
440	geographic/climate gradient and a wide range of correlating and orthogonal environmental
441	factors (e.g., differences in lake depth and morphology between sites). Medeiros et al. (2015)
442	note that the weighted averaging process reduces these secondary-gradient effects, and for cores
443	that reside within the primary temperature gradient it may not be a large factor for Arctic
444	datasets. However, users should assume larger uncertainties near both ends of the calibrated

temperature gradient. Furthermore, locations that are warmer than most of our training set 445 because of lower latitude will have different biogeographic effects on assemblages (Medeiros et 446 al. 2021). For the colder end of the gradient, < about 2 °C, there is also a biophysical limitation 447 448 to extrapolating from models due to the extensive ice coverage on lakes below this temperature; 449 the distribution of Chironomidae in perennially ice-covered lakes is poorly known. Likewise, 450 while there are a number of primarily ice-covered lakes in the dataset (which may or may not be perennially ice-covered in recent years due to warming) these are also some of the most extreme 451 northerly sites, which can have biogeographic limits to the taxa that can both distribute in a 452 single year as well as persist (Medeiros et al. 2021). The model may therefore assume a colder 453 than expected assemblage as well as a poor analogue if core intervals have high abundances of 454 taxa similar to modern analogues at these locations. As one outcome of these limitations of the 455 model, we note below that our temperature reconstructions for the Younger Dryas in South 456 Greenland are likely over-estimations. 457

458 The new transfer function performed somewhat better than older chironomid models at resolving temperature changes within the cool Allerød and very cold Younger Dryas. The less 459 460 taxonomically resolved older models lump Oliveridia and Hydrobaenus and reconstructed flat-461 lined temperatures throughout the late glacial period. In contrast, the new model, which distinguishes Oliveridia from Hydrobaenus and resolves several morphotypes of Hydrobaenus, 462 463 inferred summer temperatures up to 3 °C warmer during the Allerød than during the Younger Dryas. Although that amplitude of temperature change is still small compared with estimates 464 from the Summit, Greenland, ice cores (and thus also the estimates for Narsarsuaq), its general 465 pattern agrees with other records of climate in the North Atlantic region (Buizert et al. 2018; 466

467	Figure 5). Allerød temperature reconstructions could be overestimates if relatively thermophilous
468	taxa had not yet migrated to what would have been a pioneering first outcropping of ice-free land
469	in Greenland during regional deglaciation. Given that reconstructed temperatures of the Younger
470	Dryas fall below the calibration range of all available training sets, Younger Dryas temperatures
471	may be over-estimated. However, to support chironomids the lake must have had at least an ice-
472	free moat during some weeks of summer; thus, JJA temperatures were likely not much below the
473	reconstructed values. The new model estimated that Younger Dryas JJA temperatures at Lake
474	N14 were ~9-9.5 $^{\circ}$ C lower than modern (i.e., than temperatures modeled from the surface
475	sample, which were 0.1 °C lower than 1981-2010 instrumental measurements at Qaqortoq). That
476	estimate is intermediate between summer and annual temperature anomalies modeled for
477	Narsarsuaq based upon ice cores and climate modeling (~3-4 °C larger than the Narsarsuaq
478	summer anomaly and ~12-13 $^{\circ}$ C smaller than the Narsarsuaq annual temperature anomaly, with
479	anomalies calculated relative to results for 1981-2000 CE; Buizert et al. 2018).
480	All models except the tolerance-downweighted WA model reconstructed an abrupt
481	increase in summer temperatures at Lake N14 at the onset of the Holocene. The tolerance-
482	downweighted WA model was very strongly influenced by the narrow tolerance of the
483	Oliveridia/Hydrobaenus group in the corresponding training set (Francis et al. 2006). Our new
484	chironomid-based paleotemperature model estimated a Holocene onset warming of ~6.5 $^\circ$ C,
485	which is similar to the estimated summer warming at Narsarsuaq of ~5 $^{\circ}$ C (Buizert et al. 2018).
486	The biggest divergence between the chironomid-based reconstructions for Lake N14 and the ice
487	core- and climate model-based reconstructions for Narsarsuaq occurred between ~11,100 and
488	10,600 cal yr BP. During this period, the cold stenotherms Oliveridia and Hydrobaenus again

dominated chironomid assemblages and *Psectrocladius* disappeared – clear qualitative evidence 489 for strong cooling. Appropriately, all models inferred very cold summer temperatures during this 490 491 period. Inferred temperatures at Lake N14 returned to interglacial values shortly after ~10,600 492 cal yr BP. The centuries of very cold temperatures at this time, clearly indicated by qualitative 493 assessment of the insect assemblages, contrast with the gradual warming inferred at Summit in 494 central Greenland (and at Narsarsuag in south Greenland based on Summit data; Buizert et al. 2018) over the same time. It appears that temperatures at Lake N14 diverged from those at 495 496 Summit for several centuries, though the spatial extent and cause of the early Holocene cooling are unknown. Glacial geologic studies in the region indicate that the Greenland Ice Sheet margin 497 had retreated far inland of Angissoq Island and Lake N14's watershed by this time (e.g., Larsen 498 499 et al. 2011; Levy et al. 2020), and the island's low-relief landscape would not have hosted local 500 mountain glaciers. Therefore, glacier meltwater influx to the lake itself cannot explain the dominance of cold taxa during this time. However, outlet glaciers still fed into fjords in the 501 502 broader region, and the reconstructed early Holocene cold period at Lake N14 is consistent with some local evidence for conditions offshore of southwest Greenland, where meltwater from the 503 504 waning Greenland Ice Sheet had profound effects on sea surface conditions in the early 505 Holocene. For example, Allan et al. (2021) reported suppression of sea-surface temperatures off southwest Greenland by meltwater until the "onset of interglacial conditions at a regional scale" 506 507 at ~10,000 cal yr BP. It is increasingly recognized that both Laurentide and Greenland Ice Sheet meltwaters protractedly and repeatedly influenced sea-surface conditions in the Labrador Sea 508 throughout the early Holocene, probably suppressing temperatures over land in south and 509 510 southwest Greenland (Jennings et al. 2015; Larocca et al. 2020; Young et al. 2020; Allan et al.

511 2021; Axford et al. 2021). Angissoq Island's position offshore may have made it especially
512 susceptible to this effect, but more research in the region is needed to establish how widespread
513 any early Holocene cooling was.

514 To further test the performance of the new model for reconstructing climate across a wide 515 range of Greenland's climate zones, we compared chironomid-inferred Holocene temperatures from four lakes with independent Holocene paleotemperature evidence from the extents of local 516 ice caps near each lake. As such, chironomid-based temperature reconstructions from the four 517 518 sites using our new model were compared with the glacier-based summer temperature constraints to assess which model(s) performed best. Summer insolation forcing (Berger and Loutre 1991) is 519 known to have strongly influenced Holocene summer temperatures in Greenland, leading to 520 generally warmest Holocene climate in many parts of Greenland from ~10,000–6000 cal yr BP 521 and gradually declining summer temperatures throughout the late Holocene (Axford et al. 2021; 522 523 Figure 4a). Despite this overall broad pattern, there were distinct regional differences in Holocene temperature trends across Greenland, most notably from north to south/southwest 524 (Briner et al. 2016; Larocca et al. 2020; Axford et al. 2021), so local-scale independent 525 526 information was also needed for comparison. Prior research has established that major local ice caps near each of the lakes were smaller than their present sizes for parts of the early to middle 527 Holocene, attributed to summer temperatures elevated above those of the 20th Century (Lowell et 528 al. 2013; Levy et al. 2014; Schweinsberg et al. 2017; 2019; Axford et al. 2019). 529

To model temperatures at each of the four lakes using our new training set required merging some taxa in the new training set because it utilized finer taxonomic resolution than the published downcore identifications. However, unlike the training sets used to model previously

published temperature reconstructions for these sites, our new training set utilizes the full
taxonomic resolution of the subfossil data that were collected at the four sites. Thus, this exercise
also assessed the value of increased taxonomic resolution, albeit lower than the high taxonomic
resolution of the new model.

537 At the mid to high arctic sites Last Chance Lake (Figure 4b) and Deltasø (Figure 4c), the new model successfully reconstructed peak temperatures during the early to middle Holocene 538 periods of smaller ice cap size and higher summer insolation forcing. The new reconstructions at 539 540 these sites also mirrored the amplitudes and patterns of published midge-based reconstructions that utilized a training set from North America only (the training set of Fortin et al. 2015), 541 reflecting the importance of North American analogs to modern and past climates in the very 542 cold climates of east/northeast and northwest Greenland. No samples yielded differences 543 between published and new reconstructions that exceeded model RMSEP or sample-specific 544 uncertainties between both models. Reconstruction uncertainties were slightly improved using 545 the new model. 546

In west Greenland, the original publication noted significant differences between 547 reconstructions using Icelandic vs. North American training sets, and our new reconstructions 548 549 differed yet again (Figure 4d). Axford et al. (2013) argued that because the models used to infer past temperature from Fishtote Lake's chironomid assemblages did not adequately differentiate 550 551 Tanytarsini (which comprised up to 94% of the core's assemblage, including up to 78% *Micropsectra* spp.), the original temperature reconstructions from the lake were less precise. This 552 was especially true when applying the North American model of Francis et al. (2006), which 553 554 lumped all Tanytarsini, whereas the Icelandic model differentiated several Tanytarsini

morphotypes following the same taxonomic scheme as the subfossil data. When the dominant 555 taxa of a calibration set are merged together such that they become generalists, they effectively 556 557 become eurythermic in the temperature models utilized. The new model leverages the full 558 taxonomic resolution of the subfossil data, as did the Iceland model in the published 559 reconstructions. The new model improves upon the Iceland model by employing a training set 560 with much broader climatic and spatial coverage and thus more thoroughly characterizing the temperature optima of genus- and species-level morphotypes. At Fishtote Lake Psectrocladius 561 562 and Tanytarsini, especially, exerted strong influences on the major trends in the original reconstructions; the optima and taxonomic resolution of these taxa were significantly updated in 563 the new model (Supplemental Figure S5, Supplemental Table S3). 564

The original temperature reconstructions from North Lake, which contained a more 565 diverse assemblages than Fishtote Lake, were considered more reliable, and indicated warmer-566 than-present summer temperatures until ~3000 cal yr BP, with peak warmth occurring from 567 568 6000–4000 cal yr BP. Our new reconstruction from North Lake also indicates temperatures warmer-than-present until ~3000 cal yr BP, but with peak temperatures from the onset of the 569 570 record ~7700 cal yr BP until ~5000 cal yr BP (Figure 4d). At North Lake, Dicrotendipes was important in driving inferred warmth from 6000 to 4000 cal yr BP in the original reconstructions. 571 The lower optimum estimated for this taxon in the new training set contributed to lower modeled 572 temperatures during this warmest interval compared with previous models. 573

The new reconstructions from North and Fishtote lakes agreed better than published reconstructions with the independent summer temperature evidence from west Greenland ice caps, which were retracted beginning in the early Holocene and expanded to their current extents

between 5000 and 4000 cal yr BP (Figure 4d; Schweinsberg et al. 2017; 2019). Compared with 577 the published reconstructions using subregional training sets, the decline to Little Ice Age 578 579 minimum temperatures was more gradual through the late Holocene in the new North Lake 580 reconstruction, and the overall amplitude of multi-millennial Holocene climate change was smaller (~2 °C). This amplitude of Holocene cooling was also smaller than reconstructed in 581 582 north and northwest Greenland. The implied spatial difference remains speculative due to the paucity of quantitative temperature records from the region, but is consistent with an emerging 583 584 view that overall Holocene cooling may have been smaller in west and south Greenland than in the north (Axford et al. 2021), likely due to differing effects of meltwater-influenced sea-surface 585 conditions and ocean surface currents. Encouragingly, the new reconstructions from Fishtote 586 Lake were very similar to those from nearby North Lake throughout the period of overlap 587 588 between the two records. The Fishtote Lake core extends earlier than at North Lake and suggests that temperatures prior to ~8000 cal yr BP were suppressed relative to the middle Holocene. A 589 qualitative summer temperature reconstruction based upon sedimentary leaf wax $\delta^2 H$ supports 590 elevated temperatures and subarctic climate conditions in west Greenland ~8000-5000 cal yr BP 591 592 (Thomas et al. 2016), in good agreement with both new chironomid-based reconstructions. The 593 leaf wax record does not extend into the early Holocene. Additional proxy-based reconstructions are needed to confirm temperatures of the early Holocene (i.e., prior to 8200 cal yr BP) in west 594 595 Greenland.

In summary, at a wide range of Greenland sites we found strong agreement between
chironomid-based reconstructions using the new model and independent evidence (from ice
sheet proxies or ice cap extent) for temperature trends. In northwest and central east (mid to high

Arctic) Greenland, new reconstructions were very similar to published reconstructions but 599 reduced the uncertainty of those reconstructions. At the other sites, reconstructions using the new 600 training set appeared to be substantially improved relative to reconstructions using less 601 602 taxonomically resolved, regional-scale training sets. Specifically, the new model applied to two lakes in central west Greenland yielded Holocene temperature reconstructions that were newly 603 604 consistent with independent temperature evidence. At Lake N14 in southernmost Greenland, the new model had the unique ability to distinguish temperatures of the Allerød from those of the 605 606 Younger Dryas, despite very low species diversity in the late glacial period, because it distinguished between several morphologically similar taxa. The new model may underestimate 607 the magnitude of the Allerød-Younger Dryas cooling, however; and the cause and extent of a 608 609 surprising early Holocene cold period recorded by chironomid assemblages at Lake N14 is 610 unknown, but not a function of model performance. The new, more taxonomically resolved model confirmed the large warming at the onset of the Holocene at Lake N14, in agreement with 611 two of three existing models applied there. These improvements to paleoclimate reconstructions 612 were attributable both to the new model's finer taxonomic resolution and to its expanded 613 614 geographic/climatic coverage, which resulted in more thorough characterization of species optima. 615

616

617 Conclusion

We present taxonomically harmonized chironomid assemblage data from the surficial sediments
of 402 lakes in northern North America, Greenland, Iceland, and Svalbard. The chironomidtemperature transfer function generated with this new training set is comparable in terms of

model statistics to published models covering smaller sub-regions, but this larger dataset offers a
much broader range of climate and assemblage analogs and thus more thoroughly characterizes
the temperature optima of individual taxa. This new continent-scale training set, which offers
increased taxonomic resolution compared to the previously published regional training sets,
contains good analogs for modern and subfossil chironomid assemblages of Greenland, including
from sites in Iceland and northern Canada.

627 Downcore summer temperature reconstructions based upon new and published Greenland 628 subfossil assemblages using the new model agree well with independent summer temperature evidence. Late-glacial temperature shifts of the Allerød and Younger Dryas in south Greenland 629 are registered only by the new, more taxonomically resolved model presented here, although the 630 new model may underestimate their magnitude. In contrast, published models that merge 631 morphologically similar taxa yield flat-lined temperature reconstructions through the late glacial. 632 The new model, and the majority of published models, agree with independent evidence for the 633 magnitude of warming at the end of the Younger Dryas (i.e., onset of the Holocene) in south 634 Greenland. Elsewhere, Holocene temperature reconstructions generated by applying the new 635 636 model to published subfossil assemblages from Greenland lakes in a wide range of climate zones 637 also appear successful, judging by agreement with independent temperature evidence from ice cap extents. Differences with previously published Holocene reconstructions in east and 638 639 northwest Greenland are small, but there are some changes in reconstructions from west Greenland. There, the improved taxonomic resolution and more thorough characterization of 640 species optima in the new training set yielded temperature reconstructions that agree better 641 642 among sites and with the independent glacier evidence.

The large, taxonomically harmonized dataset presented here should be useful for a range 643 of other investigations, including but not limited to paleotemperature reconstructions on the 644 northwest North Atlantic islands and in the North American Arctic and subarctic. Notably, the 645 646 increased geographic and climatic coverage and higher taxonomic resolution of our dataset relative to the original publications allows for more precise characterization of chironomid-647 temperature relationships. One outcome should be more accurate and precise paleotemperature 648 reconstructions, especially in regions where local calibration data are limited and/or key shifts 649 650 occur between morphologically similar taxa that are newly distinguished in this dataset. While we demonstrate the utility of the broad calibration space and higher taxonomic resolution of our 651 dataset, future high-resolution identifications of subfossil chironomid assemblages at new sites in 652 the studied regions will likely glean additional information from our model. 653

654

656 Acknowledgements

657 This work was supported by the U.S. National Science Foundation's Office of Polar Programs 658 (awards 2002515 and 1454734 to Axford) and Dalhousie University. We thank Steve Brooks and 659 660 the Natural History Museum (London) for hosting a meeting on taxonomic harmonization. Jamie 661 McFarlin and Eleanor Maddison contributed to discussions on subfossil taxonomy. We thank 662 Kirsten Christoffersen, University of Copenhagen, for providing additional original sample data used in this study, as well as Klaus P. Brodersen, Konrad Gajewski, David Porinchu, Marie-663 664 Claude Fortin, and the many scientists and funding agencies who enabled collection of the valuable original data in the source publications used in this study. Permits and permissions 665 required for the collection of previously published data can be found in the original publications 666 used in this study. Tim Coston, Aaron Hartz, Laura Larocca, and G. Everett Lasher assisted with 667 field work at Lake N14, with support from Polar Field Services and Jacky Simoud/Blue Ice 668 Explorer. WHOI NOSAMS and Beta Analytic analyzed Lake N14 radiocarbon samples. Lake 669 N14 samples were collected under Scientific Survey License VU-00160 and Export Permit 670 025/2019 from Naalakkersuisut, the Government of Greenland. We thank the people of Kalaallit 671 672 Nunaat (known in English as Greenland) and the Kujalleq municipality for granting access to 673 Greenland lakes including Lake N14. We also thank the three reviewers and associate editor of Quaternary Science Reviews for their detailed comments which improved this manuscript. 674 675

Data availability Statement: Chironomid assemblage data and site temperatures from the
training set are publicly archived with the U.S. National Science Foundation's Arctic Data
Center, https://doi.org/10.18739/A27H1DN9Q. The datafiles used in this study, and associated R

- 679 scripts, are publicly available in the corresponding author's github repository;
- 680 <u>https://github.com/arcticecology/Greenland_TS</u>.
- 681

References

- Allan, E., de Vernal, A., Seidenkrantz, M.S., Briner, J.P., Hillaire-Marcel, C., Pearce, C., Meire,
 L., Røy, H., Mathiasen, A.M., Nielsen, M.T. and Plesner, J.L., 2021. Insolation vs.
 meltwater control of productivity and sea surface conditions off SW Greenland during the
 Holocene. Boreas. 50, 631-651. https://doi.org/10.1111/bor.12514.
- Anderson, M.J., 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics. 62, 245–253. https://doi.org/10.1111/j.1541-0420.2005.00440.x.
- Axford, Y., Losee, S., Briner, J. P., Francis, D. R., Langdon, P. G., Walker, I. R., 2013. Holocene temperature history at the western Greenland Ice Sheet margin reconstructed from lake sediments. Quat Sci Rev. 59, 87-100. https://doi.org/10.1016/j.quascirev.2012.10.024.
- Axford, Y., Levy, L.B., Kelly, M.A., Francis, D.R., Hall, B.L., Langdon, P.G., Lowell, T.V.,
 2017. Timing and magnitude of early to middle Holocene warming in East Greenland inferred from chironomids. Boreas. 46, 678-687. https://doi.org/10.1111/bor.12247.
- Axford, Y., Lasher, G.E., Kelly, M.A., Osterberg, E.C., Landis, J., Schellinger, G.C., Pfeiffer,
 A., Thompson E., Francis, D. R., 2019. Holocene temperature history of northwest
 Greenland–With new ice cap constraints and chironomid assemblages from Deltasø.
 Quat. Sci. Rev. 215, 160-172. https://doi.org/10.1016/j.quascirev.2019.05.011
- Axford, Y., de Vernal, A., Osterberg, E.C., 2021. Past warmth and its impacts during the Holocene Thermal Maximum in Greenland. Annu. Rev. Earth. Pl. Sc. 49, 279-307. https://doi.org/10.1146/annurev-earth-081420-063858.
- Barley, E.M., Walker, I.R., Kurek, J., Cwynar, L.C., Mathewes, R.W., Gajewski, K., Finney, B.P., 2006. A northwest North American training set: distribution of freshwater midges in

relation to air temperature and lake depth. J Paleolimnol. 36, 295-314. https://doi.org/10.1007/s10933-006-0014-6.

- Battarbee, R.W., 2000. Palaeolimnological approaches to climate change, with special regard to the biological record. Quat. Sci. Rev. 19, 107-124. https://doi.org/10.1016/S0277-3791(99)00057-8.
- Berger, A., Loutre, M. F., 1991. Insolation values for the climate of the last 10 million years. Quat. Sci. Rev. 10, 297-317. https://doi.org/10.1016/0277-3791(91)90033-Q.
- Björck, S., Bennike, O., Rosén, P., Andresen, C.S., Bohncke, S., Kaas, E., Conley, D.J., 2002.
 Anomalously mild Younger Dryas summer conditions in southern Greenland. Geology 30, 427-430. https://doi.org/10.1130/0091-7613(2002)030<0427:AMYDSC>2.0.CO;2.
- Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Analysis 6, 457-474. Bayesian Anal. 6(3): 457-474 (September 2011). DOI: 10.1214/11-BA618.
- Brandt, J. P. 2009. The extent of the North American boreal zone. Environ. Rev. 17, 101-161. https://doi.org/10.1139/A09-004.

Briner, J.P., McKay, N.P., Axford, Y., Bennike, O., Bradley, R.S., de Vernal, A., Fisher, D.,
Francus, P., Frechette, B., Gajewski, K., Jennings, A., Kaufman, D.S., Miller, G.,
Rouston, C., Wagner, B., 2016. Holocene climate change in Arctic Canada and
Greenland. Quat. Sci. Rev. 147, 340-364.
https://doi.org/10.1016/j.quascirev.2016.02.010.

- Brodersen, K.P., Anderson, N.J., 2002. Distribution of chironomids (Diptera) in low arctic West Greenland lakes: trophic conditions, temperature and environmental reconstruction. Freshwater Biol. 47, 1137-1157. https://doi.org/10.1046/j.1365-2427.2002.00831.x.
- Brodersen, K.P., Bennike, O., 2003. Interglacial Chironomidae (Diptera) from Thule, Northwest Greenland: matching modern analogues to fossil assemblages. Boreas. 32, 560-565. https://doi.org/10.1111/j.1502-3885.2003.tb01235.x.
- Brooks, S.J., Langdon, P.G., Heiri, O., 2007. The identification and use of PalaearcticChironomidae larvae in palaeoecology. Quaternary Research Association TechnicalGuide (10), Quaternary Research Association, London.
- Buizert, C., Gkinis, V., Severinghaus, J.P., He, F., Lecavalier, B.S., Kindler, P., Leuenberger,
 M., Carlson, A.E., Vinther, B., Masson-Delmotte, V., White, J.W., Liu, Z., Otto-Bliesner,
 B., Brook, E.J., 2014. Greenland temperature response to climate forcing during the last
 deglaciation. Science. 345, 1177-1180. https://doi.org/10.1126/science.1254961.
- Buizert, C., Keisling, B.A., Box, J.E., He, F., Carlson, A.E., Sinclair, G., DeConto, R.M., 2018.
 Greenland-Wide Seasonal Temperatures During the Last Deglaciation. Geophys. Res.
 Lett. 45, 1905-1914. https://doi.org/10.1002/2017GL075601.
- Danks, H.V., 2007. How aquatic insects live in cold climates. Can. Entomol. 139, 400-471. https://doi.org/10.4039/n06-100.
- Engels, S., Medeiros, A.S., Axford, Y., Brooks, S.J., Heiri, O., Luoto, T.P., Nazarova, L., Porinchu, D.F., Quinlan, R., Self, A.E., 2020. Temperature change as a driver of spatial patterns and long-term trends in chironomid (Insecta: Diptera) diversity. Glob. Change Biol. 26, 1155-1169.

- Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302-4315. https://doi.org/10.1002/joc.5086.
- Fortin, M.C., Medeiros, A.S., Gajewski, K., Barley, E.M., Larocque-Tobler, I., Porinchu, D.F., Wilson, S.E., 2015. Chironomid-environment relations in northern North America. J. Paleolimnol, 54, 223-237. https://doi.org/10.1007/s10933-015-9848-0.
- Francis, D.R., Wolfe, A.P., Walker, I.R., & Miller, G.H., 2006. Interglacial and Holocene temperature reconstructions based on midge remains in sediments of two lakes from Baffin Island, Nunavut, Arctic Canada. Palaeogeogr. Palaeocl. 236, 107-124. https://doi.org/10.1016/j.palaeo.2006.01.005.
- Gajewski, K., Bouchard, G., Wilson, S.E., Kurek, J., Cwynar, L.C., 2005. Distribution of Chironomidae (Insecta: Diptera) head capsules in recent sediments of Canadian Arctic lakes. Hydrobiologia. 549, 131-143. https://doi.org/10.1007/s10750-005-5444-z.
- Gislason, G.M., 2021. The Aquatic Fauna of the North Atlantic Islands with Emphasis onIceland. In Biogeography in the Sub-Arctic: The Past and Future of North Atlantic Biota.Pgs 105-112. Ed. E. Panagiotakopulu and J.P. Sadler. Wiley.
- Hofmann, W., 1988. The significance of chironomid analysis (Insecta: Diptera) for paleolimnological research. Palaeogeogr. Palaeocl. 62, 501-509. https://doi.org/10.1016/0031-0182(88)90070-3.
- Jennings, A., Andrews, J., Pearce, C., Wilson, L., Olfasdotttir, S., 2015. Detrital carbonate peaks on the Labrador shelf, a 13-7 ka template for freshwater forcing from the Hudson Strait outlet of the Laurentide Ice Sheet into the subpolar gyre. Quat. Sci. Rev. 107, 62-80. https://doi.org/10.1016/j.quascirev.2014.10.022.

- Juggins, S., 2013. Quantitative reconstructions in palaeolimnology: new paradigm or sick science?. Quat. Sci. Rev. 64, 20-32. https://doi.org/10.1016/j.quascirev.2012.12.014.
- Kaufman, D.S., Axford, Y. L., Henderson, A.C., McKay, N.P., Oswald, W.W., Saenger, C.,
 Anderson, S.R., Bailey, H.L., Clegg, B., Gajewski, K., Sheng Hu, F., Jones, M.C., Massa,
 C., Rouston, C.C., Werner, A., Wooller, M.J., Yu, Z., 2016. Holocene climate changes in
 eastern Beringia (NW North America)–A systematic review of multi-proxy evidence.
 Quat. Sci. Rev. 147, 312-339. https://doi.org/10.1016/j.quascirev.2015.10.021.
- Kaufman, D., McKay, N., Routson, C., Erb, M., Davis, B., Heiri, O., et al., 2020. A global database of Holocene paleotemperature records. Scientific data, 7(1), 1-34. https://doi.org/10.1038/s41597-020-0445-3.
- Langdon, P.G., Holmes, N., Caseldine, C.J., 2008. Environmental controls on modern chironomid faunas from NW Iceland and implications for reconstructing climate change.
 J. Paleolimnol. 40, 273-293. https://doi.org/10.1007/s10933-007-9157-3.
- Larocca, L.J., Axford, Y., Bjørk, A.A., Lasher, G.E., Brooks, J.P., 2020. Local glaciers record delayed peak Holocene warmth in south Greenland. Quat. Sci. Rev. 241:106421https://doi.org/10.1016/j.quascirev.2020.106421
- Larsen, N. K., Kjær, K. H., Olsen, J., Funder, S., Kjeldsen, K. K., Nørgaard-Pedersen, N., 2011. Restricted impact of Holocene climate variations on the southern Greenland Ice Sheet. Quat. Sci. Rev. 30, 3171-3180. https://doi.org/10.1016/j.quascirev.2011.07.022
- Lee, R. Denlinger, D.L., 2012. Insects at low temperature. Chapman and Hall, New York..
- Levy, L.B., Kelly, M.A., Lowell, T.V., Hall, B.L., Hempel, L.A., Honsaker, W.M., Lusas, A.R., Howley, J.A., Axford, Y., 2014. Holocene fluctuations of Bregne ice cap, Scoresby Sund,

east Greenland: a proxy for climate along the Greenland Ice Sheet margin. Quat. Sci. Rev. 92, 357-368. https://doi.org/10.1016/j.quascirev.2013.06.024.

- Levy, L. B., Larsen, N. K., Knudsen, M. F., Egholm, D. L., Bjørk, A. A., Kjeldsen, K. K., Kelly, M.A., Howley, J.A., Olsen, J., Tikhomirov, D., Zimmerman, S.R.H., Kjær, K. H., 2020.
 Multi-phased deglaciation of south and southeast Greenland controlled by climate and topographic setting. Quat. Sci. Rev. 242, 106454.
 https://doi.org/10.1016/j.quascirev.2020.106454
- Lowell, T.V., Hall, B.L., Kelly, M.A., Bennike, O., Lusas, A.R., Honsaker, W.A., Smith, C.A., Levy, L.A., Travis, S., Denton, G.H., 2013. Late Holocene expansion of Istorvet ice cap, Liverpool Land, east Greenland. Quat. Sci. Rev. 63, 128-140. https://doi.org/10.1016/j.quascirev.2012.11.012.
- Luoto, T.P., 2011. Indicator value of midge larvae (Diptera: Nematocera) in shallow boreal lakes with a focus on habitat, water quality, and climate. Aquatic Insects. 33, 351-370. https://doi.org/10.1080/01650424.2011.640333.
- McFarlin, J.M., Axford, Y., Osburn, M.R., Kelly, M.A., Osterberg, E.C., Farnsworth, L.B., 2018. Pronounced summer warming in northwest Greenland during the Holocene and Last Interglacial. P. Natl. Acad. Sci. USA. 115, 6357-6362. https://doi.org/10.1073/pnas.1720420115.
- Medeiros, A.S., Quinlan, R., 2011. The distribution of the Chironomidae (Insecta: Diptera) along multiple environmental gradients in lakes and ponds of the eastern Canadian Arctic. Can.
 J. Fish. Aquat. Sci. 68, 1511-1527. https://doi.org/10.1139/f2011-076.

- Medeiros, A.S., Taylor, D.J., Couse, M., Hall, R.I., Quinlan, R., Wolfe, B.B., 2014. Biological and nutrient responses to catchment disturbance and warming in small lakes near the Alaskan tundra–taiga boundary. The Holocene. 24, 1308-1319. https://doi.org/10.1177/0959683614540955.
- Medeiros, A.S., Milošević, Đ., Francis, D.R., Maddison, E., Woodroffe, S., Long, A., Walker, I.R., Hamerlik, L., Quinlan, R., Langdon, R., Brodersen, K.P., Axford, Y., 2021. Arctic chironomids of the northwest North Atlantic reflect environmental and biogeographic gradients. J. Biogeogr. 48, 511-525. https://doi.org/10.1111/jbi.14015.
- Millet, L., Massa, C., Bichet, V., Frossard, V., Belle, S., Gauthier, E., 2014. Anthropogenic versus climatic control in a high-resolution 1500-year chironomid stratigraphy from a southwestern Greenland lake. Quat. Res. 81, 193-202.

https://doi.org/10.1016/j.yqres.2014.01.004

- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., Simpson,G.L., Solymos, P., Stevens, M.H.H., Wagner, H., Oksanen, M.J., 2013. Package 'vegan'.Community ecology package, version, 2(9), pp.1-295.
- Porinchu, D., Rolland, N., Moser, K., 2009. Development of a chironomid-based air temperature inference model for the central Canadian Arctic. J. Paleolimnol. 41, 349-368. https://doi.org/10.1007/s10933-008-9233-3.
- Rasmussen, S.O., Andersen, K.K., Svensson, A.M., Steffensen, J.P., Vinther, B.M., Clausen,
 H.B., Siggaard-Andersen, M.L., Johnsen, S.J., Larsen, L.B., Dahl-Jensen, D., Bigler, M.,
 2006. A new Greenland ice core chronology for the last glacial termination. J Geophys.
 Res. Atmosphere. 111, D06102. <u>https://doi.org/10.1029/2005JD006079</u>

R Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <u>http://www.R-project.org/</u>.

Reimer, P.J., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Bronk Ramsey, C., Butzin, M., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hughen, K.A., Kromer, B., Manning, S.W., Muscheler, R., Palmer, J.G., Pearson, C., van der Plicht, J., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Turney, C.S.M., Wacker, L., Adolphi, F., Büntgen, U., Capano, M., Fahrni, S.M., Fogtmann-Schulz, A., Friedrich, R., Köhler, P., Kudsk, S., Miyake, F., Olsen, J., Reinig, F., Sakamoto, M., Sookdeo, A., Talamo, S., 2020. The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). Radiocarbon 62, 725-757.

Rossaro, B., 1991. Chironomids and water temperature. Aquatic Insects, 13, 87-98.

https://doi.org/10.1080/01650429109361428.

- Schmidt, S., Wagner, B., Heiri, O., Klug, M., Bennike, O. L. E., Melles, M., 2011. Chironomids as indicators of the Holocene climatic and environmental history of two lakes in Northeast Greenland. Boreas. 40, 116-130. https://doi.org/10.1111/j.1502-3885.2010.00173.x.
- Schweinsberg, A.D., Briner, J.P., Licciardi, J.M., Bennike, O., Lifton, N.A., Graham, B.L., Young, N.E., Schaefer, J.M., Zimmerman, S.H., 2019. Multiple independent records of local glacier variability on Nuussuaq, West Greenland, during the Holocene. Quat. Sci. Rev. 215, 253-271. https://doi.org/10.1016/j.quascirev.2019.05.007.
- Schweinsberg, A.D., Briner, J.P., Miller, G.H., Bennike, O., Thomas, E.K., 2017. Local glaciation in West Greenland linked to North Atlantic Ocean circulation during the Holocene. Geology 45: 195-198. https://doi.org/10.1130/G38114.1.
- Simpson, G.L., 2007. Analogue methods in palaeoecology: using the analogue package. J Stat. Soft. 22, 1-29. https://doi.org/10.18637/jss.v022.i02.

- Smol, J.P., 1992. Paleolimnology: an important tool for effective ecosystem management. J. Aquat. Ecosys. Health. 1, 49-58. https://doi.org/10.1007/BF00044408
- Steenfelt, A., Kolb, J., Thrane, K., 2016. Metallogeny of South Greenland: a review of geological evolution, mineral occurrences and geochemical exploration data. Ore Geol Rev. 77, 194-245. https://doi.org/10.1016/j.oregeorev.2016.02.005
- Stuiver, M., Reimer, P.J., Reimer, R.W., 2022, CALIB 8.2 [WWW program] at http://calib.org, accessed 2022-4-13.
- Thomas, E.K., Briner, J.P., Ryan-Henry, J.J., Huang, Y., 2016. A major increase in winter snowfall during the middle Holocene on western Greenland caused by reduced sea ice in Baffin Bay and the Labrador Sea, Geophys. Res. Lett. 43, 5302–5308. https://doi.org/10.1002/2016GL068513.
- Walker, I.R., 1990. Modern assemblages of arctic and alpine Chironomidae as analogues for late-glacial communities. In Environmental History and Palaeolimnology (pp. 223-227).
 Springer, Dordrecht.
- Walker, I.R., 1995. Chironomids as indicators of past environmental change. In The Chironomidae (pp. 405-422). Springer, Dordrecht.
- Walker, I.R., Smol, J.P., Engstrom, D.R., Birks, H.J.B., 1991. An assessment of Chironomidae as quantitative indicators of past climatic change. Can. J. Fish. Aquat. Sci. 48, 975-987. https://doi.org/10.1139/f91-114.
- Wooller, M.J., Francis, D., Fogel, M.L., Miller, G.H., Walker, I.R., Wolfe, A.P., 2004. Quantitative paleotemperature estimates from δ18O of chironomid head capsules

preserved in arctic lake sediments. J. Paleolimnol. 31, 267-274. https://doi.org/10.1023/B:JOPL.0000021944.45561.32.

Young, N.E., Briner, J.P., Miller, G.H., Lesnek, A.J., Crump, S.E., Thomas, E.K., Pendleton, S.L., Cuzzone, J., Lamp, J., Zimmerman, S. and Caffee, M., 2020. Deglaciation of the Greenland and Laurentide ice sheets interrupted by glacier advance during abrupt coolings. Quat. Sci. Rev. 229, 106091. https://doi.org/10.1016/j.quascirev.2019.106091