

Biostratigraphic evidence of human modification of high elevation aquatic ecosystems in the Intermountain West of the United States



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ABSTRACT

High resolution analysis of subfossil chironomid remains preserved in well-dated lacustrine sediment cores was undertaken to identify whether marked shifts in chironomid assemblages have occurred in recent decades in the Colorado Rocky Mountains. This study will improve our understanding of site-specific aquatic ecosystem variability in the central Colorado Rockies during the 20th and early 21st centuries. An observed increase in chironomid taxa associated with warmer, more productive lakes, e.g. *Dicoretendipes*, is consistent with the movement of these lakes towards more productive aquatic systems in recent decades. The application of a chironomid-based inference model for mean July air temperature (MJAT) to the midge stratigraphies from these sites provide centennial length reconstructions of MJAT. The chironomid-inferred reconstructions of MJAT closely track gridded MJAT estimates for much of the 20th century; however, the response of the chironomid community is muted relative to the elevated temperatures that characterize this region during the last decade. Complementary analyses of sub-fossil chironomid records, previously developed from additional high elevation lakes located throughout the Intermountain West of the United States, indicate that the rate and magnitude of faunal turnover during the late 20th and early 21st centuries surpass the rate and magnitude of faunal turnover during any preceding interval in the last century. Direct gradient analyses reveal that the chironomid assemblages in the majority of sites became increasingly similar in composition to the assemblages associated with warmer, lower elevation sites between the early 20th and early 21st century.

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1. Introduction

The magnitude and rate of biophysical changes observed during recent decades in the montane environments of the Intermountain West (IMW) are on the extreme end of the range of variations seen historically (Bonfils et al., 2008). Profound shifts in geochemical fluxes, nutrient cycling, hydrology, and ecosystem structure and function in freshwater systems have been documented (Cook et al., 2004; Westerling et al., 2006; Barnett et al., 2008; Bentz et al., 2010; Saros et al., 2012; Moore et al., 2013; Grafius and Malanson, 2015). Regional climate models indicate that mean annual temperature (MAT) at high elevations in the IMW will increase between 2.5°C and 5.5°C by the end of this century, with a clear trend in elevation-dependent warming (Pierce and Cayan, 2013).

It is critical that we improve our understanding of how aquatic ecosystems in alpine environments will be affected by on-going

and projected climate change (Catalan et al., 2013), particularly because the rate and magnitude of warming at high elevations is expected to be amplified during the coming century (Diaz et al., 2014; Pepin et al., 2015). Elevated air temperature has been identified as an important driver of changes in composition and structure of phytoplankton (Ruhland et al., 2015; Micheulutti et al., 2015), zooplankton (Nevalainen et al., 2014) and invertebrate (Eggermont et al., 2010; Reinemann et al., 2014) communities in mountain lakes during the most recent decades. In addition, projected changes in thermal conditions, and the resulting alteration of the food web structure of aquatic ecosystems, will impact threatened native Salmonid species in the high elevation aquatic ecosystems (Parker et al., 2008; Gauthier et al., 2014). Other factors, such as increased nutrient loading, have also driven the re-organization of aquatic communities in high elevation lakes in recent decades (Baron et al., 2000; Hu et al., 2014; Saros et al., 2012; Hundey et al., 2014). While many studies have endeavored to elucidate the physical and geochemical changes within these systems, greater attention should be directed at understanding how biotic communities in alpine lakes in the IMW have

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responded to elevated temperatures during the late 20th and early 21st centuries.

One method of increasing our understanding of how climate variability affects the composition and structure of aquatic communities involves extracting the remains of aquatic biota from lake sediment cores and relating changes in the abundance of aquatic taxa to observed variations in climate and limnology. Lake sediment is a powerful archive that preserves physical, geochemical, and biotic proxies that may be used to develop high-resolution reconstructions of past environment and climate (Battarbee, 2000). Multi-proxy analysis of lake sediment records provide important insights into centennial and millennial-scale climate variability and, in doing so, help society anticipate the potential impacts associated with projected climate change. Information extracted from lake sediment may also be used to develop baseline limnological information against which future changes may be compared (Smol and Douglas, 2007). This information can be utilized to further refine our understanding of how the composition, structure, and function of aquatic ecosystems will be altered in response to the changes in hydrology, limnology, and geochemical cycling that are projected to occur in mountain environments in the coming decades. For example, recent studies have documented unprecedented changes in the structure and composition of aquatic communities in high elevation lakes globally (Khamis et al., 2014; Hu et al., 2014; Michelutti et al.,

2015). Improving our knowledge of the characteristics and behavior of aquatic ecosystems in alpine environments will not only strengthen our ability to develop meaningful scenarios describing the potential future response of these freshwater systems to projected global change but also improve our ability to manage these natural systems and the freshwater water resources they contain (Catalan et al., 2013).

Here, we detail the response of chironomid communities in high elevation lakes throughout the IMW to climate and environmental change during the last century. Analysis of biostratigraphic signals preserved in sediment cores recovered from high elevation lakes in the Sawatch Range of the central Colorado Rockies was undertaken to: 1) examine the timing, rate and magnitude of 20th and early 21st century ecological and limnological change in aquatic ecosystems; and 2) to assess the correspondence between chironomid-based reconstructions of mean July air temperature (MJAT) and PRISM-based estimates of MJAT. The midge-based inference model, which incorporates a spatially extensive set of over 90 lakes from the Sierra Nevada, Uinta Mountains and central Colorado Rockies, has been successfully used to document the rate of warming during the 20th and early 21st century in the IMW (Porinchu et al., 2007, 2010; Reinemann et al., 2014). In addition, direct gradient analyses were used to assess if the change in midge assemblages observed in recent decades in the Colorado Rockies are site-specific or are

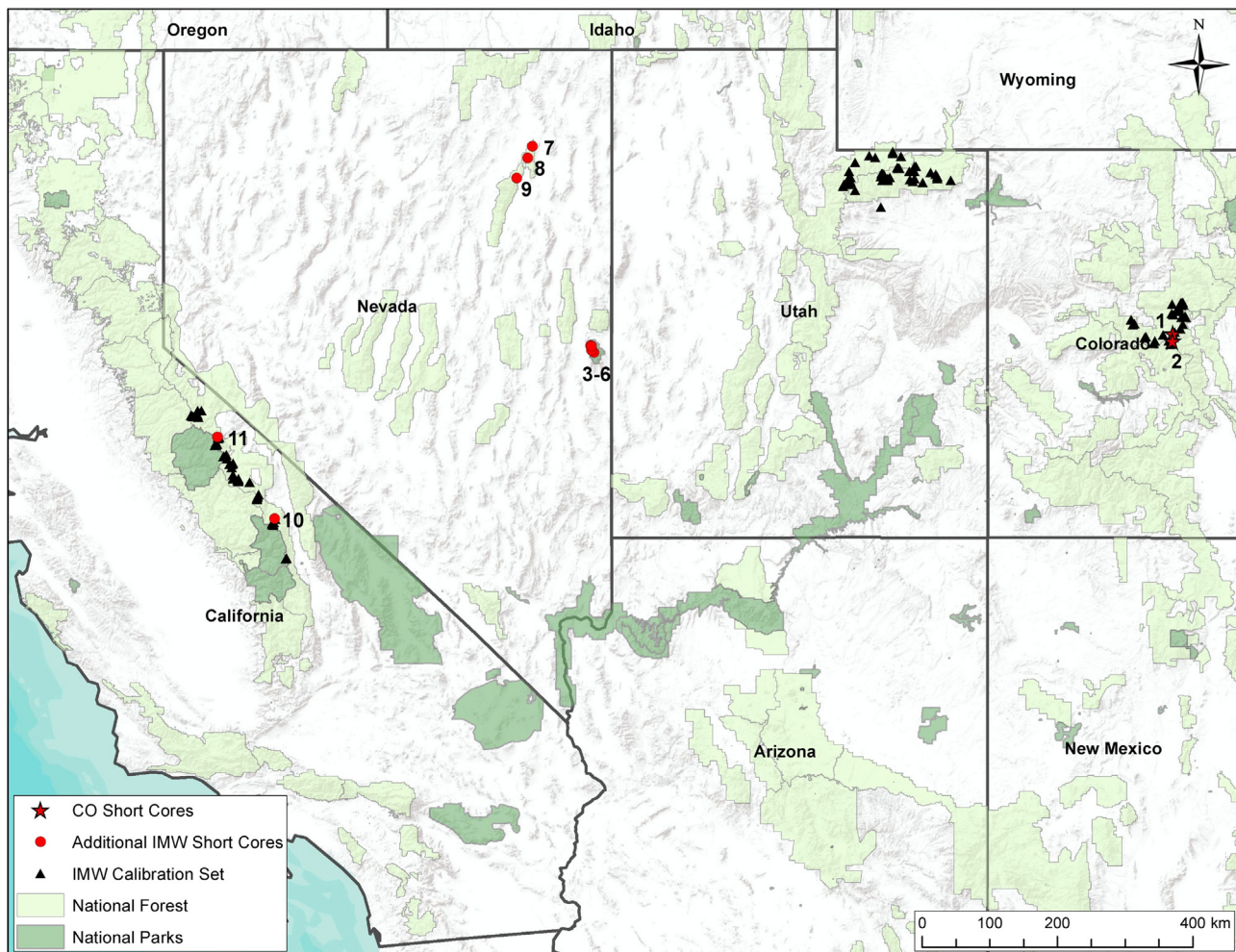


Fig. 1. Location of the lakes incorporated in the Intermountain West calibration set (Haskett and Porinchu 2014) and short core sites. The location of short core sites is depicted with numbers (see Table 1 for additional details).

indicative of a wide-spread geographic pattern in the IMW by comparing the results of this study with midge stratigraphies previously developed from high-elevation lakes in the Sierra Nevada in California and the Ruby Mountains, East Humboldt Mountains, and the Snake Range in Nevada. Analyses of these sediment archives provide insight into the spatial and temporal patterns of recent climate and environmental change in the IMW, improve our understanding of the linkage between local and regional conditions, provide a means to place recent ecological response in a longer-term context and document the profound influence of humans, via contemporaneous climate change, on aquatic ecosystems in mountain environments in recent decades.

2. Study area

Sediment cores were recovered from two alpine lakes, Linkins Lake and Grizzly Lake, located in White River National Forest in the Sawatch Range of central Colorado in July 2011 (Fig. 1; Table 1). Linkins Lake (3660m asl) is underlain by Precambrian biotitic gneisses and migmatite (Tweto et al., 1978). Linkins Lake is a small (4.55ha), moderately deep (9.25m) lake surrounded by alpine tundra with shrub willow, *Dryas* spp. and emergent grasses present along the shore. A well-defined outflow is found on the east side of the lake. Grizzly Lake (3816m asl), a small (3.10ha), relatively deep (13.7m) lake, is underlain by Oligocene andesitic lavas and breccias (Tweto et al., 1978). At the time of sampling, ~80% of the lake surface was ice covered. The resulting measurement of surface water temperature reflects the influence of the ice cover. Grizzly Lake is surrounded by alpine tundra with abundant *Dryas* spp. adjacent to the lake. The climate in the region is heavily influenced by topographic relief, which results in steep elevation gradients in temperature and precipitation. The nearest long-term climate data is available from the Independence Pass SNOTEL site (39.0754°N; 106.6117°W; 3230m asl). The SNOTEL site is located ~3km from Grizzly Lake and ~6km from Linkins Lake. Average total annual precipitation for the 1971–2000 climate normal is 84.8cm; mean January temperature is -10.54°C ; and mean July temperature is 10.95°C . Gridded air temperature data obtained from PRISM (PRISM Climate Group, 2017) provided a time series of MJAT for the interval 1900–2011 CE for Grizzly Lake and Linkins Lake. Previously developed records of recent climate and environmental change, based on sediment cores collected from high elevation lakes in the Snake Range, the Ruby and East Humboldt Mountains, and the eastern Sierra Nevada, are also incorporated in this study. Details regarding these complementary study sites are available in (Porinchu et al., 2007, 2010; Reinemann et al., 2014 and Table 1).

3. Methods

3.1. Field

Sediment cores were recovered from the approximate center of Linkins and Grizzly lakes by a messenger-operated, DeGrand gravity corer. All cores preserved the flocculent surface sediment, evidenced by little to no disturbance of the surface–water interface. The cores recovered from Linkins and Grizzly lakes both contained abundant midge tubes with a light reddish duff at the surface and measured, 21 cm and 19cm, respectively. The uppermost sediment (0–10cm) from each sediment core was extruded and sectioned in the field at 0.25cm increments using a modified version of the portable extruding device described in Glew (1988). Sediment below 10cm was sectioned at 0.5cm intervals. Sediment was stored in Whirl-paks and kept cool and dark until transported to the lab. During surface sediment collection, measurement of surface water temperature, maximum depth, pH, specific conductivity and Secchi depth were also made (see Table 1).

3.2. Laboratory

Chronologic control of the sediment cores, provided by ^{210}Pb analysis, was conducted by MyCore Scientific (Chalk River, ON). A 0.50–1.0cm sampling interval was used to constrain the chronologies for the upper portion of the cores, and a 0.50–1.5cm sampling interval was used to constrain the lower portion of the cores. Ages and sedimentation rates ($\text{gcm}^{-2}\text{yr}^{-1}$) were calculated using the constant rate of supply model (CRS), which is most robust in situations where the sediment accumulation rate changes through the core (Appleby, 2002) (Fig. 2).

The sediment cores were analyzed for sediment organic content (estimated by loss-on-ignition [LOI]) following the protocol described by Heiri et al. (2001). Sub-fossil midge analysis followed standard procedures (Walker, 2001). A minimum of 0.5mL of wet sediment was treated for 30min in a warm (30°C) 10% KOH solution and sieved through a $95\mu\text{m}$ mesh. Material retained on the mesh was backwashed into a beaker, poured into a Bogorov counting tray and sorted under a stereomicroscope at $40\text{--}50\times$ magnification. Midge head capsules were picked using forceps tweezers and permanently mounted in Entellan[®]. A minimum of 50 head capsules (Heiri and Lotter, 2001; Quinlan and Smol, 2001) were identified using a compound light microscope at $400\times$ magnification. Taxonomic determination of the sub-fossil midge remains were based predominately on Brooks et al. (2007) and a reference collection housed at University of Georgia.

Table 1

Selected limnological and environmental measurements for the study sites. Mean July Air Temperature (MJAT) values based on 1981–2010 Climate Normals obtained from PRISM at 800-m resolution. Numbers correspond to location of study sites depicted in Fig. 1. Study site abbreviations also indicated.

#	Study Sites	Latitude	Longitude	Year Cored	Elevation (m)	Depth (m)	Surface Area (ha)	Measured SWT ($^{\circ}\text{C}$)	Mean July Air Temp. ($^{\circ}\text{C}$)	Secchi Depth (m)	pH
1	Linkins Lake (LNK)	39.12876	-106.58898	2011	3660	9.25	4.55	5.64	9.1	9.25	6.55
2	Grizzly Lake (GRZ)	39.05064	-106.59427	2011	3816	13.7	3.1	1.90	8.2	13.70	7.20
3	Dead Lake (DL)	38.93574	-114.27423	2010	2916	2.00	0.1	20.15	17	Bottom	NA
4	Baker Lake (BKL)	38.95762	-114.30977	2007	3194	1.60	3.5	14.20	13.3	Bottom	6.87
5	Teresa Lake (TL)	39.00324	-114.31129	2010	3135	2.00	0.7	13.57	14.1	Bottom	NA
6	Stella Lake (SL)	39.00533	-114.31869	2011	3175	1.50	1.9	13.77	13.8	Bottom	6.98
7	Smith Lake (SMT)	41.03392	-115.09367	2010	2780	3.60	1.8	15.09	14.3	Bottom	6.41
8	Birdeye Lake (BDY)	40.91573	-115.15946	2010	2854	3.85	0.6	17.05	14	Bottom	NA
9	Cold Lake (CLD)	40.71476	-115.30172	2011	3015	6.00	0.4	10.07	13.8	5.12	7.78
10	Rocky Bottom Lake (RBL)	37.20028	-118.51722	2005	3180	10.55	2.76	15.40	11.3	7.60	8.11
11	Moat Lake (MTL)	38.05611	-119.27917	2004	3220	8.00	2.43	11.50	10.8	6.10	7.75

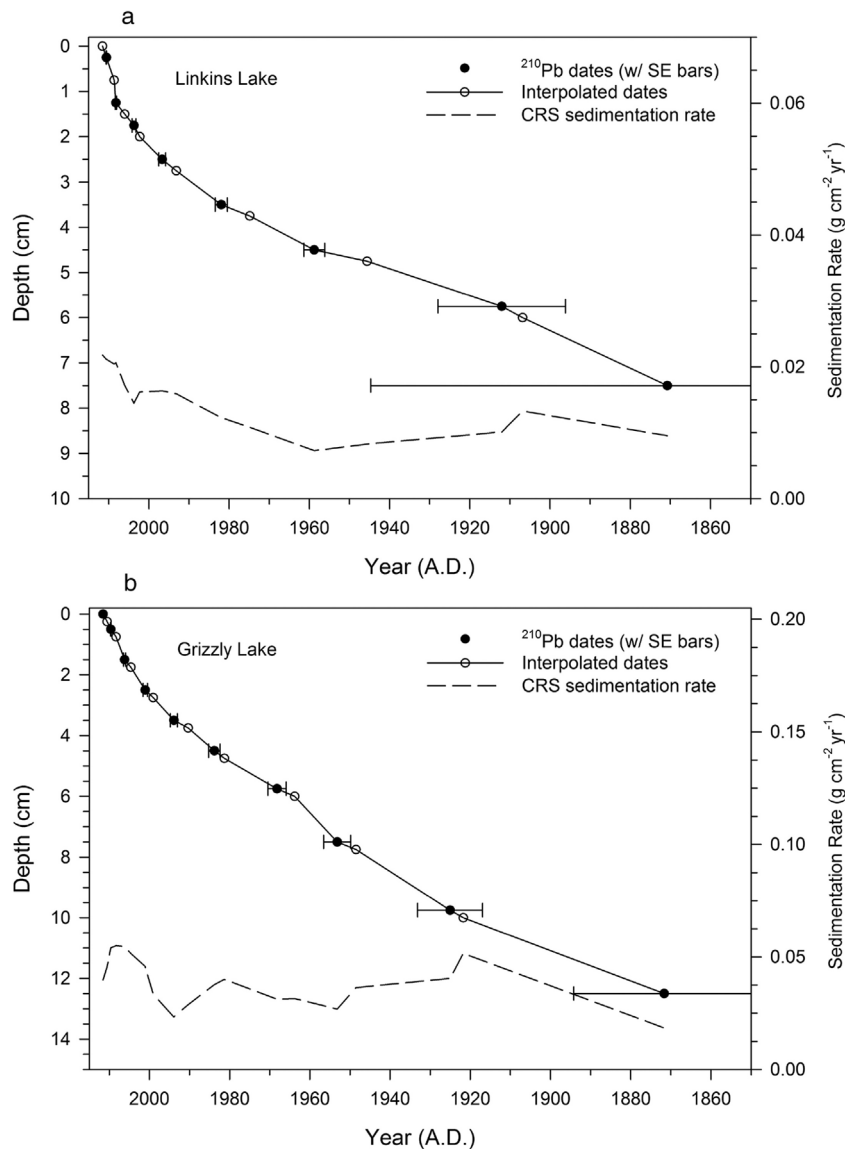


Fig. 2. ^{210}Pb chronologies for (a) Linkins Lake and (b) Grizzly Lake, utilizing the constant rate of supply model (CRS) and sedimentation rates. SE=standard error.

3.3. Statistical methods

The relative abundance of chironomid taxa was plotted stratigraphically using the Stratplot function in 'analogue' package in R (Simpson and Oksanen, 2016) with all statistical analyses based on a minimum of 45 head capsules identified/sample (Heiri et al., 2003). Optimal sum of squares partitioning, implemented by the program ZONE version 1.2 (Juggins, 1991), was used to identify zones in the midge stratigraphies. The timing and rate of faunal turnover, as a proxy of ecological change, was determined using detrended canonical correspondence analysis (DCCA) based on all taxa present in each sample, using Hill's detrending and non-linear rescaling (Hill and Gauch, 1980; Birks, 2007). DCCA, a form of multivariate direct gradient analysis, provides an estimate of compositional change, i.e. beta-diversity, with the range of sample scores capturing the total compositional change or turnover in the midge assemblages along a temporal gradient (Birks, 2007). Turnover, a measure of total compositional change over the entire stratigraphic sequence, was calculated as the difference between the highest and lowest DCCA Axis 1 values. The DCCA was performed using CANOCO version 4.0 (ter Braak and Smilauer,

2002). We calculated z-scores, based on relative abundance for *Dicoretendipes*, a thermophilous taxon commonly found in mesotrophic to eutrophic lakes with a well-defined ecology (Brooks et al., 2007; Haskett and Porinchu 2014), as a means of documenting the response of specific midge genera to environmental change during the 20th and early 21st centuries.

The calibration set used to develop the quantitative reconstructions of MJAT, which incorporates lakes from the eastern Sierra Nevada, Unita Mountains and Colorado Rockies ($n=91$), has a coefficient of determination (r^2_{jack}) of 0.61, a root mean square error of prediction (RMSEP) of 0.97°C and a maximum bias of 2.22°C (Haskett and Porinchu, 2014). The location of the lakes included in the IMW calibration set are shown in Fig. 1. The reliability of the quantitative midge-based reconstruction was evaluated by determining: 1) the total percentage of taxa present down-core that are not present in the modern calibration data set; and 2) the proportion of rare taxa present in the down-core samples. Temperature reconstructions based on subfossil assemblages are likely to be reliable if the subfossil assemblages are comprised of taxa that are well represented in the calibration set and, as a result, have robust estimates of their optima and

tolerances (Birks, 1998). A taxon is classified as rare if it has an effective number of occurrences or Hill's $N2 \leq 5$ (Hill, 1973); taxa with Hill's $N2$ values >5 in a training set can be considered well represented and will likely provide reliable estimates of temperature optima (Brooks and Birks, 2001). Sample-specific error estimates were calculated using the program C2 (Juggins, 2003). The midge-based MJAT reconstructions are compared to interpolated estimates of MJAT, obtained for Linkins Lake and Grizzly Lake, from the PRISM Climate Group (PRISM Climate Group, 2017). The estimate of MJAT values for a specific location are based on an inverse-distance squared weighting of the values of surrounding grid cell centers (PRISM Climate Group, 2017).

The composition of the subfossil chironomid assemblages preserved in the most recently deposited sediment ("top") and at the base of each sediment core ("bottom"; dating to approximately 1900 CE) at nine study sites were passively plotted in an ordination of the IMW midge calibration set constrained solely by MJAT. This approach enables an assessment of the trajectory of change between the "top" and "bottom" chironomid assemblages at the study sites relative to the modern MJAT gradient captured by the IMW midge calibration set (Haskett and Porinchu, 2014). The analysis was based on square-root transformed values of all taxa present in the subfossil assemblages and the IMW calibration set and implemented using CANOCO version 4.0 (ter Braak and Smilauer 2002). To facilitate comparison to the most updated version of the IMW training set (Haskett and Porinchu, 2014) this analysis was limited to lake sediment cores collected post-2007 CE.

4. Results

The ^{210}Pb analysis document that the sediment cores recovered from Linkins and Grizzly lakes are characterized by exponential ^{210}Pb decay profiles. The associated age-depth relationships indicate that the sedimentation rate at Grizzly Lake is slightly higher than the sedimentation rate at Linkins Lake throughout the 20th century and that sedimentation rates increase at both sites during the last two decades. (Fig. 2). The error associated with the ages increases from 0 years at the surface to 16 and 8 years for Linkins Lake and Grizzly Lake, respectively for the 20th century portion of both cores. The amount of sediment processed to yield a sufficient number of head capsules for Grizzly and Linkins lakes varied between 0.50 and 13.5 mL and 1.0 and 11.5 mL, respectively. The total number of head capsules enumerated from Grizzly Lake and Linkins Lake varied between 42.5 and 396 and 49 and 144.5, respectively. Sub-fossil midge analysis was undertaken at sub-decadal scale resolution.

4.1. Linkins Lake

A total of twenty-eight midge taxa were identified in Linkins Lake (Fig. 3a; not all taxa are plotted). The midge assemblage in Zone LNK-1 (1885 CE–2000) is characterized by the presence of *Heterotrissocladius* and *Corynocera oliveri* type and an increase in the relative abundance of a taxon associated with cool conditions, *Corynocera* nr. *ambigua*. The basal portion of this zone, which contains taxa associated with warmer, more productive lakes, e.g. *Tanytarsus* type A and *Dicrotendipes*, is also characterized by an increase in *Chironomus*, a taxon associated with the littoral of eutrophic lakes, and a decrease in *Micropsectra*. The base of the uppermost zone, LNK-2 (2000 CE–2011), is characterized by an increase in taxa associated with flowing water such as *Eukiefferiella/Tvetenia*, *Cryptotendipes* and *Limnophyes* (not shown). This zone is also characterized by an increase in temperate taxa including *Dicrotendipes*, *Microtendipes* and *Procladius* and a decrease in *Corynocera oliveri* type and *Chironomus*. The lake sediment organic matter content increases four-fold, from

approximately 4% at the base of the core to ~16% at the surface (Fig. 3a). The DCCA Axis 1 scores indicate that the largest compositional change occurs during the early during the late 20th century (~1990 CE); the remainder of the record was characterized by limited compositional change (Fig. 3a). Total turnover, measured as the range of sample scores on DCCA Axis 1, i.e. beta-diversity, for the entire sequence was 1.40. Taxon richness, which fluctuates between 9 and 17 (mean = 13.25) through the 20th century, increases to 15 in the most recently deposited sediment (Fig. 3a). The notable increase in richness that occurs between 1997 CE and 2000 CE corresponds to the large faunal turnover that occurs during this interval. The assemblage present in LNK-1 (1885 CE–2000) is dominated by *Heterotrissocladius*, *Corynocera oliveri* type and *Micropsectra*, taxa commonly associated with cold, oligotrophic lakes. This assemblage is also associated with the basal sediment.

4.2. Grizzly Lake

A total twenty-five midge taxa were identified in Grizzly Lake (Fig. 3b; not all taxa are plotted). Zone GRZ-1 (1890 CE–1970) is characterized by the high relative abundance of *Tanytarsus* type G, increasing amounts of *Tanytarsus* type B and *Paracladius*, a taxon commonly associated with cold, oligotrophic conditions, and a decrease in *Chironomus*. The assemblages present in the uppermost zone, GRZ-2 (1970 CE–2011), are more diverse with the appearance of a *Cladotanytarsus*, a taxon typically encountered in the littoral zone of warm, productive lakes. A thermophilic taxon, *Dicrotendipes*, and *Tanytarsus* type A also increase in relative abundance in GRZ-2. The lake sediment organic matter content increases five-fold, from approximately 3% at the base of the core to ~15% at the surface (Fig. 3b). The DCCA indicates notable compositional turnover in the Grizzly Lake midge assemblages during the early part of the 20th century (~1920 CE) and in the post-1980 CE interval; the mid-20th century was characterized by a muted rate of compositional change (Fig. 3b). The change in beta-diversity for the full midge stratigraphy was 0.93. Taxon richness fluctuates between 9 and 20 (mean = 12.50) through the record, peaking at 20 in 1970 CE. Richness decreases through the remainder of the late 20th century, after which it increases to 15 in the most recently deposited sediment (Fig. 3b).

4.3. Midge-based MJAT reconstruction

Application of the midge-based inference model to the subfossil chironomid stratigraphies indicate that the average inferred MJAT for the interval between 1900 CE and 2011 CE for Linkins and Grizzly lakes is 10.3°C and 8.6°C, respectively (Fig. 4 a,b). The sample-specific error estimates for Linkins Lake and Grizzly Lake vary between 0.9°C and 1.3°C and 1.1°C and 1.5°C, respectively. An assessment of the total percentage of taxa present down-core that do not appear in the modern calibration data set indicates that the subfossil midge taxa found at Grizzly and Linkins lakes are well-represented and characterized, with twenty-four of the twenty-five midge taxa present in Grizzly Lake and twenty-six of the twenty-eight midge taxa present in Linkins Lake extant in the IMW calibration set (Haskett and Porinchu, 2014). The proportion of rare midge taxa present in the down-core samples is low as reflected by the Hill's $N2$ values, with two midge taxa in Grizzly Lake (*Harnischa*, *Tanytarsus* type B) and four taxa in Linkins Lake (*Orthocladius*, *Cryptotendipes*, *Tanytarsus* type B, *Endochironomus*) having Hill's $N2$ values less than three. The PRISM-based estimates of MJAT for the same interval for Linkins Lake and Grizzly Lake are 9.1°C and 8.9°C, respectively (Fig. 4a,b). The midge-inferred MJAT values for Linkins Lake are offset and consistently higher than PRISM-based MJAT through the entire 20th century; however, the

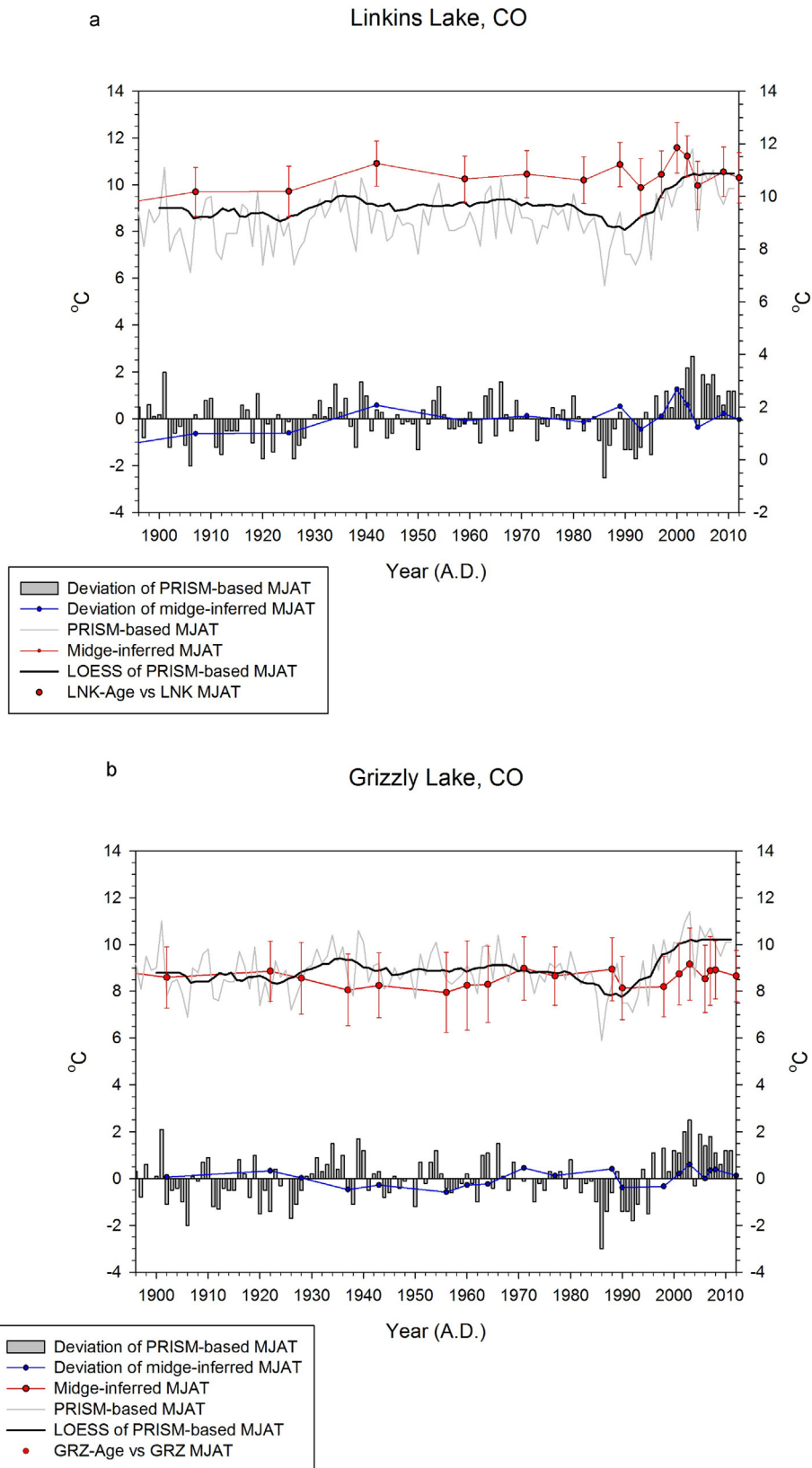


Fig. 4. Chironomid-based mean July air temperature (MJAT) reconstruction for (a) Linkins Lake and (b) Grizzly Lake for 1900 CE–2011. Points represent chironomid-based MJAT inferences (top panel) and deviations of midge-inferred MJAT estimates (bottom panel) from the long-term average. Error bars indicate the sample-specific error estimates for each midge-inferred MJAT value. Annually resolved MJAT, obtained from PRISM, is depicted in grey; the black line represents a LOWESS smooth (span=0.20) of the annual resolved PRISM data (upper panel); deviations of PRISM-derived MJAT from the long-term average over the period 1900 CE–2011 are depicted using a bar graph (lower panel).

the eight lakes in which it is extant, reveal that the post-1970 CE interval has been characterized by a dramatic increase in this taxon's abundance (1–2 SD above the long-term mean) (Fig. 6). The only site at which the relative abundance of *Dicrotendipes* has decreased during recent decades is Rocky Bottom Lake.

The ordination diagram, based on CCA, illustrates the trajectory of change in the composition of the chironomid assemblages between the early 20th century and the early 21st century in relation to the modern distribution of chironomids (captured by the IMW calibration set and constrained by MJAT) (Fig. 7). The “top” samples (~2007 CE–2012) and “bottom” samples from ~1900 CE (with the exception of Baker Lake – 1919 CE and Birdeye Lake – 1938 CE) were plotted passively with the midge assemblages present in the IMW training set (Haskett and Porinchi, 2014). In the CCA biplot the midge assemblages associated with the warmest lakes in the calibration set are positioned to the right along CCA Axis 1 and the assemblages associated with the coldest lakes in the calibration set are positioned on the left side of the ordination. The composition of the most recently deposited chironomid assemblages at seven of the nine sites have become increasingly similar to the composition of warmer, lower elevation lakes in the IMW, i.e. the trajectory of movement in the assemblages is from left to right along CCA Axis 1, reflecting the influence of MJAT. The two lakes that do not follow this trend are Teresa Lake and Grizzly Lake: the assemblages in both lakes become increasingly similar to the assemblages associated with cooler, higher elevation lakes.

5. Discussion

This study further documents the influence of climate change on the fauna present in aquatic ecosystems in central Colorado and more widely throughout the western United States (Porinchi et al., 2007; Giersch et al., 2014; Reinemann et al., 2014). The increase in taxa associated with warmer, more productive lakes such as *Dicrotendipes*, *Microtendipes*, *Procladius* and *Cladotanytarsus* in Grizzly Lake and Linkins Lake in recent decades in conjunction with the recent increases in LOI is consistent with the movement of these lakes towards more productive aquatic systems during the late 20th and early 21st centuries. The increase in the relative abundance of *Dicrotendipes* is particularly revealing as this taxon typically occurs in the littoral zone of mesotrophic to eutrophic lakes (Brooks et al., 2007). This taxon is identified as thermophilic in most modern calibration sets, including the IMW training set

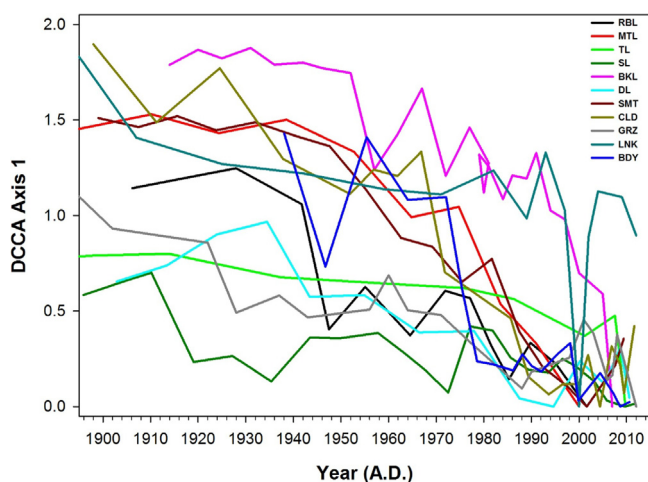


Fig. 5. DCCA of midge assemblage data from nine sites in the IMW depicting faunal turnover with the midge data constrained using dates obtained from the ^{210}Pb chronologies. Full names of study sites available in Table 1.

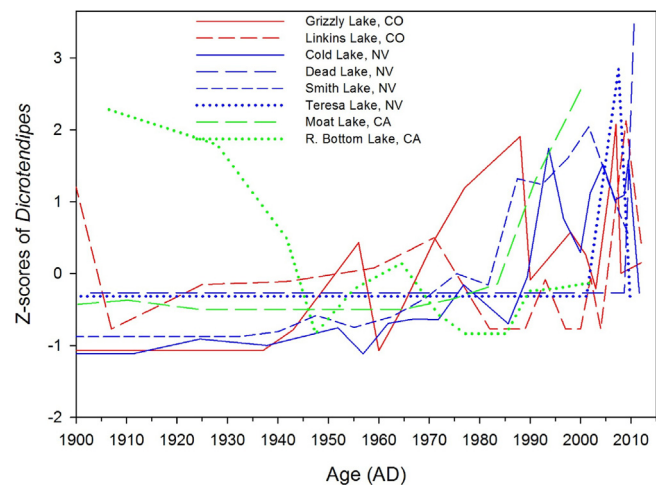


Fig. 6. Timing of increased relative abundances (z-scores) of *Dicrotendipes* in high elevation lakes in the IMW (RBL, MTL, TL, SMT, DL, CLD, LNK, GRZ).

(Haskett and Porinchi, 2014). The post-1970 CE interval is also characterized by a decrease in the relative abundance of *Chironomus*, a taxon often associated with warm, productive lakes and tolerant of the low oxygen concentrations (Wiederholm, 1983). *Chironomus* spp. have a competitive advantage in high elevation lakes that experience an extended ice-cover period due to their ability to tolerate hypoxia and extended periods of anoxia. However, as the length of the ice-cover period decreases, due to later ice-on dates and earlier ice-off dates (Magee and Wu, 2016), alpine and sub-alpine lakes will experience less severe oxygen depletion in the profundal zone, which in turn could limit the competitive advantage of *Chironomus* spp. (Granados and Manuel, 2000).

The midge-based temperature reconstructions track the relatively muted changes in MJAT that characterize much of the 20th century at Linkins Lake and Grizzly Lake. The reconstructions for both sites also capture the warming evidenced during post-1985 CE interval; however, the Linkins Lake record more clearly resolves the rapid warming that occurred between 1995 CE and 2005 CE. It is notable that the below average conditions that

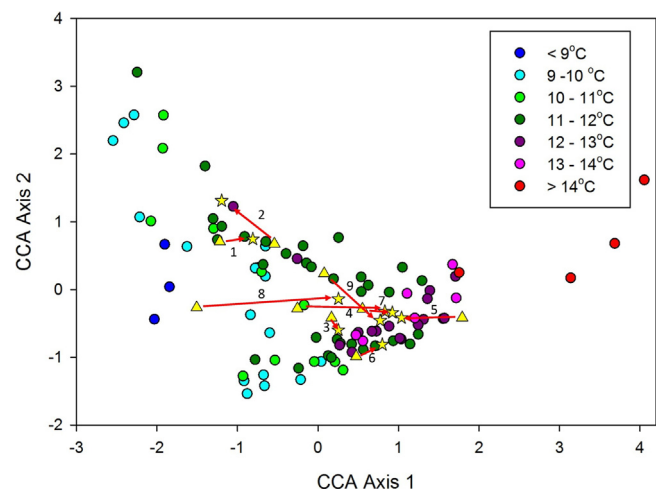


Fig. 7. CCA (constrained solely by MJAT) passively plotting fossil chironomid assemblages (top and bottom) from nine lakes in the IMW relative to the midge assemblages present in the 91-lake calibration dataset from the IMW (Haskett and Porinchi, 2014). The calibration dataset lakes are grouped according to MJAT. The arrows represent the movement through ordination space of the fossil assemblages from the early 20th century (“bottom”; triangle) to the early 21st century (“top”; star). The sites are labeled by numbers that correspond to Table 1.

typified much of the continental interior of the United States in 2004 CE, reflected in the PRISM MJAT record, is resolved in both midge-based reconstructions. Interestingly, the most recently deposited assemblages at both sites underestimate the magnitude of warming that has occurred since 2004 CE. Independence Pass was characterized by above average precipitation between 2004 CE and 2011 CE. We observed that snowfields surrounded and extended to the margin of both lakes in at the time of sediment core collection in mid-July 2011 CE. An increase in the relative contribution of snowmelt may have depressed lake water temperatures, resulting in a de-coupling of the response of midges to elevated air temperatures during this interval.

Midges are particularly sensitive to temperature (air and water) and the ecological response of midges to temperature has been well documented (Eggermont and Heiri, 2012) and demonstrated to drive the distributional changes of chironomids at the landscape scale (Walker and Cwynar, 2006; Brooks et al., 2012; Barber et al., 2013). The correspondence of the quantitative MJAT reconstructions developed for Linkins Lake and Grizzly Lake and the PRISM-based MJAT record, along with the previously developed midge-based temperature records from the IMW (Porinchu et al., 2007, 2010; Reinemann et al., 2014) support the claim that a regional-scale forcing, e.g. elevated air temperature, is driving the observed changes in the midge communities throughout the IMW. However, it is important to note that factors including habitat availability, nutrient loading, lake level fluctuations and fish introduction or stocking can influence the structure and composition of aquatic communities. For example, the elevated flux of nitrogen to high-elevation aquatic ecosystems in the Rocky Mountains and elsewhere in the western United States in recent decades has been linked to changing limnic and biotic conditions (Baron et al., 2000; Sickman et al., 2003; Wolfe et al., 2003; Moser and Ekstrom, 2010; Saros et al., 2011, 2012; Hundey et al., 2014, 2016; Spaulding et al., 2015). These recent studies clearly highlight how aquatic community composition and structure can be influenced by variations in water chemistry, lake depth and temperature and changing trophic interactions. The relative role that these processes play varies spatially and temporally, with the effects of climate and environmental change becoming increasingly important over longer timescales (Anderson et al., 2008).

The broad trends apparent in the pattern of compositional change observed in the midge assemblages preserved in the sediment recovered from lakes in central Colorado have been documented elsewhere in the IMW (Porinchu et al., 2007, 2010; Reinemann et al., 2014). For example, *Dicrotendipes* is present in eight of the eleven lakes included in this study. The increase in the relative abundance of *Dicrotendipes* in seven of the lakes in which it is currently extant in the post A.D.–1970 interval provides a distinct signal of dramatic ecological change in high elevation lakes across the IMW from the eastern Sierra Nevada to the central Colorado Rockies. In addition, the decrease in the relative abundance of *Chironomus*, observed in recent decades in Grizzly and Linkins lakes, has also been observed in the eastern Sierra Nevada (Porinchu et al., 2007b), the central Great Basin (Porinchu et al., 2010; Reinemann et al., 2014), and the Uinta Mountains (Porinchu, unpublished data) and is further indication of the alteration of the composition of benthic invertebrate communities in high elevation lakes in the IMW. The results from this study support earlier research conducted in Europe, Africa and Asia, documenting changes in midge communities in high elevation and high latitude lakes in recent decades (Granados and Manuel 2000; Battarbee et al., 2002; Solovieva et al., 2005, Eggermont et al., 2010).

The increase in taxonomic richness, which characterizes the midge communities in Linkins Lake and Grizzly Lake in recent decades, has also been observed at sub-alpine and alpine lakes

elsewhere in the IMW (Reinemann et al., 2014). The increase in richness corresponds with the apparent “movement” or change in the midge assemblages depicted in the CCA biplot (Fig. 7). Previous research assessing the influence of limnological and environmental variables on the distribution of midges in arctic and sub-arctic settings documented the existence of a relationship between taxon richness and an elevation-dependent temperature gradient, with maximum richness occurring at mid-elevation sites (Nyman et al., 2005). The ordination diagram, which captures the relationship between temperature and the composition of midge assemblages, reveals that the composition of the midge assemblages in the high elevation sites during the early 21st century are becoming increasingly similar to the assemblages associated with lower, warmer mid-elevation lakes in the IMW (Fig. 7). The chironomid assemblages in Teresa Lake and Grizzly Lake do not follow this trend. As identified above, the movement of the midge assemblage in Grizzly Lake between the early 20th and early 21st century may reflect a snowmelt-related de-coupling of the response of the midges in Grizzly Lake to elevated air temperature. The muted response of the Teresa Lake midge community may reflect the influence of local hydrology and catchment conditions. Teresa Lake is fed by a spring-water fed stream, with water temperature that is consistently at $\sim 2^{\circ}\text{C}$ through the summer (Mark, unpublished data). The depressed temperature of late summer baseflow provides additional support for the presence of a rock glacier (Van Hoesen and Orndorff (2011) and an ice-cored over-steepened protalus rampart above Teresa Lake. The composition of the midge assemblage, i.e. low alpha diversity (dominance of a limited number of midge taxa), and the de-coupling of the midge assemblage in Teresa Lake from elevated air temperatures in recent years is likely due to the influence of the melting cryosphere on lake temperature.

The effects of anthropogenically-induced global climate change can manifest at the local and regional scale. During the past 50 years, high elevation regions of the western United States have experienced an increase in surface temperatures of approximately $\sim 1.5^{\circ}\text{C}$ (Bonfils et al., 2008), with increasing rates of warming characterizing the post-1980 CE interval in Colorado (Clow, 2010). Elevated air temperature has: 1) shifted the timing of snowmelt and peak runoff to earlier in the spring (Stewart et al., 2005; Moore et al., 2007; Hidalgo et al., 2009; Clow 2010); 2) decreased the snow-water equivalent (SWE) of the winter snowpack (Mote et al., 2005; Pierce et al., 2008; Pederson et al., 2013); 3) increased the amount of rainfall relative to snowfall (Knowles et al., 2006); increased evaporation leading to severe drying in summer months (Beniston, 2003); 4) influenced the phenology of organisms (Cayan et al., 2001; Schwartz et al., 2006; Inouye 2008); and 5) decreased the spatial extent of alpine tundra (Diaz and Eischeid, 2007). Warming of this region is expected to continue through the 21st century: multimodel, multi-run ensemble simulations indicate that mean summer surface air temperature is projected to increase by $\sim 5^{\circ}\text{C}$ in the IMW under the IPCC's RCP8.5 scenario for 2070 CE–99 relative to the 1901 CE–60 base period (Stocker et al., 2013).

Sediment cores recovered from high elevation lakes in the IMW act as valuable repositories, containing and preserving the signals associated with global change. Application of a robust midge-based inference model for MJAT to the midge stratigraphies from the lakes in the mountains of eastern Nevada (Porinchu et al., 2010; Reinemann et al., 2014), the eastern Sierra Nevada (Porinchu et al., 2007), and this study indicate that changes in midge assemblages in sub-alpine and alpine lakes in the IMW track variations in air temperature during the last century. Elevated temperatures during the 20th century have been linked to shifts observed in aquatic ecosystems in alpine, arctic, and temperate sites in North America (Rühland et al., 2008). The timing of the shift in *Dicrotendipes* in the IMW is consistent with the timing of turnover in the diatom flora of

temperate lakes (i.e. 1970s) (Rühland et al., 2008, 2015; hland et al., 2008, 2015). The length of the ice-free season, the timing of ice-melt, changes in the strength or duration of thermal stratification and enhanced or prolonged nutrient suspension have been identified as the potential mechanism(s) influencing lake productivity and the ecology of high-elevation lakes (Karst-Riddoch et al., 2005; Porinchi et al., 2010; Hundey et al., 2014; Rühland et al., 2015). In terms of biological impacts of climate change, longer ice-free seasons lead to higher primary production, changes to algae and invertebrate assemblages, and enhanced nutrient suspension. Although site-specific differences in the timing and magnitude of compositional turnover in the midge assemblages exist among the IMW sites; the increase in richness and the relative abundance of warm-adapted midges, e.g. *Dicerotendipes*, together with the “upslope” movement of warm-adapted aquatic invertebrates during the 21st century, substantiates the linkage between a regional-scale forcing, e.g. elevated summer temperature, and the changes observed in midge communities throughout the IMW. The results of this research provide insight into the spatial and temporal patterns of global change-related impacts in high elevation aquatic ecosystems and help document the linkage between local conditions and drivers of regional-scale climate and environmental change in the Intermountain West of the United States.

6. Conclusion

The midge-based temperature reconstructions for Linkins Lake and Grizzly Lake, which closely track the PRISM temperature record for the 20th and 21st centuries, are able to resolve the increase in MJAT that has occurred in recent decades. The timing of faunal turnover and the similarity in the midge community response, i.e. changes the relative abundance of *Dicerotendipes* and *Chironomus* in the post-1970 CE interval provide a distinct signal and serves as marker of dramatic ecological change in high elevation lakes in the IMW in recent decades. The majority of sites analyzed using DCCA indicate that rate and magnitude of faunal turnover during the late 20th and early 21st centuries surpasses the rate and magnitude of faunal turnover during any preceding interval in the last century. The increase in midge taxa associated with warmer, more productive lakes, e.g. *Dicerotendipes*, is consistent with the movement of these lakes towards more productive aquatic systems in recent decades. A “bottom-top” analysis documents that the midge assemblages currently extant in high elevation sites in the IMW have become increasingly similar to the assemblages associated with lower, warmer mid-elevation lakes in the IMW during the last century. The correspondence of the quantitative MJAT reconstructions developed for Linkins Lake and Grizzly Lake and the PRISM-based MJAT record together with the previously developed midge-based temperature records from the IMW and the timing of faunal turnover and the similarity in the midge community response implicates a regional-scale forcing such as elevated air temperature, as driving the observed changes in the midge communities throughout this region.

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