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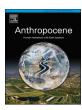
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Biostratigraphic evidence of human modification of high elevation aquatic ecosystems in the Intermountain West of the United States

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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. Dicrotendipes, 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.

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

One method of increasing our understanding of how climate variability affects the composition and structure of aquatic communities

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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 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 (3660 m asl) is underlain by Precambrian biotitic gneisses and migmatite (Tweto et al., 1978). Linkins Lake is a small (4.55 ha), moderately deep (9.25 m) 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 (3816 m asl), a small (3.10 ha), relatively deep (13.7 m) lake, is underlain by Oligocene andesitic lavas and breccias (Tweto et al., 1978).

At the time of sampling, $\sim 80\%$ 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; 3230 m asl). The SNOTEL site is located ~3 km from Grizzly Lake and ~6 km from Linkins Lake. Average total annual precipitation for the 1971-2000 climate normal is 84.8 cm; 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 19 cm, respectively. The uppermost sediment (0–10 cm) from each sediment core was extruded and sectioned in the field at 0.25 cm increments using a modified version of the portable extruding device described in Glew (1988). Sediment below 10 cm was sectioned at 0.5 cm 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 0.50–1.0 cm sampling interval was used to constrain the chronologies for the upper portion of the cores, and a 0.50–1.5 cm sampling interval was used to constrain the lower portion of the cores. Ages and sedimentation rates (g cm $^{-2}$ 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 0.5 mL of wet sediment was treated for 30 min in a warm (30 °C) 10% KOH solution and sieved through a 95 μ m mesh. Material retained on the mesh was backwashed into a beaker, poured into a Bogorov counting tray and sorted under a stereomicroscope at 40–50 \times magnification. Midge head capsules were picked using forceps tweezers and permanently mounted in Entellan $^{\circ}$. 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.

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