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NOTE

Combining lake core records with the limnologic model DYRESM-CAEDYM to evaluate lake response during the Little Ice Age and Medieval Climate Anomaly

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Abstract The Little Ice Age and Medieval Climate Anomaly are two climatic intervals within the last 2000 years that had distinctive conditions in many North American paleoclimate reconstructions. During each of these intervals, the Crevice Lake, Montana paleorecord shows distinctive limnological characteristics inferred from fossil diatoms that reflect changes in temperature seasonality and lake thermal structure. A thermodynamic-ecological model, DYRESM-CAEDYM, was used to estimate climatic conditions during these time intervals and to explore the potential for linking paleo-records with lake models to evaluate the dynamic interactions of environmental variables in influencing diatom populations over time. The model effectively simulates the timing and distribution of *Stephanodiscus* and *Cyclotella* populations evident in the modern Crevice Lake observational data. In sensitivity tests altering multiple weather inputs had a greater effect on lake temperature isotherm patterns compared with changing only single variables, which suggests the interactive effect of multiple climate variables in affecting lake thermal structure. The model simulations show the importance of the rate of climate change in affecting lake thermal structure and diatom community structure, particularly during spring and early summer. The model also provides constraints on the range of changes in solar radiation, temperature, and wind speeds that may have produced the diatom communities characteristic of the Medieval Climate Anomaly, Little Ice Age, and contemporary times.

Keywords Lakes · Paleoclimate · Rocky Mountains · DYRESM-CAEDYM · Little Ice Age · Medieval Climate Anomaly

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Introduction

The range of climate states during the late Holocene in North America was much greater than during the last century (Cook et al. 2007; Trouet et al. 2013), including during the Medieval Climate Anomaly (MCA) and the Little Ice Age (LIA), when extreme and persistent moisture and/or temperature variation (Mann et al. 2009) impacted landscape stability, biotic assemblages, and ancient civilizations (Cook et al. 2007; Diaz and Stahle 2007; Hadly et al. 1998). Current and future climate change may produce climate anomalies of similar magnitude and duration with consequent impacts on aquatic and terrestrial ecosystems, therefore, evaluating the characteristics of MCA and LIA climate can provide useful insights into climate dynamics and biotic responses under different mean states (Blois et al. 2013; PAGES 2K Consortium 2013; Woodhouse et al. 2010). In the northern Rocky Mountain region, quantitative reconstructions of climate that span the last millennium have been generated from tree-ring data (Cook et al. 2004; Pederson et al. 2011), and longer semi-quantitative estimates have been derived from other climate archives, such as lake sediments (Anderson 2013; Bracht-Flyr and Fritz 2012; Shapley et al. 2005). The majority of regional paleoclimatic reconstructions indicate a warmer climate during the MCA and cooler climate during the LIA; moisture inferences are more varied, perhaps reflecting the high spatial variability and the temporal complexity of effective moisture (Bracht-Flyr and Fritz 2012; Cook et al. 2004; Pederson et al. 2011; Steinman et al. 2014; Stevens et al. 2006).

Lakes often have highly resolved sediment records, and their physical, biological, and chemical structure responds to multiple climate variables (Fritz 2008; Saros et al. 2012; Ruhland et al. 2008). As a result, transfer functions to estimate temperature or precipitation have been generated from lacustrine biota (Eggermont and Henri 2012; Fritz et al. 2010; Ito et al. 2003; Weckstrom et al. 1997) and from geochemical variables (Ito 2001; Castaneda and Schouten 2011). Yet in most cases, the interactions of multiple factors act in concert to influence lake structure and biological communities, and these multivariate interactions are not typically captured by transfer functions (Anderson 2000; Fritz and Anderson 2013; Juggins 2013; Saros and Anderson 2015). Dynamic models are a tool for studying the complex biotic responses to climate and environmental change, both in the past and present. These models can integrate multiple simultaneously changing variables, such as nutrients, temperature, and light, and then simulate population change through time (Elliott et al. 2010; Mooij et al. 2010).

The DYRESM-CAEDYM (Dynamic Reservoir Simulation Model, Computational Aquatic Ecosystem Dynamics Model) model is a dynamic lake model that can be used to study the linkages between climate forcings, lake thermodynamics, and species assemblages (Imerito 2007; Hipsey et al. 2006a). Here we couple modeling of lake physical structure using DYRESM-CAEDYM with observed changes in biological populations through time, as reconstructed from lake sediments, in order to constrain the nature of past climate variation in the northern Rocky Mountain region and to evaluate the sensitivity of diatom populations to multiple climate variables, including temperature, precipitation, incoming solar radiation, and wind. The Crevice Lake, Montana core record (Whitlock et al. 2008, 2012) was chosen to explore this approach, because it is a highly resolved multi-proxy paleo-record, with distinct shifts in diatom community structure that can be clearly interpreted based on known ecological characteristics of the target species (Bracht et al. 2008; Interlandi et al. 1999, 2003). Thus, this study explores the potential to integrate sedimentary records and models to study the climate-environmental dynamics that drive lacustrine species interactions.

The Crevice Lake record

Crevice Lake (lat. 45.0°N, long. 110.578°W, elev. 1713 m) is located within the northern portion of Yellowstone National Park (YNP) (Fig. 1). It is a closed basin, sub-alpine, mesotrophic lake. The lake is small (7.76 ha) and 31 m deep, which results in seasonal to yearly anoxia, which aids in the formation and preservation of annual laminations (varves). The Yellowstone River runs along the eastern edge of Crevice Lake, separated from the lake by glacial till. Significant groundwater interactions probably link the lake and the river (Whitlock et al. 2008). Open forests of douglas fir (*Pseudotsuga menziesii* Franco), juniper (*Juniperus*), and pine (*Pinus*) surround the lake.

Western Montana climate is heavily influenced by the northeastern Pacific sub-tropical high-pressure system and the strength and position of the jet stream (Whitlock and Bartlein 1993). The northern portion of YNP (where Crevice Lake is located) receives the majority of its precipitation in the summer months from Gulf of Mexico moisture sources (Whitlock and Bartlein 1993).

During the winter of 2002, Crevice Lake, Montana was cored to provide a late-Holocene record of environmental change. Whitlock et al. (2008, 2012) describe this record and its interpretation in detail. The diatom record of the last 2000 year (Fig. 2) has three dominant assemblages, the *Cyclotella bodanica* Eulenstein ex Grunow 1878 -*Cyclotella michiganiana*

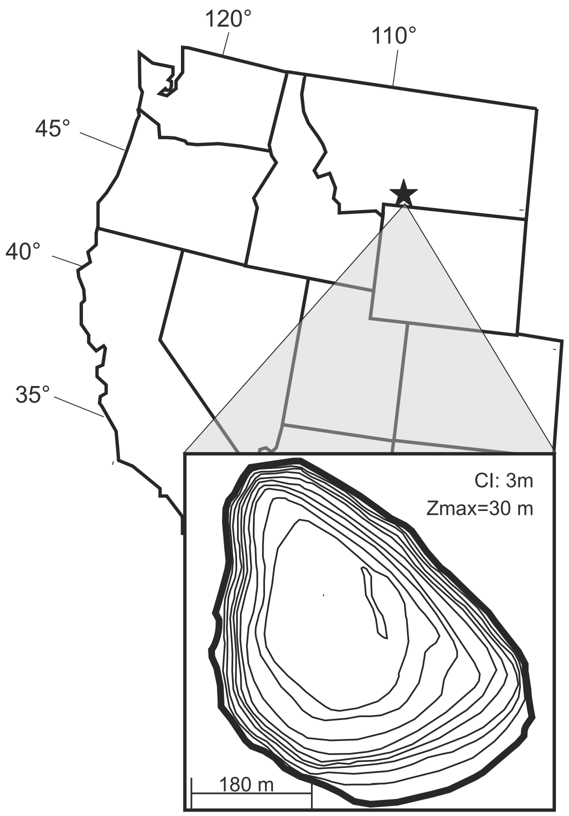

Fig. 1 Locality and bathymetric map of Crevice Lake, MT. Contour intervals are 3 m and maximum lake depth is 30 m

Skvortzov 1937 assemblage, the *Stephanodiscus minutulus* (Kutzing) Cleve and Möller 1882 assemblage, and an assemblage co-dominated by *C. bodanica* and *S. minutulus* (Bracht et al. 2008). During the MCA (~1200–800 cal year BP), the *C. bodanica* -*C. michiganiana* assemblage dominated. These two species have low phosphorus (P) nutrient requirements, dominate when nitrogen (N) concentrations are low to moderate, and in Yellowstone region lakes often bloom just above the thermocline during the summer months, when epilimnetic P concentrations are low (Interlandi et al. 1999, 2003; Kilham et al. 1996; Saros et al. 2012). Dominance of both *Cyclotella* species is favored during years with a short period of isothermal mixing in spring and extended warm summers that intensify the strength and duration of thermal stratification. Regional studies suggest that *C. bodanica* is favored during intervals when mixing depth is greater, whereas *C. michiganiana* is more abundant during warmer periods with a shallow mixing depth (Saros et al. 2012). During the LIA (~800–250 cal year BP), the *S. minutulus* assemblage dominated. *S. minutulus* is a P specialist that blooms during periods of extended water column mixing after ice-off, which regenerates P from the hypolimnion (Bradbury 1988; Interlandi et al. 1999; Kilham et al. 1996). The "modern" assemblage of the past 150 years is co-dominated by *Cyclotella bodanica* and *Stephanodiscus minutulus*. For both *C. bodanica* and *S. minutulus* to dominate the assemblage, the lake must have moderate spring mixing, as well as strong summer stratification to produce conditions favored by both *Stephanodiscus* and *Cyclotella* respectively. Although twentieth century increases in *Cyclotella* species are sometimes attributed to human-induced environmental change as a result of increased temperature and/or nitrogen deposition (Saros and Anderson 2015), the onset of the co-dominated *Cyclotella-Stephanodiscus* assemblage in Crevice Lake pre-dates the twentieth century and therefore likely reflects natural environmental variation, with growing-season climatic conditions that are intermediate relative to the MCA and LIA. Here we use these inferred changes in temperature seasonality from the Crevice Lake diatom stratigraphy in conjunction with the DYRESM-CAEDYM model to provide quantitative constraints on the range of climatic conditions that may have produced these seasonal changes in lake thermal structure and diatom community structure.

Materials and methods

Overview of DYRESM-CAEDYM

DYRESM-CAEDYM is a thermodynamic-ecological coupled model that simulates lake thermal structure, chemistry, and biology based upon weather data, surface and groundwater fluxes, lake bathymetry, and initial lake conditions (Hillmer et al. 2008; Hipsey et al. 2006b; Imberger and Patterson 1981, 1990). The complexity of the model depends upon the number of model inputs and designated outputs. The DYRESM model is one dimensional, with a layered Lagrangian scheme. It is a processed-based model, which does not require extensive calibration. CAEDYM is a nutrient, phytoplankton, zooplankton model that is capable of modeling both freshwater and marine organisms. The model is useful for forecasting the effects of nutrient

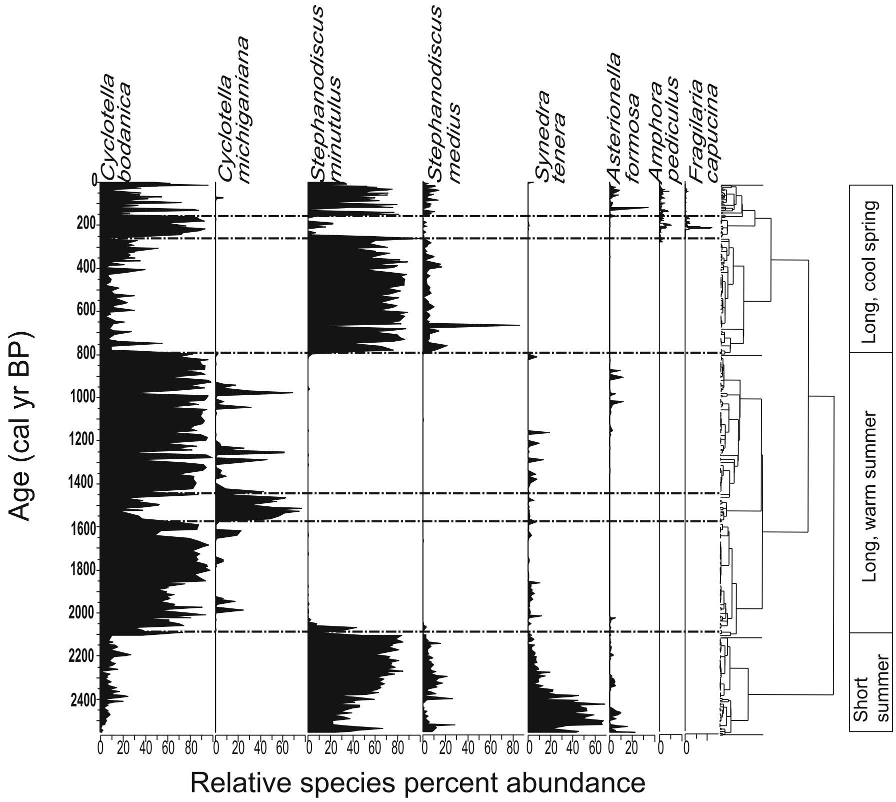

Fig. 2 Crevice Lake diatom stratigraphy, cluster analysis, and climatic interpretation (Bracht-Flyr and Fritz 2012). The *dashed lines* are zones identified by cluster analysis. The schematic portion of the diagram shows a rough interpretation of the relative depth and relative temperature, based upon the diatoms. When *Cyclotella bodanica* and *C. michiganiana* are dominant, summer seasons are protracted and warmer, in comparison to the longer and cooler springs when *Stephanodiscus minutulus* is dominant

loading, climate change, or anthropogenic influences on lakes and their associated biological communities (Stasio et al. 1996; Trolle et al. 2008). The coupled DYRESM-CAEDYM model can simulate daily changes in lake thermal structure, salinity, water chemistry, nutrient concentrations, and diatom concentrations. The model is capable of running simulations on daily or sub-daily time-steps, which is useful, because many biological indicators, such as diatoms, respond to changes in their environment at these scales.

We used DYRESM-CAEDYM in conjunction with the core record (Fig. 2) in an inverse modeling approach to quantify climate during the LIA and MCA. This involved the adjustment of model climate input variables to simulate diatom concentrations and distributions associated with the LIA and MCA periods in the Crevice Lake sediment record (Fig. 2). These climate input scenarios provide quantitative estimates of the possible dynamic combinations of temperature, incoming solar radiation, cloud cover, precipitation, vapor pressure, and wind speed characteristic of the MCA and LIA in the region. More importantly, these modeled scenarios provide insights to the dynamic interactions of these variables in affecting diatom populations. While it is not possible to derive single values for each of the variables, the inverse modeling of diatom species distributions can generate likely ranges by using a large range of test scenarios. The objective of this study was to explore whether this approach generates reasonable estimates of the climate variables that may have affected lake thermal structure in the past. The estimates provided in this paper are non-unique, and the number of model simulations was quite large, (∼300) but not exhaustive.

Weather and lake input data

A weather monitoring station was deployed at the lake in summer 2007. Continuous measurements of weather variables (June 26–October 1, 2007) and lake thermal structure (June 2007–July 2008) were collected for model calibration. We also correlated local watershed data with measurements from long-term weather stations located at Mammoth Hot Springs and Gardner, MT to determine if it was reasonable to use these longer records to extend the length of the on-site weather record to earlier in the season, thereby capturing the timing of spring ice melt. The on-site weather data were collected using a HOBO weather monitoring station that contained sensors for incoming shortwave radiation, temperature, relative humidity, precipitation, wind direction, and wind speed. Measurements for all weather sensors were taken at 3-min intervals, which were then averaged to hourly and daily measurements. The wind speed and direction sensor malfunctioned; therefore, we used daily wind speed averages from the Bozeman Gallatin Airport (NOAA). Lake thermal structure data were collected using a chain of HOBO Pro v2 water-temperature data loggers, placed at the deepest location in the lake. The thermistors were spaced at 1-m intervals from the water surface to 12 m, 2-m intervals from 12 to 20 m, and 3-m intervals to the lake bottom (31 m). Water temperature measurements were taken every 10 min and averaged to hourly and daily values. During deployment of the water temperature loggers, measurements of temperature, pH, specific conductivity (SpC), salinity, total dissolved solids (TDS), total dissolved gasses (TDG), and dissolved oxygen (DO) were taken using a HydroLab to generate the water chemistry measurements required as input data for CAEDYM. Surface water samples were also taken for measurement of total phosphorus, total nitrogen, dissolved silica, total calcium, total magnesium, total organic carbon, and other chemical concentrations (Table 1).

Table 1 Water chemistry measurements for Crevice Lake that were part of the chemistry necessary for calibration of the CAEDYM portion of the model

SC	Alk	TN	TP	Ca	Mg	Na
620	240	0.46	0.02	23.0	34.0	72.0

SC is specific conductivity, measured in μS cm^{-1}, while all other measurements are reported in mg L^{-1}. *Alk* is alkalinity, *TN* is total nitrogen, and *TP* is total phosphorus

Model setup

The DYRESM model was calibrated such that the temperature outputs were consistent with field observations, in order to confidently obtain a modern approximation of nutrient and diatom dynamics. Model calibration included both qualitative comparisons and a simple weighted least-square objective function. The meteorological variables required for calibration were either directly measured from the HOBO field station, calculated from those measurements, derived via correlations with nearby weather stations (Mammoth Hot Springs, Gardner), or taken from the Bozeman Gallatin Airport dataset. The meteorological inputs included incoming solar radiation, cloud cover, air temperature, vapor pressure, wind speed, and precipitation. The weather collection at the lake meteorological station began June 26, but many of the diatom species competitive interactions occur directly after ice-off, which occurs earlier in most years (Interlandi et al. 1999). Therefore, the 2007 weather dataset was hindcast to May 1 by using mean measurements of weather variables from Gardiner, MT, Gallatin Airfield Bozeman, MT, and Mammoth Hot Springs, WY. We extended the weather record to May 1, as this is approximately 1 week after complete ice-off (with no sign of new lake ice formation) for the 2008 spring season. The date of the ice-off transition was not included, as the stable version of DYRESM-CAEDYM available at the time of the model runs, was not capable of modeling ice. Modeling ice cover is a challenge for lake models, as the density of water is not a linear relationship, which produces model instability. Lake models that do include an ice module often require more thorough calibration and customization and instability issues can still arise.

The DYRESM model also requires detailed bathymetric information that quantifies how lake surface area changes with depth. A detailed bathymetric map and Surfer 8 were used to make these calculations. Additional model inputs include surface water inflows, outflows, and initial temperature profiles derived from the thermistor chain. The inflow and outflow variables were made negligible in the model simulations, as Crevice Lake is a hydrologically closed surface-water basin.

While DYRESM-CAEDYM is not designed to simulate two diatom species simultaneously, it is capable of modeling one freshwater diatom group and one marine diatom group simultaneously. Therefore, the marine diatom species parameters were modified to match those of the freshwater diatom group, thus allowing two freshwater diatom groups to be modeled simultaneously. The ability to access the species parameter files allows for such customization and the application of the model for many different species or groups. A second issue is that the standard distribution of DYRESM-CAEDYM can model freshwater and marine diatoms, but these modeled groups are not genera or species specific. To simulate the two specific taxa of interest, parameters were changed such that one algal group modeled *Stephanodiscus* and the other algal group modeled *Cyclotella*. Ecological parameters for *Stephanodiscus* and *Cyclotella* were either taken directly from the literature or estimated based upon the known autecology of the species.

To estimate the range of climatic conditions consistent with the nutrient and mixing requirements that fostered dominance by *Cyclotella*, *Stephanodiscus*, or both, we generated different weather scenarios that produced the lake conditions necessary for *Cyclotella* (MCA) or *S. minutulus* (LIA) dominance or coexistence between the two species (contemporary). The contemporary environment was modeled with the meteorological measurements to see how well the model simulates modern conditions. Nearly one hundred simulations were run to test the model sensitivity to certain variables, such as temperature, mixing depth, diatom concentration, etc. Each parameter was varied within the measured ranges while keeping all other variables and parameters constant. The weather inputs for the LIA and MCA simulations were generated through an inverse copula approach, which relies upon the co-variance of the measured weather inputs. To quantitatively compare the Crevice Lake core record with the model-derived abundance of *Cyclotella* and *Stephanodiscus* in the LIA and MCA intervals, the total biomass was calculated for each species for daily and model duration totals. Modeled species percent abundances were then calculated for direct comparison to the lake core species abundance record.

Results

Field data

The meteorological station data at Crevice Lake have air temperatures that differ slightly from the nearby Gardiner, MT and Mammoth Hot Springs, WY weather stations. Yet the stations measurements co-vary, and the differences among them are small and likely not significant, particularly in terms of affecting diatom communities. Average daily Crevice Lake temperature ranges from 1.8 to 26.5 °C, average relative humidity from 21 to 88 %, pressure 817–838 mbar, solar radiation 70–313 W m^{-2}, and precipitation from 0 to 17 mm day^{-1}. Average daily values are shown in Fig. 3.

The thermistor field data for June 26, 2007–October 1, 2007 are shown in Fig. 4. The lake temperatures display a typical dimictic lake stratification pattern, with the development and deepening of the thermocline throughout the summer. The lake thermal structure begins to weaken toward the end of the meteorological record during the transition from summer to fall. The DYRESM temperature outputs are shown in Fig. 4. As part of the model calibration, the thermistor data from June 26 to October 1, 2007 were compared to model simulations of lake thermal structure. To confirm proper model setup, a weighted least-square objective function was used to determine that thermodynamic parameters did not affect model simulation temperature outputs. The model effectively simulates the timing and development of the thermocline. The modeled temperature output and the field thermistor data are within 2.5 °C, at any given depth, throughout the entire season (Fig. 4).

Model simulations

We modeled three different suites of climate/lake temperature scenarios, including one for each dominant diatom mode: modern, LIA, and MCA. Table 2 shows the average values for all the climate variables from both the meteorological station and for the model simulations. This table shows that the range of individual climate variables averaged over the entire growing season is not substantially different from one scenario to the next; however, the values vary considerably among scenarios for the spring and early summer season.

Assuming that modern climatic conditions are conducive to lake conditions that foster the observed codominance of *S. minutulus* and *C. bodanica* in the surface sediments of Crevice Lake (Bracht et al. 2008), we used these conditions and the June 26–October 1 weather data as a control. This scenario produced diatom concentration patterns that show *Stephanodiscus* within the eplimnion during June and high *Cyclotella* concentrations along the thermocline throughout June and July. This pattern replicates

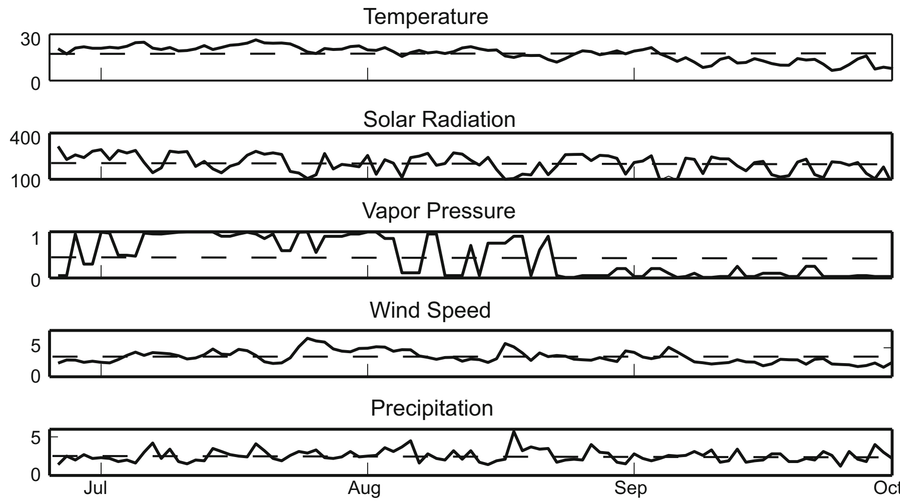

Fig. 3 Meteorological station data for the summer of 2007. The weather station included HOBO sensors for **a** temperature (C), **b** incoming solar radiation (W m^{-2}), **c** vapor pressure (mbar), **d** wind speed (m s^{-1}), and **e** precipitation. The wind direction/speed senor malfunctioned; therefore, wind speed data were obtained from Gallatin Airport. The station was located on the southeast side of the lake

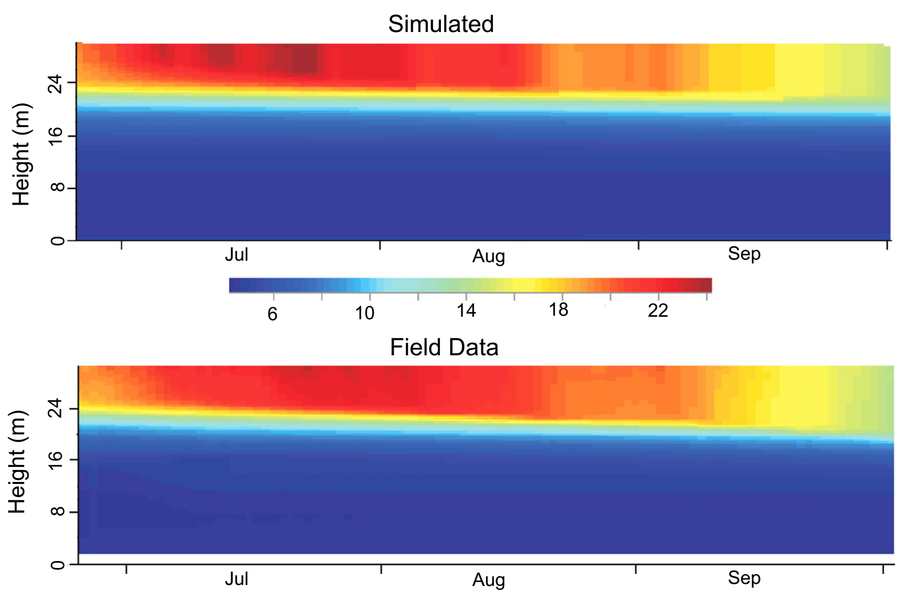

Fig. 4 Crevice Lake temperature results from both the calibrated DYRESM-CAEDYM modern model and the measured thermistor data. Results show that the modeled temperatures closely follow water temperatures, the rate at which the temperatures change, and the depth of the thermocline. The ability of the model to accurately reflect changes in the thermocline is important, as the dominant species assemblages reflect the timing, development, and relative strength of the thermocline. Surface height is the height from the lake bottom

observed diatom dynamics in other Yellowstone region lakes (Interlandi et al. 1999; Kilham et al. 1996).

As many diatom species interactions occur immediately following ice-off, and because this period was not represented in the field measurements at the lake weather station, the meteorological file (June 26–October 1) was replaced with the modeled dataset, extending the meteorological data from May 1 until October. Hundreds of model runs, with a wide range of variation in weather inputs, produced outputs consistent with modern lake dynamics. The contemporary simulation using the extended meteorological data file shows strong thermocline development by early June (Fig. 5) and summer lake temperatures similar to those observed in the 2007 thermistor data. The spring portion of the simulation shows lake thermal profiles

Table 2 Range of values of climate variables for May 1–October 1

Scenario	SW	CL	Temp	VP	Wind
June 26–October					
Met. Station	199.5	–	17.4	3.4	2.5
Contemporary	199.5–200.2	.44–.47	15.9–18.5	3.4–3.4	2.5–2.6
LIA	189.2–196.4	.35–.46	15.3–15.6	3.2–3.4	2.5–2.7
MCA	199.8–200.4	.31–.45	17.0–17.4	3.2–3.4	2.5
May 1–October 1					
Contemporary	190.5–205.7	.40–.47	15.0–17.0	2.8–3.4	2.7
LIA	179.3–189.3	.44–.54	13.9–15.1	3.4–3.6	3.1–3.3
MCA	206.3–213	.29–.46	17.6–17.9	3.1–3.6	2.6–3.1
May 1–July 9					
Contemporary	181.7–219.7	.43–.47	14.4–18.1	3.0–3.7	2.8–3.3
LIA	163.8–178.9	.45–.65	11.4–13.7	3.2–3.91	3.8–4.2
MCA	224.6–238.7	.30–.53	18.7–19.3	3.0–3.8	2.7–2.8

The meteorological station data are the average of each variable from June 26–October 1. *SW* is shortwave radiation (W m^{-2}), *CL* is cloud cover (%), *Temp* is temperature (°C), *VP* is vapor pressure (hPa), and *Wind* is wind speed (m s^{-1}). The meteorological station averages range from June 26–October 1

similar to those measured during the 2008 ice-off transition and early spring. The model outputs for *Stephanodiscus* show high concentrations from May to June, which quickly diminish, and the outputs for *Cyclotella* show moderate concentrations near the thermocline through August.

LIA model outputs of temperature and diatom concentrations are shown in Fig. 5. The greatest deviation of the climate variables from modern values occurs during spring and early summer (May 1–July 9); deviations occur at other times but are not as pronounced. Values for incoming solar radiation and air temperature are less than modern averages, while cloud cover, wind, and vapor pressure were greater (Table 2). The isotherm plot shows that strong thermocline development was delayed until mid-July, although weak thermal structure is present earlier in the season. The diatom output revealed high concentrations of *Stephanodiscus* in the epilimnion during May and June, with significantly lower abundance of *Cyclotella* occurring near the thermocline during the summer.

MCA model outputs of temperature and diatom concentrations are shown in Fig. 5. Again, deviations from the control are most apparent in the comparison of values for the May 1–July 9 period, rather than the May 1–October averages. The isotherms show strong and early development of a thermocline, which is well established by mid-May. The simulated diatom concentrations show high concentrations of *Cyclotella* from May to August along the thermocline, with almost no concentration of *Stephanodiscus* throughout the simulation. The majority of diatom growth occurs along the thermocline during May, June, and July (Fig. 5).

To quantitatively compare model results to the Crevice Lake diatom record, we calculated the total mass/volume of each genus for the length of the model simulation. Table 3 shows the percent dominance for the two modeled genera in each series of simulations. The simulated LIA percentages show that on average, *Stephanodiscus* comprises over 90 %, while *Cyclotella* is less than 10 %. Conversely, the simulated MCA percentages are approximately the reverse for both species. The simulated *Cyclotella*/*Stephanodiscus* percentages match the species distribution seen in the fossil diatom record extremely well.

Sensitivity analysis shows that the diatom concentration outputs were not particularly sensitive to changes in the thermodynamic parameters (such as light extinction coefficient) of the model, but were sensitive to the changes in ecological parameters, such as the light saturation coefficients, nutrient half saturation constants, and internal nutrient concentrations. Figure 6 shows typical results of the sensitivity analysis where changes to the thermodynamic parameters have no effect on calibration statistics, such as the root mean square error, while the ecological parameters have varying effects. The lack of calibration sensitivity to physical parameters is expected due to model design, as DYRESM is a process rather than parameter-based numerical model (Imerito 2007). The half saturation concentrations and internal silica concentration are extremely important in species resource competition and exert direct effects on the

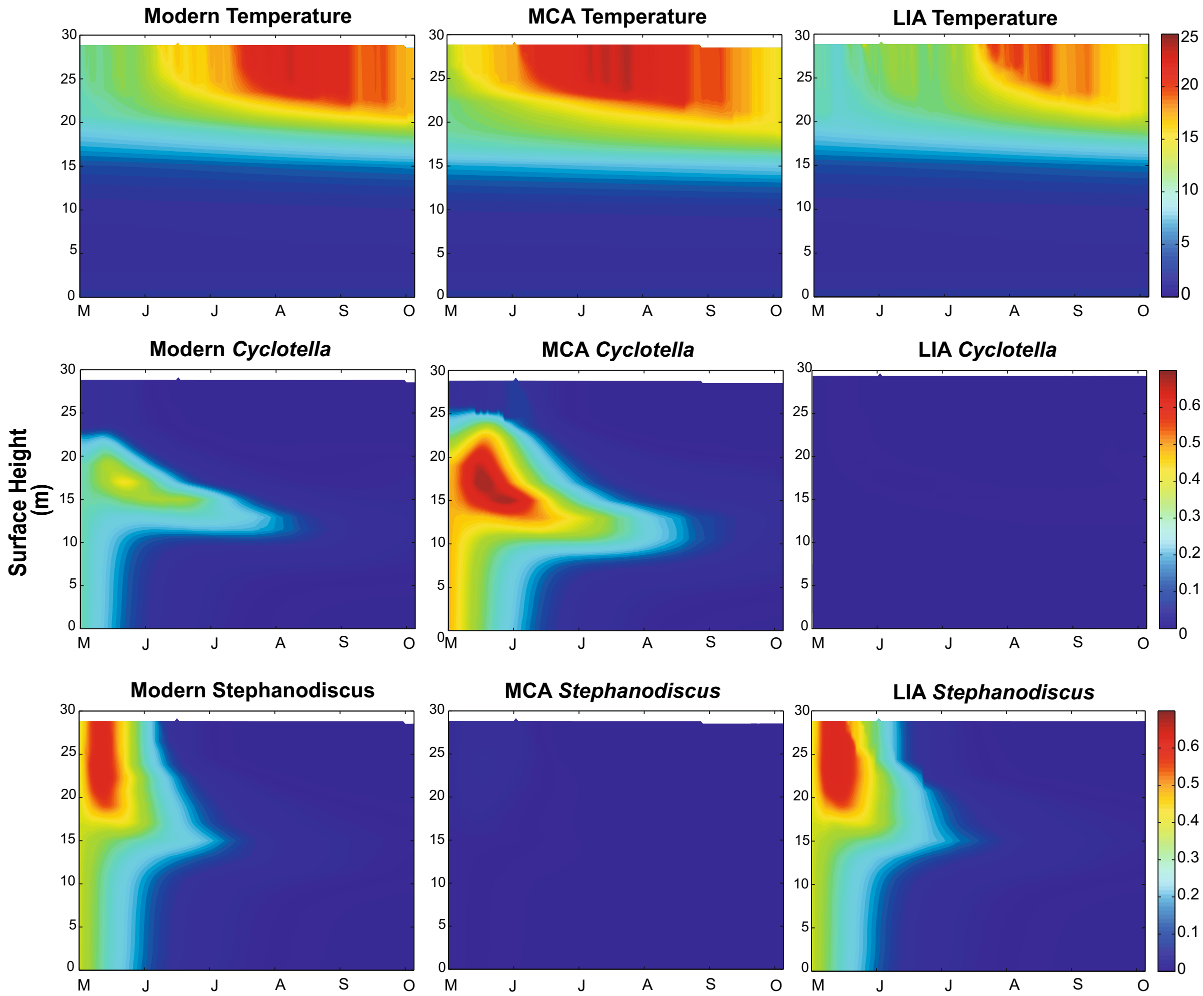

Fig. 5 Diatom concentrations and temperature profiles for three modeling scenarios, the contemporary mixed diatom assemblage, the LIA *S. minutulus* dominated assemblage, and the MCA *Cyclotella* dominated assemblage. The diatom and isotherm diagrams shown are typical model outputs for the MCA and LIA simulations. The MCA temperature profile shows strong development of the thermocline, while the LIA temperature profile shows hindered thermocline development. *Cyclotella* and *Stephanodiscus* are present in both the MCA and LIA simulations, but to use a similar scale in all simulations, it appears that only one species is present in either the MCA or LIA. Surface height is the height from the lake bottom

composition of diatom communities (Grover 1997; Tilman et al. 1982). Therefore, it is not surprising that changing these variables within the model would lead to changes in the diatom outputs.

Discussion

After confirming that the model could simulate the timing and distribution of *Stephanodiscus* and *Cyclotella*, as evident in the modern Crevice Lake observational data, we tested the sensitivity of the model to individual weather variables. Substantial changes in individual weather variables either did not produce clear changes or did not yield reasonable water-column distributions of temperature, *Stephanodiscus*, or *Cyclotella*. Altering multiple weather inputs had a greater effect on isotherm patterns compared with changing only single variables. This suggests that alterations in only one component of the climatic system are not likely to have produced the changes in lake dynamics during the LIA or MCA. It

Table 3 Percent values calculated from the contemporary, LIA, and MCA model simulations

Scenario	*Stephanodiscus* (%)	*Cyclotella* (%)
Contemporary	57	43
LIA	92	8
MCA	11	89

Percent values are calculated from the total volume of each species for the length of each simulation. This was done to quantitatively compare model results to the *Stephanodiscus* and *Cyclotella* species percentages from the Crevice Lake diatom core record. Figure 2 shows that for the LIA *Stephanodiscus* frequently constitutes ~80–90 %, and for the MCA, *Cyclotella* is frequently over ~80–90 %

also points to the interdependence of multiple climate variables in affecting lake thermal structure and diatom species composition, rather than simply temperature alone (Anderson 2000; Fee et al. 1996). The climatic variable estimates from the model are not exclusive; changing different variables by different amounts may produce model results similar to those shown. The model simulations also showed that the rate at which weather variables, such as air temperature, changed was as important in affecting lake temperatures as the magnitude of those air temperature changes. This is especially evident in Table 2, as the average for the modern, LIA, and MCA are not very different, but the rate at which the lake warms from ice-off to early July greatly influences the distribution of the diatom genera. In other words, slow warming generates *Stephanodiscus* dominated assemblages, while rapid warming of a similar magnitude produces *Cyclotella* dominance. This implies that the rapidity of change in seasonality is important in understanding lake response during the LIA and MCA.

The LIA simulation produces a delay of thermocline development until mid-July, the mixing of *S. minutulus* deep in the water column well into the

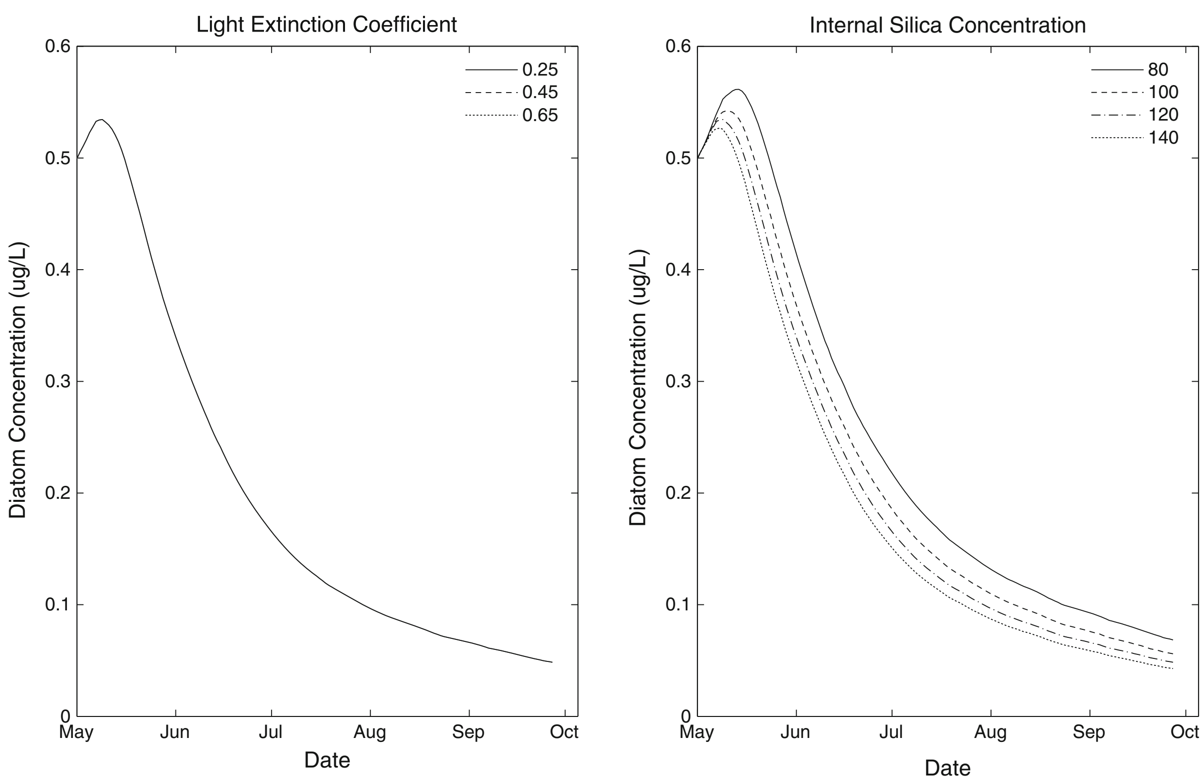

Fig. 6 Example results of the parameter sensitivity analysis for thermodynamic and ecological parameters on diatom concentrations. Thermodynamic parameters, such as the light extinction coefficient, did not have an impact on model results due DYRESM model design as a process, not parameter based design. CAEDYM (the ecological module) is parameter based, and as such, changes to those parameters did have some impact

summer, and low concentrations of *Cyclotella* along the thermocline throughout the summer (Fig. 5). In the Crevice Lake core record, *Cyclotella* is always present in low concentrations when *S. minutulus* is dominant; thus the model outputs are consistent with observational data. In general, model runs that produced diatom distributions consistent with LIA assemblages had lower solar radiation, lower temperature, and increased wind speeds. Table 2 summarizes the ranges, averaged over 3 different time intervals, that produced *Stephanodiscus, Cyclotella,* or co-dominated assemblages.

The MCA isotherm plot represents years with an early and strong development of the thermocline. Generally, model runs that produced diatom distributions consistent with MCA assemblages had higher solar radiation, higher temperatures, and decreased wind speeds (Table 2). Again, these weather values are non-unique due to the inverse modeling approach.

Table 3 shows the average species percent values, based on modeled biomass, for *Stephanodiscus* and *Cyclotella*, which are in accordance with the Crevice Lake diatom core species counts. The concordance shows that it is possible to model species or genera-specific outputs within CAEDYM. The success of our simulations in modeling the Crevice Lake record was facilitated by two characteristics of the lake and its flora. First, the diatom flora is dominated by a small number of species, whereas a more diverse flora with higher evenness might be a more difficult modeling target. Secondly, the dominant taxa in the Crevice Lake record have different and well-defined autecological tolerances. In general, this approach likely has the highest probability of success for lakes that have only a few dominant species or genera and where those taxa are significantly different in their ecological traits.

In general, the largest differences between the modeled climate variables characteristic of the LIA versus those of the MCA are for the spring and early summer period (May 1–July 9). The climate of the seasonal transition from spring into summer clearly dictates whether or not extended water column mixing produces the elevated phosphorus concentrations necessary for blooms of *Stephanodiscus*, and in the Yellowstone region lakes, internal nutrient loading is likely to be the dominant influence on diatom species composition (Kilham et al. 1996). A likely secondary influence on nutrient concentrations and diatom assemblages in regional lakes is spring runoff and the associated nutrient loading. Prior research in the Yellowstone region showed a correlation between fluctuations in lake total nitrogen concentration and winter precipitation, suggesting the importance of snowmelt and spring runoff (Theriot et al. 1997). The model does not account for external nutrient loading, but higher N would likely favor spring-blooming diatom taxa and reduce the biomass of *Cyclotella* (Kilham et al. 1996). Overall the MCA flora differs more relative to modern than the flora of the LIA (Fig. 2), and the model results suggest that this resulted from recurrent rapid warming during spring and early summer, which set up stratification early in the season and precluded development of the spring-blooming *Stephanodiscus*. In any case, the sensitivity of diatom assemblages to changes in spring to early summer seasonality rather than growing season averages is a consistent feature of the seasonal dynamics of temperate and boreal region lakes (Bradbury 1988; Kilham et al. 1996; Talling et al. 2005; Koster and Pienitz 2006).

The sensitivity analysis results (Fig. 6) are similar to those of Schladow and Hamilton (1997), who found that phytoplankton phosphorus uptake kinetics, minimum internal concentration, the half saturation constant, and the maximum uptake rate had the largest effect on chlorophyll a concentrations within model simulations. Schladow and Hamilton (1997) also found that phytoplankton growth rates, respiration, and mortality affected chlorophyll a concentrations. While chlorophyll a concentrations include all phytoplankton groups, diatom concentrations should show patterns similar to those found in the study. Model sensitivity to parameters not considered also may alter the diatom concentration outputs, such as model sensitivity to re-suspension of nutrients from the hypolimnion. Increased understanding of model response to such parameters would increase confidence in interpretation of model outputs.

The use of DYRESM-CAEDYM with the Crevice Lake core record has several limitations. The most notable limitation is that this, like most multiple variable numerical models, is an inverse modeling approach, with non-unique solutions. Another limitation is the methodology for generating weather datasets. Lack of site-specific variables for the model and short datasets (less than 1 year) prevented use of current weather generators. Therefore, the climatic variable estimates may be greatly improved with the use of a more sophisticated weather generator. Limited measurement of lake physical and thermal structure or the availability of climate data may also preclude effective model calibration and contribute to uncertainty, particularly in situations where the magnitude or nature of change in the past is very different from that in the instrumental record. In this study, the thermistor and weather data were not available during the 2007 ice-off transition; logistics prevented instrument deployment during this time, so the 2008 ice-off data were used instead. The absence of an ice module in the model also prevented evaluation of species concentrations during the ice-off transition. As such, the late-fall and winter seasons are not evaluated, although the severity of the fall and winter seasons may significantly impact the lake watershed and lake biota (Theriot et al. 1997; Saros et al. 2010). In other regional lakes, for example, paleodata suggest the input of nutrients in snowmelt or from watershed glaciers may significantly affect lake dynamics (McKnight et al. 1990; Wolfe et al. 2003; Saros et al. 2010). Therefore, the model only provides climatic parameter estimates during the ice-free season, but does not provide a complete seasonal or yearly estimate of climate. Finally, differences in temporal resolution of models and data may limit the applicability of this approach. The Crevice Lake diatom record is highly resolved and was sampled at sub-decadal resolution throughout most of the time span of the record, but slow accumulation rate sites, where samples integrate large intervals of time, may be more problematic. Despite these multiple potential limitations, the combination of lake core records with the DYRESM-CAEDYM model shows considerable promise in the analysis of paleoenvironments and therefore for understanding a broader range of environmental dynamics than is observed in instrumental data.

Conclusions

The exploration of the Crevice Lake diatom record suggests that DYRESM-CAEDYM can be successfully used in combination with paleolimnological data to explore the nature and magnitude of climate change in the past. In the Yellowstone region, the model suggests that lower temperatures than modern, along with the associated climate variables of increased cloud cover and lower incoming solar radiation, interacted to affect lake thermal structure during the LIA, with temperature depressions several degrees lower than modern. The inverse set of conditions characterized the MCA, with temperatures and incoming solar radiation higher than modern. Thus, model-based sensitivity tests help to constrain the climate conditions driving limnological change in lakes of the Yellowstone region during the LIA and MCA.

The interactive use of paleolimnological data with dynamic models might be productive with other existing paleolimnological data sets, such as to explore the relative importance of warming relative to atmospheric nitrogen deposition in affecting planktic diatom community structure (Saros and Anderson 2015) or the observed twentieth century species shifts in high-latitude lakes (Smol et al. 2005). Further development of modeling approach applied here could include modifications to accommodate other diatoms, algae, or aquatic species in the model simulations, or modeling watershed-lake interactions that affect nutrient dynamics. While this study is an initial examination of the technique, the approach shows promise for evolving our understanding of how aquatic ecosystems have responded to past environmental change and for constraining the magnitude of that change.

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