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# The Influence of Basin Morphometry on the Regional Coherence of Patterns of Diatom-Inferred Salinity in Lakes of the Northern Great Plains (USA)

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## Abstract

Sedimentary diatom profiles from saline lakes are frequently used to reconstruct lakewater salinity as an indicator of drought. However, diatom-inferred salinity (DI-salinity) reconstructions from geographically proximal sites in the Great Plains (USA) have yielded disparate results. This study explores how physical changes in lake habitat resulting from drought may affect climate inferences from salinity reconstructions. Differences in relationships among drought, lake-level change, and diatom community structure over the last century were examined for three saline lakes in the northern Great Plains with dissimilar DI-salinity records. At each site, models were developed relating available planktic:benthic (P:B) habitat area to lake-level change, and models were compared with instrumental drought records and fossil diatoms to understand how drought conditions were recorded in sedimentary diatom assemblages. The degree to which DI-salinity tracked drought variation was affected by site-specific physical characteristics that influenced the relationship between

lake-level change and P:B habitat zonation within each lake. Moon Lake showed the strongest correlation between drought and DI salinity, although this relationship was weaker during wetter conditions, as highstands resulted in a larger influx of benthic diatoms. At Coldwater Lake, a dual-basin system, P:B varied depending on lake level, which apparently reduced the correlation between DI-salinity and drought. At Lake Cochrane, the simplest and freshest of the three basins, the P:B of fossil diatoms was a better proxy for drought than DI-salinity. The integration of additional ecological characteristics into interpretations of paleoclimate records, particularly for biologically based proxies, may improve reconstructions of regional patterns of climate variation.

**Keywords:** benthic, diatom, drought, lake-level change, planktic, salinity

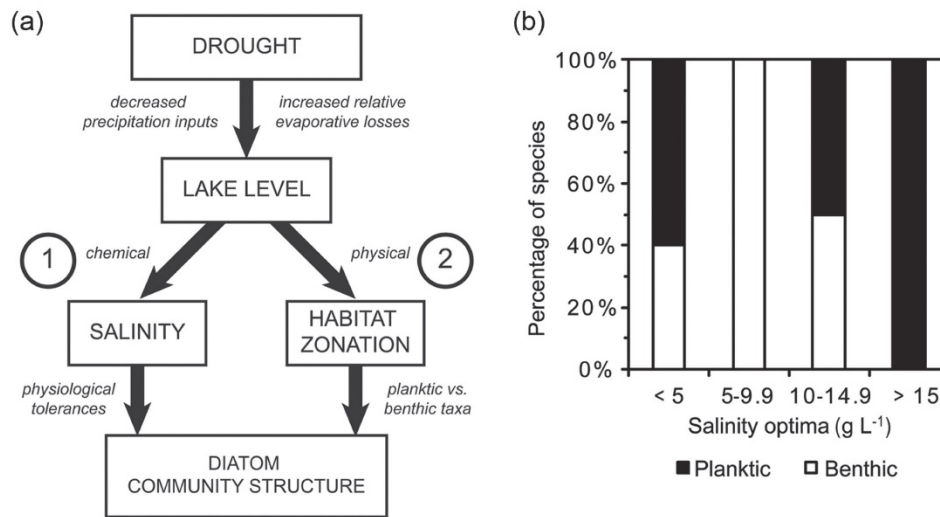
## Introduction

A key step in extrapolating single-site paleoclimate reconstructions to infer regional patterns of change is to assess the degree of synchrony in responses across lakes within a geographic region. Limnologists investigating contemporary dynamics commonly measure synchrony to evaluate the drivers of limnological change (Baron and Caine, 2000; Kratz et al., 1998; Livingstone, 2008; Magnuson et al., 1990; Rusak et al., 1999). A high degree of synchrony among lakes in limnological change through time suggests the importance of large-scale forcing of those responses, whereas low synchrony suggests a larger role for localized influences. In these studies, physical and chemical parameters are commonly moderately to highly coherent, while many biological parameters often exhibit low coherence among sites, likely due to the overriding effects of ecological processes within lakes (Kratz et al., 1998).

Spatial synchrony among biologically based paleolimnological reconstructions is commonly low to moderate in a variety of regions around the world, including Arctic (McGowan et al., 2008; Perren et al., 2009), alpine (Hobbs et al., 2011), and boreal lakes (Velle et al., 2005). For example, trophic reconstructions based on algal pigments in prairie lakes show asynchrony across systems in response to large-scale drivers (Patoine and Leavitt, 2006). In order to understand the sources of these site-specific differences in the pattern of change and ultimately to improve our interpretation of paleolimnological records, additional ecological information needs to be incorporated into reconstructions that are based on biological proxies. Recent paleolimnological research recognizes the need to better integrate ecological processes into biologically based reconstructions (Brodersen et al., 2004; Saros, 2009; Saros and Fritz, 2000; Sayer et al., 2010), and we focus here on applying these principles to diatom records in saline lakes of the northern Great Plains.

Past drought conditions in semi-arid grassland ecosystems have been reconstructed from sediment records of closed-basin saline lakes based on changes in fossil diatom assemblages driven by lakewater salinity variations. Drier periods result in reduced precipitation and decreased water levels, causing concentration of solutes and increased salinity, whereas wetter conditions result in dilution of solutes, causing decreased salinity (Gasse et al., 1997; figure 1a – pathway 1). However, diatom-inferred salinity (DI-salinity) records show low to moderate coherence when compared across sites in the Great Plains (Fritz et al., 2000), and at present, the cause of these discrepancies is unresolved. Evidence suggests

that neither differences in lake–groundwater interactions (Jovanelly and Fritz, 2011) nor local variation in climate (Benson et al., 2000) are likely responsible for these differences. Therefore, while we acknowledge that hydrologic setting can play a critical role in the response of closed-basin lakes to drought, we focus here on other factors that may influence biological responses within lakes to climatic change.



**Figure 1.** (a) Pathways by which drought influences diatom community structure in lakes. Drought may influence diatom community structure via chemical changes in lakewater chemistry (pathway 1) as well as via physical changes in habitat zonation within the lake (pathway 2). (b) Proportion of planktic and benthic taxa in relation to salinity optima in the original calibration set for the Great Plains (USA; Fritz et al., 1991).

In closed-basin saline lakes, not only salinity but also lake levels can fluctuate substantially in response to drought (Gasse et al., 1997). Because climate-driven lake-level variation is commonly highly synchronous across lake ecosystems (Magnuson et al., 1990), this response to drought has the potential to produce a regionally coherent signal that is captured by the diatom community. However, changes in lake level affect diatoms via physical changes that alter habitat zonation within the lake (figure 1a – pathway 2), and this variation in littoral versus pelagic habitat is a function of the lake’s bathymetry (Benson and Paillet, 1989; Hostetler, 1995). Ratios of planktic to benthic diatom species (P:B ratios) have been used as a metric for lake-level change in paleoclimatic studies (Wolin and Stone, 2010), assuming a positive relationship between these two variables (e.g. an increase in lake-level results in more pelagic habitat and thus a higher P:B). However, differences in basin morphometry may differentially affect changes in planktic to benthic habitat (Stone and Fritz, 2004; Wolin and Stone, 2010) and result in different diatom community changes under the same extrinsic climate signal, particularly in basins with complex morphometry.

Previous studies have demonstrated that these nonlinear changes in P:B habitat in response to climate change can be explored with three-dimensional modeling approaches (Stone and Fritz, 2004; Wigdahl et al., in preparation).

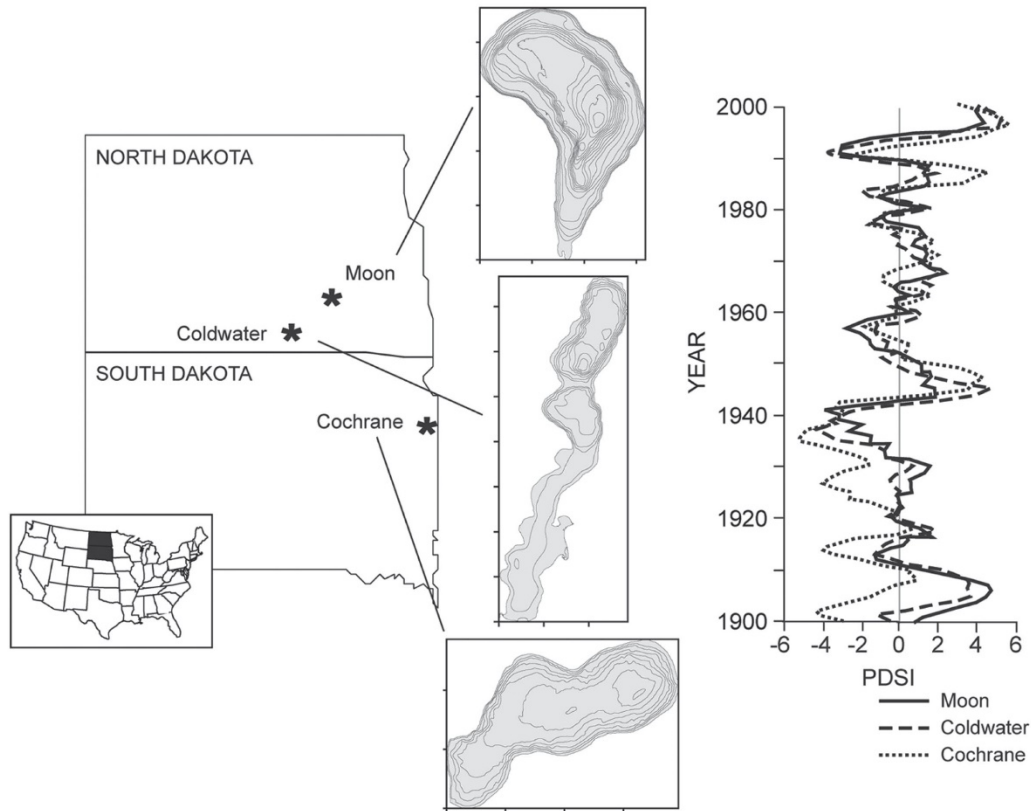
Planktic versus benthic habitat changes also have implications for diatom-based salinity reconstructions, if these ecological characteristics are unevenly distributed along gradients of interest within calibration sets. DI-salinity values are calculated using weighted averages that assume that the assemblage is representative of the complete community, even where there may be an uneven distribution of salinity optima across diatom habitats in the original calibration data set for the northern Great Plains (Fritz et al., 1991). In this case, only planktic taxa (*Cyclotella caspia* and *Cyclotella quillensis*) represent the most saline conditions (figure 1b), with mid-range salinities dominated by benthic taxa (*Cocconeis placentula* var. *lineata* and *Diatoma tenue* var. *elongatum*) and a mix of planktic and benthic species under low salinity conditions. Here, the high salinity lakes were either deep meromictic sites with planktic taxa, or shallow lakes where the diatom preservation was extremely poor—this resulted in the lack of benthic diatoms in higher end of the salinity gradient despite efforts to include these sites and ecological groups in the training set. This uneven distribution of habitat preferences results in a nonlinear DI-salinity response to changes in lake level, such that habitat-driven responses to changes in lake level interfere with weighted averages and can artificially skew the inferred values. In some cases, severe lake-level declines in saline lakes of shallow to moderate depth during drought may eliminate planktic habitat that would otherwise support the growth of the higher optima species, ultimately resulting in an underestimate of true salinity from diatom-based inferences. Additionally, increases in nutrient concentrations during lowstands may also confound the use of diatom planktic:benthic (P:B) ratios alone to infer lake-level change, with decreases in benthic production due to shading during higher planktic growth (Wolin and Stone, 2010). Because salinity and P:B habitat availability influence diatom communities in complex and differing ways, a more comprehensive assessment of diatom community response to drought incorporates both chemical drivers (figure 1a – pathway 1) and physical drivers (figure 1a – pathway 2), in the form of planktic versus benthic habitat availability.

Here we examine these relationships between diatom community structure and drought-induced change in lake level and lakewater salinity over the last century for three different lakes in the northern Great Plains. At each site, we examined instrumental drought records and aerial photographs in combination with three-dimensional models of planktic versus benthic habitat availability, in order to understand physical changes in lake-habitat zonation associated with lake-level change at each site during the last century. We then compared these data with DI-salinity and P:B ratios of diatoms in lake sediment cores to determine how chemical and physical signals of drought are reflected in the diatom record at each lake. The integration of site-specific physical characteristics and habitat preferences of diatom species with traditional paleolimnological approaches at each site provides insight into whole-lake response to environmental change and illustrates the complexity of the response of lacustrine biological communities to drought.

## Method

### Study sites

The northern Great Plains is a semi-arid region of North America containing numerous fresh (<1 g/L), sub-saline (1–3 g/L), and saline (>3 g/L) closed-basin lakes. This drought-prone region is an area of intense agricultural production with level to gently rolling topography and generally negative moisture balance (*precipitation – evaporation* < 0). Three study sites were selected in close proximity to one other (figure 2 and table 1): Moon Lake (Barnes County, ND), Coldwater Lake (McIntosh County, ND), and Lake Cochrane (Deuel County, SD). The Palmer Drought Severity Index (PDSI) from the National Climatic Data Center ([www.ncdc.noaa.gov](http://www.ncdc.noaa.gov)) shows similar drought trends at each of the three sites over the past century (figure 2).



**Figure 2.** Study locations with bathymetric maps and PDSI since 1900, from the National Climatic Data Center ([www.ncdc.noaa.gov](http://www.ncdc.noaa.gov)). Contour lines mark 1-m depth increments. PDSI averages of 36 months were used from US Climatological Divisions 6 (Moon Lake) and 9 (Coldwater Lake) in North Dakota, and from Division 7 (Lake Cochrane) in South Dakota. Negative PDSI values indicate dry conditions, and positive PDSI values indicate wet conditions. PDSI: Palmer Drought Severity Index.

**Table 1.** Select limnological characteristics of study sites

Lake	Latitude and longitude	Mean annual precipitation (cm)	Surface area (km <sup>2</sup> )	Lake-level elevation (m)	Maximum depth (m)	Average depth (m)	Salinity (g/L)	Secchi depth (m)
Moon	46°51'N, 98°09'W	46	0.35	444	15	6.7	5.2	2.3 <sup>a</sup>
Coldwater	46°01'N, 99°05'W	46	0.50	594	6	4.6	3.0	1.63 <sup>a</sup>
Cochrane	44°42'N, 96°28'W	63.5	1.44	513	7.3	4.0	2.5	1.3 <sup>b</sup>

a. Average Secchi depth for 2005–2007, from North Dakota Water Quality Assessment Report, 2005–2006 and 2006–2007.

b. Average Secchi depth for 1999 season (Stueven et al., 2000).

These lakes were also selected because they vary in basin morphometry, which allowed us to explore habitat changes in response to drought among different types of basins (figure 2). Moon Lake is the deepest of the three, with a steep-sided central basin and gently sloping shallow areas along the shoreline. Coldwater Lake is a shallow, dual-basin system. Much of the southern portion of this elongated lake is less than 3 m deep and is separated from the main basin during severe droughts. Lake Cochrane is slightly farther south and has the simplest basin with gently sloping sides. Diatom profiles spanning the last 2000 years in Moon Lake (Laird et al., 1996) and Coldwater Lake (Fritz et al., 2000) have been used to infer salinity and long-term drought patterns.

#### *Fossil diatom records*

Cores of the upper 1.0–1.5 m of sediment were taken in each lake with a 5- or 8-cm diameter polycarbonate tube fitted with a piston and operated from a boat or the ice with rigid drive rods. Visual inspection of the cores indicated complete recovery of the sediment-water interface. Cores were extracted from the deepest area of the lake and were kept upright and extruded in the field in 1–2 cm intervals and dated with <sup>210</sup>Pb methods (Eakins and Morrison, 1978) using the constant rate of supply (crs) model (Appleby and Oldfield, 1978). Diatom samples were processed with 10% hydrochloric acid and 30% hydrogen peroxide to remove organic matter, and at least 300 diatom valves were counted per sample (Battarbee et al., 2001) and identified (Krammer and Lange-Bertalot, 1986–1991; Patrick and Reimer, 1966, 1975; Spaulding et al., 2010).

DI-salinity was calculated using a transfer function from lakes of the northern Great Plains (Fritz et al., 1991). P:B ratios of fossil diatom assemblages (hereafter referred to as P:B<sub>core</sub>) were calculated for each depth in the cores based on species autecology (Krammer and Lange-Bertalot, 1986–1991; Spaulding et al., 2010). Tychoplanktic taxa were excluded from the analysis, as these species were generally a small component of the assemblages.

***Lake-level and habitat reconstruction***

Three-dimensional models of basin morphometry were developed following the methods of Stone and Fritz (2004) and used to explore changes in planktic versus benthic habitat availability in relation to lake-level changes. For each lake, a bathymetric contour map was imported into Surfer 8.03 (Golden Software 2003) and digitized to produce three-dimensional graphical images from which to calculate volume, lake-basin (sediment–water) surface areas, and planar (water–air) surfaces at a given lake-level elevation. Available planktic habitat zones were defined as the total planar surface area of the lake deeper than 0.6 m, and available benthic habitat zones were defined as total basin surface area from the lake surface to different depths of photic penetration. We calculated benthic habitat using a range of possible water clarity levels from 0.9 to 7.9 m in depth. The depth of attenuation for 10% of photosynthetically active radiation ( $K_{dPAR}$ ) for lakes in the northern Great Plains varies from 0.3 to 3.5 m (Osburn et al., 2011). Accordingly, we report models using two potential light levels for each lake (benthic zones = 0.9 m and 3.0 m in depth), as these light levels are within the regional  $K_{dPAR}$  range and best illustrate the effects of light in shaping habitat zones across all three systems. Modeled lake-level elevation was lowered in 0.3 m increments, with metrics recalculated at each vertical grid step from modern lake level to the bottom of the lake basin. From these calculations, we developed estimates of changes in planktic versus benthic habitat within each lake at a given water level (hereafter referred to as  $P:B_{model}$ ).

In order to confirm the response of lake level to drought conditions over the past century, we examined aerial photographs for each of the three lakes. Aerial photographs of each site were collected for approximately each decade spanning from the 1930s through the late 1990s, depending on image availability (for a total of eight images per lake). Images were imported into Surfer 8.03 and digitized to estimate the planar surface area at each time period. Lake levels were estimated based on visual comparison of shoreline characteristics with three-dimensional basin models, as well as by comparing calculated planar surface area with basin model estimates ( $LL_{aerial}$ ). For Lake Cochrane, the aerial photograph from 1939 was only available for a partial view of the lake.  $LL_{aerial}$  was estimated, as for other images, by a visual comparison, as well as the planar surface area for a modified model of the eastern half of the basin. The modified model was cropped to match the 1939 aerial view, and recalculated planar surface areas were compared with that from the aerial image. As there were some difficulties with this site in converting planar surface area to lake-level elevation from the models, we report planar surface area for Lake Cochrane as a metric of lake-level elevation change.

***Comparisons across and within lakes***

Relationships among PDSI,  $LL_{aerial}$ , DI-salinity, and  $P:B_{core}$  were assessed with nonparametric Spearman's rank correlations in R (version 2.14.2). As each site is located in a different US Climatological Division, 36-month averages of PDSI were used from Divisions 6 (Moon Lake) and 9 (Coldwater Lake) in North Dakota, and from Division 7 (Lake Cochrane) in South Dakota. To determine coherence across sites, we performed pairwise comparisons for each parameter between lakes ( $\alpha = 0.0167$  with Bonferroni correction for tests across

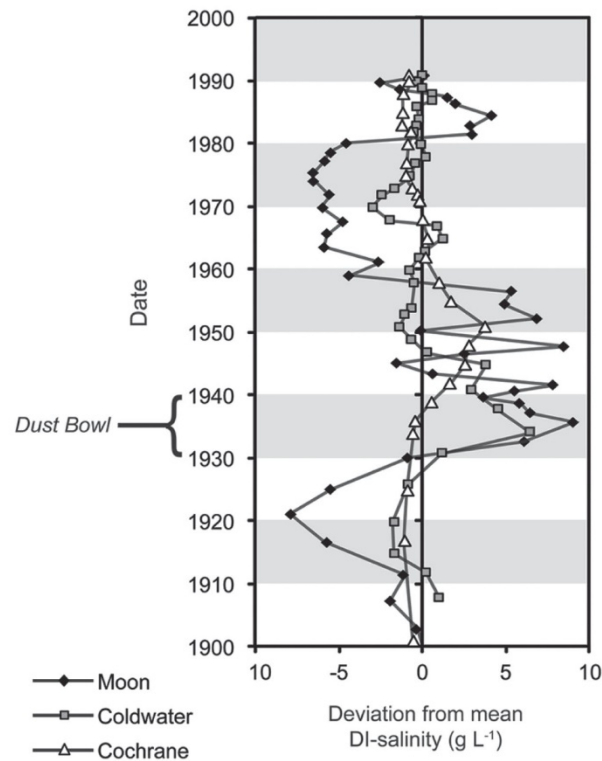


three lakes). PDSI was compared annually from 1900 until 2011. Due to availability of aerial images from slightly different years, lake-level changes were compared between lakes for similar dates ( $\leq 2$  years difference). Planar surface values from Lake Cochrane were averaged from 1965 and 1975 for comparison with 1968  $LL_{\text{aerial}}$  of Moon Lake and Coldwater Lake, and no image was available from 1960 for Lake Cochrane. In order to make comparisons among sediment core variables with different dates, values for DI-salinity and  $P:B_{\text{core}}$  at each site were averaged for 5-year increments beginning at 1905 through 1990 (1905–1909, 1910–1914, etc.). This 5-year temporal integration also smoothed out some of the uncertainty inherent in  $^{210}\text{Pb}$  dating, which averaged  $\pm 6$  to 8 years ( $\pm 2$  standard deviation) for the last century in each of the three cores. Comparisons with the Lake Cochrane core began at 1915 and skipped 1920 owing to low sample frequency at the bottom of this core. Spearman's rank correlations were also used to make pairwise comparisons between PDSI, DI-salinity, and  $P:B_{\text{core}}$  within each lake ( $\alpha = 0.0167$  with Bonferroni correction).  $LL_{\text{aerial}}$  was visually compared with PDSI but not included for analyses of within-lake coherence owing to small sample size relative to other variables.

## Results

### *DI-salinity reconstructions*

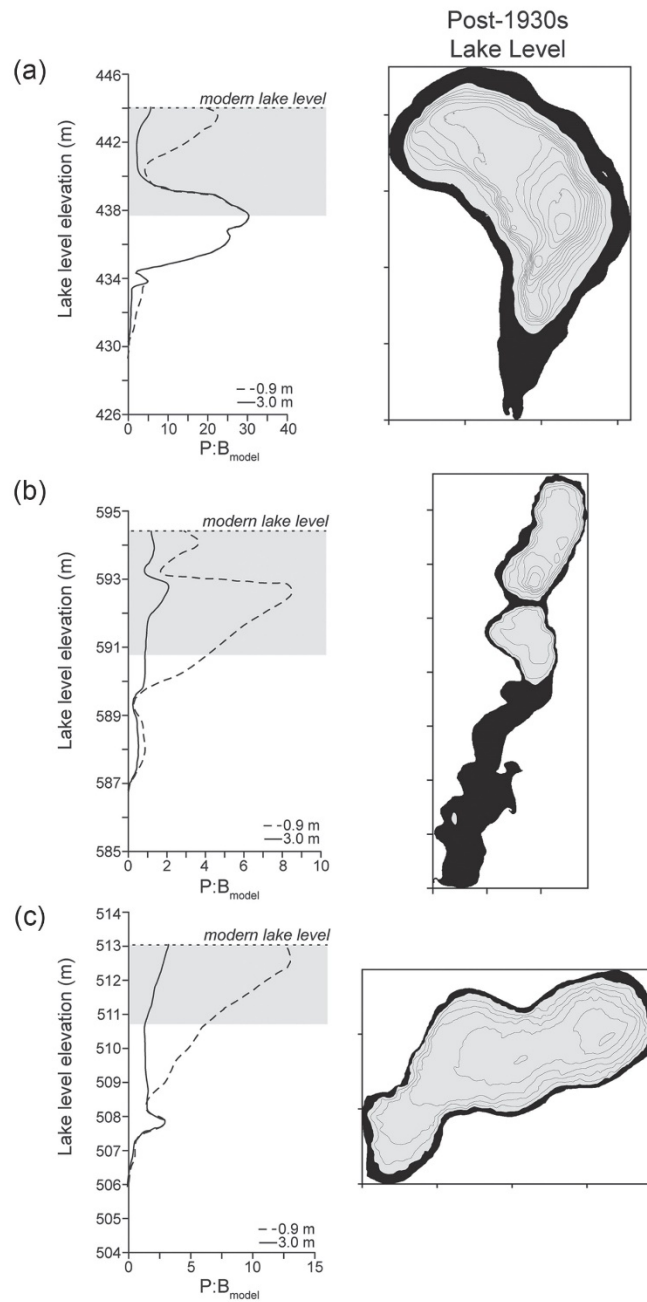
Patterns in DI-salinity varied among the three sites (figure 3). Major fossil taxa at all three sites were well-represented within the calibration set, suggesting that poor analogues were not the cause of disparities among salinity reconstructions. Moon Lake exhibited high salinity during the early 1900s, 1930s to the mid- 1950s, and 1980s, with more stable periods of low salinity during the 1960s and 1970s. Coldwater Lake's peak DI-salinity occurred at the onset of the Dust Bowl, a period of intense drought throughout the Great Plains during the early 1930s, with relatively high salinity values until the mid-1940s. Coldwater Lake also recorded its lowest DI-salinity ~1970, and values remained low and stable until the time of core collection. Lake Cochrane showed more limited fluctuations in DI-salinity throughout the core, with a peak salinity recorded around 1950.



**Figure 3.** Deviations from mean reconstructed salinity for the past century for three sites, with shaded bars alternating by decade. DI-salinity: diatom-inferred salinity.

#### *Lake-level and habitat reconstructions*

Modeled relationships between lake-level change and planktic versus benthic habitat availability varied greatly by site, depending on the basin morphometry of each lake (figure 4). These relationships were also dependent on water clarity, as shown by models for different levels of photic penetration. At Moon Lake, the maximum  $P:B_{\text{model}}$  occurred at approximately 7 m below present lake level for moderate water clarity levels (3.0 m benthic habitat depth). For low clarity conditions (0.9 m benthic habitat depth), there was also a high  $P:B_{\text{model}}$  for present water levels. At Coldwater Lake, its two basins separate when the lake level drops 1.5 m below the current level. This separation resulted in a maximum in  $P:B_{\text{model}}$  due to the isolation of extensive shallow areas in the southern portion of the lake. Lake Cochrane exhibits the most straightforward relationship between lake-level change and habitat availability, with the expected pattern of increasing  $P:B$  with increasing lake level particularly under lower water clarity conditions.

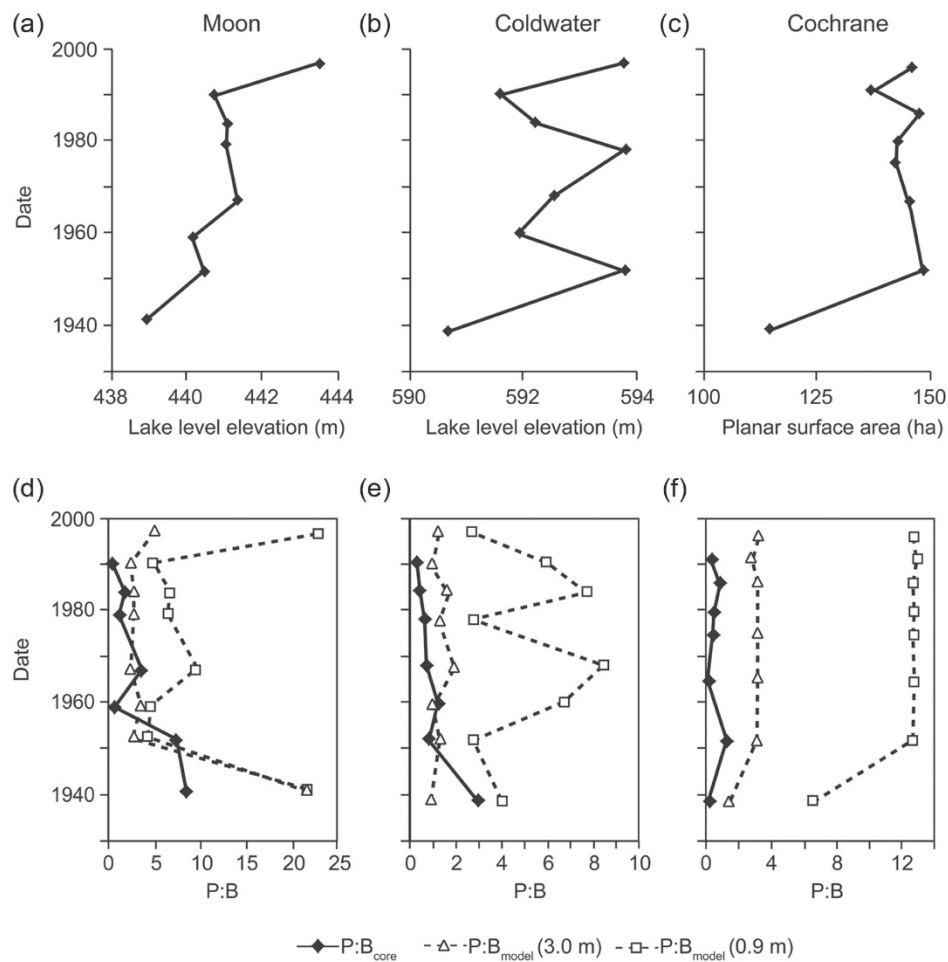


**Figure 4.** Modeled planktic to benthic habitat changes in response to lake-level change. Models of lake-level change versus  $P:B_{model}$  are shown for (a) Moon Lake, (b) Coldwater Lake, and (c) Lake Cochrane. Shaded boxes indicate the estimated range of lake-level change for the 20th century, based on aerial photographs. Bathymetric maps of changes in lake-basin area are shown for post-1930s levels (Moon Lake – 1941; Coldwater Lake – 1938; and Lake Cochrane – 1939); contour lines mark 1 m depth increments and blackened areas indicate lost elevation from modern lake levels. Scale marks on Moon Lake are 250

m apart, and scale marks on Coldwater Lake and Lake Cochrane are 500 m apart. P:B: planktic:benthic.

Based on aerial photographs, lake levels varied throughout the past century at all three sites (figure 5). The more complex shorelines and basin morphometry at Moon Lake and Coldwater Lake aided identification of lake-level change in aerial photographs, whereas lake-level change was less apparent from Lake Cochrane's simple basin. Moon Lake, the deepest site, showed the greatest magnitude of change in lake level, with post-Dust Bowl levels in 1941 approximately 4.5 m lower than the present day. Lake elevation was the most variable at Coldwater Lake, where it was approximately 3 m lower than the present day in the late 1930s, with highstands occurring in 1952, 1978, and 1997. Little change was visually evident from aerial photographs at Lake Cochrane, except during the extreme droughts of the 1930s Dust Bowl, when the lake surface dropped approximately 2 m below present-day levels. Although an outlet structure at Lake Cochrane has limited high-mark water levels since 1972 (upper limit at approximately 513 m above mean sea level), historical records still show lake-level fluctuations ranging just over a meter in elevation change since 1981 (Stueven et al., 2000).

Comparisons of bathymetric maps for modern and post-1930s lake levels (figure 4) show the most dramatic changes in basin shape at Moon Lake and Coldwater Lake in response to the 1930s droughts. Using  $LL_{aerial}$ ,  $P:B_{model}$  values were estimated for each level of water clarity and compared with  $P:B_{core}$  at all three sites (figure 5). Moon Lake and Coldwater Lake  $P:B_{core}$  values were both similar to  $P:B_{model}$  for 3.0 m benthic habitat depth. The largest mismatches between core and modeled values occurred during the late 1930s with the 3.0 m model. The discrepancies may be related to changes in turbidity associated with low lake levels during the Dust Bowl, as suggested by the closer match between  $P:B_{core}$  and the 0.9-m modeled values during this period. Lake Cochrane  $P:B_{core}$  was much lower than predicted by  $P:B_{model}$  for either 0.9 or 3.0 m benthic depth but exhibited similar patterns of change to both light level models.



**Figure 5.** Comparison of historical lake levels based on aerial photographs for (a) Moon Lake, (b) Coldwater Lake, and (c) Lake Cochrane. Planar surface area is reported for Lake Cochrane as a measure of lake-level elevation change, due to difficulties in converting surface area to elevation from aerial photographs at this site. Comparison of  $P:B_{core}$  and  $P:B_{model}$  for (d) Moon Lake, (e) Coldwater Lake, and (f) Lake Cochrane. Dashed lines indicate  $P:B$  as predicted from historical lake levels above and  $P:B$  models for different levels of water clarity.  $P:B$ : planktic:benthic.

### Coherence among lakes

Pairwise comparisons of different drought-related parameters showed varying degrees of coherence (table 2). PDSI showed strong coherence throughout the region. Moon Lake and Coldwater Lake were the most strongly correlated ( $\rho = 0.83$ ,  $p < 0.001$ ), with Coldwater Lake and Lake Cochrane ( $\rho = 0.64$ ,  $p < 0.001$ ) as well as Moon Lake and Lake Cochrane ( $\rho = 0.57$ ,  $p < 0.001$ ) also significantly correlated. Lake levels at all three sites were at their lowest in the 1930s, which is consistent with Dust Bowl drought conditions. No pairwise correlations of  $LL_{aerial}$  were significant, although there were stronger positive correlations

between Moon Lake and Coldwater Lake ( $\rho = 0.63$ ,  $p = 0.10$ ) and Coldwater Lake and Lake Cochrane ( $\rho = 0.63$ ,  $p = 0.16$ ) than for Moon Lake and Lake Cochrane ( $\rho = 0.31$ ,  $p = 0.51$ ).

**Table 2.** Coherence of drought-related parameters across and within lakes

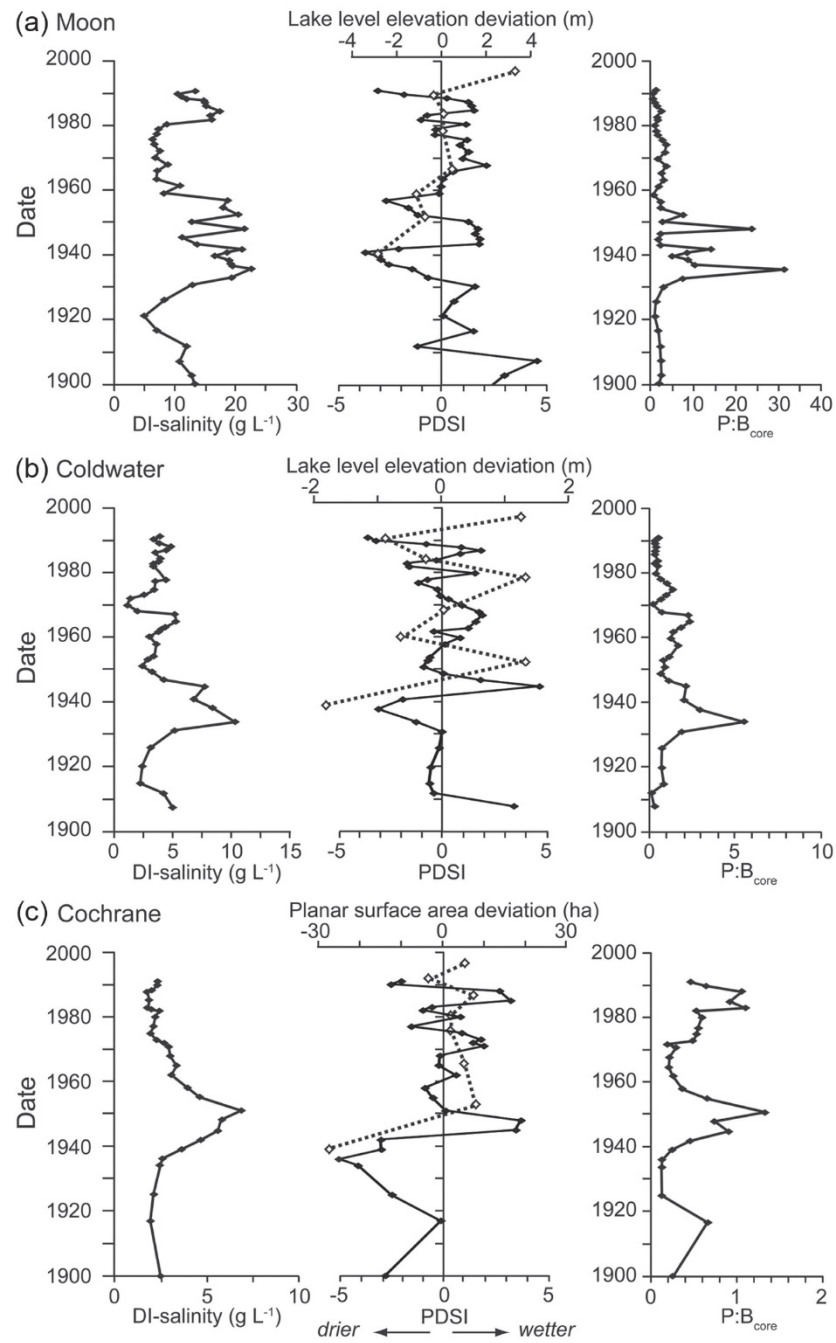
Across-lake coherence				
Site pair	PDSI	LL <sub>aerial</sub>	DI-salinity	P:B <sub>core</sub>
Moon Lake–Coldwater Lake	<b>0.83</b>	0.63	<b>0.67</b>	<b>0.62</b>
Coldwater Lake–Lake Cochrane	<b>0.64</b>	0.63	0.16	–0.54
Moon Lake–Lake Cochrane	<b>0.57</b>	0.31	0.58	–0.14
Within-lake coherence				
Site	PDSI and DI-salinity	PDSI and P:B <sub>core</sub>	DI-salinity and P:B <sub>core</sub>	
Moon Lake	–0.34	–0.07	<b>0.31</b>	
Coldwater Lake	0.08	0.003	0.28	
Lake Cochrane	0.01	<b>0.49</b>	–0.15	

PDSI: Palmer Drought Severity Index; DI-salinity: diatom-inferred salinity; P:B: planktic:benthic.

Significant Spearman's rho values are in bold ( $\alpha = 0.0167$  with Bonferroni correction) for pairwise comparisons across lakes and within-lake comparisons of PDSI – 3-year running mean with sediment core variables within sites.

Despite a strong regional coherence in instrumental records and reliable  $^{210}\text{Pb}$  dating for the cores (errors during the 1930s Dust Bowl generally  $<3$  years, data not shown), DI-salinity showed very different patterns across sites (figure 3 and figure 6). The intense drought of the Dust Bowl was captured by DI-salinity in both Moon Lake and Coldwater Lake, but not in Lake Cochrane. While Moon Lake and Coldwater Lake have some periods of similar behavior in DI-salinity and were significantly correlated ( $\rho = 0.67$ ,  $p = 0.003$ ), there were several time periods during the past century where salinity trends did not match. In particular, Moon Lake exhibited high salinity during the early 1900s, 1950s, and 1980s, whereas the DI-salinity at Coldwater Lake remained low during these times. DI-salinity in Coldwater Lake also decreased around 1970, with no corresponding change in the Moon Lake record. DI-salinity at Lake Cochrane was not significantly correlated with either Moon Lake ( $\rho = 0.58$ ,  $p = 0.027$ ) or Coldwater Lake ( $\rho = 0.16$ ,  $p = 0.56$ ). While the correlation was stronger between Lake Cochrane and Moon Lake, this may have been due to binning the data in 5-year increments for comparison between cores, which resulted in broadly similar trends at these sites; when visually comparing the records, DI-salinity at Lake Cochrane did not track the more detailed patterns exhibited by DI-salinity at Moon Lake.

P:B<sub>core</sub> was significantly and positively correlated between Moon Lake and Coldwater Lake ( $\rho = 0.62$ ,  $p = 0.007$ ), but negatively correlated between both of these sites and Lake Cochrane (Coldwater Lake and Lake Cochrane:  $\rho = -0.54$ ,  $p = 0.039$ ; Moon Lake and Lake Cochrane:  $\rho = -0.14$ ,  $p = 0.63$ ).



**Figure 6.** Within-lake comparison of drought-related parameters during the past century for (a) Moon Lake, (b) Coldwater Lake, and (c) Lake Cochrane. PDSI, for years matching core dates. Dashed lines indicate changes in lake level based on aerial photographs. Planar surface area is reported for Lake Cochrane as a measure of lake-level elevation change,

due to difficulties in converting surface area to elevation from aerial photographs at this site. PDSI: Palmer Drought Severity Index; DI-salinity: diatom-inferred salinity.

### *Within-lake coherence*

Within-lake relationships among instrumental drought indices and sediment core variables differed among sites (table 2 and figure 6). Of the three lakes, Moon Lake exhibited the strongest negative correlation between PDSI and DI-salinity ( $\rho = -0.34$ ,  $p = 0.026$ ), indicating higher lakewater salinity during drier conditions, as expected. However, some disparities between instrumental drought records and DI-salinity were still evident at this site. PDSI trends at Moon Lake indicate a shift from wet to dry conditions between 1905 and approximately 1915, while the DI-salinity record shifted from higher to lower salinity during this period (the opposite of what would be expected). DI-salinity was also very high during the 1980s, which was not a drought phase as indicated by the PDSI. The P:B ratio of diatom species at Moon Lake is significantly correlated with DI-salinity ( $\rho = 0.31$ ,  $p = 0.012$ ). With the exception of a single data point in the last century, P:B<sub>core</sub> was low during wetter times (+PDSI), and the highest DI-salinity values occurred when the fossil diatom assemblage was dominated by planktic taxa. The positive relationship between P:B<sub>core</sub> and DI-salinity contrasts with the expected inverse relationships between lake-level change and these two variables. However, the observed pattern is consistent with lake-level change and modeled P:B habitat availability at this site over the past century. Aerial photographs for Moon Lake indicated that the lowest lake level was likely near an elevation of ~439 m, which is also the elevation of maximum P:B<sub>model</sub>.

For Coldwater Lake, there was little correlation of PDSI with either DI-salinity or P:B<sub>core</sub>, except at the onset of the 1930s Dust Bowl period (table 2 and figure 6). Here, DI-salinity remained high into the 1940s (third highest salinity value for the core) during the wettest period of the last century as indicated by PDSI. DI-salinity also remained moderate and stable from approximately 1975 until the time of core collection and did not reflect the variability in PDSI during this interval. There appeared to be different relationships between DI-salinity and PDSI depending on whether conditions were wet (+PDSI) or dry (−PDSI). DI-salinity and PDSI were somewhat negatively correlated during dry periods and positively correlated during wet periods (data not shown). Like Moon Lake, the positive correlation of DI-salinity and P:B<sub>core</sub> at Coldwater Lake ( $\rho = 0.28$ ,  $p = 0.087$ ) is also in contrast with the expected relationship between these two variables. This positive correlation at Coldwater appears to be more linear in nature, primarily driven by the abundance of two planktic taxa, *C. quillensis* and *Chaetoceros elmorei* (data not shown), which have high salinity optima (20 and 11 g/L, respectively; Fritz et al., 1991). Although these taxa are classified as planktic, we note that *C. quillensis* and *C. elmorei* can do well in saline systems with relatively shallow waters (S. Fritz, personal observation). *C. elmorei*, in particular, forms cysts that preserve in dry basins and then bloom rapidly after rainfall. These features may have contributed to the lack of correlation between PDSI and P:B<sub>core</sub> at this site, along with the complex basin morphometry, which resulted in a nonlinear relationship between lake-level change and planktic versus benthic habitat availability.

Lake Cochrane showed no correlation between DI-salinity and PDSI (table 2 and figure 6). In fact, the highest reconstructed salinity values occurred just after the wettest period



in the late 1940s. Unlike Moon Lake and Coldwater Lake, Lake Cochrane showed a significant positive correlation between  $P:B_{\text{core}}$  and PDSI ( $\rho = 0.49$ ,  $p = 0.01$ ). Despite little visual evidence of major lake-level changes from aerial photographs, these subtle changes were apparently reflected by the diatom community and its response to drought. However,  $P:B_{\text{core}}$  and DI-salinity at Lake Cochrane showed an unusual nonlinear relationship, which may be related to the uneven distribution of diatom characteristics along the salinity gradient within the original calibration set.

## Discussion

While instrumental records (PDSI) showed some coherent intervals of drought across the three sites during the last century, each of the lakes responded differently to variations in moisture balance. Even those lakes with fairly synchronous lake-level changes in aerial photographs showed differences in diatom ecological response as manifested in lake sediment cores. Variations in physical lake setting as well as the ecology and internal structure of fossil diatom communities altered the relationship between drought conditions and DI-salinity, variously affecting the accuracy of reconstructed drought patterns at each site. At Moon Lake, correlations between PDSI and DI-salinity were negative, matching the predicted relationship between drought and salinity, although variation in  $P:B$  habitat availability with lake-level changes also influenced DI-salinity reconstructions. Lake Cochrane's simple basin characteristics resulted in a strong correlation of  $P:B_{\text{core}}$  with PDSI – the highest correlation between core variables and instrumental drought records at any of the three sites. By expanding the integration of diatom ecology and habitat conditions into paleoclimate inferences, we were able to strengthen our understanding of whole-lake response to climate change.

Differing bathymetry across the lakes resulted in various nonlinear relationships between modeled  $P:B$  habitat availability and lake-level variation, especially in dual-basin lakes and those with asymmetrical basin slopes. Previous work by Stone and Fritz (2004) illustrates the need for three-dimensional basin models when interpreting lake-level change from  $P:B$  ratios in sediment records. Indeed, only the simplest basin in our study, Lake Cochrane, showed the expected positive relationship between  $P:B_{\text{model}}$  and changes in lake-level elevation. As shown by modeling benthic habitat from different photic penetration depths, water clarity was an important factor affecting benthic diatom abundance. Although we explored a range of benthic habitat depths in our models, additional seasonal information on water clarity at these sites would have helped to refine our models. The combination of three-dimensional modeling and aerial photographs presented here confirmed that lake levels responded fairly synchronously to regional changes in moisture balance and demonstrated the complex relationships between lake-level change and habitat zonation within different lakes.

Differences in geomorphic setting resulted in variations in the ecological response of the study lakes to drought. Rather than being driven only by changes in water chemistry, diatom communities also responded to physical changes in  $P:B$  habitat driven by lake-level change, altering the expected negative relationship between PDSI and DI-salinity at Moon Lake and Coldwater Lake. For these two sites, complex bathymetry resulted in nonlinear

relationships among drought, lake-level change, and habitat zonation, which required an understanding of site-specific characteristics and the ecology of fossil diatom species.

At Moon Lake, the negative correlation between PDSI and DI-salinity broke down during wetter time periods, likely because of a larger influence of benthic diatoms during highstands, as indicated by basin models. Because of the internal structure of the original calibration set, which is dominated by planktic diatoms at both low and very high salinity, a high proportion of benthic taxa appeared to artificially skew the reconstructed salinity to more moderate values.

At Coldwater Lake, deviations from expected relationships were likely driven by the complex double-basin morphometry of this site and the strong influence of benthic diatom species. During highstands, such as are characteristic today, the coalescence of the two basins results in a large area of benthic habitat in the southern basin. However, when the basins were separated during lowstands (only 1.5 m below present lake level), the area of benthic habitat was greatly reduced in the main northern basin (where the sediment core was collected). This sensitivity of habitat zonation to lake-level change at Coldwater Lake resulted in complex relationships between drought conditions and diatom community structure, affecting the accuracy of diatom-based salinity reconstructions.

For Lake Cochrane, the simple bathymetry and a straightforward relationship between P:B habitat and lake-level change produced a strong correlation between P:B of diatom communities and instrumental drought records. Even during more recent decades with limited high-water marks, variations in P:B<sub>core</sub> were comparable to changes prior to the establishment of the permanent outlet, indicating that small changes in lake level at Lake Cochrane still elicited shifts in the diatom community. Although the role of nutrient concentrations in confounding P:B and lake-level change relationships is an important consideration, the response appears to be valid in sensitive closed-basin systems, such as Lake Cochrane. In similar cases, especially those with little to no relationship between drought and DI-salinity, P:B of sedimentary diatom communities may be a preferable metric over DI-salinity for lake-level change. These results may also aid in interpretations and site selection for developing diatom-based transfer functions for lake depth in other regions, such as Nebraska (USA; Shinneman et al., 2010) and Ontario (Canada; Laird et al., 2010).

The integration of instrumental and historical records with modern and paleoecological approaches provides additional insight into understanding records of past environmental change. Aerial photographs, often together with modern data, have been utilized in a variety of studies examining historical lake level and surface water changes in many different systems (e.g. Jones et al., 2001; Jovanelly and Fritz, 2011; Lyon and Drobney, 1984; Riordan et al., 2006; Van Stempvoort et al., 1993). In our study, aerial photographs provided a range of actual lake-level change over the last century to guide our interpretations of the cores and the three-dimensional models of lake elevation change. LL<sub>aerial</sub> was positively correlated across all three sites (average  $\rho = 0.52$ ), although no pairwise comparisons were significant, likely because of the small number of available images (only eight photographs per lake over the past century). As water-level fluctuations are often highly coherent among lakes in a region (Magnuson et al., 1990), the combination of aerial photographs with lake-level models and instrumental drought records allowed us to better understand whole-lake response to environmental change at each of the three sites. In this case, rather

than relying solely upon a diatom calibration set approach, examining site-specific response to large-scale climate forcing provided insight into which paleolimnological metrics best represent drought patterns in lake sediment records at individual lakes.

Other factors in addition to lake bathymetry also influence individual lake response to changing environmental conditions. Groundwater and local hydrology are particularly important for drought reconstructions, as drought-induced changes in lake level may alter groundwater flow paths and chemical signatures of lakewater in paleoclimate records (Smith et al., 1997, 2002). The relationship between salinity and drought can be complex, especially when lake basins coalesce due to rising water levels (Shapley et al., 2005). For example, ostracode salinity proxies (Mg/Ca ratios of *Candona rawsoni* shells) at Spring Lake, South Dakota, indicated high salinity during historical highstands of the 1990s. Rather than reflecting a drought signal, the high salinity was caused by the coalescence of Spring Lake with nearby systems containing much higher concentrations of solutes. The influence of basin separation and coalescence on salinity records at our sites is unclear, although a prior study concluded that this phenomenon was unlikely to account for divergent salinity patterns between Moon Lake and Coldwater Lake (Jovanelly and Fritz, 2011).

The combined effects of physical and chemical changes in response to drought have important implications for diatoms, as well as other biotic indicators in lakes. Changes in lake level and habitat zonation can alter not only diatom distributions but also macrophyte (Cheruvilil and Sorzano, 2008; Hakanson and Boulion, 2002) and zooplankton communities (Hofmann, 1998). The resulting shifts in ecological interactions among these groups could affect diatom community structure in a number of ways, including substrate availability for epiphytic diatom species, water clarity, and zooplankton grazing pressure. The complexity of potential effects and interactions on biological proxies only increases the need for a better understanding of the ecology of lakes chosen as sites for paleoclimate reconstructions. Rather than relying on a single metric within the sediment record, the use of multiple approaches (such as the combination of transfer functions and lake-level modeling presented here) is critical in order to improve the accuracy of paleoclimate inferences.

As shown here, ecological responses of lakes to changing moisture balance were unique at each of three sites due to site-specific physical characteristics that altered relationships between lake-level change and planktic versus benthic habitat zonation within the lakes. With high local variability in drought response across paleorecords of the North American interior during the early Holocene (Williams et al., 2010), the integration of additional ecological characteristics into interpretations of paleoclimate records is particularly important to constrain interpretations of limnological change and to generate more robust reconstructions of regional environmental drivers.

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