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Environmental history of a closed-basin lake in the US Great Plains: Diatom response to variations in groundwater flow regimes over the last 8500 cal. yr BP

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Abstract

Sediment records from closed-basin lakes in the Northern Great Plains (NGP) of North America have contributed significantly to our understanding of regional paleoclimatology. A high-resolution (near decadal) fossil diatom record from Kettle Lake, ND, USA that spans the last 8500 cal. yr BP is interpreted in concert with percent abundance of aragonite in the sediment as an independent proxy of groundwater flow to the lake (and thus lake water level). Kettle Lake has been relatively fresh for the majority of the Holocene, likely because of the coarse substrata and a strong connection to the underlying aquifer. Interpretation of diatom assemblages in four groups indicative of low to high groundwater flow, based on the percent of aragonite in sediments, allow interpretations of arid periods (and probable meromictic lake conditions) that could not be detected based on diatom-based salinity reconstructions alone. At the centennial–millennial scale, the diatom record suggests humid/wet periods from 8351 to 8088, 4364 to 1406 and 872 to 620 cal. yr BP, with more arid periods intervening. During the last ~4500 years, decadal–centennial scale periods of drought have taken place, despite the generally wetter climate. These droughts appear to have had similar impacts on the Kettle Lake hydrology as the “Dust Bowl” era droughts, but were longer in duration.

Keywords: closed-basin lake, diatom, groundwater flow, Northern Great Plains, paleoclimate, salinity

Introduction

Sediment records from closed-basin lakes in the climatically sensitive Northern Great Plains (NGP) of North America have contributed significantly to our understanding of regional paleoclimatology (Cumming et al., 2002; Fritz, 2008; Grimm, 2001; Laird et al., 2007; Teller and Last, 1990). Millennial-scale inferences of NGP paleoclimate over the Holocene have provided a cohesive picture of regional climate change, summarized mainly in paleoecological studies of pollen (Grimm, 2001), stable isotopes (Yu et al., 2002), and diatoms (Fritz et al., 2000; Laird et al., 2007). A comprehensive picture of climatic variation at higher frequencies (centennial to decadal) has been hindered by the limited number of lakes with a complete sedimentary archive of the Holocene, as many lakes dried up in the arid mid Holocene, by adequate preservation of paleoenvironmental proxies, and by the variability in lake response to climate because of differences in local hydrology (Fritz, 2008).

In the NGP, diatom paleoecology and the use of numerical techniques to reconstruct lake-water salinity have provided

high-resolution records of precipitation–evaporation (P–E) for periods of the Holocene (Fritz, 1990; Fritz et al., 2000; Laird et al., 1998). Sediment records also preserve geochemical evidence of groundwater flow through closed-basin lakes, in the form of authigenic precipitation of carbonate minerals, such as aragonite. In some groundwater-dominated lakes where lake water is enriched in carbonate relative to Ca, and where groundwater inflow supplies dissolved Ca, the authigenic carbonate precipitation to the lake bottom is a product of the rate of groundwater and Ca inflow (Grimm et al., 2011; Shapley et al., 2005).

Given the strong influence of both climate (P–E) and local hydrology on lakes in the NGP, robust reconstructions of Holocene environmental variations would incorporate proxies of both drivers. In this study we present a continuous high-resolution (near decadal) sediment record over the last 8500 yr (cal. BP) from a closed-basin groundwater flow-through lake, Kettle Lake, in northwestern North Dakota, USA. We use the relationship of groundwater inflow and authigenic aragonite precipitation already established for the lake (Grimm et al., 2011) to interpret the stratigraphic diatom record using a new

Figure 1. Site location map of the North American continent (A) and the Northern Great Plains (shaded area), including study site and additional sites discussed in the text (B). Bathymetry map of Kettle Lake, ND showing the uniform bowl-shape of the lake basin; contour interval is 2 m and shoreline elevation is 605 m a.s.l. (C).

statistical approach. We show that reliance on a single proxy (diatom-inferred salinity) can lead to erroneous interpretations for some periods of record. In the NGP, this is the most highly resolved diatom record of Holocene paleoenvironmental change to date.

Site description

Kettle Lake (48.607000°N, 103.624100°W, 605 m a.s.l.) is located in northwest North Dakota, USA within the NGP (Figure 1). The lake is situated within the Little Muddy aquifer, which drains to the south to the Missouri River. Kettle Lake is a small (2.2 ha) bowl-shaped closed-basin (i.e. no surface-water inflow or outflow) glacial kettle with a maximum depth of 10.2 m (Figure 1C). The region is underlain by coarse glacial outwash deposits from the Late Wisconsin glaciation. The relatively high permeability of the surrounding substratum gives the lake a strong connection with groundwater, and Kettle Lake is a flow-through groundwater-dominated lake. Indeed, the chemistry of the lake is not significantly different from the relatively fresh groundwater (1.2 g/l) of the Little Muddy Aquifer (Donovan and Grimm, 2007). Because of this strong connection with groundwater, the salinity of Kettle Lake (0.8 g/l) is somewhat anomalous in a region where lake-water chemistries are strongly driven by evaporative losses (Last, 1993). The current pH of the lake is 8.9 with a summer alkalinity of 490 mg CaCO_3/l and conductivity of 1.7 mS/cm. The climate of this region is semi-arid, with an annual deficit in precipitation–evaporation (Grimm, 2001) and lake water is depleted in Ca (30.4 mg/l) relative to HCO_3^- (549 mg/l) (Donovan and Grimm, 2007). The mean annual range in air temperature is -20°C to 28°C . The lake is surrounded by mixed-grass prairie and is currently a managed recreation site by the North Dakota Game and Fish Department. The nearshore littoral zone is dominated by emergent bullrushes of the genus *Schoenoplectus*, while submerged *Chara* sp. dominate the deeper littoral zone of the lake.

Methods

Core collection

Two overlapping cores spaced ~ 1 m apart were obtained from the deepest point in the lake in July 1996 with a Wright square-rod piston corer (Wright, 1967). The two cores were aligned stratigraphically and a composite continuous sedimentary sequence 21.87 m in length was developed (Donovan and Grimm, 2007; Grimm et al., 2011). While laminations are present throughout the core, they are not consistently annual and cannot be used for varve chronology. However, their presence is representative of anoxic bottom waters in Kettle Lake, at least for part of the year, and an alternating seasonal sedimentation of dark organic and detrital clastic layers with light aragonite layers (Donovan and Grimm, 2007).

Radiocarbon dating

The calibrated AMS radiocarbon age-model for Kettle Lake is the most detailed and comprehensive in the NGP region (Grimm, 2011). The section of the core presented in this study comprises 35 independent dates (Figure 2). Radiocarbon dates were obtained from terrestrial macrofossils, namely seeds and charcoal. Calibrated ages were obtained using Bayesian methods with BCal (Buck et al., 1999) and the INTCAL09 calibration curve (Grimm, 2011; Reimer et al., 2009). The age model uses linear interpolation between the medians of the highest posterior density regions of the calibrated ages (Grimm, 2011).

% Aragonite

Percent aragonite by mass was obtained for each sediment interval through x-ray diffraction (XRD) using a PW-1800 diffractometer (Panalytical, formerly Philips, Eindhoven, The Netherlands) with Cu-K radiation. XRD samples were air-dried, crushed, filtered through a 100 μm mesh, and mounted

Figure 2. AMS radiocarbon age-model for the section of the core presented in this paper. Dates shown are the 95% posterior density regions from BCal (simple line). There is a ~ 260 yr gap in the age model due to a slump. Material was dated and modeled above, within, and below the slump and is described in detail by Grimm (2011).

on 40 mm chemplex disks in a thin (1 mm) layer for analysis. The results were quantified with calibrated reference intensity ratios, yielding a measurement of percent mineral constituent relative to the total crystalline fraction of the sample. Further detail on the XRD data can be found in Donovan and Grimm (2007) and Grimm et al. (2011).

Diatom analysis

Samples for diatom analysis were collected from the split core at 1 cm intervals and stored wet in a cold room at 4°C. Sediments were analyzed at roughly decadal resolution, which was equivalent to 1–2 cm intervals throughout the core. Slides for diatom identification were prepared by digesting ~100 mg of sediment in 10 % HCl and 30 % H₂O₂ to oxidize carbonates and labile organic matter, respectively. Samples were allowed to settle passively, the supernatant was aspirated, and the sample was rinsed three times with deionized water. Diluted slurries were permanently mounted using Naphrax® (Battarbee et al., 2001). Diatoms were identified and enumerated with differential interface contrast light microscopy at 1000×. A number of published floras were used for identification: Patrick and Reimer (1966, 1975), Krammer and Lange-Bertalot (1986, 1988, 1991a, b), Foged (1981), and Cumming et al. (1995). We calculated an optimal counting efficiency for the slides based on the species richness (normalized by rarefaction analysis) and a ratio of efficiency based on the work of Pappas and Stoermer (1996) from an initial 30 slides with specimen counts from 400 to 600. This approach suggested a count of 335 specimens per slide would capture 95% of the species, and therefore at least this total was achieved for all samples. The same analysis, run post hoc, on 224 counts showed a 95% optimal count of 318 specimens. A number of the slides were also analyzed for diatom concentrations using microspheres.

Numerical analysis

A stratigraphically constrained cluster analysis was used to determine zones within the diatom stratigraphy based on

Bray-Curtis dissimilarity distances (Grimm, 1987). The zones were based on a uniform total sum-of-squares height and statistical significance was tested against a random broken-stick model (Bennett, 1996). A diatom-inferred salinity weighted-averaging transfer function (herein referred to as DI-salinity) was applied to the Kettle Lake core using a 77-lake training set spanning the salinity gradient of the Northern Great Plains (Fritz et al., 1993; Fritz, unpublished data, 2010). Salinity data were log transformed to reduce the right skewness and variability; consequently reconstructed salinity values as presented and discussed in this paper appear as log g/l. The salinity values from the lakes used in the training set ranged from -1.17 to 1.62 log g/l (0.06 to 41.69 g/l), with a mean of 0.36 log g/l (2.29 g/l) and median of 0.42 log g/l (2.63 g/l). The species optima obtained from the training set are then used to estimate salinity concentrations throughout the core by a weighted-averaging model (Line et al., 1994). Species were not transformed or downweighted prior to running the model, and post-hoc testing of model performance by mean-bootstrap methods over 999 cycles was used to give a root mean-squared error of prediction for the model (Line et al., 1994). All weighted-averaging calculations were made using the program C2 (Juggins, 2003).

The rate-of-change of the diatom assemblage can be interpreted as a measure of the stability of the diatom community through time. We determined the rate-of-change by linearly interpolating diatom percent abundance data to exactly 10-year intervals and calculating the chord distance between adjacent samples, a measure of dissimilarity (Jacobson and Grimm, 1986; Lotter et al., 1992). The chord distance is then divided by the amount of time (10 years) between samples, giving a rate-of-change. Interpolations were carried out using AnalySeries 2.0 (Paillard et al., 1996), while chord distance was calculated using the Analogue package in R (R Core Development Team, 2010). A detrended correspondence analysis (DCA) was used to explore associations among diatom species and their respective salinity preferences. All diatom species were included in the analysis, with downweighting of rare species. Aragonite values for each sediment interval were

passively contoured on the DCA using thinplate splines in a general additive model, in order to visualize assemblages of dominant (>10% in any one sample) diatom species over the gradient of groundwater-flow in Kettle Lake. Four groups of diatoms were identified as being associated with high, moderate-high, moderate-low, and low groundwater flow conditions based on common ranges of aragonite values. The DCA and contouring of the aragonite data was completed using R.

Results

Diatom communities and inferred salinity

A total of 263 diatom species were identified over 667 sediment intervals. The preservation of diatom frustules was reliable in those samples counted, however, a large section of dissolution is evident from 7940 to 5960 cal. yr BP, with a shorter section from 5920 to 5840 cal. yr BP (Figure 3). Salinity tolerances for the dominant species (>30% relative abundance at any point in time) throughout the core are low, suggesting mainly freshwater or subsaline conditions throughout the last 8500 years (Figure 3). In the section of core where diatom concentrations were analyzed (~3500–6000 cal. yr BP), the absolute numbers of benthic diatoms varied less than planktic species. During periods of high overall diatom concentrations, planktic species were dominant. The most prevalent diatoms throughout the core were *Stephanodiscus* spp., which are planktic and generally have low Si:P requirements (Kilham et al., 1996). *Stephanodiscus parvus* and *Stephanodiscus minutulus* are small (<5 µm), share similar ecological preferences, and are difficult to distinguish using light microscopy; we therefore combined these two species as a “complex.” Additional planktic freshwater species with moderate to high Si:P requirements include *Asterionella formosa*, *Fragilaria crotonensis*, and *Fragilaria capucina* var. *mesolepta*. A number of freshwater planktic *Synedra* spp. were present in the sediments: *S. acus*, *S. acus* var. *angustissima*, *S. tenera*, and *S. nana*. *Gomphonema clavatum*, an epiphyte, was the only abundant benthic freshwater diatom. Other gomphonemoid diatoms present were *Gomphonema olivaceum* and *Gomphonema aquaemineralis*, both epiphytic and subsaline. *Achnanthes minutissimum*, a common ‘weedy’ epipellic diatom was present throughout the core, in addition to *A. microcephalum*. Planktic diatoms with subsaline affinities include *Cyclotella meneghiniana*, *Nitzschia palea*, and *N. paleacea*. The majority of subsaline diatoms in Kettle Lake are benthic and epiphytic or epipellic. *Chaetoceros* spp. were found throughout the core, predominately in an encysted stage, and we have combined *C. elmorei* and *C. muelleri* as the cysts for these two species could not be differentiated. *Chaetoceros* is planktic with typically hyposaline tolerances. Stratigraphically constrained cluster analysis of the full diatom assemblages shows three main zones over the last 8500 years (Figure 3): 8500 to 4364 cal. yr BP (Zone 1), 4364 to 620 cal. yr BP (Zone 2), and 620 to –41 cal. yr BP (Zone 3). Subzones are distinguished within these primary zones. The independently established diatom zone 1–2 boundary at 4364 cal. yr BP is remarkably similar to the major D–E boundary in pollen and mineral data placed at 4440 cal. yr BP from the same core. This boundary was based on independent CONISS cluster analyses of mineral and pollen data and is the mean of major partitions in the dendrograms for minerals at 4290 cal. yr BP and pollen at 4590 cal. yr BP (Grimm et al., 2011). Thus, all proxies show a

major environmental regime shift at ~4400 cal. yr BP.

The DI-salinity reconstruction for Kettle Lake shows few instances when statistically significant changes in salinity (beyond the model error) have occurred over the course of the last 8500 years (Figure 4). The root-mean-square standard error of prediction for the model is 0.53 log g/l. Nonetheless, at millennial-scale resolution three stages of differing mean salinity are present; the arid mid Holocene (mean 0.06 log g/l; 8100–4364 cal. yr BP in this record), the late-Holocene wet period (mean –0.50 log g/l; 4364–2300 cal. yr BP), and an intermediate late-Holocene period (mean –0.12 log g/l; 2300 cal. yr BP to present). Relative to the modern salinity of Kettle Lake (–0.10 log g/l), the salinity in the first part of the arid mid Holocene is consistently higher (~8000–5800 cal. yr BP). This is followed by centennial periods of lower and higher salinity over the next 1200 years (5800 to ~4600 cal. yr BP), until the transition to the wetter late-Holocene period begins. Kettle Lake appears fresher today than it was for most of the late Holocene, from ~2200 cal. yr BP to present. During this period mean salinity was similar to modern, but multidecadal and centennial arid periods are prominent, producing greater variability in the DI-salinity record than previously. The current salinity of Kettle Lake and the value of the uppermost-reconstructed sample are similar, suggesting confidence in the reconstructed values. However, in some periods the reconstructed salinity is lower than at other lakes in the same region (e.g. the mid-Holocene period 5400–4800 cal. yr BP; Figure 4).

% Aragonite stratigraphy

The detailed record of authigenic aragonite for the last 8500 years in Kettle Lake is a proxy for the groundwater flow into the lake (Grimm et al., 2011). The record appears to have a multicentennial cyclicity overlaid by millennial-scale shifts in deposition (Figure 4). During the arid mid Holocene (diatom zone 1c and 1d; 8100–4364 cal. yr BP) the range in % aragonite is larger than the wet late Holocene (diatom zone 2a and 2b; 4364–1400 cal. yr BP), with concentrations averaging ~47% and 65%, respectively. The period of lowest aragonite deposition is diatom zone 1d (5400–4364 cal. yr BP), which is punctuated by prolonged droughts (Figure 4; Grimm et al., 2011). A more thorough presentation and discussion of the paleoclimatic inferences over the entire Holocene from the aragonite data can be found in Grimm et al. (2011), here we use the aragonite concentrations to improve our understanding of diatom response to changes in groundwater flow.

DCA and groundwater flow regimes

We used DCA to determine whether the distribution of the core diatom species in ordination space shows distinct grouping by salinity preference (Figure 5). No apparent grouping of species by salinity preference is evident on the first two axes. The total gradient length of DCA axis 1 is 3.3 SD units, suggesting a uni-model diatom response, and the explanatory power of the first and second axes is 19% and 14%, respectively. To aid in the interpretation of the core diatom distribution the aragonite concentration for each corresponding sediment sample was then passively introduced to the ordination space and contoured. This approach has the advantage of incorporating both axes of variation within ordination space, as the aragonite is contoured across both. The gradient of aragonite across the ordination space represents a gradient of high (high aragonite concentra-

Figure 3. Stratigraphic record of diatom percent abundances for Kettle Lake, ND. Only strongly dominant diatoms (>30%) are shown, ordered by increasing salinity preference from left to right. Stratigraphically constrained cluster analysis results of the statistically significant diatom zones based on sum-of-squares distance and tested against a broken-stick model. Strength of the zonation shown as thick solid line, strongest; solid line, strong; dashed line, significant. Large shaded area is the zone of diatom dissolution.

Figure 4. Diatom-inferred salinity reconstruction in log g/l. The root-mean squared error of prediction for the model is present for each data point as a grey error bar. Solid line is the current salinity of Kettle Lake (-0.09 log g/l), while millennial-scale mean salinity for the mid- and late-Holocene periods shown in dashed lines (0.053 , -0.503 , and 0.117 log g/l). Aragonite concentrations as % mineral fraction. Diatom zones are overlain as per Figure 3.

Figure 5. DCA of all diatom species classified according to salinity preference. Corresponding aragonite concentration (% mineral fraction) for each sample is passively contoured in ordination space

tion) and low (low aragonite concentration) groundwater flow and groundwater elevation (Figure 5).

Diatom-inferred lake states

The visualization of high and low groundwater flow enables us to semi-quantitatively define the diatom assemblages that are associated with flow regimes over the two main gradients (DCA axis 1 and 2) of diatom change. In so doing we can establish the dominant (>10% at any point in the record) diatoms present during high (group 1; > 62% aragonite), moderate-high (group 2; 56–62% aragonite), moderate-low (group 3; 50–56% aragonite), and low (group 4; < 50% aragonite) groundwater flow. The modern ecological affinities of the diatom assemblages associated with each groundwater regime are used to elucidate physical and chemical attributes of the lake during the four broadly defined states (Figure 6), as discussed in detail in the subsequent sections.

Discussion

DCA-defined diatom groups (Figure 6)

Diatom group 1: High groundwater flow, deep lake. This group of diatoms is dominated by freshwater euplanktic species (predominantly *Stephanodiscus* spp.) (Figure 6). The small domi-

nant (<5 μm) *Stephanodiscus parvus-minutulus* complex typically blooms in the spring during lake overturn when Si:P is low, but can survive into stratification (Kilham et al., 1996; Støermer and Håkansson, 1984). These diatoms imply that the lake state during high groundwater flow is likely dimictic and that most diatom growth is taking place after ice-out, when hypolimnetic phosphorus is being recycled from the sediments into the photic zone (Bradbury, 1988). *Stephanodiscus niagarae* and to a lesser extent *Stephanodiscus medius* are also present in this group. *S. niagarae* commonly blooms following the onset of stratification and into the late summer, typically occupying hypolimnetic waters (Bradbury, 1988; Kilham et al., 1996).

Asterionella formosa is euplanktic, forms stellate colonies, and has an intermediate to high Si:P requirement (Saros et al., 2005; Tilman et al., 1982). *A. formosa* can bloom in the late spring or the late summer during periods of low phosphorus regeneration and high silica. *A. formosa* is often found in association with *Fragilaria crotonensis* (as it is in the Kettle Lake sediments), which has similar resource requirements to *A. formosa* and has been observed at high abundances near the thermocline after spring mixing (Bradbury, 1988). *F. crotonensis* blooms in the late spring and early summer when stratification is establishing and phosphorus is becoming depleted.

Benthic diatoms in this group are low in relative abundance, reflecting the relatively low proportion of benthic habitat (Wolfin and Stone, 2010) (Figure 6). The narrow littoral bench of

diatom group	groundwater flow (aragonite concentration)	strongly dominant diatoms (>30% relative abundance)		inferred mixing regime	salinity	inferred diatom habitat (white area)	inferred lake environment
		freshwater	saline				
1	high (>62 % mineral fraction)	<ul style="list-style-type: none"> • <i>Asterionella formosa</i> • <i>Stephanodiscus medius</i> • <i>Stephanodiscus niagarae</i> • <i>Stephanodiscus parvus-minutulus</i> complex 	<ul style="list-style-type: none"> • <i>Fragilaria crotonensis</i> • <i>Nitzschia agnita</i> • <i>Amphora copulata</i> 	dimictic; strong spring mixing	fresh (0.4 - 0.9 g L ⁻¹)		
2	moderate-high (56 - 62 % mineral fraction)	<ul style="list-style-type: none"> • <i>Fragilaria capucina</i> var. mesolepta • <i>Synedra acus</i> • <i>Stephanodiscus hantzschii</i> • <i>Nitzschia linearis</i> var. tenuis • <i>Hantzschia amphioxys</i> 	<ul style="list-style-type: none"> • <i>Martyana olseni</i> • <i>Achnanthis microcephalum</i> • <i>Gomphonema olivaceum</i> • <i>Craticula halophila</i> • <i>Navicula oblonga</i> • <i>Nitzschia palea</i> • <i>Chaetoceros elmorei-muelleri</i> complex 	weak spring mixing; lower water level	slightly saline (0.5 - 4.0 g L ⁻¹)		
3	moderate-low (50 - 56 % mineral fraction)	<ul style="list-style-type: none"> • <i>Fragilaria tenera</i> • <i>Gomphonema clavatum</i> 	<ul style="list-style-type: none"> • <i>Cyclotella meneghiniana</i> • <i>Coconeis placentula</i> • <i>Achnanthis minutissimum</i> • <i>Gomphonema aquaeumeralis</i> 	dimictic to polymictic; possibly meromictic	saline to strongly saline (0.3 - 2.5 g L ⁻¹)		
4	low (< 50 % mineral fraction)	<ul style="list-style-type: none"> • <i>Synedra acus</i> var. angustissima • <i>Synedra nana</i> • <i>Nitzschia linearis</i> 	<ul style="list-style-type: none"> • <i>Nitzschia paleacea</i> 	dimictic to polymictic or meromictic	strongly saline to freshwater lens over dense saline water (0.45 - 0.50 g L ⁻¹)		

Figure 6. Diatom-inferred lake environments for the DCA defined diatom "groups" over the range of high to low groundwater flow (as inferred from aragonite). Only the strongly dominant diatoms (> 30% relative abundance) are listed, however diatom groups are defined based on all 263 taxa found in the sediment core. Inferred mixing regimes and salinity are based on modern ecological affinities of the dominant diatoms. Available diatom habitat and inferred lake levels are based on the modern diatom ecology and inferred groundwater flow regime depicted on the modern lake bathymetry (plan view and cross-section)

Kettle Lake is the sole area suitable for diatom growth, because it is unlikely that the photic zone is sufficient to reach the lake bottom at high water levels and high groundwater flow given modern Secchi depths of approximately 4.5 m.

Diatom group 2: Moderate-high groundwater flow, lower lake-level. During somewhat lower groundwater flow, the diversity of benthic diatoms increases dramatically. A number of freshwater and subsaline epiphytic species of the genus *Gomphonema*, *Cocconeis*, *Achnanthisidium*, *Amphora* and *Cymbella* are present, suggesting a greater abundance of submerged or emergent aquatic vegetation on the littoral bench of the lake. This would be expected as lake level and groundwater flow is slightly lower, and suitable habitat becomes available. A number of epipellic diatoms with subsaline affinities (e.g. *Mastogloia smithii* and *Craticula halophila*) also occur, in addition to a number of *Nitzschia* spp. that are generally found in waters of high ionic strength (Cumming et al., 1995). The increased dominance of epipellic diatoms is likely a result of the photic zone extending to the lake bottom and increasing the proportion of benthic habitat (Wolin and Stone, 2010) (Figure 6).

The inferred increase in salinity is supported by the presence of the planktic, hyposaline *Chaetoceros muelleri-elmorei* complex. The colonial euplanktic *C. muelleri-elmorei* complex can form heavily silicified resting cells (which is the predominant form found in the sediment records), thus it is meroplanktic and dominates during periods of strong mixing. The increase in inferred salinity would result from greater evaporative loss from the lake due to lower groundwater flow. Changes in salinity in response to the P-E balance of closed-basin lakes have proven a robust relationship in the NGP (Fritz, 1990; Laird et al., 1996; Last, 1993).

Diatom group 3: Moderate-low groundwater flow, low lake-level. During periods of a low groundwater gradient, the lake level drops, and an increase in evaporative loss would favor diatoms with saline affinities. Indeed, the planktic diatom *Cyclotella meneghiniana*, which has a subsaline affinity, is dominant in this group. *C. meneghiniana* is a common species in the lakes of the NGP throughout the Holocene (Fritz et al., 1993, 2000; Laird et al., 2007) and has been observed to bloom in the late summer in Kettle Lake (J. E. Saros, personal communication, 2010), presumably during periods of strong stratification, conditions that are common in this genus (Bradbury, 1988; Winder et al., 2009). *C. meneghiniana* is also an efficient user of Si and generally has a low Si:P requirement (Tilman and Kilham, 1976). Additional spring-early summer blooming planktic species present in this group (*Synedra tenera* and *Stephanodiscus hantzschii*) suggest that fresher conditions perhaps prevailed soon after winter ice-out, despite the lower groundwater flow and lake level. *Synedra tenera*, a freshwater planktic diatom, is associated with *C. meneghiniana* in the fossil assemblages and is competitive under similar lake thermal characteristics and low P (Interlandi et al., 1999). The presence of *S. hantzschii* in group 3 is somewhat unexpected as the other *Stephanodiscus* spp. with low Si:P are associated with group 1 and high groundwater flow, however previous studies show that *S. hantzschii* is favored in lakes with high alkalinity (Brugam, 1983).

The benthic community of this group is less diverse than group 2 but contains some epiphytic taxa commonly associated with saline conditions, namely *Cocconeis placentula* and *Gomphonema aquaemineralis*. The presence of epipellic *Nitzschia*

perminuta and *N. liebtruthii*, which have salinity optima in the mesosaline (> 20 g/l) and hyposaline (3–20 g/l) range, respectively, and which are the highest salinity ranges found throughout the sediment record, adds further evidence of saline conditions during periods of low groundwater flow. A number of epipellic *Navicula sensu lato* species (e.g. *Luticola mutica* and *Navicella pusilla*) with freshwater and subsaline affinities are also present in this group.

Diatom group 4: Low groundwater flow, meromictic lake. Few diatom species are associated with low groundwater flow conditions in Kettle Lake. Salinity is likely to be at its highest during periods of the lowest groundwater flow and lake level, however, the planktic freshwater diatoms *Synedra acus* var. *angustissima*, *S. nana*, and *Nitzschia linearis* are dominant at these times. These three species share similar life strategies and form stellate colonies which facilitate their euplanktic habit. *S. acus* var. *angustissima* has high Si:P requirements and implies weak or no mixing of the water column (Bradbury, 1988). Brugam (1983) showed that *S. nana* is typical in naturally meromictic lakes in Minnesota. Therefore these two species imply that at the lowest groundwater flow, the lake becomes meromictic. *S. acus* var. *angustissima* and *S. nana* bloom in the spring and need a freshwater mixolimnion, which snow and ice-melt would provide. This freshwater lens would remain chemically isolated from deep saline waters under meromictic conditions.

Nitzschia paleacea is also dominant in this low groundwater flow group and can inhabit periphytic and planktic environments, forming both rosette and stellate colonies, respectively. It is commonly found in alkaline, slightly brackish waters. It has been described as an obligatory nitrogen heterotroph and is tolerant of heavy organic pollution (Hürlimann and Schanz, 1993; Lange-Bertalot, 1978). It is unclear where in Kettle Lake this diatom would have been growing, but likely it occurred below the mixolimnion, where conditions would be more alkaline and ammonium supply from the sediments would be plentiful. Interestingly, *N. paleacea* and *S. acus* var. *angustissima* are present in alternating time periods in the sediment record (Figure 3), suggesting varied degrees of meromixis, with *N. paleacea* signifying a greater monimolimnetic habitat. The modern and historical association of *Synedra acus* var. *angustissima* and *Nitzschia paleacea* in meromictic systems is not without precedent and has been elegantly presented using varved sediments, sediment traps, and phytoplankton samples in a Turkish lake (Woodbridge and Roberts, 2010). No benthic diatoms are dominant in this group.

Diatom-inferred lake water salinity

The reconstructed diatom-inferred salinity for Kettle Lake varies over decadal, centennial, and millennial timescales for the last 8500 cal. yr BP (Figure 4). The DI-salinity suggests that Kettle Lake has been significantly fresher than today during multiple periods throughout its history, including during part of the arid mid-Holocene period. This is particularly surprising during the period 5400–5000 cal. yr BP, when groundwater flow appears to be at its lowest and group 4 diatoms dominate (Figure 7). While we have established that the weighted-averaging salinity model is statistically significant for Kettle Lake, the diatom species in “group 4” are not well represented within the training set. The two dominant diatoms for this group, *Nitzschia*

Figure 7. Diatom stratigraphy for Kettle Lake, ND grouped in accordance with defined assemblages of high (group 1) to low (group 4) groundwater flow. Diatom assemblage rate-of-change represents the stability of the diatom communities through time, expressed as departure from the mean of chord distance per 10 yr. Stratigraphic zones are defined by original zones of all taxa as shown in Figure 3.

paleacea and *Synedra acus* var. *angustissima*, are present in nine and eight of the 77 training set lakes, respectively. More importantly, the relative percent abundance of these diatoms does not exceed 2% within the training set, meaning that the salinity optima of these two species of diatoms is not well constrained. Therefore during periods of the salinity reconstruction when these two diatoms dominate the assemblage (up to >80% relative abundance), the inferred lake environment is not represented by the training set. We infer that periods of the record that are dominated by group 4 diatoms and the lowest groundwater flow actually represent a much more arid period than suggested directly by the salinity reconstruction. The taxa found in group 4 suggest a meromictic water column and are likely growing in a fresh mixolimnion lens overlying a highly saline monimolimnion. Thus, the diatom-inference of fresh surface waters likely is correct, but in this case relatively fresh surface waters occur during arid climatic conditions.

Overall the DI-salinity of Kettle Lake has a small range in variability over the last 8500 years. Kettle Lake's modern salinity is comparatively very low for the NGP, because it is a groundwater flow-through lake in a very coarse substratum that is fed by fresh groundwater (Donovan and Grimm, 2007; Grimm et al., 2011). Our salinity reconstruction results suggest that Kettle Lake has maintained this strong connection to the groundwater system throughout the last 8500 years, thus buffering the lake's response to drought.

Environmental history of the Kettle Lake region

The stratigraphic summation and presentation of the defined "groups" of diatoms reduces the complexity of a species-rich community, while offering a temporally detailed view of diatom response to variations in groundwater over the last 8500 years (Figure 7). We now discuss the environmental history of Kettle Lake through the three main zones of the core in the context of regional environmental change.

Zone 1 (8500–4364 cal. yr BP). The base of the Kettle Lake diatom record (8500 cal. yr BP), dates to the mid-Holocene arid period of the NGP (Dean et al., 1996). The base of zone 1 (zone 1a; 8500–8351 cal. yr BP) represents a period of moderate-low groundwater flow into a well-mixed deep saline lake (Figure 7). Subsequently, the diatoms indicate a shift to wetter climate at 8351 cal. yr BP (zone 1b, Figure 6; 8320–8088 cal. yr BP) or at least a fresher lake from greater groundwater flow (Figure 7). This shift, which appears abrupt in the diatom record, culminates a gradual and variable increase in aragonite following the major drought and aragonite minimum at ~9250 cal. yr BP (Grimm et al., 2011). So whereas the aragonite indicates a gradual increase in moisture, the diatoms may indicate a threshold response. A brief event occurring at ~8200 cal. yr BP where diatom Groups 2 and 3 become dominant suggests more saline conditions and an arid climate. This observation is similar to other studies in this region where a cool, windy, dry period is inferred in response to this climatic event (Alley et al., 1997; Dean, 1993). This event is not extraordinary during the early mid Holocene, but does correspond with one of the lowest aragonite minimums and by inference severe droughts of the Holocene (Grimm et al., 2011), and the synoptic climatology associated with the 8.2 ka event in Greenland may have exacerbated a cyclical NGP drought owing primarily to other causes.

At approximately 8100 cal. yr BP Kettle Lake became dra-

matically more saline, and the diatom assemblages subsequently were less stable (zone 1c, Figure 7). The timing of this transition corresponds with abrupt expansion of prairie to the east at Elk Lake, Minnesota (Dean et al., 1996). To the northwest of Kettle the transition to the mid-Holocene arid period began earlier (c. 9000 cal. yr BP), as lake level dropped in Ceylon Lake and the basin became closed (Last, 1990). At Kettle Lake diatoms were lost from the sediments because of dissolution beginning ~7920 cal. yr BP. This phenomenon commonly occurs in highly saline environments (Ryves et al., 2009) and lasted in Kettle until ~5950 cal. yr BP. The period of diatom dissolution also corresponds with an intensely dry period, based on other proxies (Grimm et al., 2011).

From 5950 cal. yr BP until 4364 cal. yr BP, the diatom assemblages have a high rate-of-change, suggesting an unstable community, fluctuating among lake states on decadal to centennial timescales (Figure 7). A saline, well-mixed lake dominated by group 2 and 3 diatoms was prevalent above the diatom dissolution zone, similar to the lake state prior to the dissolution (Figure 7). At 5700 cal. yr BP Kettle became intermittently fresher for ~200 years, followed by a dramatic shift to high salinity and inferred arid conditions at 5419 cal. yr BP (zone 1d, Figure 6). This climatic inference from diatoms corresponds well with the inference from aragonite data, which indicate an extended pluvial period ~5700–5600 cal. yr BP, followed by an intense drought centered at ~5400 cal. yr BP (Figure 4; Grimm et al., 2011). At this time Kettle Lake enters a period where meromixis (group 4 diatoms) becomes a dominant lake state (Figure 7), alternating with saline conditions and moderate-low groundwater flow (group 3 diatoms) (Figure 7).

Evidence for meromictic conditions during this time period also comes from authigenic mineral deposits of struvite (hydrous Mg-ammonium-phosphate), in the same Kettle Lake core between 8700 and 4650 cal. yr BP (Donovan and Grimm, 2007). Struvite is a guano mineral, occurring in animal waste and requiring an anoxic sedimentary environment, such as is characteristic of a meromictic lake. Donovan and Grimm (2007) hypothesized that during the arid mid Holocene, the relatively deep Kettle Lake would be one of a small number of lakes in the NGP that still contained water, causing a dramatic increase in migratory waterfowl, guano deposition, and preservation of struvite. The presence of this mineral and the dominant diatom *Nitzschia paleacea* (an obligate N heterotroph, tolerant of heavy organic pollution) further supports the inference of a meromictic lake environment at this time. Meromixis could become established under continued warm and arid conditions which drive further lowering of groundwater flow and increased evaporative loss from the lake, which continued to increase salinity and produced strong chemical stratification. As a result of infilling, the lake basin would have been approximately 10 m deeper or double the present depth at this time, making meromictic conditions easier to establish (Figure 8). It appears that while group 4 diatoms suggest meromictic conditions, their abundance is not necessarily related to the strength or stability of meromictic conditions. This is demonstrated by the sustained high values of group 4 diatoms in the lower half of zone 1d from ~5400 to 5000 cal. yr BP (Figure 7) which correspond with a sustained period of intermediate aragonite values with little variability, suggesting relatively dry, but not intensely dry, conditions, and thus a sustained drought of intermediate intensity. It is perhaps the persistence of low lake-levels and a relatively large monimolimnion that favors group 4 diatoms dur-

Figure 8. Schematic cross-sections of Kettle Lake, ND through time as defined by the main diatom zones. Historical lake depths and infilling are based on linear interpolations of basin morphology and the age-model. The estimated range in lake levels are shown as dashed lines, subjectively inferred from the diatom defined lake states, with the predominant groundwater level as the lake level. The vertical axis represents the depth from modern water surface in meters.

ing this time. In addition, throughout the entire mid Holocene the sediment is finely laminated (Grimm et al., 2011), and the period of struvite occurrences overlaps with a large zone of diatom dissolution (Donovan and Grimm, 2007), suggesting that meromictic conditions are not specific to periods when group 4 diatoms dominate.

A ~200 year period of fresher conditions prevailed from 4750 to 4550 cal. yr BP, prior to the most significant shift (greatest sum-of-squares height in the diatom cluster analysis) at 4364 cal. yr BP, when the mid-Holocene arid period switched abruptly to a wetter late-Holocene period. This 200-year period also corresponds with wet conditions implied by the aragonite data (Figure 4; Grimm et al., 2011). The age of this shift in diatoms falls between the major breaks in pollen and mineral data respectively at 4290 and 4590 cal. yr BP. Thus, all proxies (minerals, pollen, and diatoms) indicate a major climatic mode shift during this period.

Zone 2 (4364–620 cal. yr BP). Kettle Lake was generally fresh, dimictic, and influenced by high groundwater flow during zone 2 (Figures 7 and 8). The sedimentation rate also increased at ~4500 cal. yr BP, possibly as a result of increased aquatic production (Figure 2). This sharp transition to zone 2 is also the strongest shift in the pollen and mineral records for Kettle (Grimm et al., 2011). The dramatic shift to a wet late-Holocene period is well documented in a number of records from the NGP (Laird et al., 2007). Indeed, the timing of this transition in Ceylon and Waldsea Lakes to the north of Kettle Lake (Figure 1) occurred within ~50 years of the event at Kettle Lake. To the east of the NGP, Lake 239 in Ontario and Elk Lake, Minnesota recorded dramatic secular changes at 4435 cal. yr BP and ~4200 varve years before AD 1980, respectively (Bradbury and Dieterich-Rurup, 1993; Laird and Cumming, 2008). To the west of Kettle, Foy Lake in the Rocky Mountains of Montana also exhibits large diatom assemblage shifts at c. 4500 cal. yr BP (Stone and Fritz, 2006). Here, Stone and Fritz (2006) present evidence for a significant climate state change associated with an apparent reduction in strength of forcing by the Pacific Decadal Oscillation. Such a shift in the relative influence of Pacific versus Atlantic sea-surface temperature might be associated with an increase in moisture from low-level summer southerly air masses from the Gulf of Mexico, as hypothesized in other regional paleoclimatic studies (Dean et al., 1996).

Multidecadal to centennial length drought periods dominated by the saline diatoms in group 2 or 3, are evident dur-

ing the wetter period in Kettle Lake from 4364 to 1406 cal. yr BP (e.g. 3442 to 3268 cal. yr BP and 1950 to 1700 cal. yr BP (Figure 7)). However, there is no evidence of a mega-drought beginning at c. 4200 cal. yr BP and persisting for several hundred years, as has been observed in a number of North American paleoclimatic records (Figure 7; Booth et al., 2005). In contrast, Kettle Lake shows evidence of moister conditions at c. 4200 cal. yr BP. At other times in zone 2 are short sporadic decadal periods of strongly saline water or meromixis (diatom group 3 and 4), suggesting dramatic fluctuations in the groundwater-table and lake levels. These drought periods predictably show higher diatom community instability during an overall zone of relative assemblage stability (Figure 7).

Around 1406 cal. yr BP, there is an increased abundance of benthic diatoms (group 2). While the reconstructed DI-salinity is similar to Kettle Lake's current salinity (Figure 4), the community assemblage is relatively unstable. A diatom subzone from 1406 to 872 cal. yr BP (zone 2c, Figure 6) is characterized by some of the highest rate-of-change values, lower groundwater flow and much drier conditions (group 2, 3, and 4 diatoms) (Figure 7). The base of this subzone corresponds closely with the base of mineral/pollen zone E3, which these proxies indicate as drier than underlying zone E2 (Grimm et al., 2011). Zone E3 exhibits a tripartite dry-wet-dry sequence. The earliest dry interval dating to 1460–900 cal. yr BP corresponds closely with diatom zone 2c and is coincident with the 'Medieval Climate Anomaly' (MCA; Bradley et al., 2003). Drought was common during the MCA and has been documented in a number of other western paleoclimatic records (Herweijer et al., 2007; Woodhouse, 2004). Regionally, this shift is coincident with Ceylon Lake to the northwest, which also shows a transition from high lake levels at ~2000 cal. yr BP to a low level at ~1500 cal. yr BP and a return to high lake levels by ~1000 cal. yr BP (Teller and Last, 1990). In Kettle Lake the abrupt increase in salinity at 1406 cal. yr BP is followed by large decadal fluctuations in salinity, returning to fresher conditions. At ~872 cal. yr BP, another abrupt diatom assemblage shift takes place (zone 2d, Figure 7), where fairly stable, freshwater diatom communities dominate from 872 to 620 cal. yr BP (Figure 3 and 7). Zone 2d corresponds closely with the wet middle section of mineral/pollen zone E3 dated to ~900–600 cal. yr BP, which also indicates wetter conditions (Grimm et al., 2011). Other diatom records from North Dakota show a complex response both temporally and spatially during this period, with evidence of arid and wetter periods (Fritz

et al., 2000). It is becoming evident that the heterogeneity of lake responses to arid periods is related to the lake's connection to the groundwater table (Almendinger, 1993; Fritz et al., 2000; Laird et al., 2007). Indeed, the strong connectivity of Kettle Lake to the Little Muddy Aquifer would lead to its relative biological stability during climatically instable periods.

Zone 3 (620 cal. yr BP to present). Zone 3 in the diatom record of Kettle Lake represents the transition into the 'Little Ice Age' (LIA) and a rapid transition to a more arid climate and unstable diatom communities until 113 cal. yr BP (zone 3a, Figure 7). Each of the four diatom groups dominates at some point during this period, suggesting variable lake levels and groundwater flow from a more variable climate (Figure 7). Group 2 diatoms, which include both freshwater and subsaline benthic species, are prominent during the early LIA, suggesting that cold spring temperatures and moderately arid climate prevailed (Fritz et al., 1994). Colder temperatures could also favour benthic diatoms, as a long period of lake-ice cover would mean a reduced spring mixing and short planktonic growing season. Freshwater conditions (group 1 diatoms) dominate near the end of the LIA (~350 to 113 cal. yr BP), suggesting a gradual transition to wetter conditions. This pattern of a cool arid early-LIA transitioning into a cool, moist late-LIA (~350 cal. yr BP) also was apparent to the east in Elk Lake, Minnesota (Bradbury and Dieterich-Rurup, 1993). It should be emphasized that although zone 3 is somewhat drier than the preceding 300 years (Figure 7), the magnitude of this aridity is nowhere near that of the mid Holocene. Other records from North Dakota, including Devils, Moon, Coldwater, and Rice Lakes, all have a much more complex response to the LIA climate (Figure 1; Fritz et al., 1994, 2000).

The modern period (zone 3b, Figure 6; 113 cal. yr BP to present) continued as relatively arid and unstable, with all four lake regimes dominating at some point. Decadal periods of meromixis occurred early in this period following a transition from group 2 to 3 diatoms. This pattern suggests a gradual lowering of lake level in response to reduced groundwater flow. The large 'Dust Bowl' era drought of the 1930s is recorded in an abundance of group 3 and 4 diatoms, however, the corresponding salinity during this time is only slightly above the modern value (Figure 4). Comparing the inferred lake state and salinity of the 'Dust Bowl' with the rest of the record, suggests that droughts more severe than the Dust Bowl, both in duration and aridity, were prevalent throughout the last 8500 years at Kettle Lake. The diatom rate-of-change for the modern period and the end of the LIA also suggests that the recent climate is generally more unstable than any other extended period over the last 8500 years.

Conclusion

The regional climatic and hydrologic gradients in the NGP are strong and pose a significant challenge to reconstructing a coherent picture of North American climate. We have shown that the use of an independent proxy of groundwater flow provides an effective means to interpret the biological response through time, in a closed-basin lake ecosystem that is intimately tied to the local aquifer. At the millennial-scale there is strong evidence for regional climatic re-arrangements, particularly at ~4500 cal. yr BP. Both the diatom and

geochemical record from Kettle Lake, suggest periods of meromixis during the mid Holocene and the last 600 years. At the decadal-centennial scale the diatom record from Kettle Lake shows no clear cyclic trends over the last 8500 years. However, periods of prolonged (~100 years) and rapid (20–30 years) drought have taken place throughout the mid to late Holocene. These droughts appear to have had similar impacts on the Kettle Lake hydrology as the 'Dust Bowl' era droughts, but were longer in duration.

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