

A 1600-year record of human impacts on a floodplain lake in the Mississippi River Valley

Richard B. Brugam · Samuel E. Munoz

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Abstract In North America, land use practices of the last two centuries have strongly influenced aquatic communities and freshwater quality, but the impacts of prehistoric land use on freshwater resources remain poorly documented. Here we investigate the influence of prehistoric and historical land use on Horseshoe Lake, Illinois, USA, an oxbow lake in a floodplain of the Mississippi River that is adjacent to Cahokia, the largest prehistoric indigenous population center north of Mexico. Diatom assemblages from Horseshoe Lake's sedimentary record track shifts in aquatic environmental conditions over the last ca. 1600 years. During the period of prehistoric population growth and agricultural intensification associated with Cahokia's emergence (ca. 600–1200 CE), the relative abundance of *Aulacoseira granulata*—a planktonic diatom associated with shallow eutrophic lakes—increased. Following the abandonment of Cahokia in the 14th century CE, the diatom flora of the lake shifted from

planktonic *Aulacoseira* taxa to the epiphytic taxa *Cocconeis* and *Gomphonema*. This shift in diatom assemblages is consistent with a reduction of nutrient inputs to the lake and/or reduced fishing pressure as prehistoric populations abandoned the area. Following the intensification of historic settlement after 1800 CE, diatom assemblages shift to epipelagic species of small *Staurosira* and *Fragilaria*, indicating a reduction in aquatic macrophytes and increased turbidity. Our results document prehistoric indigenous impacts on a freshwater system beginning nearly 1000 years before European colonization of the Americas and demonstrate the antiquity of human impacts on freshwater resources in North America.

Keywords Horseshoe lake · Cahokia · Mississippian · Floodplain · Oxbow lake · Diatoms · Eutrophication

R. B. Brugam (✉)
Department of Biological Sciences, Southern Illinois
University Edwardsville, Edwardsville, IL 62025, USA
e-mail: rbrugam@siue.edu

S. E. Munoz
Department of Marine and Environmental Sciences,
Marine Science Center, Northeastern University, Nahant,
MA 01908, USA

S. E. Munoz
Department of Civil and Environmental Engineering,
Northeastern University, Boston, MA 02115, USA

Introduction

Human activities exert a fundamental control on aquatic ecosystems and freshwater quality (Smith et al. 1999; Jackson et al. 2001; Dudgeon et al. 2006). Managing freshwater resources to improve water quality depends, in part, on understanding the sensitivity of aquatic ecosystems to environmental changes that occurred in the recent past and in prehistory (Smol and Stoermer 2010). At sites across North America,

instrumental datasets and paleolimnological records document declines in freshwater quality beginning in the 19th and 20th centuries because of enhanced nutrient loading and pollutants (Cumming et al. 1992; Hall et al. 1997; Carpenter et al. 1998; Smol 2010). Despite the abundance of evidence documenting recent historical degradation of freshwater resources, paleolimnological records of prehistoric human impacts on aquatic ecosystems in North America are scarce. In one prominent set of studies, Ekdahl et al. (2004, 2007) demonstrated that an Iroquoian settlement around a small lake in southern Ontario, Canada caused a shift to more eutrophic conditions in the 13th century CE. Yet, whether prehistoric human impacts on freshwater ecosystems were widespread in North American remains unclear. Paleolimnological evidence from South and Central America demonstrates that indigenous populations in those regions influenced freshwater ecosystems thousands of years before European colonization (Haberyan and Horn 2005; Slate et al. 2013; Bush et al. 2016), but were similar impacts north of Mexico confined to the relatively recent past? Prehistoric populations in some areas of eastern North America, particularly in the Midwest and Southeast, were large, sedentary, and cultivated a variety of plant foods for thousands of years prior to European colonization (Smith 2009; Milner 2005), but their influence on freshwater ecosystems remains poorly documented.

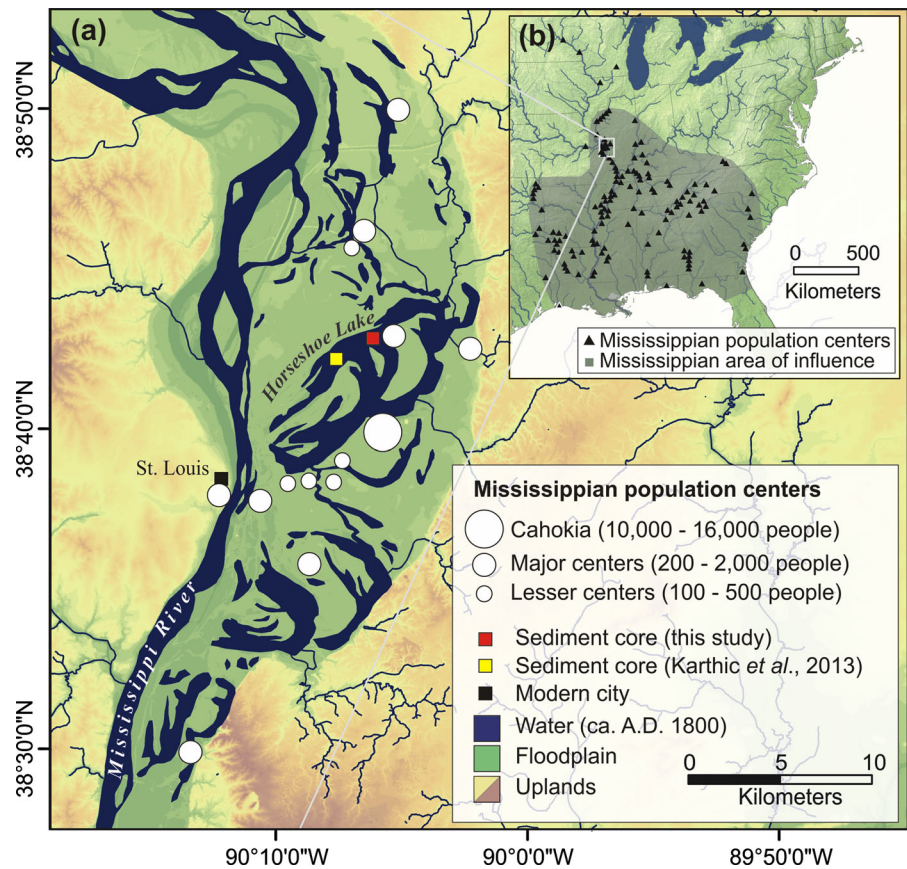
In this study, we present diatom assemblages in a sedimentary record from Horseshoe Lake, Illinois (USA)—an oxbow lake that is adjacent to Cahokia, the largest prehistoric indigenous settlement north of Mexico. Because of its size and cultural prominence, Cahokia is one of the most intensively studied archaeological sites in North America, and its demographic and land use history are well-documented (Pauketat and Lopinot 1997; Milner 1998; Simon and Parker 2006; Munoz et al. 2014). We use diatom assemblages from Horseshoe Lake to examine the impacts of prehistoric populations on freshwater quality and ecosystems. We show that this large lake has been highly sensitive to human activities over the past 1600 years and exhibited signs of cultural eutrophication as early as 600 CE.

Study area

Horseshoe Lake is a large (860 ha) and shallow (3 m) oxbow lake near Saint Louis, Missouri (Fig. 1). Horseshoe Lake is in a wide section of the middle Mississippi River's floodplain known as the 'American Bottom' (Milner 1998). The lake formed from a neck cut-off of the Mississippi River about 1800 years ago and developed plugs along its arms that limited its hydrological connectivity with the main channel (Hajic 1993). Several small streams originating from the loess-capped uplands to the east drain into Horseshoe Lake directly or via adjacent lakes and wetlands. In the late 19th and 20th centuries, many wetlands of the American Bottom were drained and artificial levees were constructed along the Mississippi River to encourage development and manage flood risk (Hajic 1993). Prior to the establishment of these artificial levees, high-magnitude flood events of the Mississippi River periodically deposited sediment into Horseshoe Lake (Munoz et al. 2014, 2015). Today, Horseshoe Lake is managed by the Illinois Department of Natural Resources for fishing and waterfowl hunting, and the lake's watershed contains a mix of agricultural, industrial, and urban land use.

During the Late Woodland (ca. 400–1050 CE) and Mississippian (ca. 1050–1350 CE) archaeological periods, the floodplain and uplands around Horseshoe Lake were populated by indigenous peoples who hunted, fished, and cultivated a variety of domesticated plant foods (Fig. 2). During the Late Woodland Period, inhabitants of the area incorporated the cultivation of indigenous seed crops of the Eastern Agricultural Complex (EAC; Smith 1987), including goosefoot (*Chenopodium berlandieri*), sumpweed (*Iva annua*), knotweed (*Polygonum erectum*), little barley (*Hordeum pusillum*), and sunflower (*Helianthus annuus*) into a mixed and mobile subsistence strategy (Johannessen 1984; Fortier and Jackson 2000; Koldehoff and Galloy 2006). Late Woodland peoples began cultivating maize (*Zea mays* subsp. *mays*) in conjunction with indigenous seed crops of the EAC after ca. 800 CE (Milner 1998; Simon and Parker 2006), although hunting, fishing, and foraging for wild plant foods remained important into the Mississippian Period (Fritz 1990; Lopinot 1997). During the subsequent Mississippian Period, beginning around 1050 CE, Cahokia emerged as a major political, economic, and religious center, drawing thousands

Fig. 1 Map of the study area in the middle Mississippi River Valley, showing: **a** locations of sediment cores collected from Horseshoe Lake, and Mississippian population centers (after Pauketat and Lopinot 1997), and historic (ca. 1800 CE) positions of the Mississippi River, floodplain lakes, and streams (modified from Milner 1998); **b** location of the study area within eastern North America, with major Mississippian population centers and area of Mississippian influence (ca. 1000–1600 CE)



of people from across the region into a hierarchically-organized, sedentary, and predominately agricultural lifestyle (Milner 1998). The area's population size, including Cahokia and neighboring settlements, reached its height around 1200 CE, followed by a period of sociopolitical dissolution and gradual out-migration until the area was almost completely abandoned by 1350 CE. Following Cahokia's dissolution, the area was sparsely occupied by various indigenous groups until around 1700 CE, when Euro-American farmers, fur traders, and missionaries first settled the area (Esarey 1984; Brown and Sasso 2001). Populations increased rapidly after 1800 CE as Euro-American peoples settled the area, initially establishing farms and later industries along the Horseshoe Lake's shoreline and its watershed (Esarey 1984; Karthic *et al.* 2013). Given the long and well-documented demographic and land use history of the Horseshoe Lake area, we analyzed diatom assemblages in a lake's sedimentary record to examine the influence of prehistoric and historic land use on the

lake's ecology. We hypothesize that prehistoric occupation of the lake and its watershed shifted the lake towards more eutrophic conditions, and that nutrient inputs declined following the abandonment of Cahokia.

Materials and methods

Field sampling

Four sets of sediment cores were taken across the apex of Horseshoe Lake using a Livingston piston corer in May 2012 (Fig. 1). Here, we analyze the core collected from the in-filling former thalweg of the Mississippi River (HORM12-4; 90.081279°W, 38.704767°N; water depth 1.09 m). This 578-cm-long sediment core was split longitudinally, described, photographed, sectioned into 1 cm increments and stored in WhirlpakTM bags in a refrigerator. The core analyzed in this study is the same core as the one used

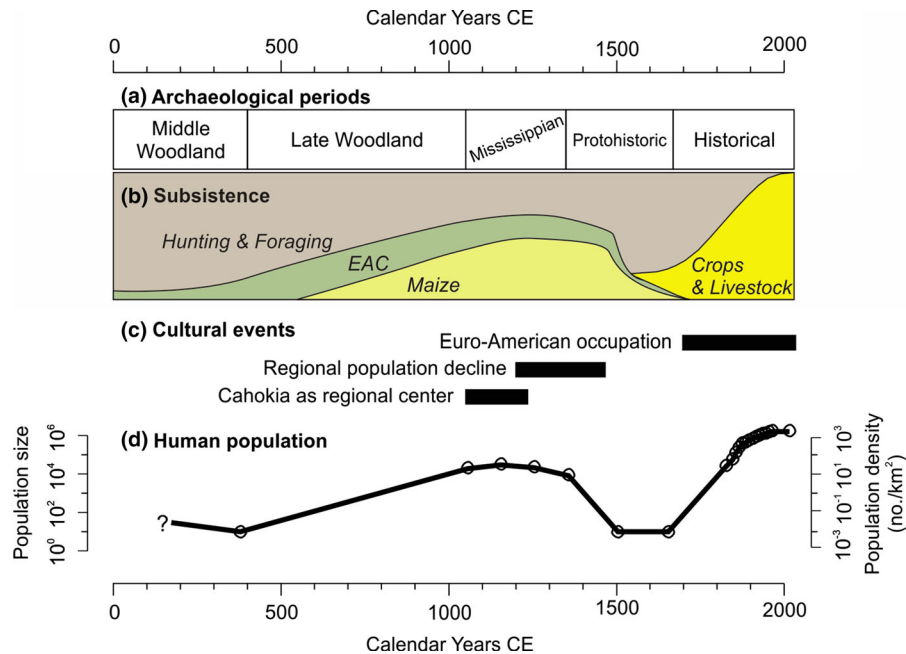


Fig. 2 Timeline of cultural, land use, and demographic change in the study area: **a** archaeological periods of the American Bottom after Fortier et al. (2006); **b** subsistence strategies modified from Simon and Parker (2006), where EAC denotes the ‘Eastern Agricultural Complex’, a set of plant foods domesticated in eastern North America (see text for details);

c timing of important cultural and demographic events; **d** human population size and density in the study area (prehistoric population levels after Milner (1998), with archaeological hiatuses from Fortier et al. (2006) representing very sparse occupations); historical populations for the study area are based on the historical census

in the paleoecological (fossil pollen, stable carbon isotopes) and paleohydrological (grain size) reconstructions described by Munoz et al. (2014, 2015), and additional details on this sedimentary record can be found in those publications.

Chronological control

The age model for the core is the same as that used by Munoz et al. (2014), and is a modified smooth spline developed using Clam 2.2 (Blaauw 2010). The age model is based on 9 accelerator mass spectrometry ¹⁴C dates on terrestrial macrofossils, calibrated using the IntCal13 calibration curve (Reimer et al. 2013). The rise in *Ambrosia* pollen found by Munoz et al. (2014) was assigned the date of 1825 ± 25 CE based on McAndrews (1988). This differs slightly from the 1809 date previously assigned to the *Ambrosia* rise by Karthic et al. (2013) for a 73-cm-long core from Horseshoe Lake (Fig. 1). Additional details of this sediment core’s age model can be found in Munoz et al. (2014).

Diatom preparation and identification

Diatom samples were made at approximately 8-cm intervals in the core except between 64.5 and 80.5 cm where the sampling interval was 2 cm. In some core levels there were no diatom microfossils preserved. These levels were scanned for diatoms and discarded.

Diatom microfossils were prepared from the Horseshoe Lake core using a method similar to Moos et al. (2005). Approximately 0.5 gm of sediment was placed in a glass centrifuge tube. The organic matter in the sample was removed from the sediment using a solution of 50% HNO₃ and 50% H₂SO₄. The solution was heated to 90 °C for 4 h using a block heater. The samples were removed from the block heater and allowed to cool and settle for 24 h. The acid was aspirated off and replaced with de-ionized water. This process was repeated every 24 h until the remaining acid was removed. Subsamples of the diatom suspension were dried on coverslips and mounted in NaphraxTM mounting medium, and diatoms were identified using a Leitz Laborlux microscope with a

100× oil immersion lens. Diatom preservation in the Horseshoe Lake core was highly variable so numbers counted varied from a low of 68 at 144.5 cm depth to a high of 524 at 725 cm. Diatom identification followed Siver and Hamilton (2011), Kramer (2000, 2002), Lange-Bertalot (2001), and Siver et al. (2007).

Statistical analysis

Constrained incremental sums of squares cluster analysis (CONISS)

Diatom assemblages from the Horseshoe Lake core were compared using the computer program CONISS, which performs a stratigraphically constrained cluster analysis (Grimm 1992). In contrast with ordinary cluster analysis, only stratigraphically adjacent clusters are merged. The dissimilarity metric used was chord distance.

Non-metric multidimensional scaling (NMDS)

In contrast to CONISS, Non-metric Multidimensional Scaling (NMDS) is not constrained by depth, and instead compares samples independently of depth. Minchin (1987) showed that this non-parametric method is relatively robust to variations in community models and is an appropriate choice for most ecological applications. Paleolimnologists have more frequently used Detrended Correspondence Analysis (DCA) to ordinate fossil diatoms from cores. DCA assumes that diatom taxa are organized in unimodal response functions along environmental gradients in a bell-shaped pattern. The technique is subject to an “Arch Effect,” a computational artifact in which the second ordination axis is a function of the first. DCA attempts to account for this effect by “detrending” or compressing the high and low values on the first axis. NMDS is a non-parametric method that assumes no particular response function (Minchin 1987), thereby avoiding the “Arch Effect” and modifications of ordination axes. NMDS was used by Schroeder (2016) to study the human impacts on diatom assemblages in a core from an Ohio reservoir.

Non-metric multidimensional scaling (NMDS) ordination was performed on diatom taxa using PC-Ord version 6.01 (Peck 2010). Taxa are ordinated by calculating the weighted average of the coordinates of samples containing them. This weighted average

indicates which taxa are important in controlling the location of particular samples in ordination space. In our analysis, we used 24 taxa with abundances in at least 1 sample of > 5% (Table 1). This number of taxa is smaller than the total number of taxa in the dataset because many taxa from the total dataset were too rare for inclusion in the statistical analysis (Peck 2010). Members of the genus *Gomphonema* were summed. We used all 33 depths from the Horseshoe Lake core and used the Bray–Curtis distance metric.

Results

Diatom assemblages are present throughout most of Horseshoe Lake’s sedimentary record (Figs. 4, 5), but we encountered poor diatom preservation in sections that were identified by Munoz et al. (2015) as sediment deposited during major flood events of the Mississippi River (Fig. 3). Here, we use sections in which diatom assemblages are well preserved to interpret limnological changes at Horseshoe Lake over the last 1600 years. Stratigraphically constrained cluster analyses based on CONISS divides the diatom assemblages from Horseshoe Lake into 4 zones numbered HORMD1 through HORMD4 (Fig. 3).

Zone HORMD1 (393 cm, 390 CE)

Zone HORMD1 contains only one sample. Diatom assemblages in this sample are dominated by *Aulacoseira distans* (79%), a taxon that is not present in any other sample (Fig. 4). There are small percentages of *Cyclotella meneghiniana* and *Stephanodiscus minutus*. The unique diatom assemblage in this zone reflects conditions prior to intensive prehistoric settlement and/or the aquatic ecosystem shortly after the lake’s formation, but because it contains only one sample it is not used in our interpretation of the Horseshoe Lake record (below).

Zone HORMD2 (345–45 cm, 610–1400 CE)

Core zone HORMD2 is separated from zone HORMD1 by 56 cm of sediment without identifiable diatom microfossils. This zone is also interrupted from 225 to 185 cm by another region with poor diatom preservation. After this interruption, diatom accumulation continues with the same assemblage that existed

Table 1 Taxa used in NMDS ordination, listed in order of abundance

Taxon number	Species name	Authority
1	<i>Aulacoseira granulata</i>	(Ehrenb.) Simonsen
2	<i>Nitzschia amphibia</i>	Grunow
3	<i>Fragilaria vaucheriae</i>	(Kütz.) Petersen
4	<i>Staurosira construens</i> var. <i>venter</i>	(Ehrenberg) Hamilton
5	<i>Aulacoseira distans</i>	(Ehrenberg) Simonsen
6	<i>Aulacoseira ambigua</i>	(Grunow) Simonsen
7	<i>Stephanodiscus minutus</i>	Pantocsek
8	<i>Amphora ovalis</i>	(Kütz.) Kütz.
9	Sum of <i>Gomphonema</i> species	
10	<i>Cocconeis placentula</i>	Ehrenb.
11	<i>Rhopalodia gibba</i>	(Ehrenberg) O. Müller
12	<i>Aulacoseira muzzanensis</i>	(F.Meister) Krammer
13	<i>Navicula lanceolata</i>	(C.Agardh) Ehrenb.
14	<i>Craicula cuspidata</i>	(Kütz.) D.G. Mann
15	Unidentified <i>Aulacoseira</i>	
16	<i>Lyrella hennedyi</i>	(W.Smith) Stickle & D.G. Mann
17	<i>Aulacoseira granulata</i> var. <i>angustissima</i>	(O.Müll.) Simonsen
18	<i>Cyclotella meneghiniana</i>	Kütz.
19	Unidentified <i>Pinnularia</i>	
20	<i>Synedra rumpens</i>	Kütz.
21	Unidentified <i>Navicula</i>	
22	<i>Surirella linearis</i>	W. Smith 1853
23	<i>Staurosira construens</i>	Ehrenberg 1843
24	<i>Sellaphora pupula</i>	Kütz.

Taxon numbers are keyed to Fig. 7

before the hiatus. That assemblage is dominated by *Aulacoseira granulata* (Fig. 4), a planktonic species of shallow, alkaline lakes (Brugam 1993), with abundances varying from 15 to 81%. *A. granulata* is accompanied by another variety of the same species, *A. granulata* var. *angustissima*. Other planktonic species that are present are *Aulacoseira muzzanensis* and *Stephanodiscus minutus*. These planktonic species are accompanied by a wide variety of epiphytic species at low abundances (Fig. 5). The most abundant of these are *Cocconeis placentula* and *Amphora ovalis*. Both of these species are moderately abundant at deeper core levels, but decline in abundance at shallower core depths until they nearly disappear at 250 cm (990 CE).

Zone HORMD3 (145–57 cm, 1400–1780 CE)

Zone HORMD3 begins between 169 cm (1310 CE) and 145 cm (1410 CE) with a decline in *A. granulata*

from 58.9 to 2.9% (Fig. 4) and a rise in total epiphytic taxa from 11.2 to 92.6% (Figs. 4, 5). *Cocconeis placentula* and *Amphora ovalis* return in higher abundances than in diatom zone HORMD2. This change represents a major shift in diatom assemblages at Horseshoe Lake from planktonic taxa to epiphytic ones (Fig. 3). The sample from 145 cm is unusual, with a high abundance of *Nitzschia amphibia*. Just after this sample (145–97) there is another hiatus in diatom preservation. After the hiatus, accumulation of diatoms continues with an assemblage that has high epiphytic percentages and lower planktonic species percentages (Fig. 3). This zone contains a peculiar diatom species—*Lyrella hennedyi* (Fig. 4)—which reaches 12.8% at 57 cm (1780 CE). This is a species generally found epipelically in marine sandy environments (Mann and Stickle 1993). Other, more common epipellic species like *Staurosira construens* var. *venter* and *Staurosira vaucheriae* begin to appear at this level.

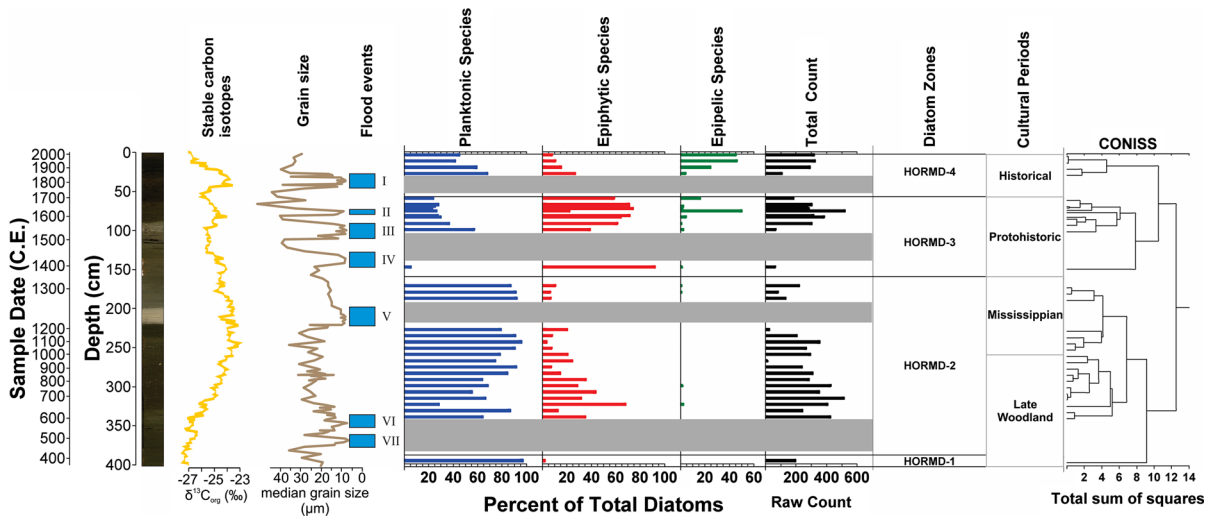
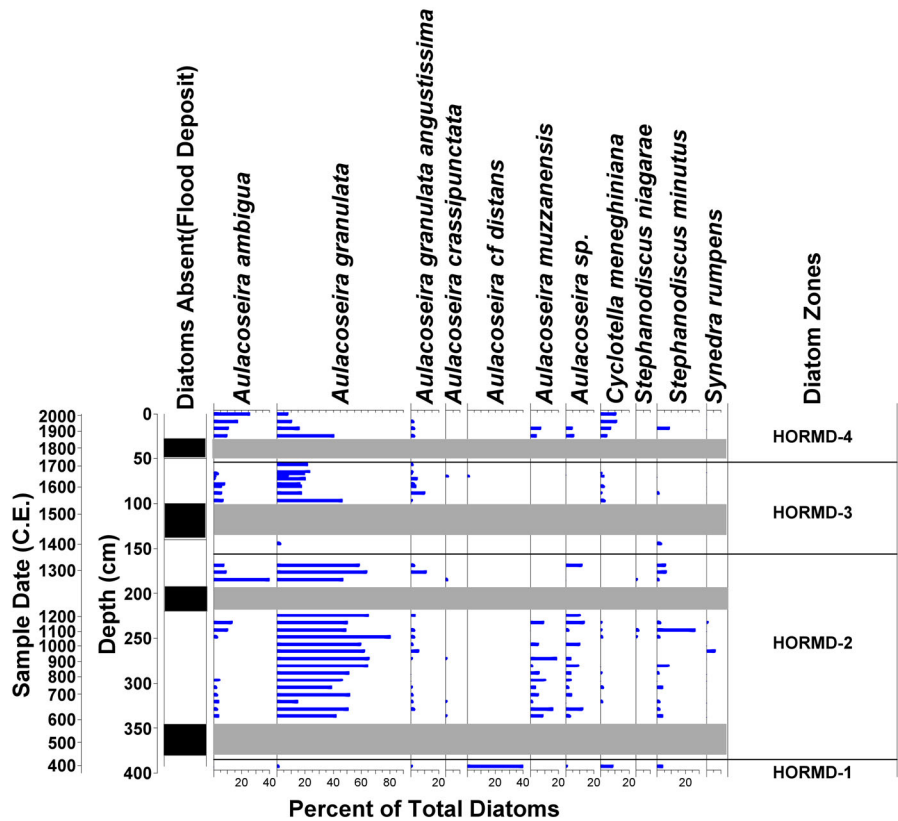


Fig. 3 Summary diagram of diatom microfossils from the Horseshoe Lake core. Diatom taxa are grouped by life form. The dendrogram shows the stratigraphically constrained incremental sums of squares (CONISS) cluster analysis used to determine diatom zone boundaries. Thin black horizontal lines indicate zone boundaries combining diatom zones and cultural periods

(after Fortier et al. 2006). Gray rectangular bars indicate core regions where diatoms are not preserved. Flood deposits (blue rectangles), sediment grain size, stable carbon isotopes ($\delta^{13}C_{org}$) and a core photograph from Munoz et al. (2015) are shown in the panels to the left

Fig. 4 Planktonic diatom microfossils from the Horseshoe Lake core. Thin black horizontal lines indicate diatom zone boundaries. Black rectangles on the left column (labeled “Diatoms absent”) and gray bars indicate core regions where diatoms are not preserved



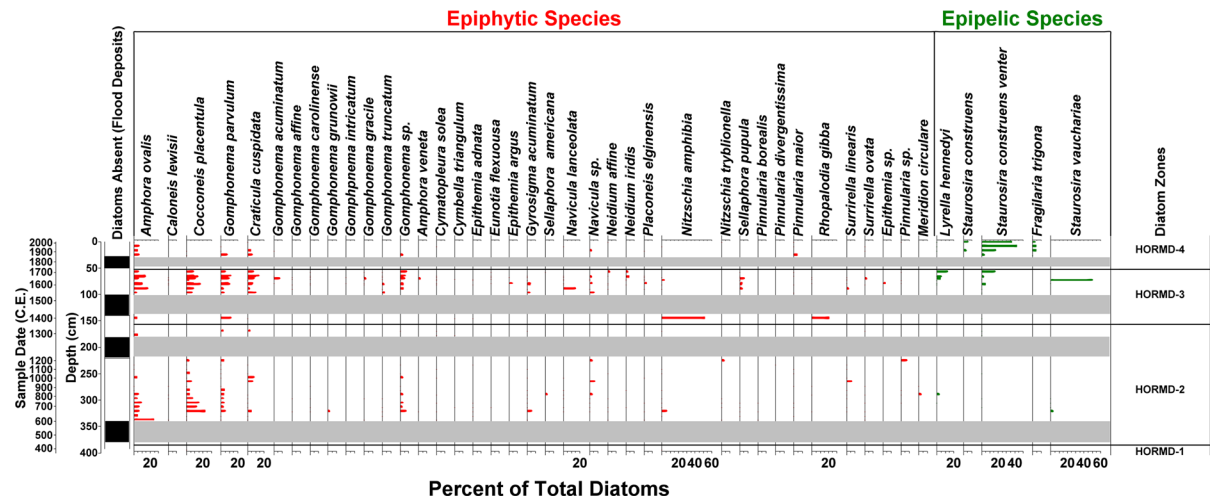


Fig. 5 Epiphytic and epipellic diatom microfossils from the Horseshoe Lake core. Thin black horizontal lines indicate diatom zone boundaries. Black rectangles on the left column

Zone HORMD4 (57–1 cm, 1810–2010 CE)

This zone begins with a layer without diatom fossils. The later, fossil-containing layers have more epipellic taxa (*S. construens* var. *venter*, *S. construens* and *Fragilaria trigona*; Fig. 5). *L. hennedyi* percentages, however, are reduced. *Cyclotella meneghiniana* appears in abundance for the first time. Epiphytic taxa decline and are replaced by epipellic taxa (Fig. 5).

Ordination results

For diatom assemblages in Horseshoe Lake, NMDS ordination differentiates samples before the abandonment of Cahokia ca. AD 1350, from those deposited afterwards (Fig. 6). This result agrees with the CONISS results (Fig. 3). Samples prior to the abandonment of Cahokia have low scores on Axis 1, whereas samples from after the prehistoric abandonment of the region score higher on Axis 1. The groupings of diatom assemblages were highly significant ($p = 0.001$) using Analysis of Similarities (ANOSIM). The overlap among pre- and post-abandonment samples implies that shifts in communities were gradual, similar to the lagged community response observed in a reservoir in Ohio (Schroeder et al. 2016). In Horseshoe Lake, we also observe a lagged community response following historic Euro-American settlement, although the most recent samples score highly on Axis 2 (Fig. 6).

(labeled “Diatoms absent”) and gray bars indicate core regions where diatoms are not preserved

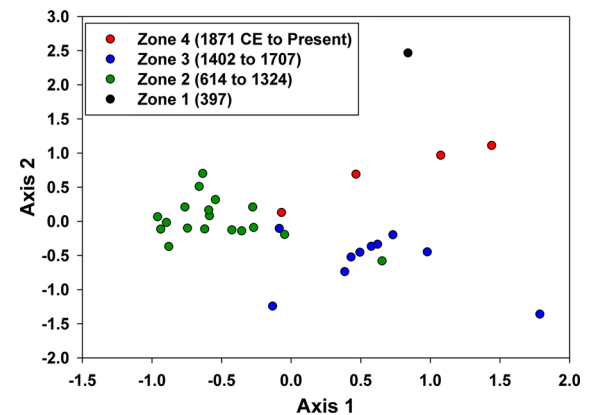


Fig. 6 Non-metric multidimensional scaling (NMDS) ordination of diatom assemblages at various core depths

The weighted averages of taxa provide insight into the distribution of individual samples, with Axis 1 defined by taxa that were abundant prior to and immediately after Cahokia’s abandonment, and Axis 2 defined by taxa that have dominated diatom assemblages since historic Euro-American settlement (Fig. 7). Planktonic taxa (*Aulacoseira granulata* and *Stephanodiscus minutus*) are most abundant in samples with Axis 1 coordinates < 0 (pre-abandonment). Epiphytic taxa (*Amphora ovalis*, *Cocconeis placentula*, *Gomphonema* spp. and *Navicula lanceolata*) are > 0 (post-abandonment). Taxa abundant following historic Euro-American settlement (*Staurosira*

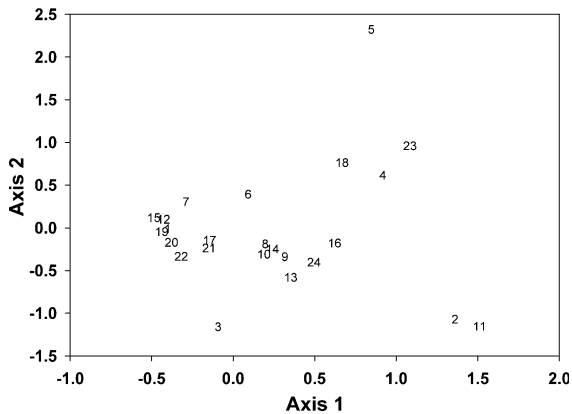


Fig. 7 Diagram of weighted averages of diatom species in ordination space. Numbers are keyed to taxa names in Table 1

construens, *S. construens* var. *venter*, *Cyclotella meneghiniana*) occur at high Axis 2 values.

Summary

The diatom assemblages from Horseshoe Lake’s sedimentary record are divided into three main zones, as HORMD1 contains only one sample: (1) During the period of Cahokia’s emergence, HORMD2 (610–1400 CE) is dominated by planktonic taxa – especially *A. granulata*; (2) Following Cahokia’s abandonment, HORMD3 (1400–1780 CE) assemblages shift from plankton to epiphytic taxa; (3) With intensification of Euro-American settlement, diatom assemblages in HORMD4 (1810–2010 CE) shift towards epipellic taxa.

Discussion

Diatoms in floodplain lakes

Sediments, diatoms, and other materials deposited in oxbow lakes are sourced from the lake itself (autochthonous) or its watershed (allochthonous), but during flood stages the main river channel may also deposit material in the lake (Toonen et al. 2012; Bhattacharya et al. 2016), which represents an extra-local source of allochthonous material. In a previous study of Horseshoe Lake’s sedimentary record, Munoz et al. (2015) used grain-size analysis to identify the timing of major overbank flood events of the Mississippi River (Fig. 4). Prior to the establishment of

artificial levees, the Mississippi River periodically inundated the floodplain around Horseshoe Lake, depositing a layer of well-sorted and fine-grained sediment in the lake. We encountered levels in which diatom preservation was poor that correspond to levels identified by Munoz et al. (2015) as consisting mainly of suspended sediment delivered from the Mississippi River during overbank floods (Fig. 3). The absence of diatoms in these levels allows us to interpret the diatom assemblages that are present in the sediment as being primarily autochthonous. Low diatom concentrations in the extra-local allochthonous sediments are a consequence of (1) low diatom concentrations in the suspended load of floodwaters and/or (2) diatom dissolution. Diatoms are stable in sediment where the interstitial water is saturated with respect to biogenic silica (BSi), but dissolve in environments where the solubility product for BSi is not exceeded (Van Cappellen and Qui 1997a, b), so exposure of diatoms to low-silicate water may have caused them to dissolve. Throughout the remainder of this discussion, we interpret the diatom assemblages in Horseshoe Lake as being sourced primarily from the lake and its watershed.

Wiklund et al. (2010) compared modern communities of epiphytic diatoms in periodically flooded and non-flooded lakes in the Peace–Athabasca Delta in Alberta, Canada and found large differences in lake water silicate and taxon abundance between lake types. At Horseshoe Lake, we found Wiklund et al. (2010) “flood-indicator” and “non-indicator” taxa mixed together in sediment assemblages. This may be a result of comparing living communities with sediment fossil assemblages. The diatom-poor levels in the Horseshoe Lake core could result from poor preservation—not differential survival of living diatoms.

Diatom assemblages associated with prehistoric human populations

The most prominent shift in diatom assemblages at Horseshoe Lake as shown in stratigraphic diagrams, CONISS clustering, and NMDS ordination occurs in the 14th century CE, and coincides with the abandonment of Cahokia and surrounding communities in the floodplain and adjacent uplands. Diatom assemblages at this time shift from being dominated by planktonic *Aulacoseira granulata* to dominance by epiphytic *Cocconeis* and *Gomphonema* spp (Figs. 3, 4, 5, 7). The

diatom taxa we observe before and after the prehistoric abandonment of the Horseshoe Lake area differ in their modern distributions: *A. granulata* is associated with shallow, eutrophic, alkaline lakes, whereas *Gomphonema* and *Cocconeis* are taxa that live on the leaf surfaces of aquatic plants (Brugam 1993; Hoaglund et al. 1982; Kilham and Kilham 1975). The observed shift in diatom assemblages is indicative of a major shift in Horseshoe Lake's ecology when prehistoric indigenous people abandoned the area.

We interpret the dominance of *A. granulata* in diatom assemblages as an indicator of eutrophic conditions in Horseshoe Lake when prehistoric populations were growing and becoming increasingly agricultural. A review of the ecology of *A. granulata* by Kilham and Kilham (1975) found that it is common in eutrophic lakes with high pH and alkalinity, particularly in rivers and shallow floodplain lakes with high water turbulence. Kilham and Kilham (1975) classify *A. granulata* as meroplanktonic, depending on turbulence for periodic resuspension from the bottom sediments where it survives in a dormant state until mixed into the water column. In Sweden, Yang et al. (2016) found *A. granulata* to be a major part of eutrophic Lake Erken's spring phytoplankton during warmer winters with a shorter period with ice cover because the taxon can survive in lake sediment and return to the plankton when lake turbulence increases at ice-out. In general, *A. granulata* is found in shallow eutrophic lakes around the world, including reservoirs in Spain (Goméz et al. 1995) and Brazil (Fontana et al. 2014), floodplain lakes in Mozambique (Siteo et al. 2015) and shallow prairie lakes in Saskatchewan, Canada (Hall et al. 1999). In Adams Bayou, a floodplain lake in Arkansas (USA), 20th-century sediments are dominated by a group of *Aulacoseira* species including *A. granulata*, whereas *Gomphonema parvulum* and other epiphytic taxa were more abundant before this time. This change was interpreted as a change from a clear-water mesotrophic system to an enriched turbid system caused by an increase in local land clearance (Bhattacharya et al. 2016). The dominance of *A. granulata* in Horseshoe Lake's diatom assemblages during diatom zone HORMD2 (610–1400 CE) indicates that the lake was more eutrophic during the prehistoric occupation of the area, as population densities and agricultural production increased (Milner 1998; Simon and Parker 2006; Pauketat 2009).

Eutrophication of Horseshoe Lake during the Late Woodland and Mississippian Periods is consistent with stable organic carbon isotopic ($\delta^{13}\text{C}_{\text{org}}$) measurements reported by Munoz et al. (2014) (Fig. 3). Stable carbon isotopes in lake sediments are sensitive to lake trophic status because high photosynthetic rates cause reduced isotopic discrimination among aquatic autotrophs (Hollander and McKenzie 1991; Hollander et al. 1992; Brenner et al. 1998; Meyers 2003; Belle et al. 2017; Earley et al. 2017; Mays et al. 2017). In Horseshoe Lake, Munoz et al. (2014) reported that $\delta^{13}\text{C}_{\text{org}}$ values gradually increased beginning around 450 CE, and reached a stable maximum around -23‰ from 900 to 1200 CE, tracking the development of Cahokia and inferred lake eutrophication. Following a decline when Cahokia was abandoned, $\delta^{13}\text{C}_{\text{org}}$ increased again following Euro-American settlement ca. 1800 CE. In the same study, Munoz et al. (2014) also report shifts in pollen assemblages associated with prehistoric and historical deforestation that track trends in $\delta^{13}\text{C}_{\text{org}}$ values. In an independent study of $\delta^{13}\text{C}_{\text{org}}$ in surface sediment cores from Horseshoe Lake, Karthic et al. (2013) found $\delta^{13}\text{C}_{\text{org}}$ values ranging from -26 to -24‰ for the historic period, confirming the patterns reported by Munoz et al. (2014).

Recently, paleolimnologists have used weighted averaging models of diatom assemblages to infer past total phosphorus concentrations in lakes (Enache et al. 2012; Reavie and Edlund 2013; Cumming et al. 2015; Reavie et al. 2017). We were unable to apply this approach to the diatom assemblages in Horseshoe Lake because of the lake's shallow depth and the presence of epiphytic diatom taxa. As discussed by Juggins et al. (2013), epiphytic diatom taxa hinder reconstructions of total phosphorus because these taxa are sensitive to multiple environmental factors. Species composition of benthic and epiphytic communities are controlled by factors other than phosphorus, particularly the amount of light reaching the sediment surface, so quantitative reconstructions of total phosphorus levels are challenging in shallow lakes like Horseshoe Lake. Heathcote et al. (2015) encountered similar problems interpreting the paleolimnology of eutrophication in shallow Minnesota lakes, leading them to employ qualitative reconstructions of trophic status based on environmental preferences of diatom species and sediment geochemistry.

In this study, we applied a qualitative approach developed by Scheffer et al. (1993) to describe the trophic status of shallow lakes. Scheffer et al. (1993) argued that shallow lakes have alternative stable states that are controlled by nutrient concentrations. One stable state is a low-nutrient, clear-water state that enables light to penetrate to the lake bottom and encourages high macrophyte abundance; the alternative stable state has high nutrient concentrations that cause dense blooms of plankton, preventing sunlight from reaching the lake bottom (Scheffer et al. 1993). Prior work by Randsalu-Wendrup et al. (2014, 2016) demonstrated that these alternative states—and shifts between them—can be inferred using diatom assemblages in sedimentary records because diatom taxa can be classified as planktonic or epiphytic. Similar state changes have been inferred using diatom records from shallow lakes, which show shifts from epiphytic to planktonic taxa in response to more eutrophic conditions, as aquatic macrophytes are replaced by planktonic algae in response to an increase in nutrient delivery to the lake (Bhattacharya et al. 2016; Sayer et al. 2010). At Horseshoe Lake, we interpret the prominent shift in diatom assemblages in the 14th century as a shift from a eutrophic to more mesotrophic state when prehistoric populations abandoned the area and nutrient inputs to the lake from settlements and agricultural fields in the watershed declined.

An alternative ‘top-down’ model for trophic state shifts in shallow lakes views predatory fish as playing a fundamental role in a lake’s trophic status (Hobbs et al. 2012, 2016). Using paleolimnological techniques on small shallow lakes in the Prairie Pothole region of Minnesota and South Dakota, Hobbs et al. (2012, 2016) found larger fish stocks in plankton-dominated lakes, whereas fish were absent in macrophyte-dominated lakes. This finding led Hobbs et al. (2016) to propose that changes in top-down controls were an important driver of regime shifts, and that changes in nutrient delivery need not be invoked to explain shifts in the trophic state of shallow lakes.

Indigenous populations in the study area consumed large amounts of fish for dietary protein (Milner 1998), and prehistoric fishing in Horseshoe Lake may have contributed to a shift in the lake’s trophic state. The importance of fish in the diet of prehistoric populations in the study area is indicated by the presence of fish bones, scales, and hooks in archaeological contexts

(Kelly and Cross 1984; Kelly 1997; Yerkes 2005), and stable carbon isotope measurements of human bone collagen and apatite (Kellner and Schoeninger 2007). Modern experiments also demonstrate that substantial amounts of fish can be harvested with minimal energy expenditure from a Midwestern oxbow lake using a simple net (Limp and Reidhead 1979). Given the large prehistoric population that lived around Horseshoe Lake, fishing in the lake may have acted as a ‘top-down’ control that removed carnivorous taxa like bowfin (*Amia calva*), which is a common fish remain in archaeological contexts (Kelly and Cross 1984; Kelly 1997). Reduced populations of predatory fish would enable expansion of zooplanktivorous fish populations and an increase in phytoplankton (Hobbs et al. 2016), creating diatom assemblages similar to those observed in Horseshoe Lake when prehistoric human population densities were high. When indigenous populations declined at the end of the Mississippian Period, carnivorous fish populations in Horseshoe Lake would have recovered. This, in turn, would have increased predatory pressure on zooplanktivorous fishes, enabling proliferation of zooplankton that graze on phytoplankton, thereby resulting in clearer water and expansion of aquatic macrophytes. Although this ‘top-down’ mechanism provides a plausible explanation for the inferred shifts in trophic state at Horseshoe Lake, a decrease in nutrient inputs to the lake as a result of declining indigenous populations may also have been responsible for the inferred shifts in the lake’s ecology.

Other factors aside from prehistoric human land use, namely environmental factors affecting the climate and hydrology of the Mississippi River and its basin, may have also influenced diatom assemblages in Horseshoe Lake, although the characteristics of the observed changes around the time of abandonment of Cahokia implicate human activities. For example, the transition of the lake from a turbid eutrophic state to a more mesotrophic state in the 14th century roughly coincides with the onset of the ‘Little Ice Age’ (Mann et al. 2009), when the frequency of high-magnitude flooding on the Missouri and Upper Mississippi Rivers increased (Munoz et al. 2015), while localized drought around Cahokia became more common (Benson et al. 2009). It is possible that an increase in the frequency of overbank floods enhanced the connectivity of Horseshoe Lake with the Mississippi River and contributed to the observed transition

towards a more mesotrophic state, although the mechanism responsible for this is not clear. These environmental changes associated with the Little Ice Age, however, may have influenced the decision of prehistoric populations to abandon Cahokia and the surrounding region (Benson et al. 2009; Munoz et al. 2015), reducing human impacts on Horseshoe Lake indirectly. Examining diatom assemblages from other floodplain lakes along the Mississippi River that were not as heavily settled by prehistoric populations as Horseshoe Lake could provide additional insight into the role of late Holocene climate variability on aquatic communities.

In short, evidence from fossil diatom assemblages and stable carbon isotopes indicates that, as prehistoric populations abandoned the Horseshoe Lake area in the 14th century, the lake shifted from a turbid eutrophic state to a more mesotrophic state, dominated by aquatic macrophytes. This inferred shift in trophic state was most likely the result of reduced nutrient inputs from indigenous settlements around the lake and/or the recovery of fish populations, as fishing pressure was relaxed. In either case, our data demonstrate that the ecology of a large lake in North America was substantially affected by prehistoric indigenous peoples beginning around 600 CE, nearly a millennium prior to European colonization of the Americas. Our findings add to the existing evidence of prehistoric cultural eutrophication in North America (Ekdahl et al. 2004) and demonstrate that large Mississippian population centers, which were located across much of eastern North America, also adversely influenced freshwater quality. In the case of Cahokia, human impacts on aquatic ecosystems, and on terrestrial ecosystems (Munoz et al. 2014), persisted for hundreds of years.

Diatom assemblages associated with historical settlement

In the early 19th century, diatom assemblages in Horseshoe Lake shifted from epiphytic taxa to epipellic ones of the genera *Staurosira* and *Fragilaria*, as historical settlement of the area intensified. This shift in diatom assemblages is similar to that reported in Horseshoe Lake by Karthic et al. (2013), who examined the upper meter of the lake's sedimentary record. In the longer diatom record presented in this study, the abundance of *A. granulata* during the

historical period is not as high as during the prehistoric occupation of the area in the Late Woodland and Mississippian Periods. These differences in diatom assemblages associated with prehistoric and historical occupations reflect, at least in part, industrialization of the area in the late 19th and early 20th century. For example, lead smelting operations on the lakeshore in the early 20th century left the uppermost sediments contaminated with heavy metals, and wastewater from a coking plant that has operated since the 1920s continues to be a large source of nitrates to the lake, both of which may influence historic diatom communities (Karthic et al. 2013). Epipellic diatoms of the genera *Staurosira* and *Fragilaria* first appear in diatom assemblages ca. 1800 CE, prior to industrialization of the area, implying that other factors also contribute to the unique diatom assemblages present in Horseshoe Lake today. Artificial levees and other hydrological alterations to Horseshoe Lake, for example, isolate the lake from the Mississippi River and maintain more consistent lake levels. Extensive aquatic macrophyte beds, which we infer to have been present following the prehistoric abandonment of the area, are no longer present on Horseshoe Lake, and may be inhibited by increased turbidity as the lake gradually fills in. In short, historical land use practices from the early 19th century onwards have markedly altered Horseshoe Lake, but these recent changes represent a second and distinct period of human influence on the lake's freshwater ecology over the last 1600 years.

Conclusions

Fossil diatom assemblages in a sedimentary record collected from Horseshoe Lake, an oxbow lake in the floodplain of the middle Mississippi River, demonstrate that between 600 and 1400 CE, the lake shifted to a eutrophic state when the area was heavily occupied by prehistoric indigenous populations. After the abandonment of the area by prehistoric populations in the 14th century CE, the lake became less eutrophic and supported extensive beds of aquatic macrophytes. Beginning in the early 19th century, historic settlement of the area altered the aquatic ecosystem and adversely affected water quality. Our work implies that human activities profoundly influenced the ecology of a large lake in North America

nearly a 1000 years prior to European colonization of the continent.

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