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Inferring lake depth using diatom assemblages in the shallow, seasonally variable lakes of the Nebraska Sand Hills (USA): Calibration, validation, and application of a 69-lake training set

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Abstract
The Nebraska Sand Hills are a distinctive eco-region in the semi-arid Great Plains of the western United States. The water table underlying the Sand Hills is part of the High Plains/Ogallala aquifer, an important water resource for the central Great Plains. Lake levels are affected directly by fluctuations in the water table, which is recharged primarily by local precipitation and responds quickly to climatically induced changes in regional water balance. Instrumental records are available for only 50–100 years, and paleolimnological data provide important insights into the extremes and variability in moisture balance over longer time scales. A set of 69 lakes from across Nebraska was used to establish a statistical relationship between diatom community composition and water depth. This relationship was then used to develop a diatom-based inference model for water depth using weighted averaging regression and calibration techniques. Development of the inference model was complicated by strong intra-seasonal variability in water depth and the linkages between depth and other limnologic characteristics, including alkalinity, water clarity and nutrient concentrations. Analysis of historical diatom communities from eight lakes allowed for the reconstruction of lake-level fluctuations over the past several thousand years. Comparisons of the more recent portion of these reconstructions with the instrumental Palmer Drought Severity Index (PDSI) showed that sediment records may not faithfully reflect short-term fluctuations in water level, except where sedimentation rates are very high. However, large and persistent changes in moisture availability were discernible even in longer, low-resolution records. Thus, diatoms are a useful addition to the tools available for understanding past drought in the central Great Plains, especially when trajectories of change are constrained by data from multiple sites or other proxies.

Keywords: Nebraska, Sand Hills, diatoms, inference model, shallow lakes, lake-level

Introduction

The Nebraska Sand Hills are the largest sand dune region in the Western Hemisphere, covering roughly 58,000 km^2 in Nebraska and a small part of South Dakota. The water table underlying the Sand Hills is part of the High Plains/Ogallala aquifer, an important water resource for the central Great Plains region (Bleed and Flowerday 1998). The aquifer reaches the surface in many interdune depressions, creating thousands of lakes and wetlands, which support this unique ecoregion and both provide habitat for many animals, including a large migratory bird population, and also support the local ranching economy. Droughts in the recent, instrumental record have had significant effects on water availability in ground water and ground-water-fed lakes and streams (Chen et al. 2003; Chen and Chen 2004; Burbach and Joeckel 2006), with profound effects on aquatic ecosystems (Covich et al. 1997). Yet research throughout the Great Plains and western United States has shown that fluctuations in moisture availability in the twentieth century have been relatively small in comparison with earlier periods in the Holocene, which experienced much more persistent and more severe droughts (Woodhouse 2004).

Prior paleoclimate research in the Sand Hills used paleosol records in dunes, optically stimulated luminescence (OSL) dates from dune sand, and sediment core records of inter-bedded lake mud, sand, and peat to identify at least three major periods of significant aeolian activity during the Holocene: 700–900, 3,200–4,000, and 6,000–9,000 calendar years before present (Loope et al. 1995; Mason et al. 1997, 2004; Nicholson and Swinehart 2005). Times of inferred dune mobility were attributed to prolonged periods of drought (Mason et al. 2004; Nicholson and Swinehart 2005). Such inferences can be complicated, however, by the interdependence of vegetation, fire, and various aspects of climate on dune stabilization or mobilization (Mason et al. 2004; Nicholson and Swinehart 2005). Thus, the nature and duration of the antecedent conditions that led to decreased dune vegetation and allowed dunes to migrate are unclear.

Diatoms have been shown to be an effective tool to qualitatively and quantitatively infer changes in moisture balance over time in arid and semi-arid environments (Fritz et al. 1999; Gasse 2002). Here we investigate their use to infer past water levels from shallow natural lakes in western Nebraska and their utility as a proxy to further constrain the history of regional drought. Previous research on lakes in the Sand Hills has focused primarily on understanding the controls on the chemical evolution of these lakes and their hydrology (Gosselin 1997; Bennett et al. 2007). Less attention has been paid to the effects of this variability on the biologic structure of the lakes. Previous studies have cataloged some of the most abundant groups of aquatic organisms (La Baugh 1986) but did not investigate the differences in biological communities as they related to differing physical and chemical characteristics of the lakes. Inference models based on modern relationships between biota such as diatoms and the environment are routinely applied to fossil biological data in order to infer quantitative environmental characteristics for periods without adequate instrumental data coverage (Kauppila et al. 2002; Ramstack et al. 2003; Siver et al. 2003). Here we devise a diatom-based model to infer maximum lake depth, based on weighted averaging regression and calibration methods applied to a calibration set of 69 lakes across the state of Nebraska. We then reconstruct lake depth for eight lakes from the Sand Hills and compare the results with twentieth century instrumental records of Palmer Drought Severity Index (PDSI) and with longer tree-ring based reconstructions of PDSI (Cook et al. 2004). The newly developed inference model is also applied to the Holocene diatom stratigraphy of two additional lakes, which have been previously published (Schmieder 2009), and the results are compared with interpretations of drought generated from other proxies for moisture availability.

Study area

Lakes selected for calibration set development included natural lakes, reservoirs, and sand pits located throughout Nebraska (Figure 1). Lake selection was based on needs of state agencies, and accessibility. Sand pits, or borrow pits, are remnants of gravel mining, mostly from excavations during the construction of a major interstate highway in the 1960s, which have since been naturally flooded. Reservoirs and sand pits are more common in the eastern part of the state. A large east–west gradient in precipitation exists across the state, with rainfall in the northwest averaging about 360 mm year^{-1}, increasing to more

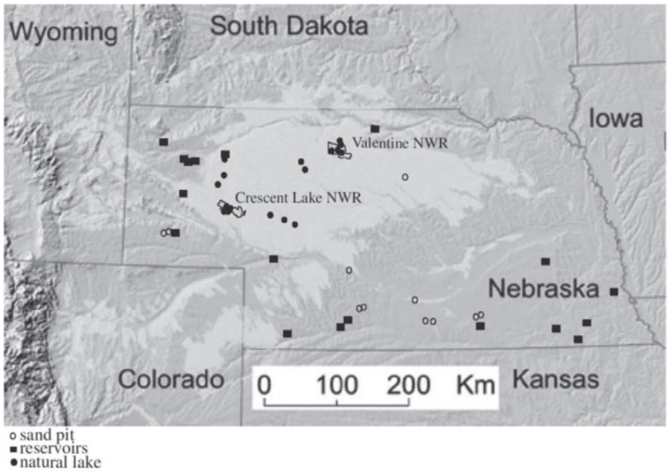


Figure 1. Map of Nebraska with sites used in the calibration set identified by type. Longer sediment cores were collected from the Valentine and Crescent Lake National Wildlife Refuges (outlined in *black*). Both areas are within the Sand Hills eco-region (*light shading*).

than 860 mm year^{-1} in the southeast (Bleed and Flowerday 1998). Generally, evaporation exceeds precipitation on an annual basis, except in the eastern-most part of the state. Nebraska is primarily an agricultural state, with urban centers and small agricultural farms in the eastern and southeastern part of the state, and smaller rural communities farther west, where land is used primarily for cattle grazing.

Cores collected for use in paleolimnological reconstructions were taken from eight lakes in two natural areas in the Sand Hills region of western Nebraska: the Valentine National Wildlife Refuge (VNWR) and the Crescent Lake National Wildlife Refuge (CLNWR) (Figure 1). Two additional core records from prior studies, Beaver and Swan lakes, also were taken from the Sand Hills (Schmieder 2009). The Sand Hills landscape is characterized by stabilized dunes that are the product of aeolian activity in the late Tertiary to Holocene (Loope et al. 1995). In the inter-dune valleys the water table reaches the surface, creating permanent lakes, which are generally shallow and eutrophic (Bennett et al. 2007). Groundwater is the primary source of water and solutes for the lakes, and evaporative concentration of solutes is the main control on the salinity and chemical composition of the lakes. Local precipitation is the primary source for groundwater recharge (Gosselin et al. 1994).

Methods

Water sample collection

Water samples were collected on an approximately monthly basis from May to September from 1999 to 2002. Not all lakes were sampled every month or during all years. Samples were collected from 49 water bodies (19 natural lakes, 18 reservoirs, and 12 sand pits) with the following 22 physical and chemical variables measured for each lake: water depth, water temperature, latitude, longitude, dissolved oxygen (DO), pH, alkalinity, conductivity, total nitrogen (TN), total phosphorus (TP), nitrogen to phosphorus ratio (N:P), orthophosphate (OP), total dissolved phosphorus (TDP), total kjeldahl nitrogen (TKN), nitrite + nitrate (NN), total suspended solids (TSS), Secchi depth, turbidity, light penetration, and concentrations of the pesticides Atrazine, Alachlor, and Metalochlor. Twenty additional lakes in the CLNWR were sampled in 2004 (Zlotnik et al. 2007) with a limited suite of six variables collected (water depth, alkalinity, pH, conductivity, Secchi depth, water temperature). All water samples were taken from approximately 0.5 m water depth and were collected monthly from the same location in the lake, identified using GPS coordinates. Sample sites were located at approximately the deepest point as determined during a transect of the lake with an acoustic depth finder. From monthly samples, yearly means ware calculated.

Water samples for alkalinity, turbidity, TSS, nutrients, and pesticides were collected using a polyurethane resin Van Dorn bottle. Water samples were transported on ice to the laboratory in acid-cleaned polyethylene bottles. Alkalinity was determined in the laboratory within 6–10 h, using water warmed to in-lake temperature (Lind 1985). Nutrient samples were filtered within 6–10 h and frozen for 1–3 weeks. Total phosphorus (TP), TDP, OP, TN, and NN were determined using methods described by Lind (1985), D'Elia et al. (1976) and Downes (1978). All remaining analyses were performed based on methods described by the American Public Health Association (1995). Turbidity was measured in the field using a field turbidimeter (Model 2100P, Hach, Loveland, CO). Conductivity, salinity, and pH were measured in the field at approximately 0.5 m below the water surface with a multiprobe and surveyor (Model 4a, Hydrolab, Austin, TX).

Diatom surface sediment and sediment core collection

Short sediment cores were obtained from each lake at the same point water samples were taken. Cores were taken using a gravity corer and immediately sectioned with an extruding device (Glew 1989). The sections were stored in Whirl-pak plastic bags and maintained in a dark moist environment at 4°C. The upper-most centimeter section of the sediments from each short core was used as a diatom surface sediment sample for the development of a modern calibration data set. Sediment samples for diatom analyses were processed with 10% HCl to remove carbonates and with cold 30% hydrogen peroxide to oxidize organic matter (Battarbee 1986). A minimum of 300 diatoms per slide were counted in each sample. Diatoms were identified using standard iconographs (Krammer and Lange-Bertalot 1986–1991; Patrick and Reimer 1966) and other published literature. Counts were transformed to percent relative abundance for all analyses. Diatom surface sediment samples were compared with yearly mean water chemistry values from the year of collection to develop the calibration set. Additionally, longer sediment cores from eight lakes were collected in 2000 and 2003 with either a piston (Verschuren 1993) or gravity corer. Cores were sectioned into 1-cm increments in the field and stored in Whirl-pak plastic bags at 4°C until analyzed.

Age-depth models for the eight sediment cores were based on ^{210}Pb dating. Lead-210 was measured through its grand-daughter product ^{210}Po (Eakins and Morrison 1978), and the constant rate of supply model (c.r.s.) (Appleby 2001) was used to estimate age, with confidence intervals calculated by first-order error analysis of counting uncertainty (Binford 1990). Lead-210 is useful to approximately 150–200 years before present; dates from before approximately AD 1850 were estimated by extrapolation of linear sediment accumulation rates in the earliest sections of the ^{210}Pb record. This extrapolated chronology is very approximate (pre-1800 dating uncertainty ≥100 years) and is used only to provide a rough comparison with broad, century-scale trends in tree-ring records.

Statistical analysis and comparison with other records

Modern diatom assemblages from surface sediment samples were compared with 22 physical and chemical variables in 49 lakes and 6 physical and chemical variables in the full suite of 69 lakes. Environmental data were log (or log+1 for data containing zeros) transformed prior to analysis to normalize their distributions. Diatom taxa were included in ordination analyses if they were present in at least 2% relative abundance in one or more lakes.

Multivariate ordinations were used to explore relationships among lakes and diatom assemblages. Relationships among lakes were explored using Principal Components Analysis (PCA) and between diatoms and environmental data using Canonical Correspondence Analysis (CCA). A CCA was performed individually on all 22 physical and chemical variables, including all water chemistry data, as well as site latitude, longitude, and water depth to identify those variables that were significantly ($P \leq 0.005$) related to diatom community composition. Manual forward selection among individually significant variables was conducted using permutation testing, with 200 unrestricted Monte Carlo permutations, to determine those variables with significant explanatory power. To assess whether each individually significant variable explained a unique fraction of the variance in the diatom species assemblages, a partial CCA (pCCA) was run for each variable individually and with other significant variables as conditional co-variables. This allowed for the separation of the unique explanatory power of each variable of interest. All ordination analyses were run in R software with rare species downweighted before analysis using default functions in the vegan package of R (R Development Core Team 2006; Oksanen et al. 2008).

Species optima and tolerances were calculated for environmental variables with significant explanatory power. Additionally, a transfer function was developed for lake depth. These models were developed and the predictive ability assessed using a weighted-averaging approach with bootstrap error estimation in C2 software (version 1.4; Juggins 2003). The strength of each model was assessed using the coefficient of determination (r^2) and the root mean square error (RMSE). Because the same data were used to generate and evaluate the model, these assessments were not entirely independent, and the validation step of bootstrapping with 1,000 cycles was used to generate a bootstrapped coefficient of determination (r_{boot}^2) and a root mean square error of prediction (RMSEP), which more realistically portrayed error estimates (Fritz et al. 1999).

Results of the depth reconstructions for the eight cores were compared with instrumental records of moisture availability from the region. The most recent 100 years were compared with records of the Palmer Drought Severity Index (PDSI) available from the National Climatic Data Center (NOAA 2009). The PDSI is a standardized drought index based on time series data including precipitation, air temperature, and soil moisture (NOAA 2009). Records from the six divisions covering the Sand Hills region (divisions 176, 177, 161, 162, 145, and 146) were averaged to create a composite annually resolved record for the region. Additionally, because the centimeter sediment sections integrated different time increments, a variably smoothed record of PDSI was also created and compared with each sediment record. For the variably smoothed record, each dated core section was matched with a PDSI composed of an average of the same number of years prior as was integrated in the core section. Depth reconstructions over the past several thousand years were compared with a published tree-ring based reconstruction of PDSI for division 161 (Cook et al. 2004). Depth reconstructions were also developed and compared with records of sediment composition (mean grain size and weight percent sand) from Beaver and Swan lakes (Schmieder 2009).

Results

Environmental variables

Lakes were chosen to cover a wide range of limnological conditions (Table 1). Most natural lakes were small and shallow (less than 2 m in depth) in contrast to reservoirs (typically 4–10 m). The lakes ranged from less than a few hectares to 35,700 ha in area. In the set of 49 lakes with 22 total measurements, an initial principal components analysis (PCA) showed the first axis was strongly correlated with nutrients, turbidity, and related parameters (Figure 2). There was additionally a large group of outliers related to pesticide concentrations in several of the reservoirs (Oxbow Trails, Prairie Owl, Claytonia, Cub Creek, Prairie, Big Indian). A PCA of the six variables and full 69-lake data set showed a similar pattern, with the strongest gradient related to water depth and water clarity (Figure 2). These results agree with the findings of a study of the hydrologic characteristics of over 250 natural and man-made Nebraska lakes, where the main axis of variation was related to trophic state variables, including nutrients and Secchi depth (Bennett et al. 2007).

Natural lakes were generally shallower and more saline than the reservoirs and sand pits and also showed greater variability in trophic status, major ion chemistry, and other characteristics (Table 1; Figure 2). Aside from the reservoirs with high pesticide and nitrate concentrations, most reservoirs and sand pits clustered closely together at a point on the ordination consistent with deep lakes, with relatively little variation along other gradients.

Modern diatom distribution

Over 500 taxa were identified in the natural lakes, reservoirs, and sand pits of Nebraska. Calibration and transfer function development were based on only those taxa that occurred in a relative abundance greater than 2% in at least one lake; this reduced the number of species in the calibration set to 157. Most of the dominant taxa in the lakes were common benthic forms, including *Nitzschia*, *Synedra*, *Planothidium*, and *Cocconeis* species. Planktonic species, including abundant *Aulacoseira ambigua* and *Stephanodiscus hantzschii*, were common in the calibration set, but occurred mainly in the deeper reservoirs and sand pits and had more limited distribution in the shallower natural lakes of western Nebraska. Generally salt tolerant taxa, such as *Anomoeoneis costata* and *Craticula cuspidata*, were found in greater abundance in the western natural lakes, although some species, including *Craticula halophila* were widely distributed across the study area.

While some variables, such as pesticide concentrations, showed interesting distribution among the lakes, they were not significantly related to the pattern of diatom species distribution. Using CCA for each physical and chemical variable in the 49-lake calibration set, only nine variables (TKN, depth, alkalinity, TP, TN, TSS, Secchi depth, pH, and N/P ratio, in decreasing order of significance) had significant

Table 1. Chemical data for the nine variables which had significant individual relationships with diatom distributions in the data set and site location information.

Lake	Longitude (dec. degree N)	Latitude (dec. degree W)	Depth (m)	pH	Alkalinity (mg L^{-1} $CaCO_3$)	Secchi (cm)	TSS (mg L^{-1})	TP (µg L^{-1})	TN (µg L^{-1})	TKN (µg L^{-1})	N:P
Sand Hills lakes											
Big Alkali	100.62	42.63	1.87	9.1	327	59	40	94	1,833	1,828	19.40
Crane	102.37	41.73	0.92	9.1	184	18	79	580	6,453	6,256	11.01
Dewey	100.63	42.54	1.71	9.2	177	64	41	447	3,082	3,074	6.89
Diamond Bar	102.48	42.28	2.00	8.4	516	19	40	300	5,584	5,443	18.51
Dry 2000	101.29	41.66	1.15	9.0	1,276	19	83	2,486	9,272	9,133	3.73
Dry 2002	101.29	41.66	0.76	9.5	2,436	12	66	4,120	11,590	11,524	2.81
Duck I	100.73	42.54	0.50	8.4	190	50	16	132	2,391	2,349	18.16
Island 1999	102.40	41.74	1.64	8.5	200	32	54	125	3,609	3,501	28.76
Island 2003	102.40	41.74	1.64	8.9	254	14	130	291	3,260	3,260	11.21
Pony	100.51	42.49	1.24	9.7	163	81	23	463	3,587	3,578	7.75
Roundup	102.41	41.75	0.63	9.2	858	12	146	1,005	8,721	8,710	8.78
Schick	101.26	41.55	0.80	9.6	174	70	9	321	3,729	3,684	11.76
Shaup	101.12	42.35	1.35	9.5	111	43	14	318	2,289	2,283	7.94
Smith	102.45	42.40	1.95	8.4	158	146	6	170	1,965	1,945	11.56
Swan	101.48	41.73	0.74	9.4	100	15	149	477	7,019	7,006	17.04
Tree Claim	102.50	41.78	0.60	9.1	2,820	14	194	433	16,422	16,400	37.93
Two Mile	101.16	42.40	1.34	10.3	154	17	153	676	8,173	8,155	14.65
West Long	100.72	42.53	1.03	9.6	213	110	7	518	1,956	1,953	4.61
Wickson	102.59	42.16	0.50	9.6	4,628	30	115	373	14,634	14,625	39.29
Reservoirs											
Big Indian	96.69	40.06	4.61	7.9	88	20	47	209	2,964	902	8.47
Box Butte	103.10	42.46	4.61	8.7	186	334	7	34	545	540	15.92
Carter P. Johnson	103.52	42.68	3.87	8.6	179	115	13	40	363	467	11.80
Chadron	103.00	42.45	4.32	9.0	192	162	10	25	325	308	12.57
Champion	101.45	40.28	1.30	8.7	194	46	30	90	1,167	528	5.86
Claytonia	96.52	40.29	3.06	8.3	133	18	31	505	2,415	1,024	2.03
Cub Creek N	99.91	42.83	7.46	8.8	147	159	7	41	737	647	17.34
Cub Creek S	97.05	40.24	2.87	8.1	76	10	37	952	4,996	976	2.67
Hayes Center	100.56	40.35	1.86	8.8	310	35	33	176	998	865	4.91
Isham Dam	102.47	42.55	4.46	9.3	367	139	9	54	1,740	1,206	22.28
Kilpatrick	103.17	42.05	1.90	9.4	313	49	18	80	1,329	945	12.73
Minatare	103.30	41.55	5.87	8.7	243	95	10	50	746	511	10.23
Ogallala	101.65	41.21	10.56	8.5	181	126	8	46	1,296	684	17.41
Oxbow Trails	97.17	41.08	2.28	8.5	192	23	55	259	2,805	1,980	9.68
Prairie	98.29	40.32	6.30	8.8	109	23	38	435	1,889	920	2.11
Prairie Owl	96.05	40.63	2.26	8.3	156	29	56	248	3,567	1,402	11.57
Welfleet	100.44	40.45	2.50	8.7	305	63	15	112	959	685	5.98
Whitney	103.18	42.47	2.42	8.8	251	43	79	329	1,569	483	2.24
Sand pits											
Alda	98.29	40.48	4.50	8.7	191	135	9	17	2,755	830	47.77
Blue Hole	99.36	40.69	4.00	8.7	178	107	12	91	808	947	20.72

Lake	Longitude (dec. degree N)	Latitude (dec. degree W)	Depth (m)	pH	Alkalinity (mg L^{-1} CaCO$_3$)	Secchi (cm)	TSS (mg L^{-1})	TP (µg L^{-1})	TN (µg L^{-1})	TKN (µg L^{-1})	N:P
Brady Interchange	100.22	40.60	3.10	8.4	171	179	8	15	1,154	574	38.84
Bufflehead	99.01	40.40	2.70	9.0	136	166	7	27	1,142	474	17.78
Cheyenne	98.36	40.46	3.50	8.5	167	168	8	20	1,603	470	26.02
Cochran	99.17	40.41	4.20	9.3	293	19	78	312	5,748	5,348	17.91
Coot Shallow	99.44	42.22	3.50	8.5	162	244	5	19	1,141	477	26.49
Cozad	100.40	41.06	2.30	9.1	253	185	5	56	1,939	1,662	30.00
Fremont Slough	103.56	41.56	4.40	8.6	164	140	7	31	827	370	12.77
Morill	103.56	41.56	8.20	9.2	328	73	11	78	1,446	924	11.73
War Axe	98.44	40.43	5.20	8.5	197	123	10	16	3,138	473	35.37
West Gothenburg	100.18	40.59	4.80	8.6	159	188	7	36	767	484	13.78
Crescent Lake NWR lakes											
Bean			0.30	10.3	21,275	0					
Christ			0.50	10.0	182	2					
Gillet			0.50	10.2	19,249	50					
Gimlet			0.50	10.7	355	50					
Hackberry 2002			1.00	9.4	385.5	25					
Hackberry 2003			1.00	9.8	236	19					
Heswett			0.10	9.7	405	2					
Lost			0.10	7.6	14,690	1					
Lower Harrison			1.00	9.2	20,262	10					
Maverick			0.20	8.9	405	10					
Perin			1.00	9.2	684	100					
Pond 28			0.10	10.4	8,105	2					
Read Head			0.80	9.5	785	50					
Reno			0.53	10.5	33,027	53					
Rush			0.50	9.1	684	2					
School Section			0.10	10.5	76,489	2					
Shafer			0.50	10.3	223	30					
Upper Tree Claim			0.50	9.8	13,170	4					
Whitehead			0.65	9.6	3,470	55					
Windmill			0.71	9.0	1,425	9					

($P \leq 0.005$) explanatory power. Manual forward selection was used to determine the strongest explanatory variables related to the distribution of diatoms in regional lakes, and the results showed that water depth, alkalinity, TKN, and TP comprised the best model for the 49-lake data set. Using the same manual forward selection process in the 69-lake and 6-variable data set, water depth, alkalinity, and Secchi depth were identified as key variables (Figure 3). The gradient in alkalinity in the 49-lake set was related mainly to two outlier lakes, Wickson and Tree Claim; when these lakes were removed, alkalinity became an insignificant part of the 49-lake model (Table 2). These two lakes were, however, within normal range in the 69-lake data set.

Although diatom assemblages in the lakes had significant individual relationships with nutrient variables (TKN, TP, Secchi depth), alkalinity, and depth, not all were independent of one another. Using a partial CCA, where each of these variables was assessed for significance with the remaining variables used as conditional co-variables, only depth and alkalinity consistently showed a significant and independent relationship with the diatom assemblages

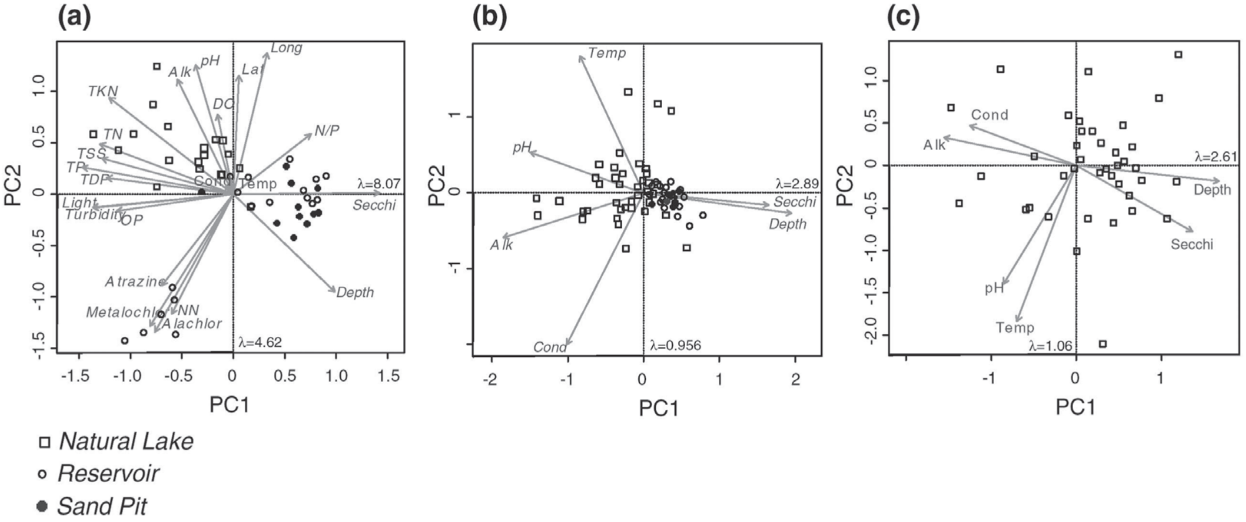


Figure 2. Principal components analysis (PCA) of **a)** all physical and chemical data in the 49-lake, 22-variable data set **b)** all data in the 69-lake, 6-variable data set **c** all natural lakes, with sites identified by type.

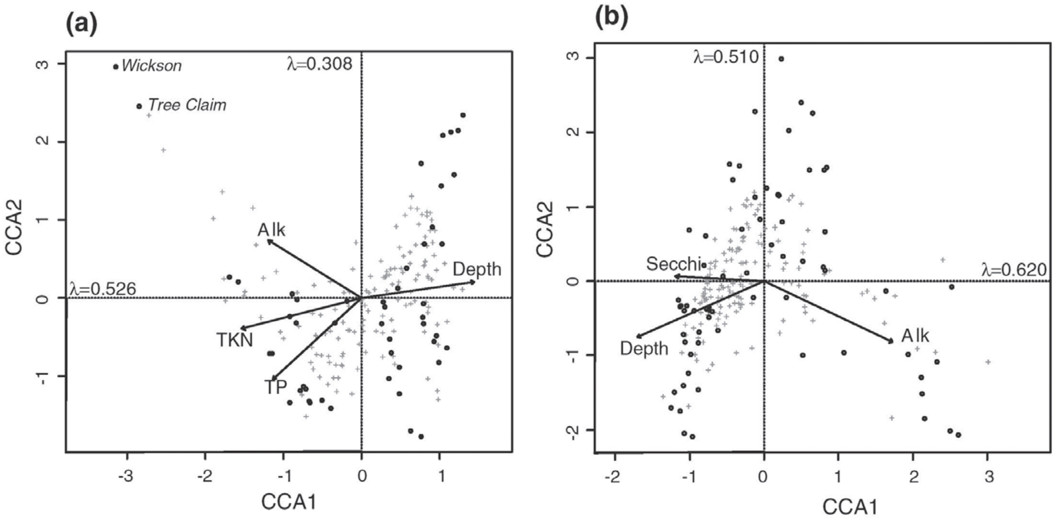


Figure 3. Constrained correspondence analysis (CCA) for the significant variables in **a)** the 49-lake, 22-variable data set and **b)** the 69-lake, six-variable data set. Note that the inclusion of alkalinity as a significant variable depends on the presence of two outlier lakes in **a**. Sites are shown as *black circles*, species as *grey crosses.*

(Table 2). The importance of alkalinity in explaining the diatom distributions was dependent on including a small number of high alkalinity lakes; however, it did not have as strong an influence along the entire gradient.

Dating models

Total ^{210}Pb activity in the dated cores declined from surface values ranging from 5 to 10 pCi g^{-1} to background values of 0.3–1.0 pCi g^{-1} (Figure 4). The shape of the activity profiles was broadly similar among most sites: a very gradual change in the upper core sections followed by an abrupt (near-exponential) decline beginning at depths ranging from 10 to 40 cm. According to the constant rate of supply (c.r.s.) model, the sections of exponential decline indicate fairly uniform sedimentation rates, while the flat, i.e., vertical, sections represent periods of accelerating sediment input. The ^{210}Pb profiles from West

Table 2. Total (for each variable individually) and unique (for each variable when others are considered as conditional co-variables) variance explained for each of the most significant variables in the 49-lake and 69-lake datasets.

Variable	Total variance explained in 69-lake set	Unique variance explained in 69-lake set	Total variance explained in 49-lake set	Unique variance explained in 49-lake set
Depth	5.2% ($P \leq 0.005$)	3.2% ($P \leq 0.005$)	5.6% ($P \leq 0.005$)	2.9% ($P \leq 0.005$)
Alkalinity	5.4% ($P \leq 0.005$)	3.1% ($P \leq 0.01$)	4.9% ($P \leq 0.005$) with two outlier lakes; 1.5% ($P = 0.77$) without	3.1% ($P \leq 0.005$)
Secchi	3.4% ($P \leq 0.005$)	2.3% ($P \leq 0.01$)	3.8% ($P \leq 0.005$)	2.2% ($P = 0.17$)
TKN			5.9% ($P \leq 0.005$)	2.4% ($P = 0.06$)
TP			4.8% ($P \leq 0.005$)	2.5% ($P = 0.02$)

Significance is given in parentheses

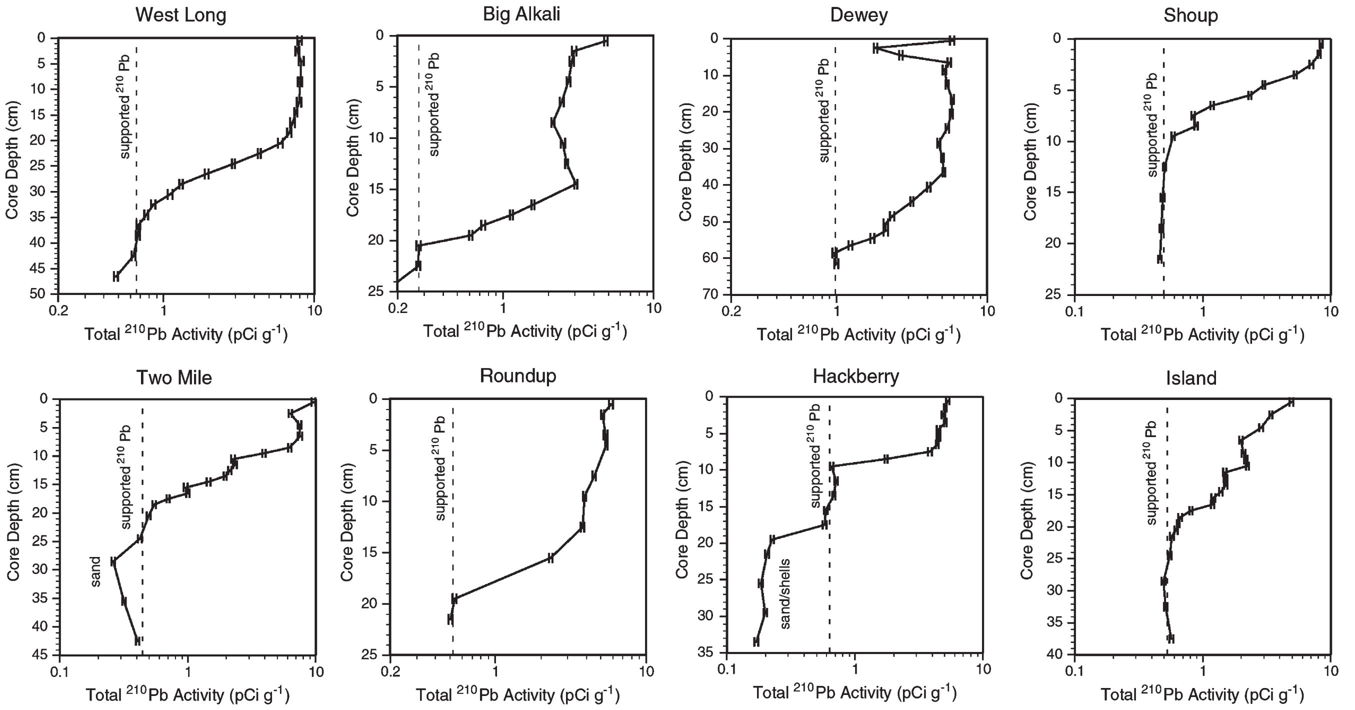


Figure 4. Profiles of ^{210}Pb activity versus depth. A smooth decline in unsupported ^{210}Pb to an obvious break to background (supported) ^{210}Pb indicates continuous sedimentation (see West Long and Shoup). Short interruptions in the smooth declines may indicate sediment pulses (Dewey) or a hiatus in sedimentation (Hackberry).

Long, Big Alkali, Shoup, Two Mile, Roundup, and Island were generally monotonic, but did contain small kinks and flat sections that likely represent changes in sedimentation. A smooth transition between sediments containing unsupported ^{210}Pb and older sediments with only supported (background) ^{210}Pb was present in West Long, Shoup, Two Mile and Island, while Big Alkali and Roundup dropped more abruptly to background values. No sample material remained for dating between 16 and 19 cm in Roundup, contributing to the few samples with supported ^{210}Pb and the lack of older dates for that lake. In Big Alkali this abrupt transition to background may indicate a hiatus in sedimentation; however, even if there was a hiatus, the amount of missing ^{210}Pb would be fairly small, and errors would be large only for the oldest dates (pre-1900). Hackberry showed relatively constant ^{210}Pb in the upper 7–8 cm, followed by a sharp drop to supported values below 9 cm. This sharp transition is either a hiatus or represents a period of very slow sediment accumulation; the latter is assumed by c.r.s model calculations.

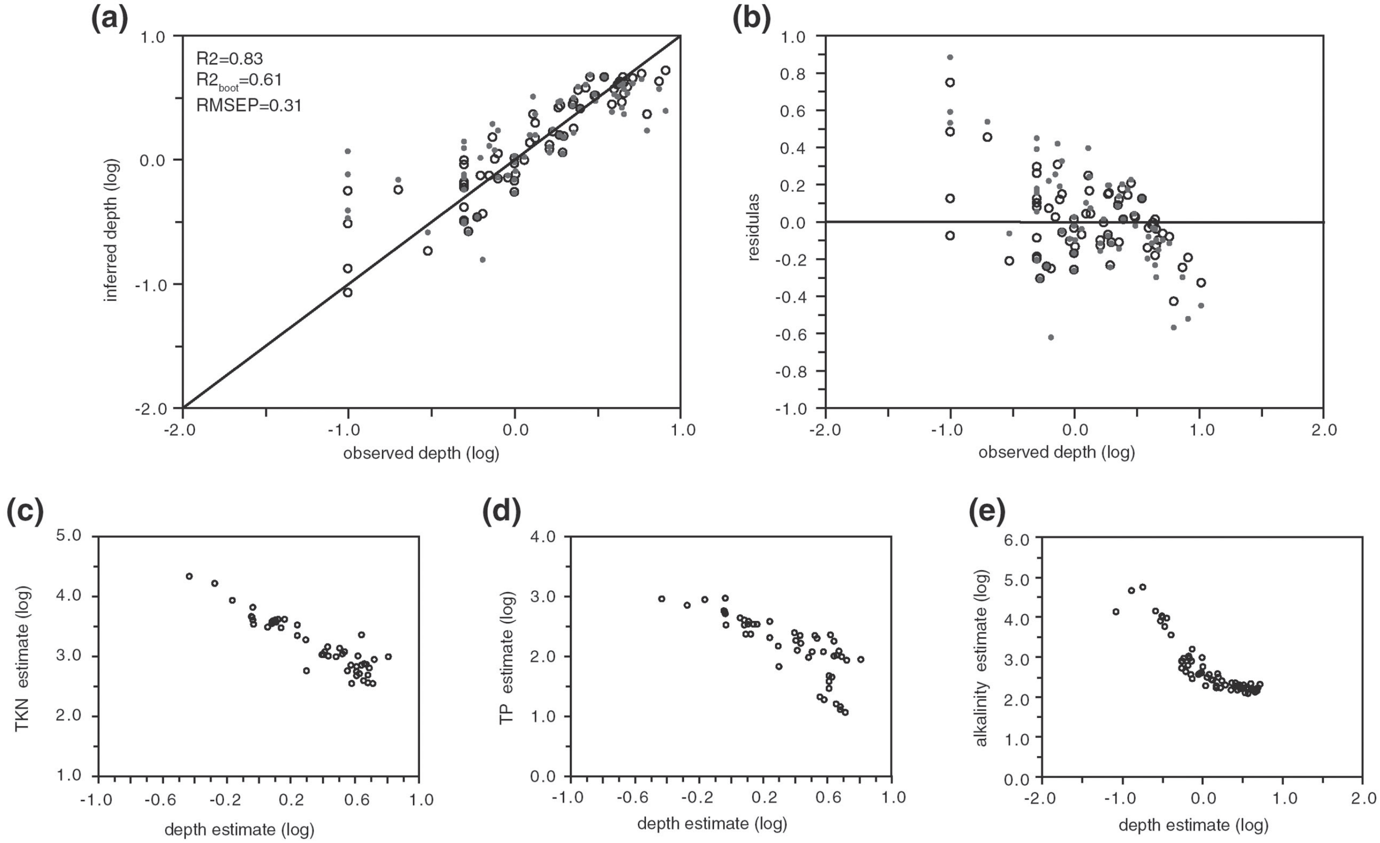


Figure 5. a) Water-depth values inferred from the transfer function compared to observed water depth in the calibration set and **b)** the residuals from the relationship. *Large open circles* show original values; *smaller closed circles* are bootstrapped values. The calculated optima for depth for each species had strong relationships with other variables including **c)** TKN **d)** TP and **e)** alkalinity.

In both Hackberry and Two Mile there was a clear break between supported and unsupported ^{210}Pb, followed by a further drop in total ^{210}Pb which was attributed to observed changes in core lithology (sand and shells); these values were not used to calculate supported ^{210}Pb. The Dewey Lake core also showed a sharp drop in ^{210}Pb activity just below the surface (defined by two data points); this feature was modeled as a spike in sediment flux.

Transfer function

Optima and tolerances were calculated for depth, alkalinity, TKN, and TP, and a transfer function was developed for depth, which was the most consistently significant explanatory variable (Table 2; Figure 5). The transfer function was developed using a weighted-averaging calculation with classic de-shrinking; both classic and inverse de-shrinking were evaluated and gave very similar r^2 and RMSEP values. De-shrinking corrects the overestimation of low values and underestimation of high values caused by averaging in both the regression and calibration steps of model development (initial log depth = −0.0496 + 1.399*observed log depth; Birks 1990). The r^2 values for the depth model were high ($r^2 = 0.83$, $r_{\text{boot}}^2 = 0.61$) and, although errors were not large in absolute terms (RMSE = 0.13 log (meters), RMSEP = 0.31 log (meters)), they were large relative to the range of measured depth in Nebraska natural lakes (0.1–2 m; −1 to 0.3 log (meters)). A slight trend was apparent in the residuals (Figure 5), indicating the possibility of overestimating depth in shallow conditions and underestimating inferences of deeper water conditions.

The nutrient (TKN and TP) and alkalinity optima had a strong negative correlation with depth optima. Taxa with a high depth optima had low nutrient and alkalinity optima and vice versa (Figure 5). Such strong relationships underscore the lack of independent relationships between diatoms and the multiple individually significant physical and chemical variables.

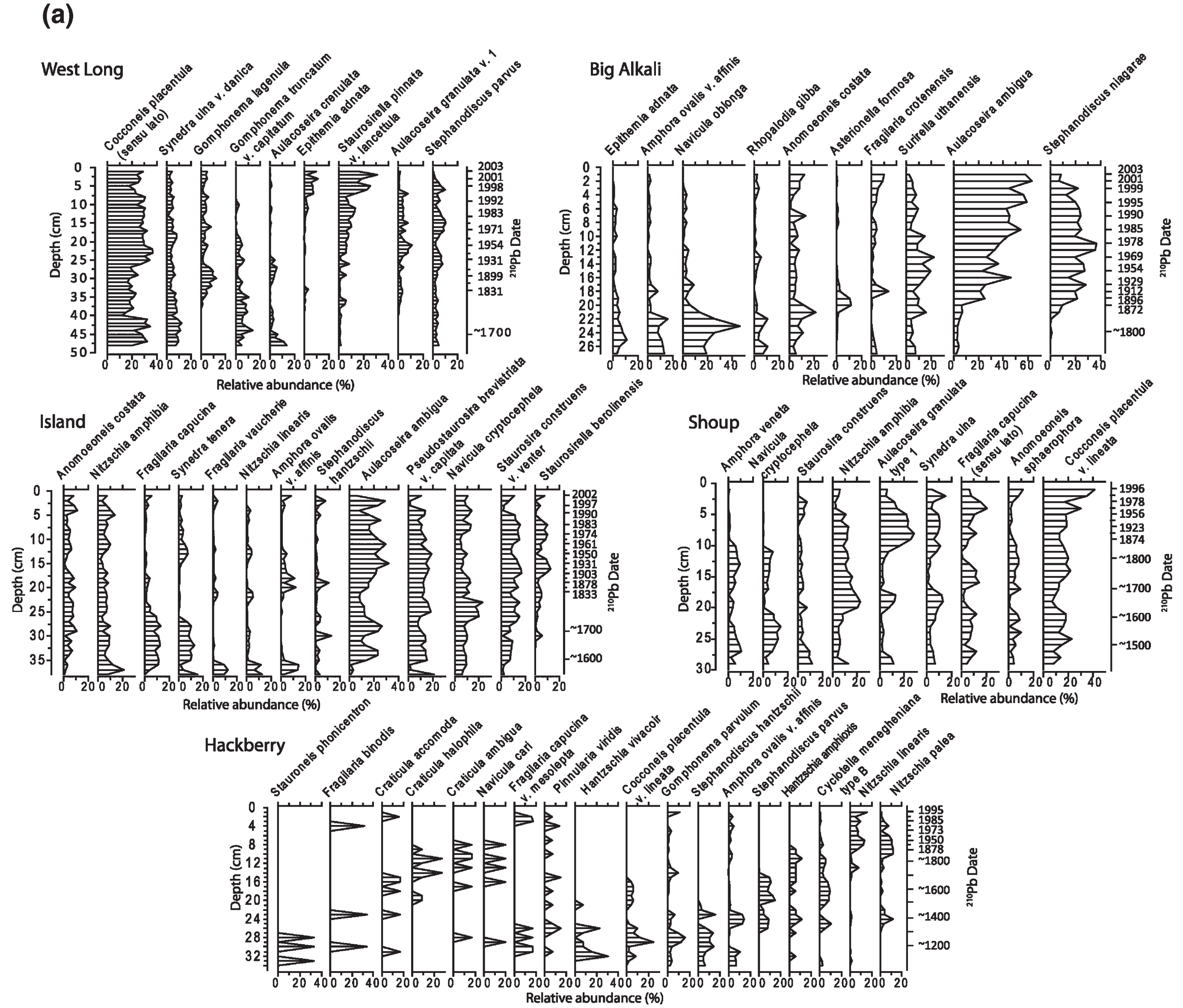


Figure 6. Stratigraphic profiles for the most abundant diatoms in the eight sediment cores. Profiles for West Long, Big Alkali, Island, and Shoup lakes show all species with abundance >10% in at least two intervals. Profiles for Dewey, Hackberry, Roundup and Two Mile show selected abundant species; many species had at least one occurrence of 10% or greater, but not all can be shown here. Dates based on ^{210}Pb are shown in *black*, estimated dates are shown in *grey.*

Core records and lake level history

Four of the lakes cored in this study (West Long, Big Alkali, Shoup, Island) had diatom communities dominated by a small number of species that shifted in relative abundance through time (Figure 6). All four of these lakes were dominated by species such as *Aulacoseira*, *Stephanodiscus*, and *Cocconeis*, which are common in many shallow, relatively eutrophic lakes of the Midwest and Great Plains (Reavie and Smol 2001; Ramstack et al. 2003). The remaining four lakes (Dewey, Two Mile, Hackberry, Roundup) had highly variable species composition through time. In these lakes a few or even a single species was typically dominant in a given interval, with relative abundances up to 100% (not shown), but those taxa became absent or occurred in very low relative abundances in subsequent intervals. These four lakes had a wide diversity of assemblages, comprised predominantly of benthic species (Figure 6).

The diatom communities in Dewey, Two Mile, Hackberry, and Roundup lakes had extremely high

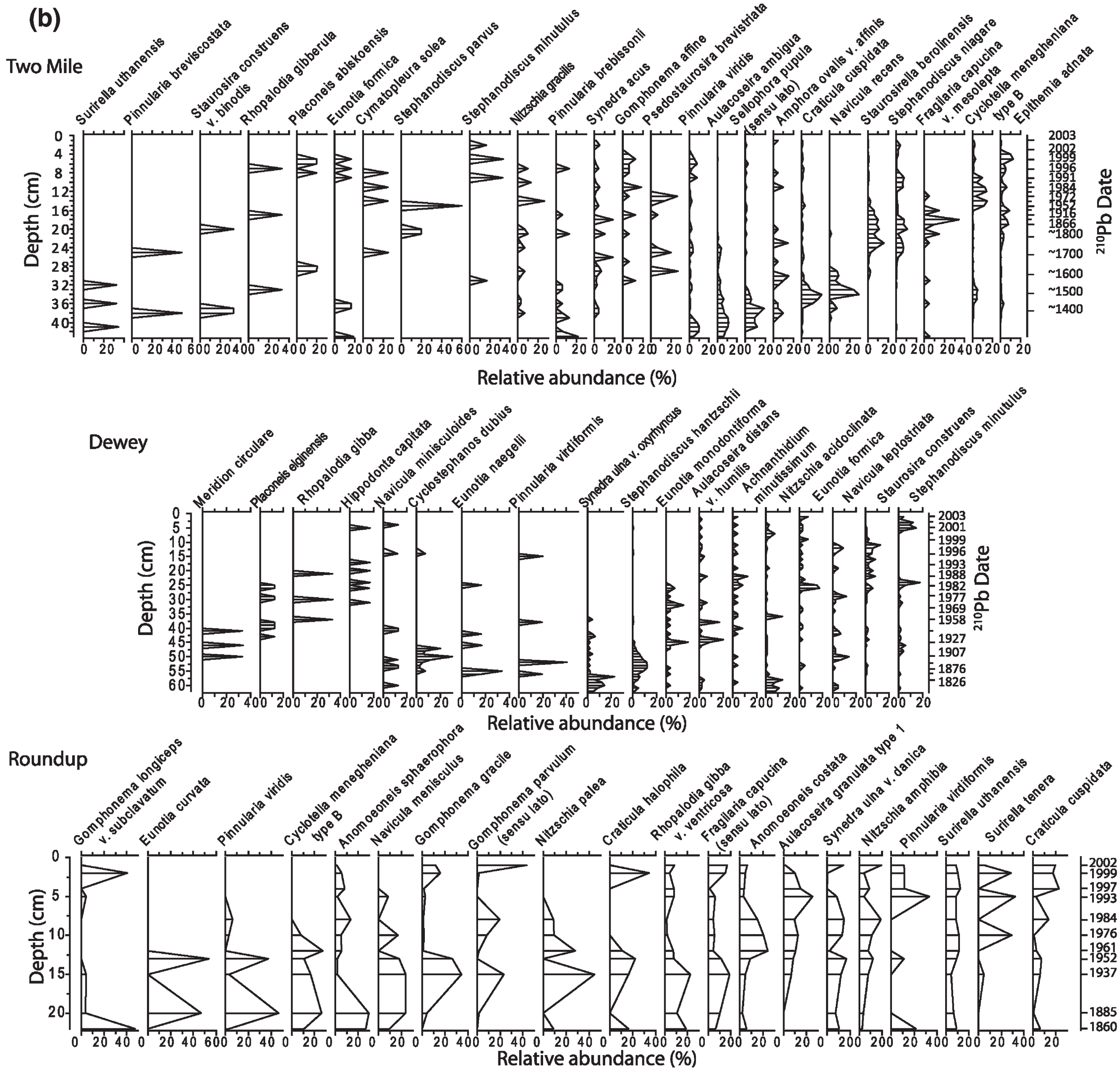


Figure 6. *(Continued)*

year-to-year variability and, subsequently, an assessment of whether or not distinct changes in species composition occurred through time was difficult. In the four lakes with more stable diatom communities (West Long, Big Alkali, Shoup, and Island), the records had two synchronous periods of assemblage shifts, one around 1700 AD and another in the late 1800s to 1900 AD. In West Long Lake, the relative abundance of *Cocconeis placentula* dropped by about half during the 1700s AD and remained low through 1900 AD, with small increases in a number of other taxa. Slight increases in planktonic taxa, including *Stephanodiscus parvus* and *Aulacoseira granulata*, took place with the return of higher abundances of *Cocconeis placentula* around 1900 AD. In Big Alkali Lake, the biggest change in community composition occurred between 1800 and 1900 AD with a large increase in the relative abundance of planktonic taxa, including *Aulacoseira ambigua* and *Stephanodiscus niagarae*, which occurred in step with

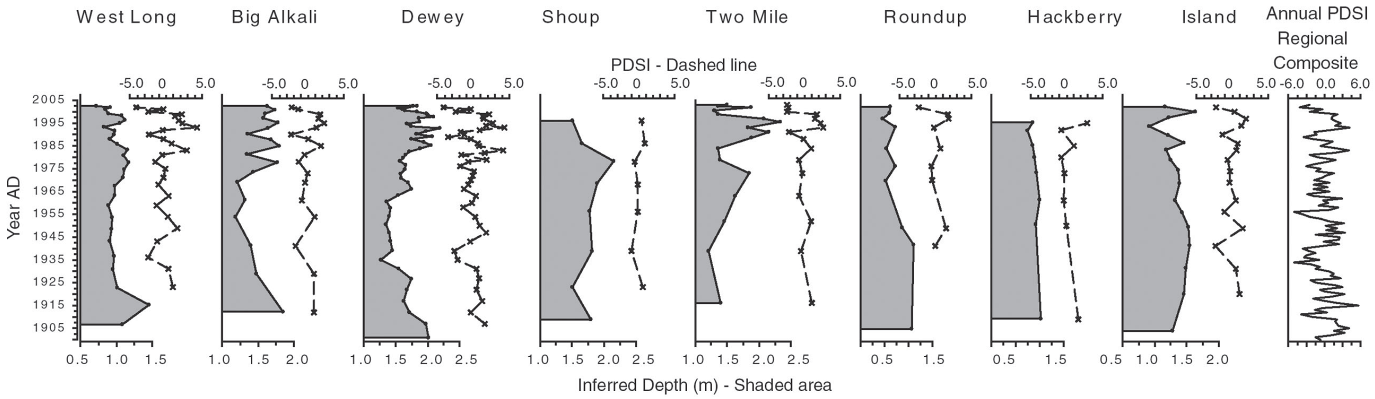


Figure 7. Reconstructed water depths (*shaded*) for the last century with comparison to variably smoothed (*dashed lines*; see text) PDSI records and the instrumental PDSI regional composite.

a decrease in benthic *Amphora*, *Navicula*, and other species. The diatom assemblage in Shoup Lake was predominantly benthic, with varying dominance of several benthic species, including *Cocconeis placentula*, *Nitzschia amphibia*, and several fragilariod species. An increase in the planktonic *Aulacoseira granulata* between the mid-1800s and mid-1900s AD showed similarities in timing to the changes in West Long and Big Alkali. Island Lake, similar to Shoup Lake, preserved decreased abundances of planktonic *Aulacoseira* between about 1700 and 1900 AD, with an increase in the early 1900s and subsequently decreasing abundances in the last several decades. Periods of low relative abundance of *Aulacoseira ambigua* in Island Lake corresponded with increased abundance of *Navicula cryptocephala* and several fragilariod taxa. Relatively few major changes occurred in the diatom assemblages preserved in any of the lakes during the last century.

Reconstructed depths showed relative stability in the last century (Figure 7). None of the changes in reconstructed depth over the last 100 years exceeded model error; however, lakes did show some common patterns in depth reconstructions. In the more eastern lakes in and near the Valentine NWR, average sediment accumulation rates during the last century (0.02–0.15 g cm^{-2} $year^{-1}$) were higher than those in the Crescent Lake NWR (0.01–0.08 g cm^{-2} $year^{-1}$). This allowed for more resolution in each centimeter section and consequently, greater temporal resolution in the recent record. West Long, Big Alkali, and Dewey lakes, within the VNWR, all showed stable and moderate to low inferred depth in the early part of the century, moderate increases in the 1970s, decreases in the early- to mid-1980s, increases in the mid-1990s, and decreases in the late 1990s. Two Mile and Shoup lakes, to the west, both had an inferred depth increase in the 1970s. Resolution in Shoup was limited; however, Two Mile Lake also recorded a decrease in the mid-1980s, increase in the early 1990s, and decrease in the late 1990s, similar to the pattern in the lakes of the VNWR. Roundup and Hackberry lakes, in the CLNWR, had very limited resolution over the last century, but showed some changes in inferred depth that were synchronous with those in the more eastern lakes, including the recent decrease in inferred depth in Roundup. Island Lake recorded very little change in inferred depth until two relatively recent fluctuations, which were similar in pattern, but temporally off-set from changes in the other lakes.

Recent records were compared with the twentieth century instrumental records of Palmer Drought Severity Index (PDSI) (Figure 7; NOAA 2009). When compared with the annually resolved PDSI, low inferred lake levels are weakly correlated with periods of extended drought, and high lake levels with periods of extended above average moisture availability. Because the core records do not have the same yearly resolution as instrumental PDSI data, the inferred depths were also compared with a variably smoothed PDSI record, where the PDSI record was composed of a running average between core dates. These records show much greater similarity; even large droughts are smoothed in the very low-resolution record of PDSI, which is reflected in profiles such as Roundup and Shoup, where very little change was inferred.

By extrapolating the ^{210}Pb dates over the length of the cores, changes in diatom assemblages could

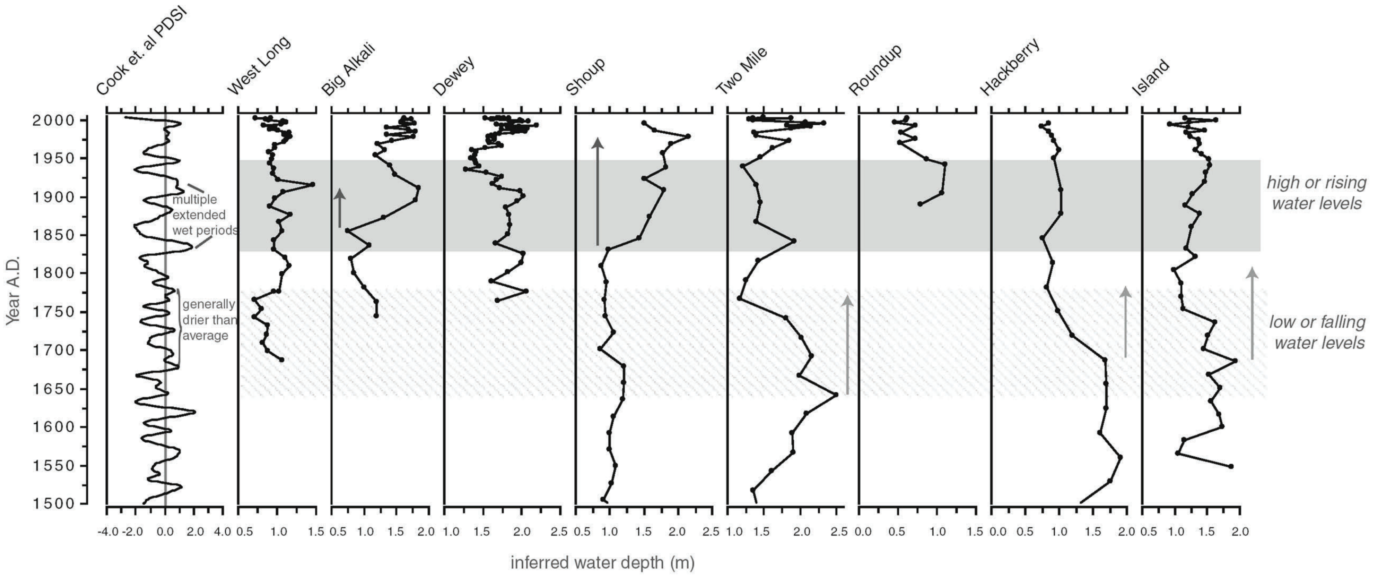


Figure 8. Reconstructed water depths for the full length of the cores with comparison to a published 20-years smooth of tree-ring-inferred PDSI (Cook et al. 2004). Intervals with change in excess of RMSEP are indicated with *arrows* that span the period of significant change; *dark* and *light arrows* indicate significant increases and decreases in inferred lake levels, respectively. *Y*-axis dates are based on the tree-ring record, with cores plotted at corresponding ^{210}Pb or extrapolated dates.

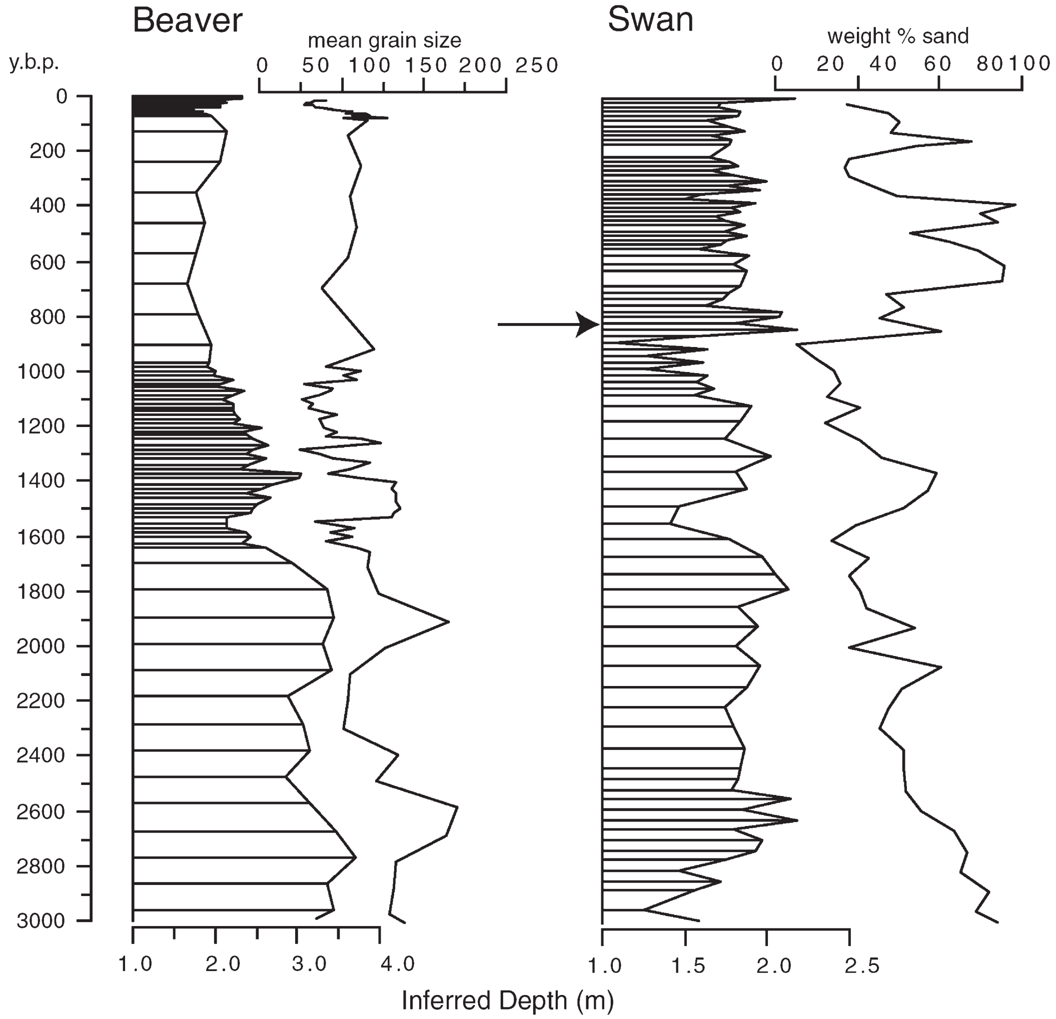
be compared with tree-ring inferred PDSI over several hundred years. The most marked changes in species composition and in inferred depth, and the only changes in inferred depth to exceed the range of RMSEP in the eight cores collected in this study, occurred between 1600 and 1900 AD, as inferred lake levels dropped between approximately the 1600s to 1700s AD and increased again in most lakes in the early 1800s–1900 AD (Figure 8). When compared with a 20-year smooth of reconstructed PDSI based on tree-ring widths (Cook et al. 2004), the decrease in inferred depths around 1700 AD corresponded with a period inferred to be generally dry, while multiple extended wet periods occurred during the increase in inferred lake levels from 1800 to 1900 AD (Figure 8). The inferred decrease in lake level also occurs concurrently with periods of inferred drought, lowered lake levels, and increased markers for dry conditions, in other parts of the Great Plains (Valero-Garces et al. 1997; Xia et al. 1997; Yu et al. 2002).

Comparison with other Holocene records

The depth transfer function was also applied to longer Holocene core records from the Sand Hills region (Schmieder 2009). Cores from Beaver Lake and Swan Lake in the Sand Hills were evaluated previously for sediment proxies thought to reflect changing moisture conditions over the Holocene: percent sand size grains in Swan Lake and mean grain size in Beaver Lake. Larger grain size and increased sand content are thought to reflect drier conditions, when sand dunes were mobilized and a lowered water table allowed larger grains to be deposited farther into the lake basin (Schmieder 2009; Nicholson and Swinehart 2005). Changes in diatom-inferred depth track the timing of major changes inferred from these other proxies, although the relationship between sediment composition and inferred depth is not constant in the lakes over time (Figure 9).

Diatom-inferred depth over the previous several thousand years showed high variability, including several intervals of synchronous change. Both lakes had low or decreasing depth from approximately 2,100 years before present to 1,500 calendar year BP, with a marked drop in lake level at approximately 1,600 calendar year BP. The lakes record a short deeper-water interval around 1,300 calendar year BP, before lake levels again decreased. Lake levels were generally high from about 1,000 calendar year BP to modern times in Swan Lake, with stable and moderate inferred depth values in Beaver Lake. Both lakes record higher than average lake level in the last 100 years, as compared to the previous 3,000 years.

Figure 9. Inferred water depth (*bars*) applied to previously published diatom records from the Sand Hills. Inferred depths are compared with proxies for the input of allochthonous material (*lines*). The peak in inferred depth at approximately 800 years BP in Swan (*arrow*) was the only inferred change in depth to exceed model error.



Swan Lake showed a general correspondence between lower lake levels and increased large sand fraction in the sediment. An exception occurred during a brief, rapid increase in lake level at around 800 calendar year BP, during the only statistically significant increase in lake level. In contrast, Beaver Lake showed a general correspondence between higher lake level and larger grain size throughout most of the core. Although the relationships differ between cores and over time, periods of major change occurred synchronously in both sediment properties and inferred depth (Figure 9).

Discussion

Calibration

Depth had the most robust and significant independent relationship with diatom assemblages; however, other variables, including TKN, TP, and alkalinity, were closely linked. While depth appears to be the variable most directly controlling changes in species composition, it does not change in isolation. In many shallow lakes, fluctuations in water depth can have important effects on the ecology and functioning of the system (Coops et al. 2003), and this appears to hold true for the shallow natural lakes of western Nebraska. Shallow lakes are known to exhibit multiple responses to water-level fluctuations, including increased or decreased nutrient concentration (Hoyer et al. 2005). In the Sand Hills lakes, shallower water depths generally corresponded with increased nutrient concentrations, possibly due to increased wind mixing and sediment re-suspension. Shallower water depth also corresponded with increased alkalinity, potentially related to evaporative concentration of salts. Calculated species optima for the three significant variables were highly correlated (Figure 5), and it is likely the case that the diatom community is responding to a multi-faceted change in the lake ecosystem driven by changes in depth, lake area, and resultant changes in habitat availability, sediment resuspension, and internal nutrient cycling.

The depth gradient in the calibration set was divided between shallow natural lakes and deeper reservoirs; however, a PCA of natural lakes alone showed that depth remained a significant explanatory variable when sand pits and reservoirs were removed. The PCA also showed that the same relationship exists between nutrients, alkalinity, and depth in natural lakes alone. Because these relationships were consistent across all subsets of the data, the largest set of lakes was used for the development of the transfer function.

Although conductivity in regional lakes is responsive to seasonal changes in precipitation (Gosselin 1997; Bennett et al. 2007), and studies in other parts of the Great Plains have successfully used fluctuations in salinity as a proxy for moisture balance (Fritz 1990; Fritz et al. 1993), no significant relationship was found between lake salinity and diatom assemblages. Specific conductance had an insignificant relationship with diatom distribution in both the full data set and in natural lakes alone, while TSS had a weak relationship only in the full data set. Six brackish to saline natural lakes were removed from the calibration set due to poor diatom preservation, and it may be that a longer salinity gradient would result in a stronger connection with diatom distribution. However, a wide range of salinities was represented, and many salt-tolerant taxa such as *Amphora*, *Anomoeoneis*, and *Chaetoceros* species were present in the calibration set. This suggests that although salinity may be quite variable across the region, it does not have a pronounced effect on diatom distributions.

Lake-level reconstructions

Lake-level fluctuations have been reconstructed successfully using changes in diatom assemblages in other regions (Punning and Puusepp 2007; Laird and Cumming 2008). Diatom-inferred changes in depth have been employed most successfully in lakes where the ratio of planktonic to benthic species was the dominant change during a deepening or shallowing of the lake (Brugam et al. 1998; Laird and Cumming 2008). Often these models reflect an increase in planktonic taxa with increasing water depth as shallow, littoral areas are inundated. In our Nebraska calibration set, the species with deep-water optima included both planktonic taxa (*Stephanodiscus*, *Cyclotella*, and *Asterionella* species), as well as taxa generally considered to be benthic, shallow-water species (e.g. *Cocconeis*, *Nitzschia*, and *Cymbella* species) (Table 3). In shallow lakes, or lakes with complicated basin morphometry, changes in depth can increase or decrease the extent of the littoral zone and the habitat available for attached species (Stone and Fritz 2004). Because the Nebraska lakes are very shallow and often situated in broad interdune valleys, increased water volume in the lake likely contributes to a substantial expansion of the lake surface area as well as an increased maximum depth. The combined increases in depth and littoral zone extent may lead to an increase in both planktonic and benthic taxa under wetter conditions. It is possible that a calibration set for lake area or littoral zone extent would provide a more direct link with changes in diatom community composition and thereby a more robust measure of moisture availability in these shallow systems.

The strong correlation between depth and other variables, including nutrient levels and alkalinity, may also lead to the possibility of spurious changes in inferred depth due to unrelated changes in one of these confounding variables. Nutrient concentrations and alkalinity may change as a result of, or in concert with, changes in depth; however, an unrelated change in one of these variables would cause a change in the depth reconstruction which is not reflective of the true lake level history.

An additional potential complication in the water-depth calibration was that the deepest end members of the calibration set were artificially developed systems, such as reservoirs and sand pits. These systems are different in many ways from the natural lakes and may be poor analogues for a deep-water condition in the natural lakes; however, the natural lakes are so uniformly shallow that a calibration set using only natural lakes had an ineffectively short gradient. This again points to the possibility of improving the resolution of this calibration with a lake-area measure, where a longer gradient may be available within natural lakes alone.

Relatively few major changes occurred in the diatom assemblages preserved in any of the lakes during the last century, in contrast to many other shallow Midwestern lakes that have undergone heavy anthropogenic impacts during that time period, such as eutrophication as a result of the expansion of mechanized farming and chemical fertilizer in use since the middle of the last century (Reavie and Smol 2001; Ramstack et al. 2003). More pronounced changes in diatom assemblages in previous periods (prior to 1900), although synchronous, are variable among lakes in terms of species composition changes. Thus, the nature of a regionally synchronous shift may vary from planktonic to benthic assemblages, among benthic species, or from benthic to planktonic assemblages in different lakes. Although the lakes have differing responses in terms of species composition, the changes occur during similar time periods. This indicates that larger regional changes are discernible in the diatom record though interpretation may be difficult.

Comparison of inferred water depth with records of sediment composition from two longer core records from the Sand Hills again demonstrated that the timing of major changes in the diatom communities are temporally coherent, although the relationships can be variable and interpretations complex. In Swan Lake, lowered lake levels generally corresponded with increased allochthonous input, probably driven by greater mobility of surface soil on the drier terrestrial landscape. An exception occurred during a period of rapid inferred depth increase around 800 calendar years BP. Increased water depth may in some situations lead to increased shoreline erosion, and alternatively increase sediment input with increasing water depth. Although the sand substrate and high groundwater inputs to these lakes typically make overland flow a minimal contributor to the water budget, increased precipitation and runoff may increase the load and size of sediment input to the lakes during wet periods, creating a relationship similar to that evident in Beaver Lake.

Resolution and dating

Previous studies of hydrology in the Sand Hills region determined that groundwater recharge rates are rapid and lakes respond quickly to changes in local precipitation. In the Crescent Lakes NWR, changes in lake extent, measured as lake surface area, were highly correlated with precipitation over the preceding 45 days (Gosselin et al. 2000). Several years of lake-elevation measurements at Island Lake in the CLNWR showed variability of over a meter in a single season and nearly 2 m over the 7-year period of record (Gosselin et al. 2000). Natural lakes monitored over several months for the development of this calibration set had single-season variation that ranged from 0.1 to >1.0 m per season, with even greater variability between two summer seasons.

A centimeter-thick sediment section preserved from several months to 10 years of sediment deposition at the tops of cores to as much as 30 years of deposition at the bottom of the cores. Therefore, some core intervals integrated a large range of depth conditions over time. In these situations, a substantial change in average conditions was needed to produce a marked change in the diatom assemblage. Even the relatively large change in precipitation during recent drought events may not be of sufficient magnitude to produce a major shift in the sediment record. For example, modeling studies have shown that between 1979 and 1990, when precipitation was decreased to half of the long-term average, the regional water table dropped by an average of 0.89 m (Chen and Chen 2004). This may reflect a large change for a lake in a single year, but could easily fall within the range experienced over a decade and make the drop difficult to distinguish in the diatom record. The more pronounced and regionally consistent changes during major climate shifts prior to the last century are better recorded in the regional diatom record.

Diatom-inferred records of lake depth were weakly correlated with the annual instrumental record of PDSI for the Sand Hills region over the last several decades; however, known droughts early in the twentieth century, including the Dust Bowl era, were not well defined in inferred lake level reconstructions. The recent drought of the late 1980s was reflected in many of the inferred lake-level changes, especially from lakes in the VNWR (West Long, Big Alkali, Dewey) where records had higher temporal resolution. However, the much larger and longer Dust Bowl drought of the 1930s was not well reflected in the core records; the only lake to show decreased depth in the 1930s was Dewey, the record with the highest resolution during this period. While there may be reasons for greater sensitivity and increased variability in the last several decades, including changes in ground-water withdrawal for ir-

Table 3. Occurrence and optima and tolerance data for the 25 most frequently occurring diatom species in the calibration set. Species are ordered by decreasing depth optima.

Taxa	# lakes	Depth optima (m)	Depth tolerance (m)	TKN optima (µg L^{-1})	TKN tolerance (µg L^{-1})	TP optima (µg L^{-1})	TP tolerance (µg L^{-1})	Alk optima (mg L^{-1} $CaCO_3$)	Alk tolerance (mg L^{-1} $CaCO_3$)
Navicula menisculus	13	4.6	1.5	2,040	3	105	3	149	1
Asterionella formosa	15	4.5	1.6	626	1	104	3	166	1
Cyclotella ocellata	13	4.4	1.3	507	1	21	1	180	1
Fragilaria crotonensis	18	4.2	1.8	1,240	2	97	3	225	2
Gyrosigma acuminatum	12	3.6	1.3	908	2	48	3	224	2
Denticula kuetzingii	15	3.5	1.5	513	1	29	2	173	1
Amphora pediculus	15	3.4	1.8	532	1	53	2	190	1
Achnanthidium minutissimum	26	3.4	1.5	583	2	51	3	178	1
Stephanodiscus hantzschii	22	3.3	1.9	1,286	2	145	3	188	1
Navicula capitatoradiata	13	3.3	2.0	2,996	3	179	3	178	2
Pseudostaurosira brevistriata sensu lato	11	3.2	1.5	484	1	31	2	156	1
Synedra tenera	12	3.1	2.6	1,179	2	100	2	312	2
Navicula radiosa	12	3.0	2.0	889	2	79	3	215	2
Nitzschia perminuta	11	3.0	1.6	1,168	3	104	5	239	2
Aulacoseira granulata type 1	15	3.0	1.9	1,666	2	130	3	274	2
Cyclotella meneghiniana	15	2.4	2.0	784	2	67	3	350	4
Cymbella cymbiformis	16	2.4	2.1	1,055	2	60	3	198	1
Hippodonta capitata var capitata	12	2.3	2.1	843	2	101	3	234	2
Planothidium lanceolatum	22	2.1	2.2	484	1	196	6	355	3
Achnanthidium exiguum	12	2.1	2.7	890	2	73	3	236	2
Synedra acus	32	2.1	2.4	1,212	2	146	4	322	3
Stephanodiscus niagarae	12	2.1	2.0	2,289	3	214	2	225	2
Fragilaria capucina sensu lato	28	2.1	2.3	1,537	3	176	5	304	2
Navicula trivialis	15	2.0	1.9	1,569	2	135	3	307	3
Synedra ulna	42	1.9	2.7	1,039	2	88	4	257	2
Craticula halophila	12	1.8	2.6	941	2	165	3	567	5
Amphora ovalis var affinis	37	1.7	2.5	1,391	3	111	4	237	2
Aulacoseira ambigua	17	1.7	1.7	2,609	2	172	2	218	2
Rhopalodia gibba sensu lato	19	1.7	2.6	1,675	3	121	4	342	2
Staurosira construens sensu lato	13	1.6	1.7	1,976	3	187	3	182	1
Nitzschia linearis sensu lato	30	1.5	2.5	1,494	3	188	4	238	2
Encyonema silesiacum sensu lato	13	1.4	2.0	1,988	3	149	3	182	1
Nitzschia palea	18	1.3	1.9	3,435	2	329	3	277	2
Cocconeis placentula var lineata	19	1.2	1.9	2,789	2	328	4	254	2
Fragilaria capucina var mesolepta	16	1.2	3.3	2,444	2	198	3	571	6
Gomphonema truncatum sensu lato	13	1.0	1.8	3,191	2	275	3	241	2
Hantzschia amphioxys	26	1.0	2.0	3,001	3	383	4	657	5
Sellaphora pupula sensu lato	20	0.9	1.9	1,255	2	195	2	353	2
Amphora veneta	26	0.9	2.6	3,020	3	374	2	514	4
Gomphonema parvulum sensu lato	20	0.9	2.6	2,687	3	298	3	310	2

Table 3. *Continued*

Taxa	# lakes	Depth optima (m)	Depth tolerance (m)	TKN optima (μg L^{-1})	TKN tolerance (μg L^{-1})	TP optima (μg L^{-1})	TP tolerance (μg L^{-1})	Alk optima (mg L^{-1} CaCO$_3$)	Alk tolerance (mg L^{-1} CaCO$_3$)
Fragilaria vaucheriae	24	0.9	2.8	1,314	2	136	3	310	3
Navicula oblonga	26	0.8	2.4	2,040	3	132	5	658	4
Nitzschia amphibia	30	0.8	2.1	4,958	2	593	3	909	5
Gomphonema longiceps var subclavatum	12	0.8	2.0	2,162	2	315	2	366	3
Epithemia adnata sensu lato	24	0.7	2.5	4,379	2	316	3	663	4
Nitzschia frustulum	18	0.7	2.1	2,963	3	168	3	1,249	4
Navicula cryptocephala	25	0.7	2.5	695	2	182	4	615	4
Craticula cuspidata	25	0.6	2.5	4,910	3	339	3	591	3
Cocconeis placentula sensu lato	19	0.6	3.1	2,239	2	238	3	331	2
Anomoeoneis costata	35	0.4	2.3	8,279	2	425	3	5,719	6

rigation in the region (McGuire 2004), more likely the decreasing resolution with sediment compaction down-core simply smoothed the record of changes in diatom communities. Intra-seasonal and inter-annual variability is high in these shallow, groundwater-fed lakes and without extremely high sedimentation rates and excellent chronological resolution in the cores, rapid variations are undetectable. Thus, only large changes in the mean state of the lakes produce identifiable trajectories in core records with low to average resolution.

Other studies have shown that small variations in lake level are difficult to capture using diatom-based inference models. Laird and Cumming (2008), for example, compared diatom-inferred depths with instrumental records from an Ontario lake; they found that lake level decreases of 0.2–0.3 m during the drought of the 1980s were not reflected by the diatom-based record of depth, but larger changes of several meters to tens of meters over the Holocene matched well with changes in depth inferred from other proxies. Some studies have shown that more robust models for diatom variability with depth can be developed by using a calibration set based on shallow-to-deep water transects within an individual lake rather than by using a suite of lakes with a range of maximum depths as has been done here (Punning and Puusepp 2007; Laird and Cumming 2008).

Dating results were better than initially expected, given the potential for disruption of sedimentation in these shallow lakes. Most ^{210}Pb profiles exhibited fairly smooth declines with depth, indicating reasonably conformable sedimentation. Although we were able to model dates for all eight cores, there is a possibility that some profiles are truncated by desiccation events, leading to increased model errors. Uncertainty of the dates based on counting precision (a minimum error) is less than ± 5–10 years over the last century. Dates extend back to the mid-1800s for all cores except Roundup; mid-1800 dates have errors on the order of several decades for most cores and dating error rises substantially for the oldest dated intervals in West Long and Dewey, approaching 25 years at the bottom. Pre-nineteenth century dates extrapolated from the ^{210}Pb dating are based on assumptions of continuous sedimentation at a constant rate prior to the earliest ^{210}Pb dated interval, which is likely to lead to large errors in these older dates. Even given the large errors, long-term shifts in the lakes are likely comparable to century-scale changes recorded in the tree-ring records, though offsets from the dates given here are probable. Even with the most robust dating models, the potential for dating errors or offsets between cores must be considered when comparing these records with instrumental data and with one another. The largest changes in inferred lake level occur synchronously, span relatively long time periods, and correlate well with instrumental records; however, offsets such as the timing of lake level change in Island Lake may be related to dating models rather than an asynchronous response to changes in regional climate.

Conclusions

The modern diatom assemblages in 69 Nebraska lakes were compared with modern water chemistry data to understand the controls on diatom distribution in the region. Diatom distributions are controlled by a number of factors, including nutrient concentrations, alkalinity, and water depth. The multiple controls on diatom distributions made it difficult to develop a strong calibration for a single variable, as many interacting effects influence changes in diatom community composition through time. The most robust relationship was between diatoms and water depth, and this relationship was used to develop a model to infer past water depth from sub-fossil diatom assemblages in sediment cores. Nutrient concentrations and alkalinity were also strongly linked to both diatom community composition and to water depth, however, they did not show strong independent relationships with diatom distributions in the calibration set.

The transfer function for depth was applied to eight newly collected sediment cores from the Nebraska Sand Hills. Comparison of the inferred depth record with instrumental records showed that Sand Hills sediment records may not faithfully reflect short-term (inter-annual to decadal) fluctuations in water level, but they do reflect large and persistent change in moisture availability. Diatom-inferred depth did correlate with short-term changes in effective moisture in some lakes where sedimentation rates were high and assemblages from an individual season were distinguishable. Due to the high inter-annual variability in lake depth, samples that integrated more than a few years because of slow sedimentation showed very little change over short time scales. Inferred depth histories for two previously published, longer core records showed that lower resolution records do distinguish large shifts in the average depth of the lake that are persistent over long periods of time. In nearly all lakes, large changes in climate that produced major shifts in the mean state of the lakes, such as those associated with the 'Little Ice Age,' were discernible in most sediment records. The transfer function had relatively large error, and few changes in inferred depth exceeded model error. Nonetheless, many changes were synchronous among lakes and matched well with instrumental and other proxy data, indicating that diatoms in these shallow, variable systems are a useful addition to the tools available for understanding past drought, especially when trajectories of change are constrained by data from multiple sites or other proxies.

Recent droughts were of short duration compared with those in previous centuries and millennia and had relatively little impact on the diatom communities. When combined with additional regional information about drought occurrences, diatom-based inferences of depth may provide an important source of additional information on quantitative changes in moisture availability.

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