

# Response of temperate lakes to drought: a paleolimnological perspective on the landscape position concept using diatom-based reconstructions

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**Abstract** The hydrological position of a lake within the landscape can affect a number of lake chemical, physical, and biological features, as well as how lakes respond to environmental change. We present a paleolimnological test of the model for landscape position and lake response to climate change proposed by Webster et al. (2000). To investigate how diatom communities have responded to drought relative to landscape position, we examined sedimentary diatom profiles extending through the twentieth century from an upland site (Crystal Lake) and a lowland site (Allequash Lake) in the Northern Highlands region of north-central Wisconsin (USA). To explore changes in diatom communities at each site, we developed a

calibration set and transfer functions from 48 lakes in Wisconsin's Northern Highland Lake District. We further determined planktic:benthic ratios in the two target lakes, developed lake level models, and investigated the sensitivity of planktic:benthic diatom ratios to climatic variability over the past century. In the upland lake, diatom communities responded indirectly to climate via drought-induced changes in lake level, which resulted in shifts in planktic versus benthic habitat availability. This response of diatoms to changes in habitat availability provides an alternative approach for tracking climate change in upland lakes, though careful consideration must be given to the effect of the bathymetry and its relationship to lake level change and habitat zonation at individual sites. In the lowland lake, changes in diatom communities were related to temperature (and possibly lakewater chemistry) and physical changes secondarily. These results are consistent with the model by Webster et al. (2000), with chemical changes occurring in the lowland system and little chemical response in the upland system. However, the biological changes in sediment records presented here provide additional insight into how lake response to climatic change is shaped by landscape position, contributing to a clearer understanding of potential changes in ecosystem structure and function during drought conditions.

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## Introduction

Landscape position determines the hydrologic setting of lakes, including their position within regional groundwater flowpaths and the relative importance of groundwater, surface inflow, and precipitation in their hydrologic budgets (Almendinger 1990; Webster et al. 1996; Kratz et al. 1997; Riera et al. 2000). Though lakewater chemistry is influenced by a number of factors, including evaporative losses, atmospheric deposition, and local geology, it is also related to groundwater inputs and hence, lake location in the regional groundwater flowpath (Webster et al. 1996; Soranno et al. 1999; Baines et al. 2000). As groundwater is often enriched in solutes relative to precipitation or surface inflow (Kenoyer and Anderson 1989), lowland lakes receiving more groundwater tend to have higher concentrations of major cations than upland lakes that are less connected to groundwater sources.

Hydrologic budgets of lakes are often linked with regional drought conditions (Shuman and Donnelly 2006), which can alter the relative importance of water sources and cause differential responses in chemistry and lake level depending on the landscape position of sites (Webster et al. 1996). As the hydrology of upland lakes is precipitation-dominated, these sites are more likely to show physical responses related to lake level change during drought conditions, rather than the chemical responses from groundwater flow changes seen in lowland lakes. Lake-level changes cause variations in habitat zonation within lakes depending upon individual site bathymetry (Benson and Paillet 1989; Hostetler 1995), and can have important implications for biological community structure (e.g. planktic versus benthic areas, Wolin and Stone 2010). Thus, the landscape setting of lakes can be critical in illuminating potential mechanisms influencing different responses in lakes to the same large-scale driver, such as drought.

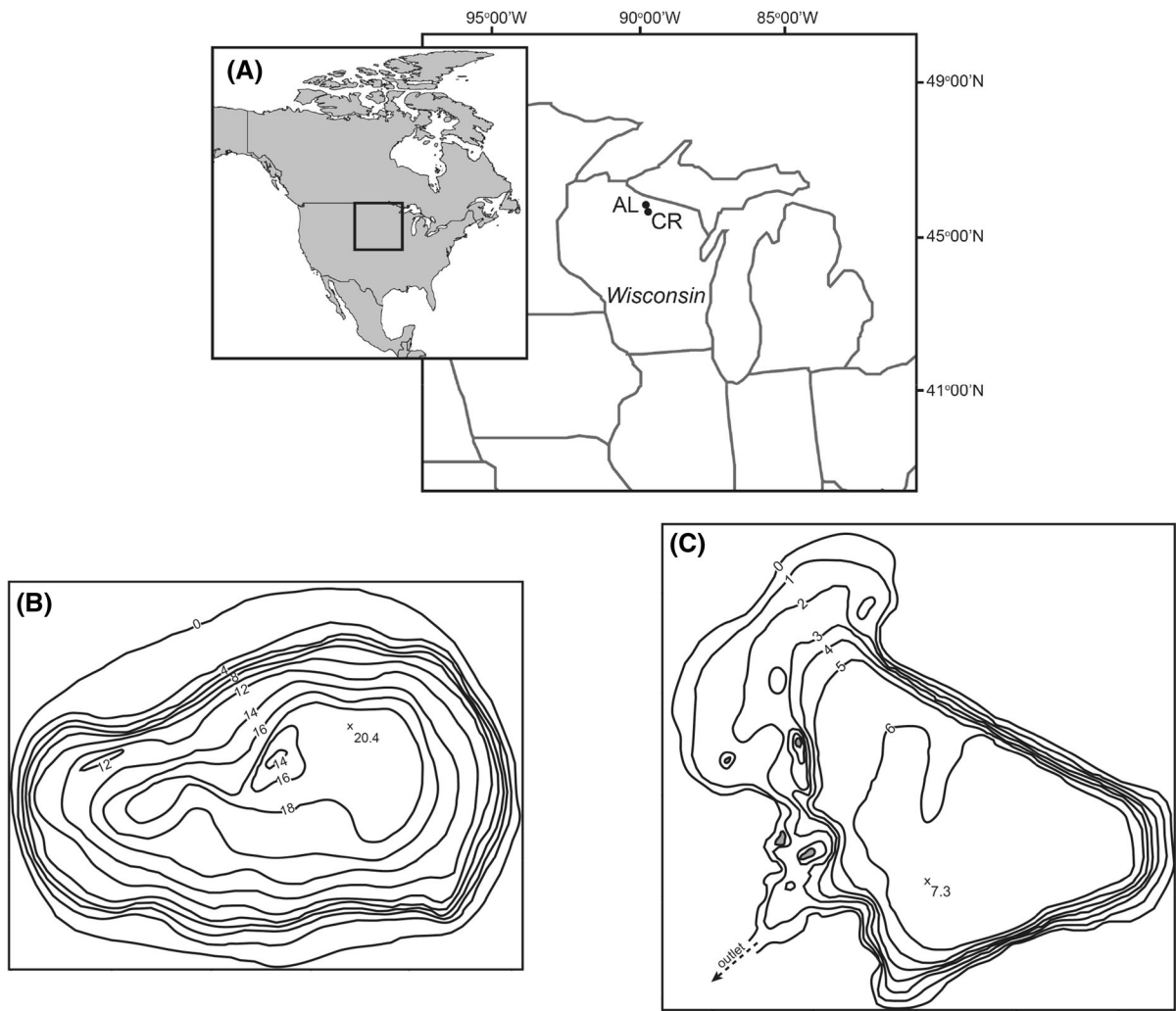
Using a monitoring dataset spanning 13 years, Webster et al. (2000) developed a framework for understanding lake chemical response to drought based on hydrology and landscape position within a watershed in northern Wisconsin. Sites lower in the watershed showed more coherent chemical responses to a 4-year drought during the late 1980s than upland lakes, due to stronger influences of groundwater at lowland sites. Upland systems did not show similar signals of changes in water chemistry during drought conditions.

Paleolimnological records contain histories of such responses to drought, including events of longer duration and higher severity than seen during the historical period. Biological indicators in sediments also provide insight into changes in ecosystem structure and function, and the sensitivity of diatom communities to environmental change has been used to reconstruct past changes in a number of variables, from water chemistry to physical habitat changes (Birks et al. 1990; Dixit et al. 1999; Fritz et al. 1991; Stone and Fritz 2004). By comparing sedimentary diatom records for lakes occupying different landscape positions, we aim to expand our current understanding of differential lake responses to climatic change.

We present a paleolimnological test of the model for landscape position and lake response to climate change proposed by Webster et al. (2000). Based on this model, we would predict that lower elevation drainage lakes would show the strongest relationships between water chemistry and climate, whereas higher elevation lakes (hydraulically mounded) would be more likely to show relationships between lake level and climate. To investigate whether diatom communities record differences in lake response to twentieth century drought due to landscape position, we collected sediment cores from a lowland lake (Allequash Lake) and an upland lake (Crystal Lake), located in northern Wisconsin. We then used multiple approaches to assess the changes in fossil diatom assemblages in response to drought over the past century. We developed a calibration set from a suite of lakes in the North Temperate Lakes—Long Term Ecological Research site (NTL-LTER), to explore relationships between lake features and diatom community structure, and then applied the new transfer functions to fossil diatom communities. We also used planktic:benthic ratios in combination with lake level modeling to assess the role of drought-induced habitat changes in shaping diatom communities. We compared reconstructed variables and ecological characteristics with community structure changes and climatic conditions (temperature, precipitation, and drought) over the past century.

### Site description

The Northern Highland Lake District of northern Wisconsin and the upper peninsula of Michigan



**Fig. 1** a Regional maps and bathymetric maps for b Crystal Lake and c Allequash Lake (contour lines illustrate depths in meters, with “x” indicating maximum depth at each site)

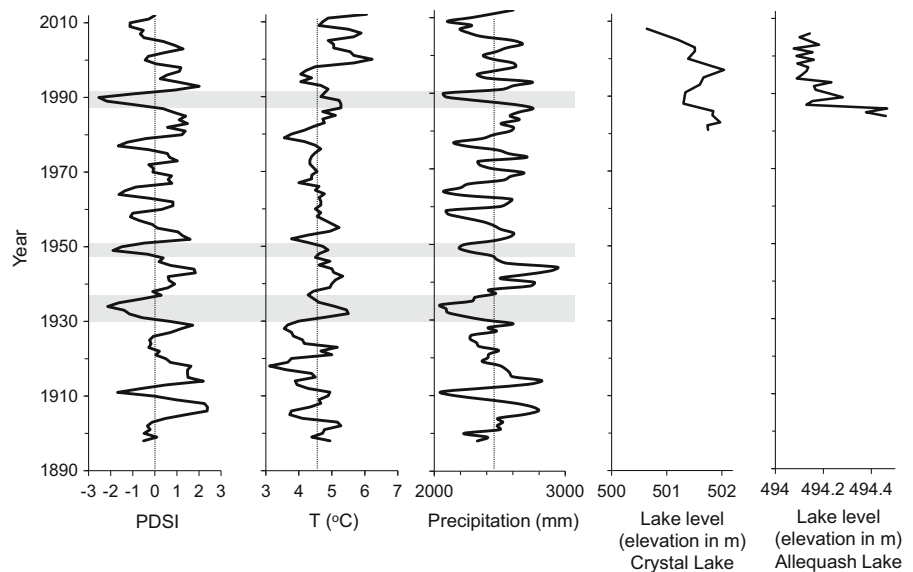
contains about 2500 lakes, and is the site of the North Temperate Lakes—Long Term Ecological Research program (NTL-LTER). Here, glacially formed lakes are situated over about 40 m of sandy outwash made of low-carbonate materials (Attig 1985; Kenoyer and Bowser 1992), with significant groundwater fluxes to the lakes due to this porous matrix (Kenoyer and Anderson 1989).

To explore the role of landscape position in shaping diatom community response to drought, we collected sediment cores from Crystal Lake, an upland system, and Allequash Lake, which is lower in elevation (<http://lter.limnology.wisc.edu/>, Fig. 1). Crystal Lake is an ultra-oligotrophic seepage lake at 500.5 m

elevation that receives most of its water from precipitation inputs, receiving only 6 % of its hydrologic budget from groundwater, while Allequash Lake is a meso-oligotrophic drainage lake at 494.1 m elevation that receives about 31 % of its hydrologic budget from groundwater (Webster et al. 1996). Crystal Lake has a simple bathymetry, with a regular sandy shoreline and a shallow area on the northern and southern sides of the basin. Allequash Lake is a more complex basin, with an irregular shoreline, four small islands within the lake, and a surface outlet.

Regional climate data since A.D. 1900 for Wisconsin Climatological Division 2 (which contains both Allequash and Crystal Lakes) were obtained from the

**Fig. 2** Environmental data for study region from the National Climatic Data Center ([www.ncdc.noaa.gov](http://www.ncdc.noaa.gov)) for Wisconsin Climate Division 2 since 1900. Data include 36-month averages for Palmer Drought Severity Index (PDSI), temperature (T), and precipitation accumulation (Precipitation), as well as measured lake-level elevation at both Crystal and Allequash Lakes. *Shaded bars* highlight periods of intense drought, and *vertical dashed lines* indicate means over the past century



National Climatic Data Center ([www.ncdc.noaa.gov](http://www.ncdc.noaa.gov)). Parameters included 36-month averages for the Palmer Drought Severity Index (PDSI), temperature, and precipitation (Fig. 2). Since 1900, this area has experienced several periods of drought, most notably in the early 1930s, the late 1940s, and the late 1980s. Lake levels at both sites have been monitored as part of the NTL-LTER program, with measurements taken at Crystal since 1981 and at Allequash since 1984.

## Methods

### Core collection and chronology

To investigate diatom community changes through time, sediment cores were collected from Allequash and Crystal Lakes with a modified piston corer in January 2007. A 93-cm-long core was collected from Allequash Lake and a 50-cm-long core was collected from Crystal Lake, each with intact sediment–water interfaces. On the same day and within a few meters from where the piston core was collected in Crystal Lake, a frozen sediment core one meter in length was collected using a wedge-shaped freeze coring device filled with ethanol and dry ice. All cores were taken back to the University of Wisconsin’s Trout Lake Field Station, where piston cores were extruded into contiguous 0.5-cm intervals and frozen sediment cores were removed from the freeze corer. Crystal’s freeze

core was wrapped in foil, kept frozen, and transported to the National Lacustrine Core Repository (LacCore) at the University of Minnesota where it was cleaned with a planer, imaged, and sectioned into 0.2-cm depth intervals using a microtome-like slicing device. Remaining core samples and core sections are archived at the National Lacustrine Core repository (LacCore) at the University of Minnesota.

Age-depth chronologies for the piston cores collected from Crystal and Allequash lakes were established with  $^{210}\text{Pb}$  distillation and alpha spectrometry methods (modified from Eakins and Morrison 1978), and dates were determined using the constant rate of supply model (Appleby 2001). An age-depth model for Crystal’s freeze core was constructed by aligning freeze core sediment depths stratigraphically with sediment depths in the  $^{210}\text{Pb}$ -dated piston core collected from Crystal based upon changes in profiles of *Ambrosia*-type pollen observed in both cores. Depth alignments between piston and freeze cores collected from Crystal Lake were confirmed using high-resolution ( $\sim 1$ -cm depth intervals) profiles of organic matter content and pollen percentage data obtained in both cores.

### Sedimentary diatom analysis

For the sedimentary diatom assemblages, sediment was digested with 10 % HCl and 30 %  $\text{H}_2\text{O}_2$  according to Battarbee (1986). Permanent slides were made

by settling solutions on cover slips and mounting cover slips with Naphrax. A Nikon E600 microscope using Nomarsky differential interference contrast (DIC) was used to count processed diatoms. Diatom taxonomy was based on Krammer and Lange-Bertalot (1986–1991) and Camburn and Charles (2000). A total of 500 frustules were counted on each slide and the percentage of each species was calculated. Planktic:benthic ratios of diatom community structure in sediment cores ( $P:B_{\text{core}}$ ) were calculated for full assemblages at each depth in the cores, based on ecology of the species present (Krammer and Lange-Bertalot 1986–1991; Spaulding et al. 2010), with tychoplanktic taxa excluded from the analysis. For Crystal Lake, diatom counts were integrated from the piston and freeze cores in order to maximize sample resolution in more recent decades and expand the temporal range of the study at that site. The most recent samples from 1986–2008 were from the freeze core, and earlier samples (1900–1968) were from the piston core. Intermediate samples were blended based on  $^{210}\text{Pb}$  dates and shifts in assemblages.

#### Development of diatom-based inference models

Surface sediment samples were collected in 2003 from 48 lakes using a small gravity corer, with samples processed for diatom analysis as described above. Chemical data were collected from these lakes as part of the University of Wisconsin-Madison's Biocomplexity Project, with methods and data available on the project website (Lottig and Carpenter 2012, <https://lter.limnology.wisc.edu/project/north-temperate-lakes-biocomplexity-project>). The following variables were selected to explore patterns in diatom distributions: specific conductance ( $\mu\text{S cm}^{-1}$ ), dissolved organic carbon (DOC;  $\text{mg L}^{-1}$ ), dissolved inorganic carbon (DIC;  $\text{mg L}^{-1}$ ), pH, total nitrogen (TN,  $\mu\text{g L}^{-1}$ ), total phosphorus (TP,  $\mu\text{g L}^{-1}$ ), secchi depth (m), chlorophyll *a* ( $\mu\text{g L}^{-1}$ ) and maximum depth (m). Specific conductance was measured with a YSI Model 32 Conductance Meter from 125 ml of unfiltered water at 25 °C. The pH was analyzed from 20 ml of unfiltered lake water the same day with a Fisher Accumet 950 Meter probe. TP and TN were acidified back at the lab with the addition of 1 ml OPTIMA HCl to 100 ml of unfiltered lake water and were quantified in a Technicon Autoanalyzer II according to the Long Term Ecological Research (LTER)-Geochemistry Lab

protocol. DIC & DOC were analyzed from 15 ml of filtered water for Model 700 OI TOC Analyzer, and lakewater was filtered for chlorophyll analysis by methanol extraction on a Kontron 930 Spectrophotometer, according to LTER protocols.

Canonical correspondence analysis (CCA) was used to relate diatom species distributions to the measured environmental variables across the suite of lakes (R, version 2.10.1). After examining histograms and normality plots, all parameters except pH were  $\log_{10}$  transformed to improve normality. Rare diatom taxa (taxa comprising <5 % of the assemblage in all lakes or those only found in one lake) were eliminated from analyses. With considerations for co-variation among environmental parameters and ecological relevance, manual forward selection and variance partitioning were used to identify significant ( $p < 0.05$ ) variables to be included in the CCA model.

Transfer functions were developed to infer each parameter over time from fossil diatom assemblages for a sub-set of environmental variables that were identified as significant in the CCA model, using the program C2 (version 1.6.6, Steve Juggins). Weighted averaging with bootstrap error estimation (1000 cycles) was used, a robust approach for small (<50 sites) datasets. Model diagnostics were run using deshrinking (classic and inverse) and weighted averaging (basic and tolerance-downweighted), and the best models were determined by examining the coefficient of determination ( $r_{\text{boot}}^2$  value), the root mean square error (RMSE), and the root mean square error of prediction ( $\text{RMSEP}_{\text{boot}}$ ) based on bootstrapping errors of 1000 cycles. Transfer functions were then applied to the full fossil diatom assemblages from sediment cores of Crystal and Allequash lakes using C2.

#### Statistical analysis

To examine patterns of change in diatom communities over the past century, principal components analysis (PCA) was performed on fossil diatom assemblages at Crystal Lake, and detrended correspondence analysis (DCA) was used for the Allequash core (due to longer gradient length at this site). Species that comprised >1 % of the assemblage in any core sample were included in the ordination, with species data untransformed and rare taxa downweighted. Spearman's nonparametric rank correlations in R (version 2.14.2)

were used to assess relationships among variables at each site for Crystal Lake and Allequash Lake. Pairwise comparisons with Bonferroni corrections among core and climatic variables identified potential links between diatom community changes and environmental conditions.

### Lake level models

Three-dimensional models of basin morphometry were developed following the methods of Stone and Fritz (2004), to explore changes in planktic versus benthic habitat availability relative to lake level changes. For both Crystal Lake and Allequash Lake, a bathymetric contour map was imported into Surfer 8.03 (Golden Software 2003) and digitized to produce three-dimensional graphical images. Bathymetric maps were developed by the Wisconsin Department of Natural Resources in 1971 for Crystal Lake and in 1969 for Allequash Lake (Fig. 1). As the original map measurements were in feet, data points were converted to elevation in meters after digitizing was complete. For both sites, the Kriging gridding method produced models that were most consistent with the original contour maps. We calculated volume, lake-basin (sediment–water) surface areas, and planar (water–air) surfaces at a given lake-level elevation. Available planktic habitat zones were defined as the total planar surface area of the lake from the surface elevation to a depth of 1.8 m (Bradbury and Winter 1976; Haworth 1979), and available benthic habitat zones were defined as total basin surface area from the lake surface to different depths of photic penetration. Multiple models were run for each site, using benthic zone depths ranging from 0.9 to 10.0 m, in order to identify major patterns in the relationship between lake level change and shifts in habitat zonation. For each benthic limit, modeled lake level elevation was lowered in approximately 0.3 m increments, with metrics recalculated at each vertical step from modern lake level to the bottom of the lake basin (Fig. 1). These calculations were then used to estimate changes in habitat for planktic and benthic habitat zones within the lakes at each water level ( $P:B_{\text{model}}$ ). Using average secchi depth (NTL-LTER data, from 1981–2013 with underwater viewer during open-water seasons) as a guideline for individual sites, we selected two models with different benthic zone limits at each lake, to capture possible seasonal variation in water clarity and

any sensitivity of the models to different benthic zone limits. For Crystal with an average secchi depth of 7.51 m, we used benthic limits of 6.9 and 10 m, and for Allequash with an average secchi depth of 3.26 m, we used benthic limit depths of 3.0 and 5.1 m for the models presented here.

To assess the range of possible lake level changes over the past century (prior to the initiation of direct measurements at the sites), aerial photographs were examined for both lakes (USGS EarthExplorer, <http://earthexplorer.usgs.gov/>) with approximately one photograph available per decade from the 1930s to the late 1990s. These aerial images were compared with the bathymetric maps and three-dimensional models for any shoreline changes to estimate lake level ranges over the past century, and therefore to understand limitations in using our models to relate lake-level changes with diatom planktic:benthic ratios at these sites.

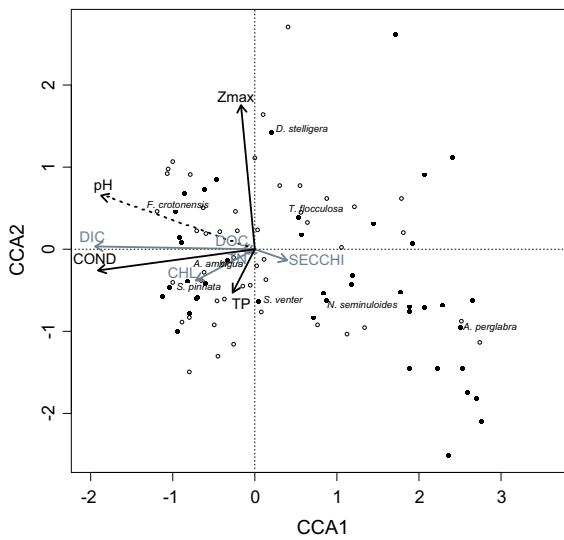
## Results

### Calibration set and transfer functions

The range in selected physical and chemical variables for the 48 lakes is provided in Table 1. After removal of rare taxa, 43 diatom species were included in the calibration set. CCA models for all 48 lakes identified four significant environmental parameters: specific conductance, maximum depth, pH, and TP (explaining 23.4 % of total variance, Fig. 3). Conductance and pH were most closely correlated with axis 1, maximum depth with axis 2, and TP with axis 3. As there are issues with reconstructing multiple parameters from a calibration set, we developed transfer functions for two parameters that explained independent portions of variance within the training set (conductance and maximum depth), with the goal of identifying which variable most strongly influences diatom communities at each lake site. Using variance partitioning for these two variables, conductivity independently explained 10.2 % of the total variance and maximum depth explained 5.6 % of the total variance. Tolerance downweighted averaging equations were used for conductance (RMSE = 0.121, RMSEP = 0.156,  $R^2 = 0.854$ , bootstrap  $R^2 = 0.822$ ) and weighted averaging equations were used for maximum depth (RMSE = 0.149, RMSEP = 0.205,  $R^2 = 0.559$ ,

**Table 1** Summary of lake features for 48 lakes in the calibration set

Parameter	Average	Median	Range
Specific conductance ( $\mu\text{S cm}^{-1}$ )	61	64	13–120
Chlorophyll a ( $\mu\text{g L}^{-1}$ )	5	4	1–13
Secchi depth (m)	4	3	<1–10
DOC ( $\text{mg L}^{-1}$ )	5	4	2–13
DIC ( $\text{mg L}^{-1}$ )	7	7	1–16
Total N ( $\mu\text{g L}^{-1}$ )	351	340	188–563
Total P ( $\mu\text{g L}^{-1}$ )	13	13	<1–34
pH	7.7	7.9	5.9–8.7
Maximum depth (m)	12	11.7	3–26



**Fig. 3** Canonical correspondence analysis for calibration set data. *Black arrows* indicate significant environmental parameters, with *solid black arrows* indicating variables used to develop transfer functions and *dashed arrows* indicating variables that were not reconstructed for core samples. *Gray arrows* illustrate other environmental parameters not used in the final CCA model. *Open circles* designate sites, and *closed circles* designate diatom species, with notations for dominant taxa found in the sediment core samples

bootstrap  $R^2 = 0.268$ ). Performance of the conductivity transfer function in surface sediments was very close to measured values for both Crystal (measured:  $13 \mu\text{S cm}^{-1}$ , diatom-inferred:  $12.7 \mu\text{S cm}^{-1}$ ) and Allequash lakes (measured:  $87 \mu\text{S cm}^{-1}$ , diatom-inferred:  $85.6 \mu\text{S cm}^{-1}$ ). Maximum depth reconstructions from surface sediments underestimated the deeper upland system (Crystal-measured: 20.4 m, diatom-inferred: 14.2 m) and overestimated for the shallower lowland lake (Allequash—measured:

7.3 m, diatom-inferred: 10.5 m). The major taxa present in the cores were well-represented within the calibration set, with the exception of *Asterionella ralfsii* var. *americana* Körner and *Pinnularia biceps* var. *pusilla* Camburn & Charles present in Crystal Lake as well as *Asterionella formosa* Hassall present in Allequash Lake.

**Crystal Lake core**

At Crystal Lake, unsupported  $^{210}\text{Pb}$  dates extended back to 1790, at 20.5 cm core depth (Fig. 4a). Chronology errors at this site ranged from  $\pm 1.43$  years in recent sediments to  $\pm 3.72$  years around 1900. Fossil diatom communities at Crystal Lake over the past century (Fig. 5a) were dominated by *Asterionella ralfsii* var. *americana*, *Pinnularia biceps* var. *pusilla*, and *Tabellaria flocculosa* Roth (primarily Str. III), with smaller proportions of *Aulacoseira perglabra* (Østrup) Haworth, *Navicula seminuloides* Hustedt, *Stauroneis nobilis* var. *gracilis* Kobayasi, and *Synedra subrhombica* Nygaard also present in the assemblages. *Tabellaria flocculosa* was lowest in relative abundances earlier in the century yet steadily increased towards the top of the core. *Asterionella ralfsii* var. *americana* became slightly more common after the late 1960s, making up at least 25 % of assemblages after that time.  $\text{P:B}_{\text{core}}$  ratios at Crystal steadily increased from the early part of the century to present, with benthic taxa dominating the assemblage for much of the record. Similar to the pattern in  $\text{P:B}_{\text{core}}$  ratios, diatom-inferred maximum depth (DI- $Z_{\text{max}}$ ) steadily increased since the early part of the century, to maximum values at present (Fig. 6a). Diatom-inferred conductance (DI-conductance) was generally stable over the past century, with small peaks in

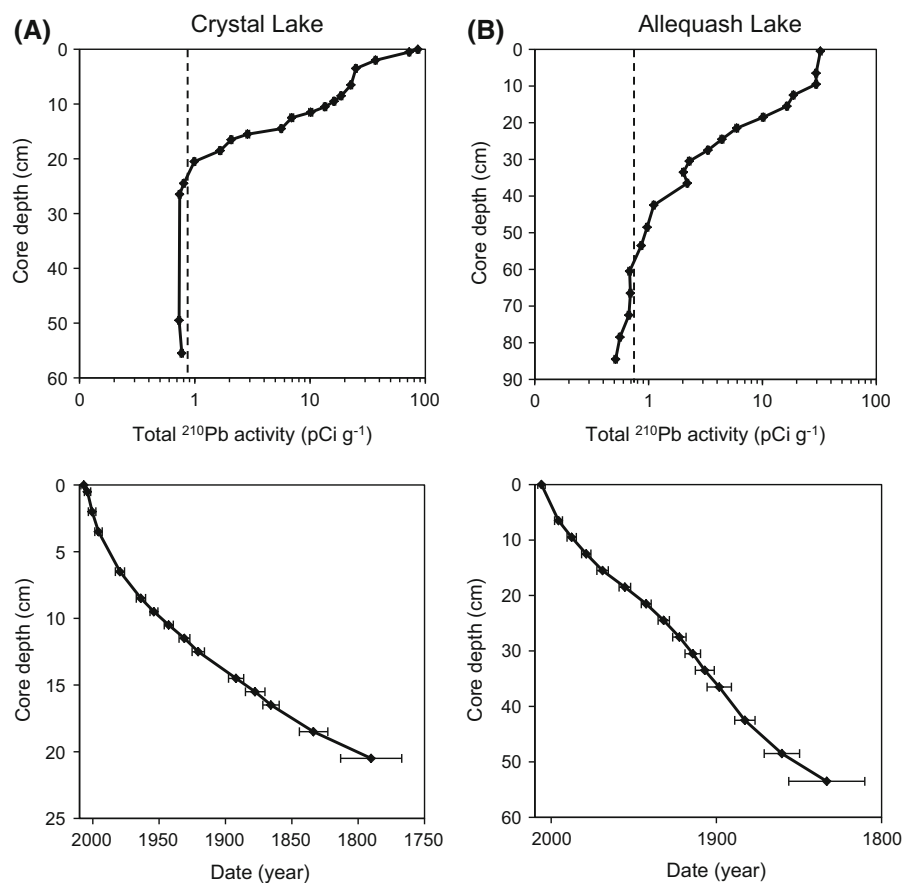
inferred values occurring in the late 1970s and mid 2000s. In Crystal Lake, measured lake levels were high in the early 1980s, and declined during the droughts of the late 1980s into the early 1990s. During these droughts, groundwater inputs to Crystal were reduced to zero (Anderson and Cheng 1993). After a peak in 1997, the lake level declined to its lowest point in recent years.

Based on downcore PCA scores, diatom community changes were primarily related to physical variables (Tables 2, 3). PCA scores on the first two axes were correlated with P:B<sub>core</sub> (PCA 1:  $\rho = 0.67$ ,  $p < 0.001$ , PCA 2:  $\rho = -0.56$ ,  $p = 0.003$ ). There was strong covariation among reconstructed variables and P:B<sub>core</sub> at this site, with more planktic taxa associated with higher lake levels (P:B<sub>core</sub> with DI-Z<sub>max</sub>:  $\rho = 0.88$ ,  $p < 0.001$ ). Planktic species were also

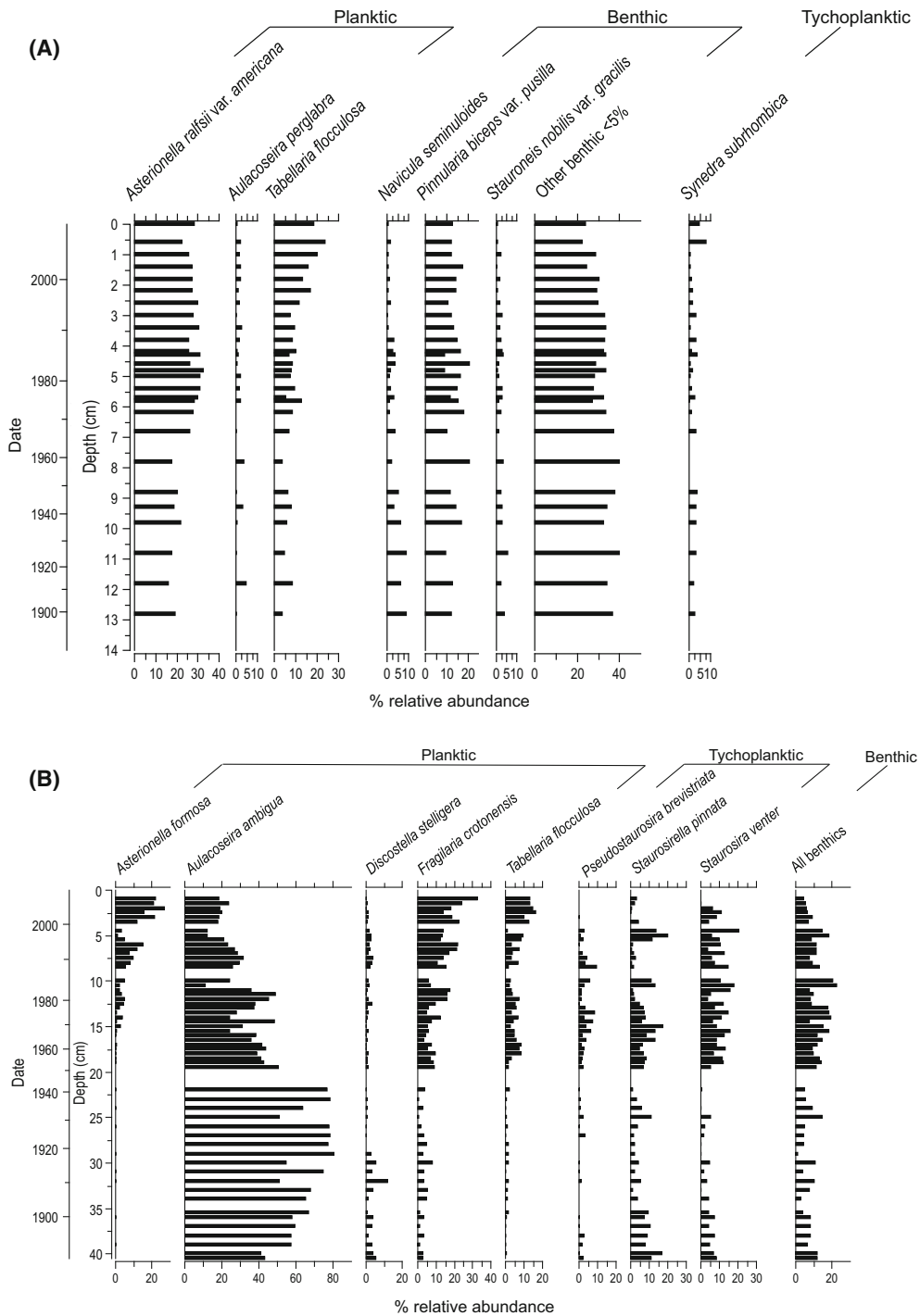
associated with higher specific conductance (P:B<sub>core</sub> with DI-conductance:  $\rho = 0.44$ ,  $p = 0.022$ ), though the range of reconstructed conductance was narrow (10 to 15  $\mu\text{S cm}^{-1}$ ). None of the three environmental parameters were significantly related to changes in the diatom community structure as indicated by PCA scores. While chronology was tightly constrained at this site, the lower resolution available deeper in the core may have reduced accuracy of comparisons between 36-month average environmental data and estimated dates for sediment core parameters.

Changes in measured lake levels were linked to climatic variables at the upland site (Table 3). Measured lake levels were related to PDSI ( $\rho = 0.78$ ,  $p < 0.001$ ), as well as precipitation ( $\rho = 0.72$ ,  $p < 0.001$ ) and temperature ( $\rho = -0.54$ ,  $p = 0.002$ ) individually, meaning that higher lake levels occurred

**Fig. 4** Lead-210 based chronology for cores from **a** Crystal Lake and **b** Allequash Lake. *Dashed lines indicate supported  $^{210}\text{Pb}$  levels*

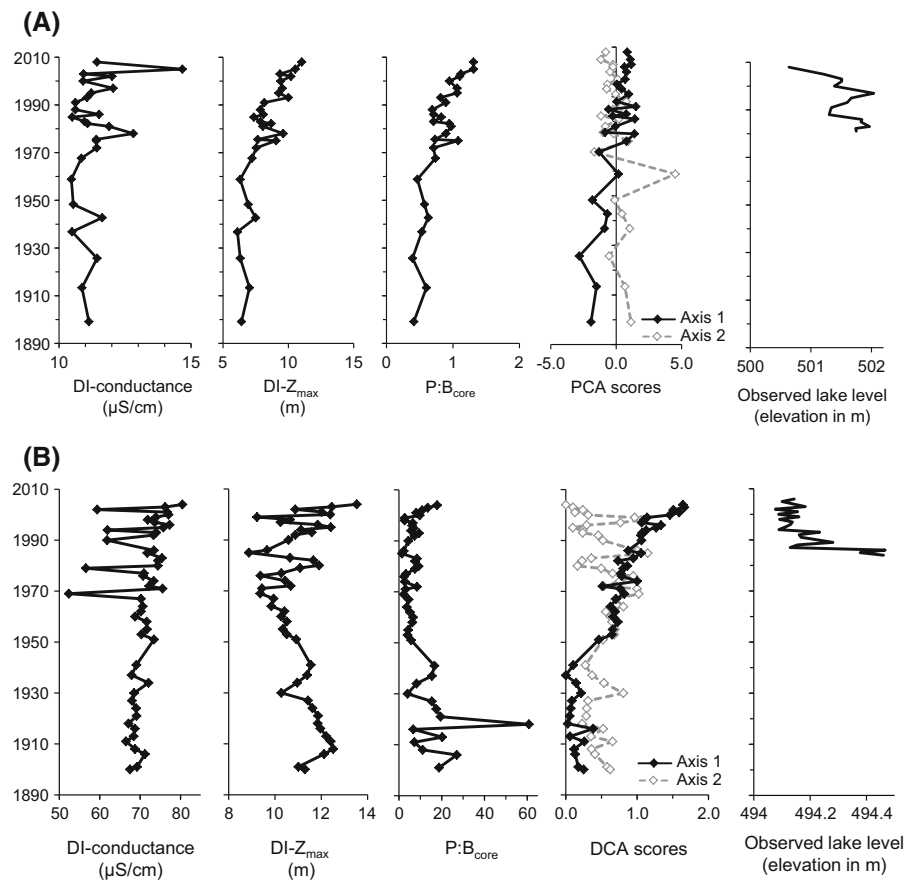






**Fig. 5** Sedimentary diatom community profiles for **a** Crystal Lake (species >5 % relative abundance in any one sample) and **b** Allequash Lake (species >10 % relative abundance in any one sample). Crystal Lake samples are combined from freeze and extruded cores, and “Other benthic <5 %” indicates the sum of all other benthic taxa not presented separately here, due to low abundances of individual taxa. For Allequash, as no single benthic taxon met the >10 % threshold, benthic species abundances were summed and presented here in the “All benthics” category

**Fig. 6** Sedimentary diatom community features with measured changes in lake level for **a** Crystal Lake and **b** Allequash Lake, including diatom-inferred conductance (DI-conductance), diatom-inferred maximum depth (DI-Z<sub>max</sub>), planktic:benthic ratios (P:B<sub>core</sub>), and principal components analysis (PCA, Crystal) and detrended correspondence analysis scores (DCA, Allequash) for the first and second axes



**Table 2** Spearman’s nonparametric rank correlation values ( $\rho$ ) for environmental variables with diatom community structure changes at Crystal Lake and Allequash Lake, as indicated by

principal components analysis (PCA) or detrended correspondence analysis (DCA) scores for the first and second axes

	Crystal Lake		Allequash Lake	
	PCA Axis 1	PCA Axis 2	DCA Axis 1	DCA Axis 2
PDSI	0.14	-0.05	0.10	-0.16
Temperature	0.36	-0.12	<b>0.33</b>	0.04
Precipitation	0.22	0.12	0.18	-0.08

PDSI = Palmer Drought Severity Index Bolded values indicate significant correlations (significance level with Bonferroni corrections for environmental variables:  $\alpha = 0.05/3 = 0.02$ )

during cool, wet time periods at this site. During droughts of the late 1980s and more recently the late 2000s, lake levels dropped, ranging approximately 1.5 m from a maximum of 502 m elevation in 1997 to a minimum of 500.5 m elevation in 2009. The greater drop in lake level during the 2000s (compared to the 1980s) may have been due to generally higher

temperatures during this time period, resulting in more extreme changes in effective moisture than the drought in the late 1980s.

Though lake levels at this site responded to climatic change in a typical manner, relationships with sediment core-inferred variables showed opposite trends than expected. Measured lake levels were negatively

**Table 3** Spearman’s nonparametric rank correlations ( $\rho$ ) among environmental parameters, core metrics, and measured lake level at Crystal Lake and Allequash Lake

	Crystal Lake				Allequash Lake			
	DI-cond	DI-Z <sub>max</sub>	P:B <sub>core</sub>	LL	DI-cond	DI-Z <sub>max</sub>	P:B <sub>core</sub>	LL
PDSI	0.16	0.08	0.16	<b>0.78</b>	0.10	0.14	0.12	0.27
Temperature	−0.14	0.39	0.35	<b>−0.54</b>	0.28	−0.05	−0.06	0.09
Precipitation	0.09	0.13	0.12	<b>0.72</b>	0.17	0.07	0.11	0.54
LL	0.13	−0.45	−0.40	−	−0.04	−0.34	−0.31	−

DI-cond diatom-inferred conductance, DI-Z<sub>max</sub> diatom inferred maximum depth, PDSI palmer drought severity index, LL measured lake level

Bolded values indicate significant correlations (significance levels with Bonferroni corrections:  $\alpha = 0.05/4 = 0.013$  for diatom-inferred values and P:B<sub>core</sub> comparisons;  $\alpha = 0.05/3 = 0.02$  for LL comparisons)

related (nonsignificantly) to reconstructed maximum depth ( $\rho = -0.45$ ,  $p = 0.094$ ), as well as P:B<sub>core</sub> ( $\rho = -0.40$ ,  $p = 0.15$ ), such that higher lake levels were actually associated with shallower reconstructed maximum depths and more benthic species. However, due to the low bootstrap  $R^2$  value for the maximum depth model ( $R^2 = 0.268$ ), the overall predictive ability of the reconstructed depth values is low. The lack of statistical significance between P:B<sub>core</sub> and measured lake levels may also be due to the reduced sample size when measured lake-level beginning in the late 1980s is matched with core samples. Though the depth model itself is poor, the negative relationship between measured depth and P:B is consistent with models for extent of benthic habitat at this site, which showed a maximum P:B<sub>model</sub> at approximately 3 m below maximum lake-level elevation (Fig. 7a). Though measured lake levels are currently at their lowest since measurements began in the early 1980s, it is possible that lake levels were slightly higher during the wetter time period of the early 1970s when the bathymetric map for Crystal was produced. Examinations of aerial photographs did not find any clear changes in shoreline or the exposure of the shallow shelf along the northern portion of the basin, indicating that the lake levels at Crystal did not drop below 500 m elevation over the past century for extended periods. This suggests that levels during the timespan of this study were within the range of elevation where lake-level change and P:B<sub>model</sub> are inversely related, such that planktic species are less abundant as lake levels rise (opposite from what is often assumed about lake-level change and diatom community P:B).

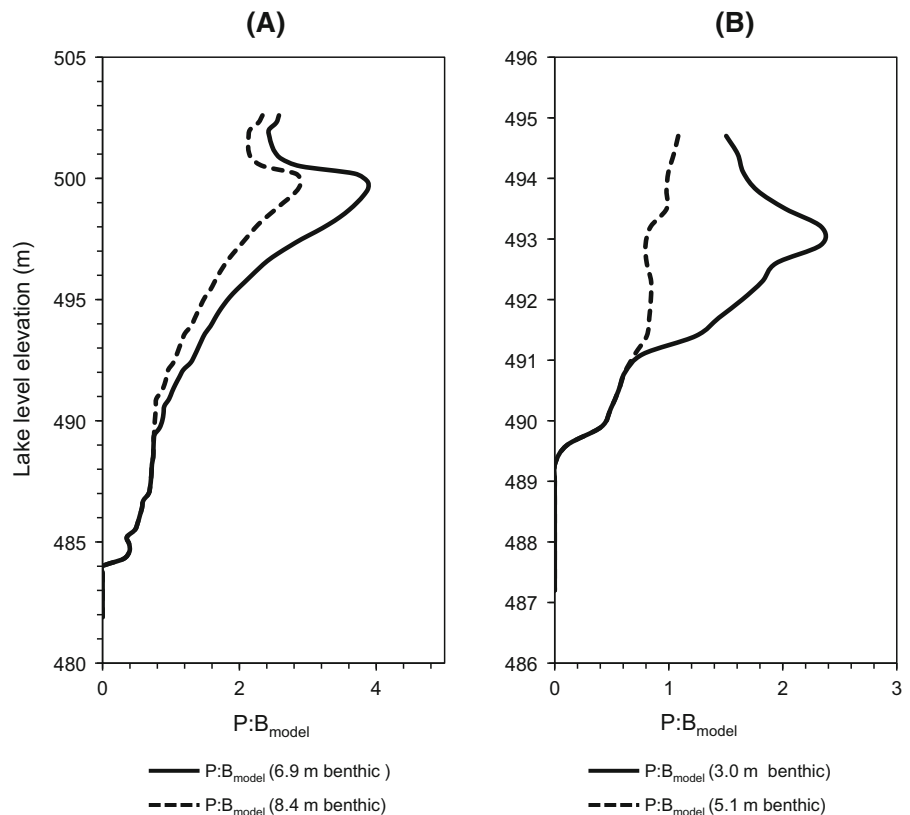
Models were similar in pattern for both water clarity levels.

#### Allequash Lake core

At Allequash Lake, unsupported  $^{210}\text{Pb}$  dates extended back to 1833, at 53.5 cm core depth (Fig. 4b). Activities were slightly flattened at the top of the core for the sample at 0.5 cm and 6.0 cm depth, but otherwise showed steady decline downcore. Estimates of chronology error were somewhat higher than at Crystal, with  $\pm 2.23$  years in uppermost sediments for Allequash and  $\pm 5.72$  years near 1900.

Fossil diatom assemblages at Allequash Lake were dominated by *Aulacoseira ambigua* (Grunow) Simonsen over the past century (Fig. 5b), often comprising >60 % of the community, with lower relative abundances in more recent sediments. A shift occurred around mid-century, with increasing abundances of *Fragilaria crotonensis* Kitton, and *Tabellaria flocculosa*. *Pseudostaurosira brevistriata* (Grunow) Williams and Round, *Staurosira venter* (Ehrenberg) Cleve & Moller and *Staurosirella pinnata* (Ehrenberg) Williams and Round also increased at this time, with later decreases in the upper portion of the core. *Asterionella formosa* has increased since 1970, comprising over 20 % of the assemblage in the most recent sediments. The ratio of planktic:benthic taxa (P:B<sub>core</sub>) peaked in 1918, 1941, and 2004, and was lower from the 1950s through the early 2000s. The highest peak in P:B in 1918 was due to this sample containing the lowest proportion of benthic species in the core (down to only 1.5 % of the assemblage) as well as the highest proportion of planktonic taxa (93 %).

**Fig. 7** Modeled relationships between lake level change and planktic:benthic habitat changes ( $P:B_{\text{model}}$ ) for **a** Crystal Lake and **b** Allequash Lake, including different benthic zone limits



At this site, DI-conductance over the past century showed a slight increasing trend from about  $70 \mu\text{S cm}^{-1}$  in the early part of the century to approximately  $80 \mu\text{S cm}^{-1}$  at present, with slightly lower values occurring intermittently since the late 1960s (Fig. 6b). These intermittent low values appear to be driven partly by small fluctuations in *Staurosira venter* (conductivity optimum =  $49.7 \mu\text{S cm}^{-1}$ ) in more recent sediments, as *Aulacoseira ambigua* declines (optimum =  $66.8 \mu\text{S cm}^{-1}$ ) and *Asterionella formosa* becomes more common (less than 5 % abundance in calibration set, not utilized for reconstructions).  $\text{DI-Z}_{\text{max}}$  decreased around 1930 but was otherwise fairly stable until 1970, and has been increasing with more variability to its highest value in most recent sediments. The magnitude of lake level change was smaller at Allequash Lake than at Crystal Lake. Measured lake levels at both sites were highest during the early 1980s, and dropped during the droughts of the late 1980s. Levels were low and stable from the mid 1990s to present. Allequash Lake has a more complex basin, with an irregular shoreline and four small islands within the lake, and

lake level models at this lowland site were sensitive to different depths of benthic limits. For clearer conditions and a deeper benthic zone (5.1 m model), maximum  $P:B_{\text{model}}$  occurred at the highest lake level, but less transparent conditions (3.0 m benthic zone limit) resulted in a maximum  $P:B_{\text{model}}$  at approximately 1.5 m below maximum lake-level due to flooding of shallow shorelines at high water-level (Figs. 1, 7b). As at Crystal Lake, maximum modeled elevation is higher than present levels, as lake levels were likely higher during the late 1960s (when the bathymetric map was produced). However, the magnitude of lake level change is smaller at Allequash Lake than at Crystal Lake (from a maximum of 494.5 m elevation in 1986 to a minimum of 494.1 m in 2002). Such small changes are difficult to identify on aerial photographs; however, the stability of the shoreline in the images indicated that the lake level of Allequash likely did not drop below 493 m in elevation over the past century (no major shoreline changes or variations in island size/exposure). Shifts

in  $P:B_{\text{model}}$  within this range are small but in different directions for the two benthic zone models.

Based on DCA scores, diatom community changes at Allequash Lake were primarily related to temperature and secondarily to physical variables (Tables 2, 3). While DCA axis 1 scores were correlated to  $P:B_{\text{core}}$  ( $\rho = -0.36$ ,  $p = 0.01$ ), axis 2 scores showed a stronger relationship with this variable ( $\rho = -0.76$ ,  $p < 0.001$ ). Qualitatively, axis 1 scores track the slight increase in DI-conductance, so this axis may reflect diatom community changes in response to water chemistry shifts, based on this calibration set. Temperature was the only climate parameter significantly correlated with changes in diatom community structure in Allequash, as indicated by DCA scores (axis 1,  $\rho = 0.33$ ,  $p = 0.02$ ).  $P:B_{\text{core}}$  was strongly correlated with  $DI-Z_{\text{max}}$  ( $\rho = 0.90$ ,  $p < 0.001$ ), such that more planktic taxa were associated with higher reconstructed lake levels. However,  $P:B_{\text{core}}$  was not significantly related to measured lake levels from 1985–2004 ( $\rho = -0.31$ ,  $p = 0.24$ ) or other climate variables. Diatom-inferred variables were not significantly related to climatic parameters at this site. There may be issues with comparisons between sediment core parameters and environmental data due to slightly higher error estimates for the core chronology, though there is a higher resolution of samples in this core, consistent through 1900 (approximately every 3–5 years). Measured lake levels were associated with diatom community changes for axis 1 DCA scores ( $\rho = -0.51$ ,  $p = 0.042$ ), and were most strongly related to precipitation ( $\rho = 0.54$ ,  $p = 0.032$ ) with higher lake levels occurring during wetter time periods.

## Discussion

Landscape position can strongly affect a number of lake chemical, physical, and biological features (Kratz et al. 1997), as well as how lakes respond to environmental changes (Webster et al. 2000). The sedimentary diatom profiles presented here for north temperate lakes allowed us to examine biological response to climatic variability over the past century for two systems in different positions within the hydrological landscape. In upland Crystal Lake, diatom communities responded to drought-induced

changes in lake level, which altered planktic versus benthic habitat availability, rather than lakewater chemistry. In the lowland Allequash Lake, shifts in diatom community structure were primarily related to changes in temperature (and possibly chemistry) and secondarily to physical changes. While the lack of chemical response in the higher elevation system is consistent with previous studies (Webster et al. 1996, Webster et al. 2000), our results suggest that biological change in this lake may be more tightly coupled to climate than that in the lowland lake, via changes in lake level. This indicates that higher elevation, hydraulically mounded sites may have more potential than lowland drainage sites for tracking drought over time in biological records, depending on the role of ecological features in shaping climatic response at individual sites.

The upland site responded physically to drought conditions, with measured lake levels significantly related to PDSI since 1981. During droughts of the late 1980s (1988–1991) and more recently the late 2000s, Crystal Lake levels dropped, ranging approximately 1.5 m from its maximum elevation in 1997 to its minimum elevation in 2009. Biological changes at this site were indirectly related to climate, with diatoms responding to drought conditions through the filter of physical changes in lake level, rather than lakewater chemistry changes. While the correlations between measured lake level and planktic:benthic ratios in the core were not statistically significant, this may be due to the comparably shorter record of lake level which was initiated in the 1980s. Given fewer time points when the records are matched for analysis, we contend that these relationships (though not statistically significant) represent important ecological changes within the system recorded by diatom communities, particularly given that the comparison of annual lake level records to environmental data show significant correlations to PDSI at Crystal Lake. Variations in lake level resulted in shifts in habitat zonation that altered the relative proportions of planktic and benthic taxa represented in the sediment record. Therefore, though indirect, changes in the planktic:benthic ratio of fossil diatom assemblages signaled climatic changes in the record at Crystal Lake. However, careful consideration of lake-level models was critical in order to understand site-specific features influencing the relationship between  $P:B$  and lake level changes.

In contrast, the lower elevation lake showed no significant correlations between reconstructed parameters and climate variables, though changes in diatom community structure as measured by DCA scores were significantly correlated with mean annual temperatures. Our inability to detect direct correlation of reconstructed parameters to climate parameters in the lowland lake may be due to relatively small indicators of change, the presence of the surficial outlet at this site, or lags in response caused by the larger proportion of groundwater in the hydrologic budget (Webster et al. 1996). Diatom communities in Allequash Lake showed a limited range of variation for DI-conductance over the past century (increasing about  $10 \mu\text{m cm}^{-1}$  from 1900 to present), and therefore may represent a weak signal of conductivity recorded by diatoms, or relatively stable conditions in this record. Clear links between diatom-based reconstructions and climate were not evident in this lowland site's paleolimnological record, as has been found in other modern ecological studies (Webster et al. 1996, 2000).

The diatom calibration set for lakes in the NTL-LTER captured both chemical and physical gradients across the set of 48 lakes. Though significant variables included four parameters (maximum depth, conductance, TP, and pH), we focused on conductance and maximum depth for paleolimnological reconstructions presented in this study. These two variables were associated with different axes of change in the CCA, thereby possibly explaining separate portions of variation in diatom community structure. Conductance and pH covaried in the same direction along axis 1 (such that higher conductance values were associated with higher pH values), likely due to groundwater sources of higher concentrations of base cations and other solutes along the landscape position gradient in this dataset (Webster et al. 1996). Though the transfer function for conductivity may have been confounded by concurrent changes in pH, a comparison to the pH optima in similar lakes in the Northeast US (Camburn and Charles 2000) suggests no distinct patterns of changes in relative abundance of major taxa with higher or lower pH optima. For example, at Allequash Lake (current pH = 8.1), key community changes included a decline in *Aulacoseira ambigua* since 1950 (pH optimum reported by Camburn and Charles 2000: 6.47), whereas *Asterionella formosa* (optimum 7.24), *Fragilaria crotonensis* (optimum 7.59), and

*Tabellaria flocculosa* (optimum 6.10) generally increased since 1950. The current pH is lower at upland Crystal Lake (6.1), and more recent shifts occurred in the early 1980s from communities dominated by *Asterionella ralfsii* var. *americana* (pH optimum 5.13 for larger form,  $>45 \mu\text{m}$ ), *Pinnularia biceps* var. *pusilla* (optimum 5.65), and *Navicula seminuloides* (optimum 6.76) to a stronger presence of *Tabellaria flocculosa* (optimum 6.10) with *A. ralfsii* var. *americana*. The lack of pattern in pH optima among these dominant species shifts suggests that pH changes are not likely the primary chemical driver of changes in diatom communities at our study sites.

Webster et al. (2000) found coherent drought-induced changes in water chemistry at lowland sites, though our results indicate that changes recorded by diatom community structure were not as clearly driven by chemical changes at the lowland site. Rather than finding strong relationships between diatom-based reconstructions and climatic variables over the past century at Allequash Lake, changes in diatom community may suggest potential shifts in nutrient concentrations at this site. Particularly from the early 1980s to present, both *Asterionella formosa* and *Fragilaria crotonensis* (along with *Tabellaria flocculosa*) increase in relative abundance in the sediment record, while *Aulacoseira ambigua* declined. Reported TP optima for Minnesota lakes (Ramstack et al. 2003) for the declining *A. ambigua* ( $29 \mu\text{g L}^{-1}$ ) are higher than the taxa that increased: *A. formosa* ( $23 \mu\text{g L}^{-1}$ ), *F. crotonensis* ( $22 \mu\text{g L}^{-1}$ ), and *T. flocculosa* ( $11 \mu\text{g L}^{-1}$ ). Optima reported by Camburn and Charles (2000) are generally lower, with *A. ambigua* ( $7 \mu\text{g L}^{-1}$ ) having lower TP optima than the increasing taxa (*A. formosa* =  $12 \mu\text{g L}^{-1}$ , *F. crotonensis* =  $9 \mu\text{g L}^{-1}$ , *T. flocculosa* =  $8 \mu\text{g L}^{-1}$ ). The TP optima from the calibration set in this study, however, were similar across these species, and were also between the values reported by Ramstack et al. (2003) and Camburn and Charles (2000): *A. ambigua* at  $13 \mu\text{g L}^{-1}$ , *F. crotonensis* at  $12 \mu\text{g L}^{-1}$ , and *T. flocculosa* at  $11 \mu\text{g L}^{-1}$  (*A. formosa* was not in high enough abundances in our calibration set to calculate an optimum). In other studies, *A. formosa* and *F. crotonensis* are indicators of increasing nitrogen concentrations rather than phosphorus (Yang et al. 1996; Saros et al. 2005), though it is unclear if this is also the case for this study. The community shift from *A. ambigua* to *A. formosa* and *F. crotonensis* in the

latter portion of the century may suggest changing nutrient conditions as a confounding factor to isolating and tracking lake response to climatic signals using the diatom record. Though the nature of changes in nutrient conditions at this lowland site requires further clarification (particularly for more recent dates), these results support that chemical rather than physical controls are the primary drivers of diatom assemblage changes. With increased human usage at lowland sites (e.g., densities of cottages and resorts, Riera et al. 2000), understanding the role of nutrients (both phosphorus and nitrogen) in shaping diatom communities will be particularly important in predicting response to larger-scale climatic drivers at lakes positioned lower in the landscape.

A recent paper by Juggins (2013) reiterates the need for careful examination of reconstructed parameters and confounding variables in calibration sets, including understanding the ecological mechanisms that drive changes in biological community structure. In this case, the accuracy of depth reconstructions was sensitive to relationships between lake level change and availability of planktic versus benthic habitat at individual sites. With a positive relationship between P:B and maximum depth in the training set (data not shown) and P:B<sub>core</sub> significantly correlated to DI-Z<sub>max</sub> at both sites, shifts in planktic and benthic taxa within the sediment record were clearly related to changes in lake depth. However, in contrast with the traditional assumption that planktic habitat is reduced at lower lake levels, lake level models of Crystal Lakes bathymetry showed that potential P:B habitat actually increases as lake levels decline. This resulted in an inverse relationship at Crystal Lake in more recent sediments between diatom-inferred and measured lake levels (recorded since 1980). Additionally, if the diatom community at this site is primarily driven by these changes in physical habitat rather than changes in chemistry, the accuracy of diatom-inferred conductance is unclear for this upland lake. In addition to such fluctuations in lake-level and planktic:benthic habitats, climatic drivers can have important effects on water column stability and turbulence within lakes. The more recent shifts at Allequash Lake have also been observed at other sites, with declines in *Aulacoseira* taxa, which prefer turbulent conditions, and increases in planktonic species such as *Asterionella formosa* and *Fragilaria crotonensis*. Increases in *A. formosa* and *F. crotonensis* at other locations have

been attributed to warming temperatures over the past century (Solovieva et al. 2005, 2008) and subsequent changes in thermal stability and circulation patterns (Bradbury et al. 2002). Interactions between lake mixing and nutrients are also likely important, as mixing depth preferences for other diatom taxa have been shown to be influenced by nutrient concentrations (Saros et al. 2012), and increased water-column stability may allow these planktonic taxa to be more competitive if such a shift increases access to nutrients around the thermocline (Bradbury et al. 2002; Ruhland et al. 2010). Higher abundances of heavily silicified *Aulacoseira* species at Elk Lake, MN may also have been linked to the influence of logging at this site, via increasing nutrients and turbulence within the water column (Bradbury et al. 2002). In addition to temperature and nutrient factors, changes in water clarity could also influence diatom productivity and community composition. The lake level models presented here showed different sensitivity to benthic limits at each site, with Allequash showing more variability in the relationships between P:B<sub>model</sub> and lake level change depending on the benthic limit selected. This could be further refined by additional fieldwork to test the influence of water clarity changes on changes in P:B habitat extent and establish benthic ranges. Exploring these complex relationships between climatic variables and physical conditions within lakes may also benefit from the types of site-specific models applied here. Our approach of combining contemporary ecological data and lake basin modeling with traditional paleolimnological tools improved our interpretations of diatom-based reconstructions using this calibration set.

It is important to recognize that the selection of core sites can affect the sensitivity of paleolimnological reconstructions, in particular those reconstructing depth (Laird et al. 2011). Depth models have been developed using transects of cores within individual systems (Laird and Cumming 2008) as well as multiple sites (Brugam et al. 1998; Moser et al. 2000). Comparisons between these approaches suggest that within-lake model development may be more appropriate than multi-lake training sets for reconstructing depth (Laird et al. 2011) in part due to sensitivities of benthic taxa to site-specific factors and challenges in applying data from multiple lakes to a single site (Moser et al. 2000). Laird et al. (2011) also found that the coring locations focusing on depth

reconstructions should be  $\sim 1$  m below the P:B boundary, with this ecotone falling between 6 and 15.8 m in boreal lakes of Ontario. As light availability is a key control on the depth of this boundary, further consideration of the role of dissolved organic carbon in individual systems would also aid in identifying fluctuations in the P:B ecotone. Additional detailed exploration of diatom-depth relationships at individual sites (Kingsbury et al. 2012), using repeated surface sediment sampling at different water depths, would improve the accuracy of P:B<sub>core</sub> in representing lake level changes, particularly with respect to the tychoplanktic taxa. Our use of P:B models here in combination with paleo techniques also supports the importance of understanding site-specific characteristics in shaping biological response to large-scale environmental changes. The diatom-inferred maximum depth values presented here generally appear to be underestimated for the deeper Crystal Lake and overestimated for the shallower Allequash Lake, a similar pattern as seen by other studies (Brugam et al. 1998). While there are concerns with the absolute values reconstructed here, we focus on the trends in P:B<sub>core</sub> and DI-Z<sub>max</sub> to better understand overall patterns in lake-level change over the past century related to landscape position (Moser et al. 2000). DOC was included in our calibration set, but we did not find this to be a significant parameter controlling diatom community changes across the entire dataset. However, the role of DOC at individual lakes, in conjunction with additional studies of the P:B boundary location, should be included in future work utilizing upland systems to track biological response to climate.

Different responses to the same large-scale climatic drivers between the lakes in this study demonstrate the importance of understanding how landscape position shapes lake biological, chemical, and physical responses to changing environmental conditions. The diatom profiles and diatom-based reconstructions presented here, in combination with lake basin modeling, provide longer temporal perspectives on lake response to drought conditions. Our results agree with predictions based on the model for lake response to climatic change by Webster et al. (2000), with little chemical response in the upland system. However, we did see an indirect biological response to climatic variation in the upland site to drought-induced changes in lake level and habitat zonation. Though exploring physical changes in lake depth at Crystal

allows us to better understand the biological response of lakes (particularly upland sites) to climate change, it must be interpreted with caution due to the role of planktic:benthic habitat shifts in driving response to lake level changes, as discussed above. We strongly recommend that applications of this transfer function be accompanied by modeling the relationship between lake level change and planktic:benthic habitat availability at individual sites (Stone and Fritz 2004). These results highlight differences in drivers of biological changes in upland versus lowland sites, as well as the importance of incorporating modern ecological techniques into our interpretations of sediment records. A clearer understanding of potential changes in ecosystem structure and function during intense drought conditions will allow for more effective management decisions regarding the fate of these valuable aquatic resources.

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