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Response of the Phytoplankton Community in an Alpine Lake to Drought Conditions: Colorado Rocky Mountain Front Range, U.S.A.

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Abstract

Lakes may serve as sentinels for the impacts of changing climate in alpine areas. In the Rocky Mountain region, 2002 was a year with extremely low snowpack. We examined the summer phytoplankton community in Green Lake 4 for a 6-year period that included the summer of 2002. The phytoplankton community variation was examined in the context of the changes in physical and chemical properties of Green Lake 4. The physical changes associated with the 2002 drought included warmer surface water temperatures and greater hydraulic residence times; whereas the chemical changes included higher concentrations of acid neutralizing capacity (ANC) and major ions. During the summer of 2002 the phytoplankton community was dominated by *Synedra* sp. and *Ankyra* sp.; two previously rare species. The growth of *Synedra* sp. was sufficient to cause a decrease in silica concentrations, which has not been observed in other summers in the water quality monitoring record. The results of a redundancy analysis (RDA) indicated that concentrations of major ions and ANC were aligned with *Synedra* sp. and *Ankyra* sp. during the 2002 drought year. Following the 2002 drought year, *Chrysococcus* sp. and *Chlorococcum* sp., which became abundant, were aligned with nitrate in the RDA. These results indicate that the response of the phytoplankton community to the extreme drought was most strongly correlated with water quality changes that occurred, rather than temperature and hydraulic residence time. The dominant species in the post-drought phytoplankton community were found to be associated with nitrate, which is brought to the watershed by atmospheric deposition and may represent an anthropogenic driver of phytoplankton community composition.

Introduction

The harsh environmental conditions characteristic of alpine environments suggest that alpine organisms are on the edge of their environmental tolerances (Williams et al., 1998). Consequently, these organisms and biogeochemical processes mediated by them may be sensitive to small environmental changes in climate and other parameters (Williams et al., 2002). The hydrology of alpine catchments is dominated by the annual snowmelt event, the magnitude of which depends on accumulation of snow in winter and climatic conditions in the spring. Therefore, alpine areas are considered to be especially sensitive to environmental changes and may be early indicators of climate change (Hauer et al., 1997; Williams et al., 2002). Because algal populations are typically diverse and respond rapidly to environmental changes over time scales of weeks (Reynolds, 1984), measurements of phytoplankton community composition in alpine lakes can provide valuable insight into climate-driven ecological change in these sensitive catchments (Hauer et al., 1997; Moraska Lafrancois et al., 2003; Strecker et al., 2004; Anneville et al., 2005).

An important change in alpine lakes has been the timing of loss of ice-cover (ice-out) in spring. In alpine catchments of the Front Range of the Rocky Mountains in Colorado, U.S.A., the date of ice-out has moved forward in time by two weeks since 1981 (NWT-LTER database: http://culter.colorado.edu). Dates of ice-out and ice-cover (freeze-up) determine the portion of the year when phytoplankton growth is limited by low-light availability (ice-cover) and the portion with high light availability (ice-free) (Hauer et al., 1997). Furthermore, changes in alpine lake phytoplankton community composition in summer have been found to be related to changes in hydrological regime, especially residence time, during and after snowmelt (McKnight et al., 1990). Moreover, annual variation in the hydrology at the watershed scale has the potential to impact surface water quality (e.g. Brooks and Williams, 1999). The changes in precipitation and temperature in alpine catchments, drivers for earlier ice-out dates, may also influence water column stratification and residence time in summer. Thus, these direct and indirect climatic controls on the lake environment may interact along with nutrient concentrations and abundance of invertebrate grazers to influence phytoplankton community composition (Hauer et al., 1997; Lotter and Bigler, 2000; Battarbee et al., 2002; Anneville et al., 2005).

For these reasons, changes in the hydrologic cycle associated with drought may have a particularly strong influence on phytoplankton community structure in alpine lakes (Thomas et al., 1991). Across Colorado and the Western U.S.A., drought conditions prevailed in the early 2000s. In Colorado, the year of 2002 was the driest year in a 110-year record, 1895–2005 (NOAA,

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2006) and was the fifth consecutive year of below normal precipitation in Colorado. Statewide average precipitation in 2002 was 257 mm, about half the annual average of 403 mm from 1895–2005 (NOAA, 2006). The combination of below average precipitation, above average temperatures, high evaporation rates, and continued depletion of water supplies resulted in severe stress for the state's private, commercial, and agricultural sectors (Pielke et al., 2005). These regional scale shifts in climate have the potential to alter the hydrologic regime, and subsequently water quality, at the catchment scale.

An additional driver of environmental change for alpine ecosystems in the Colorado Front Range is anthropogenic nitrogen deposition. Nitrogen enters the atmosphere from both urban and agricultural sources and is transported to pristine, high elevation areas during easterly, upslope wind events (Baron et al., 2000; Williams and Tonnessen, 2000). Nitrogen loading has been associated with increases in certain diatom species coincident with the introduction of nitrogen fertilizers to agricultural areas of the Front Range (Wolfe et al., 2001), nitrogen saturation of the phytoplankton community (Gardner et al., 2008), and episodic acidification (Williams and Tonnessen, 2000). Thus, high nitrogen availability associated with anthropogenic N deposition may have some influence on the phytoplankton community response to drought conditions.

There is some urgency in improving our understanding of how changes in climate may affect lake and stream ecosystems in seasonally snow-covered catchments. Recent climate analyses have shown widespread declines in the winter snowpack of mountain ecosystems in western North America and Europe that are associated with positive temperature anomalies (Laternser and Schneebeli, 2003; Scherrer et al., 2004). For example, northern hemisphere snow cover observed by satellite over the 1966 to 2005 period decreased in every month except November and December, with a stepwise drop of 5% in the annual mean in the late 1980s (Brown, 2000). Magnuson et al. (2000) showed that for lakes and rivers in the northern hemisphere, the freeze-up date has become later at a rate of 5.8 $\pm$ 1.6 days per century, while the ice-out date has occurred earlier at a rate of 6.5 $\pm$ 1.2 days per century.

The goal of this study was to understand the relationships between drought, the physical and chemical conditions in an alpine lake, and the response in phytoplankton abundance and community composition. To address this goal, we collected weekly limnological measurements during the summers of 2000–2005 from an alpine lake, Green Lake 4, which is studied as part of the Niwot Ridge Long-Term Ecological Research project (NWT-LTER). The monitoring data included water column physical and chemical environments, phytoplankton community composition, and algal biomass. In addition to examining differences in the water quality and phytoplankton community characteristics among the years, we employed principal component and redundancy analyses to identify dominant relationships during and after the drought years.

Methods

SITE DESCRIPTION

The upper Green Lakes Valley is an east-facing glacial valley, headed on the Continental Divide in the Colorado Front Range (40°03′N, 105°35′W). Named for a series of shallow paternoster lakes, the Green Lakes Valley is the headwaters of North Boulder Creek and lies within the City of Boulder Watershed with no public access. The upper valley is approximately 225 ha in area, and the elevation ranges from 4084 m at the Continental Divide to 3515 m at the outlet of Green Lake 4 (GL4; Fig. 1A). The floor of Green Lakes Valley has the stepped form of a glaciated mountain valley. At the foot of the north-facing Kiowa Peak is the Green Lake 5 rock glacier (RG5), a lobate rock glacier approximately 8 ha in area and at an elevation of 4000 m, where extensive research on hydrochemistry has been conducted (Williams et al., 2006, 2007). Niwot Ridge, the northern boundary of the Green Lakes Valley, is the site of other experimental areas, including an Aerometrics wet-chemistry precipitation collector at the Saddle site (Fig. 1A), operated by NWT-LTER as part of the National Atmospheric Deposition Program (NADP).

The continental, high mountain climate of Green Lakes Valley has been recorded continuously at the D-1 meteorological station on Niwot Ridge (Fig. 1A) for over 50 years and for shorter periods on the valley floor. At an elevation of 3750 m, the D-1 station is the highest continuously operating weather station in North America. The climate is characterized by long, cool winters and a short growing season (Williams et al., 2002). Mean annual temperature at D-1 is -3.7 °C (Williams et al., 1996). Almost 80% of the approximately 1000 mm of recorded annual precipitation falls as snow (Caine, 1996). The bulk snowpack temperature remains below 0 °C until late spring, causing a lag in the hydrological cycle by concentrating the release of meltwater in a short, intense period of runoff (Caine, 1996).

GL4 is an oligotrophic alpine lake with low summer chlorophyll *a* concentrations and dilute surface waters (NWT-LTER database: http://culter.colorado.edu). The average depth is 4.0 m, while the maximum depth is 13.1 m. GL4 has a surface area of 5.34 ha. The lake has become thermally stratified in mid-summer since limnological monitoring began in 2000. In general the lake mixes soon after ice-out and then becomes more stratified until the end of July when the differences in temperature between the epilimnion and hypolimnion decrease until fall mixing occurs in early September. The lake is generally ice free from the beginning of July until mid-late September, though there are large year-to-year variations. Historically, the lake was fishless, but due to accidental stocking in 1998, Yellowstone cutthroat trout now inhabit both GL4 and the upstream Green Lake 5.

FIELD SAMPLING AND MEASUREMENTS

Discharge from GL4 has been measured continuously since 1983 from about 1 May to 30 October (Williams and Caine, 2001). Hydraulic residence times were calculated by dividing the volume of the lake by the discharge.

The GL4 limnological monitoring program began in 2000; in-lake physical, chemical, and biological parameters were collected according to protocols in Gardner et al. (2008) during the ice-free period of the summer months of June, July, and August, 2000–2005. The first sampling date each summer occurred shortly after the ice had melted on the lake.

Using an inflatable raft to reach the deepest part of the lake, grab samples were collected at the surface and at depths of three and nine meters (Fig. 1B) with a Van Dorn sampler. The surface and 3 m sampling depths are representative of the epilimnion in terms of water quality. The surface samples may also reflect any effects of photoinhibition on the phytoplankton community. The 9 m depth is representative of the water quality and phytoplankton community in the hypolimnion. The hypolimnion accounts for a small portion of the lake volume, but is in closer contact with lake sediments. Subsamples were taken for algal biomass, phytoplankton community composition, and water quality analysis. Samples were stored in polyethylene bottles that were rinsed three times with sample water at the time of collection. Water samples were transported the same day as collection to the laboratory.

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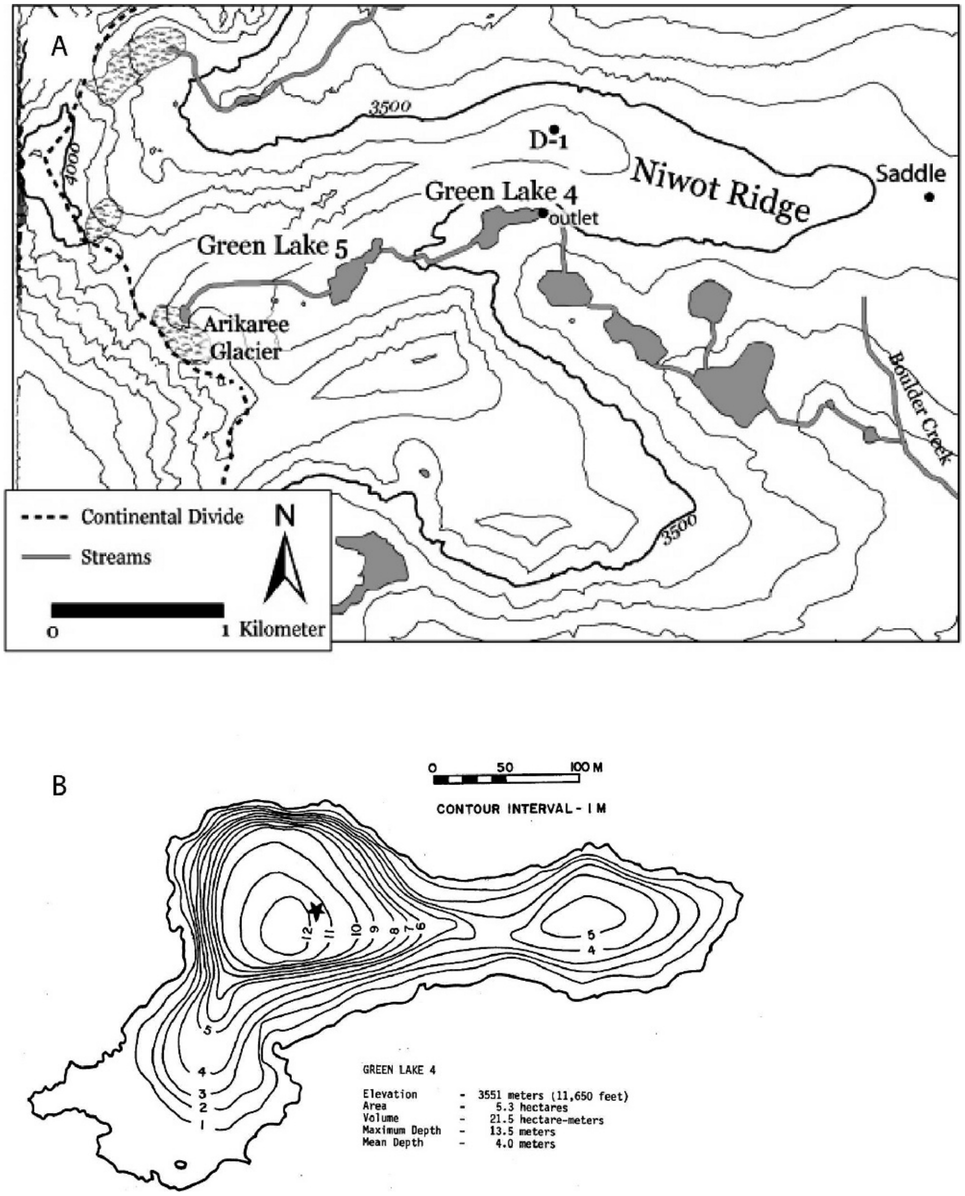

FIGURE 1. (A) Study location at the Niwot Ridge Long-Term Ecological Research (NWT-LTER) site. Contour interval is 100 m. (B) Bathymetric map of Green Lake 4. Monitoring samples were taken from the point marked with a black star (40.05°N, 105.64°W).

Temperature, dissolved oxygen, and solar irradiance measurements were measured from the raft at each depth using a YSI dissolved oxygen meter and a Li-Cor datalogger. Secchi depth readings were taken all years except 2004.

PHYSICAL AND CHEMICAL PARAMETERS

Water samples were analyzed for pH, acid neutralizing capacity (ANC), conductance, major ions, reactive silicate (Si), and dissolved organic material, following the protocols presented in Williams et al. (1996). ANC and pH were measured immediately on return to the laboratory using the Gran titration technique. Subsamples for major ions and nutrients were immediately filtered through pre-rinsed (300 mL), 47 mm Gelman A/E glass-fiber filters with 1.2 μm pore size. DOC samples were also filtered in the laboratory on the same day as collection using pre-combusted 47 mm Whatman glass-fiber filters (pore size 1.2 μm) and a hand-pump filtration system. Filtered samples were stored in the dark at 4 °C and analyzed within 1–4 weeks. Anions were measured by ion chromatography (Dionex DX 500) with chemical ion suppression and conductivity detection. Calcium, magnesium, sodium, and potassium were analyzed with a Varian AA6 atomic absorption spectrophotometer. Total phosphorus (TP) and total dissolved phosphorus (TDP) were measured on a Lachat QuikChem 8000, where dissolved organic phosphorus (DOP) is equal to TDP minus inorganic phosphorus (IP), and IP was measured as orthophosphate, PO_4^{3-}. Analytical precision for inorganic solutes and nutrients was less than 2% and detection limits less than 1 μeq L^{-1}. Dissolved organic carbon (DOC) concentrations were determined by high-temperature catalytic oxidation using a Shimadzu Total Organic Carbon Analyzer. Three replicate analyses were done for each sample. Standard deviation was typically 0.06 mg C L^{-1} with a range of 0.01–0.22 mg C L^{-1}.

Chlorophyll *a* samples were filtered within 12 hours through Whatman glass fiber filters (pore size 1.2 μm) with a hand-pump filtration system, and filters were frozen in aluminum foil until processing. The filters were extracted with hot ethanol, and chlorophyll *a* was quantified spectroscopically as described by Marker et al. (1980) and Nusch (1980).

Table 1 lists GL4 environmental characteristics and associated abbreviations used in later analyses.

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TABLE 1

A subset of Green Lake 4 environmental variables, and corresponding abbreviations, used in analyses.

Environmental parameter	Abbreviation
% Saturation Dissolved Oxygen	%DO
Acid Neutralizing Capacity*	ANC
Ammonium*	NH_4^+
Calcium*	Ca^{2+}
Chloride*	Cl^-
Chlorophyll *a*	chl *a*
Conductivity*	COND
Dissolved Organic Carbon	DOC
Dissolved Organic Phosphorus*	DOP
Dissolved Oxygen	DO
Hydraulic Residence Time‡	HRT
Magnesium*	Mg^{2+}
Light Attenuation	1% attenuation
Nitrate*	NO_3^-
Particulate Phosphorus*	PP
pH*	pH
Phosphate*	PO_4^{3-}
Potassium*	K^+
Secchi Depth	Secchi
Silica†	Si
Sodium*	Na^+
Sulfate*	SO_4^{2-}
Total Dissolved Phosphorus*	TDP
Total Phosphorus*	TP
Water Temperature*	TEMP

* Variables used in both the principal components analysis (PCA) and redundancy analysis (RDA).

† Varible used in the PCA only.

‡ Variable used in the RDA only.

TABLE 2

Species list of algae found in Green Lake 4 samples. Corresponding symbols next to species indicate those species aggregated together into taxonomic groups for the ordination analyses. Abbreviations indicated represent taxa in statistical analyses.

Division	Taxa	Group	Abbreviation
Bacillariophyta	Bacillariophyte spp.		
	Synedra famelica	ξ	Syn
	Synedra sp.	ξ	
	Fragilaria sp.		
Chlorophyta	*Ankyra judayi*	*	Ank
	Ankyra sp.	*	
	Chlamydomonas sp.	≡	Chlam
	Chlamydomonas spp.	≡	
	Chlorella minutissima	▽	
	Chlorella sp.	▽	
	Chlorococcum sp.		Chlor
	Chlorophyte spp.		
	Coenochloris polycocca		
	Monomastix sp.		
	Raphidocelis microscopica		
	Scenedesmus ecornis	✦	
Chrysophyta	*Chromulina* sp.		
	Chrysococcus sp.		
	Dinobryon sp.		
Cryptophyta	*Plagioselmis nannoplanctica*	⊕	Plag
	Plagioselmis sp.	⊕	
Cyanophyta	*Aphanocapsa delicatissima*	Ψ	
	Aphanothece clathrata	Ψ	
	Aphanothece minutissima	Ψ	
	Cyanophyte spp.	Ψ	
	Dactyloccoccopsis sp.	Ψ	
	Oscillatoria limnetica	Ψ	
	Rhabdoderma sp.		
	Rhabdogoea scenedesmoides	Ψ	
Haptophyta	*Chrysochromulina* sp.	✦	Chrys
Pyrrophyta	Pyrrophyte sp.		
Unknown spp.			

PHYTOPLANKTON ENUMERATION

Samples taken for phytoplankton community composition analysis were preserved with Lugol's solution (1%) and stored at room temperature. A 50-, 40-, 20-, 10- or 5-mL subsample was settled in Utermöhl or Hydro-Bios settling chambers overnight and identified at 1000× with an inverted microscope. A minimum of 400 cells were identified and counted in each sample.

Consistency in identification of algal taxa by the four phycologists involved in this study was maintained by consultation and use of photomicrographs. To minimize potential identification bias, taxa with very similar morphotypes, and hence greater difficulty to resolve, were considered as combined taxonomic groups in the statistical analysis. Table 2 includes a species list of algae and taxonomic groups found in Green Lake 4 samples, and acronyms used to represent taxa in subsequent analyses.

Algal biomass was calculated based on lake-specific algal biovolumes, a technique that evaluates biomass and expresses abundance of each species (Wetzel, 2001). Mean dimensions of the cells (ca. five measurements per taxa) determined average cell volume (μm^3) by corresponding geometric equations (Tikkanen, 1986). Several taxa were analyzed individually to illustrate the temporal patterns seen in the phytoplankton community, but all of the counts were utilized to calculate the total biomass by division or phyla.

Statistical Analysis

To evaluate differences in the physical and chemical variables among the years, data for the first 6 weeks after ice-out were analyzed using a one-way analyses of variance (ANOVA), followed by the Student-Newman-Keuls multiple comparison test if needed. The fixed period after ice-out was employed for the comparison because concentrations of inorganic ions gradually increase after ice-out. A similar analysis was performed on the biovolume-weighted Shannon-Wiener Diversity Indices (H′), the total phytoplankton biovolume, and the biovolume-weighted abundances of 6 taxa: *Ankyra* sp., *Chlamydomonas* sp., *Chlorococcum* sp., *Chrysococcus* sp., *Plagioselmis* sp., and *Synedra* sp. The abundances of the individual taxa were fourth root transformed to meet the normality and homogeneity of variance assumptions of the ANOVA. All of these tests were considered independent and no adjustments to *p*-values were used (Moran, 2003).

A principal components analysis (PCA) was used to examine interannual variability in the physical and chemical parameters. All 18 variables that were sampled simultaneously with the phytoplankton were included in the analysis (Table 1). The PCA was performed in PC-ORD 4 using the correlation matrix.

The species composition was evaluated with both indirect and direct ordination techniques. The relationships among species were assumed to be linear after a preliminary detrended correspondence analysis (DCA) indicated the species gradient was less than 2 and linear ordination methods (PCA; redundancy analysis [RDA]) would be appropriate (ter Braak, 1995). Prior to the ordinations, the fourth root of the biovolume weighted abundance was calculated to reduce the influence of small yet

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dominant algae which otherwise dominate the analysis and to improve the distribution of the data (Clarke and Warwick, 1998). To avoid the "double-zero" problem (cf. McCune and Grace, 2002), the data were transformed such that the Hellinger distance would be the distance measure used instead of the Euclidean distance typically used for PCA (Legendre and Gallagher, 2001). First a PCA was performed on the transformed species matrix with the environmental variables available as *a posteriori* supplementary variables. Secondly, an RDA was performed which explicitly used the matrix of environmental variables to explain the variability in the species composition. In short, this technique begins with a multiple regression of each algal species on the environmental variables followed by a PCA performed on the predicted values from the multiple regressions. All of the 18 environmental variables that were included in the PCA were evaluated for use in the RDA with the exception of silica and the addition of hydraulic residence time (Table 1). Because multiple regression–based techniques can be sensitive to redundancy in the variables (McCune and Grace, 2002), a subset of significant variables were selected utilizing the approach of Sweetman and Smol (2006). First, partially constrained RDAs were performed with each pair of highly correlated variables ($r > 0.8$); one variable was selected as the explanatory variable and the correlated variable was used as a covariable. If the explanatory variable was not significant based on Monte Carlo permutation tests ($p < 0.05$), then it was removed from consideration. Second, the variance inflation factors (VIF) were examined in a RDA with the remaining variables as a way to remove superfluous variables. The variable with the highest VIF was removed and the RDA recalculated until the VIF for all the remaining variables was less than 8. Finally, forward selection was used to determine the fewest number of significant variables ($p < 0.05$) to include in the model. The significance of the resulting first two RDA axes was evaluated with Monte Carlo permutation tests (999 unrestricted permutations, $p < 0.05$). Variance partitioning was used to determine the influence of each of the significant variables individually (Zuur et al., 2007). Because most of the variability in the predictor variables was between years, (R^2 up to 96% based on the one-way ANOVAs), year of sampling was explicitly excluded from the RDA analysis and the temporal pattern was evaluated after the ordination. The ordinations were performed in CANOCO 4.5 on all 103 samples and the 18 taxonomic groups. The resulting RDA correlation triplot depicts the relationship among the samples, species, and environmental variables. The length of the arrows for both species and environmental samples represent the correlations with the first and second RDA axes. The position perpendicular to the species and environment arrows represents the approximate ordering of the samples.

Results

PHYSICAL AND CHEMICAL CONDITIONS OF GREEN LAKE 4

During the six-year study, precipitation was at or below average throughout 2000–2002; which corresponded to the last three years of the five year regional drought. Precipitation was above average throughout 2003–2005 (Fig. 2A). In 2002, precipitation was the lowest at 860 mm (Fig. 2A) (Williams et al., 2006). Since 1951, the mean summer temperature has averaged 6.8 °C (Fig. 2B). The mean summer temperature was higher during the first three years and lower during the final years of the study, with 2002 the warmest summer at 9.3 °C (Fig. 2B). Thus, average or below average precipitation and above average temperatures

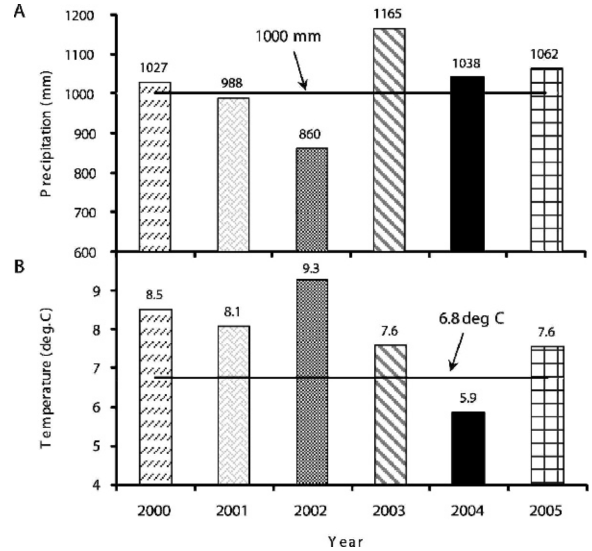

FIGURE 2. Broad-scale climatic factors and historical average values as measured at NWT-LTER D-1 alpine station. Lines indicate the historical average from 1953 to 1996. (A) Total Water Year Precipitation (Oct–Sept); B) Mean summer (Jun–Jul–Aug) temperatures.

typified the years of 2000 through 2002. Further, the extreme drought conditions which occurred in 2002 in the Green Lakes Valley were consistent with the extreme drought conditions prevalent throughout the State of Colorado that year.

The environmental conditions of Green Lake 4 reflected the climatic changes over the study period, especially during the 2002 drought (Table 3). The annual discharge of 1,200,000 m^3 during the 2002 drought was 20% lower than the next lowest discharge and only 65% of the historical average from 1983 to 2005. The average summer hydraulic residence time (HRT) in 2002, 21.5 days, was almost 40% longer than the historical average HRT. The date of ice-out in 2002, June 8, was about one month earlier than the historical average. Further, the length of the ice-free season of 132 days in 2002 was the longest over the 6-year study period.

Concomitant with these drought related hydrologic extremes, the mean summer water temperature was highest in 2002 at 10.9 °C. Moreover, although the lake is generally only weakly stratified, stratification was accentuated in 2002 with a maximum epilimnetic water temperature of 14 °C (at the surface) while hypolimnetic temperatures remained at about 7 °C, similar to other years (Fig. 3). The water temperature was lower during the post-drought period, 2003–2005. The pH of 6.7 and conductivity of 19.3 $\mu S\ cm^{-1}$ were significantly higher in 2002 compared to other years. In contrast, light penetration, dissolved oxygen, and percent saturation of dissolved oxygen remained relatively constant throughout the six-year period. DOC was lowest in 2000–2001, averaging 0.6 mg L^{-1}, and was highest in 2002, 2004, and 2005, averaging 1.0 mg L^{-1}.

In all years, the concentrations of most major cations and anions gradually increased following the loss of ice-cover. For example, there was a significant negative linear relationship between Ca^{2+} concentrations and discharge ($p < 0.05$), with an overall range for Ca^{2+} concentrations from 62 to 122 $\mu eq\ L^{-1}$. In contrast, DOC concentration gradually decreased during the summer. The changes in major ion concentrations and DOC during the summer period were greater than the variation in concentration with depth on a given sampling date (NWT-LTER database: http://www.culter.colorado.edu). Therefore, to examine

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TABLE 3

A summary of Green Lake 4 physical and chemical characteristics as measured during the summer monitoring period at the outlet to the lake, between 24 May and 31 August 2000–2005. Differences among years for each variable were tested with a one-way ANOVA followed by the Student-Newman Keuls post-hoc test: those differences significant at $p < 0.05$ are indicated with lower case letters, where statistically distinguishable means between years are indicated by varying letters, proceeding from highest mean value(s) (i.e., a) to lowest mean value(s) (e.g., b, c, d, e, or f). (nd= no data; *number of days between ice out and ice cover; §sum of discharge gage measurements at the GL4 outlet, 24 May–31 August; ¶computed as discharge divided by GL4 volume, 24 May–31 August).

Parameter	Unit	2000	2001	2002	2003	2004	2005
Number of Samples		18	14	15	14	18	18
Date of Ice Out		1 July	2 July	8 June	12 July	7 July	16 July
Ice Free Season*	(days)	122	101	132	108	112	113
Discharge§	(m^3)	1,488,614	1,618,566	1,119,548	1,995,454	1,463,523	1,962,613
HRT¶	(days)	15.4^{b}	14.8^{b}	21.5^{a}	12.4^{c}	16.3^{b}	13.0^{c}
1% Attenuation	(m)	10.5	13.0	11.7	10.2	nd	nd
Secchi	(m)	nd	4.2	3.8	4.1	nd	3.4
TEMP	(°C)	9.5^{ab}	9.2^{ab}	10.8^{a}	7.9^{b}	8.3^{b}	8.7^{b}
COND	(μS/cm)	10.6^{f}	14.4^{c}	19.2^{a}	13.3^{d}	18.5^{b}	12.6^{e}
pH		6.6^{b}	6.46^{c}	6.65^{a}	6.52^{bc}	6.34^{d}	6.35^{d}
DO	(mg/L)	8.0^{ab}	nd	7.4^{b}	8.7^{a}	8.3^{ab}	8.1^{ab}
% DO	(%)	111.9	nd	105.2	111.1	106.2	104.2
DOC	(mg/L)	0.51^{b}	0.62^{b}	0.90^{a}	nd	1.16^{a}	0.99^{a}

interannual variation, we compared the average concentrations of major cations, anions, and nutrients for the six-week summer period subsequent to ice-out in GL4 (Fig. 4). The average concentrations of major cations were high in the summers of 2002 and 2004 compared to the other years, and the concentrations of Ca^{2+} and K^{+} were at their maximum in 2002 (115 and 7 $\mu eq\ L^{-1}$, respectively). The anions SO_4^{2-} and Cl^{-} also exhibited highest concentrations in summer 2002 (90 and 4 $\mu eq\ L^{-1}$, respectively), whereas ANC concentrations generally decreased during the study. However, ANC concentrations were greater in 2002 than in 2001 or during the post-drought years. Furthermore, it should be noted that ANC concentrations peaked at the end of the summer 2000; whereas ANC concentrations peaked in mid-July in 2002.

The variations in summer nutrient concentrations followed different patterns than those for major ions. The nitrate concentrations generally decreased following ice-out (NWT-LTER database: http://www.culter.colorado.edu). Concentrations of ammonium, phosphate, and total dissolved phosphorus (TDP) were low with no consistent pattern of variation following ice-out. The concentrations of Si, a required nutrient in the growth of diatoms, remained relatively constant throughout the summer in all years except for 2002, when a sustained decline occurred in July (Fig. 5). The silica concentrations measured during the 2002 ice-free sampling season (mid June to end of August) were the lowest measured during any ice-free sampling season over the 10 year period from 1995 to 2005. Also, the average silica concentration during the 2002 ice-free season was lower than the average over the entire 10 year period.

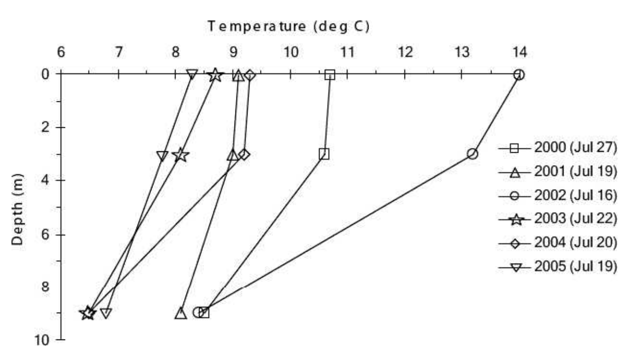

FIGURE 3. Green Lake 4 temperature depth profile circa 20 July, peak growing season, 2000–2005.

In terms of interannual variation, average summer NO_3^- concentrations were highest in 2004 at 19.6 $\mu eq\ L^{-1}$ and lowest in 2000 at 7.1 $\mu eq\ L^{-1}$ (Fig. 4). Average concentrations of NH_4^+ were highest in 2003 at 1.3 $\mu eq\ L^{-1}$, and there was no significant difference among the other years. Concentrations of PO_4^{3-} and TDP fluctuated in a similar manner, with higher values of PO_4^{3-} occurring in 2000, 2002, and 2005.

The PCA of the environmental variables indicated that the overall chemical composition of the lake water was unique for each year of the study (Fig. 6). The first two components explained 54% of the variance in the environmental data. ANOVA confirmed that differences between loadings of yearly averages were statistically significant for all yearly comparisons on Axis 1 and for all yearly comparisons with the exception of 2001 and 2003 on Axis 2 ($p < 0.0001$). The first axis was associated with the concentrations of most of the major cations and anions with a gradient from low concentrations in 2000 to high concentrations in 2002 and 2004. The variables loading most on the second PCA axis included temperature, silica, ANC, and pH as well as nitrate, which distinguished the environmental conditions in 2002 from 2004. The various forms of phosphorus were only weakly correlated with the first two PCA axes.

PHYTOPLANKTON ABUNDANCE AND VARIATION

Over the course of the study, chlorophyll *a* concentrations were consistently greater in the hypolimnion as compared to the epilimnion (Flanagan, 2007). This was especially true during the summers of 2002 and 2005. In general, chlorophyll *a* concentrations increased in mid-late July (epilimnion maximum concentrations ~2–4 $\mu g\ L^{-1}$; hypolimnion maximum concentrations ~4–10 $\mu g\ L^{-1}$) and decreased by the end of the summer sampling season. In general, the changes in phytoplankton species composition throughout the summers were much greater than the variation with depth, despite the greater hypolimnetic chlorophyll *a* concentrations (Flanagan, 2007).

The average algal biovolume increased following the extreme regional-scale drought in 2002 (Fig. 7). A one-way ANOVA followed by the Student-Newman Keuls post-hoc test indicates that the

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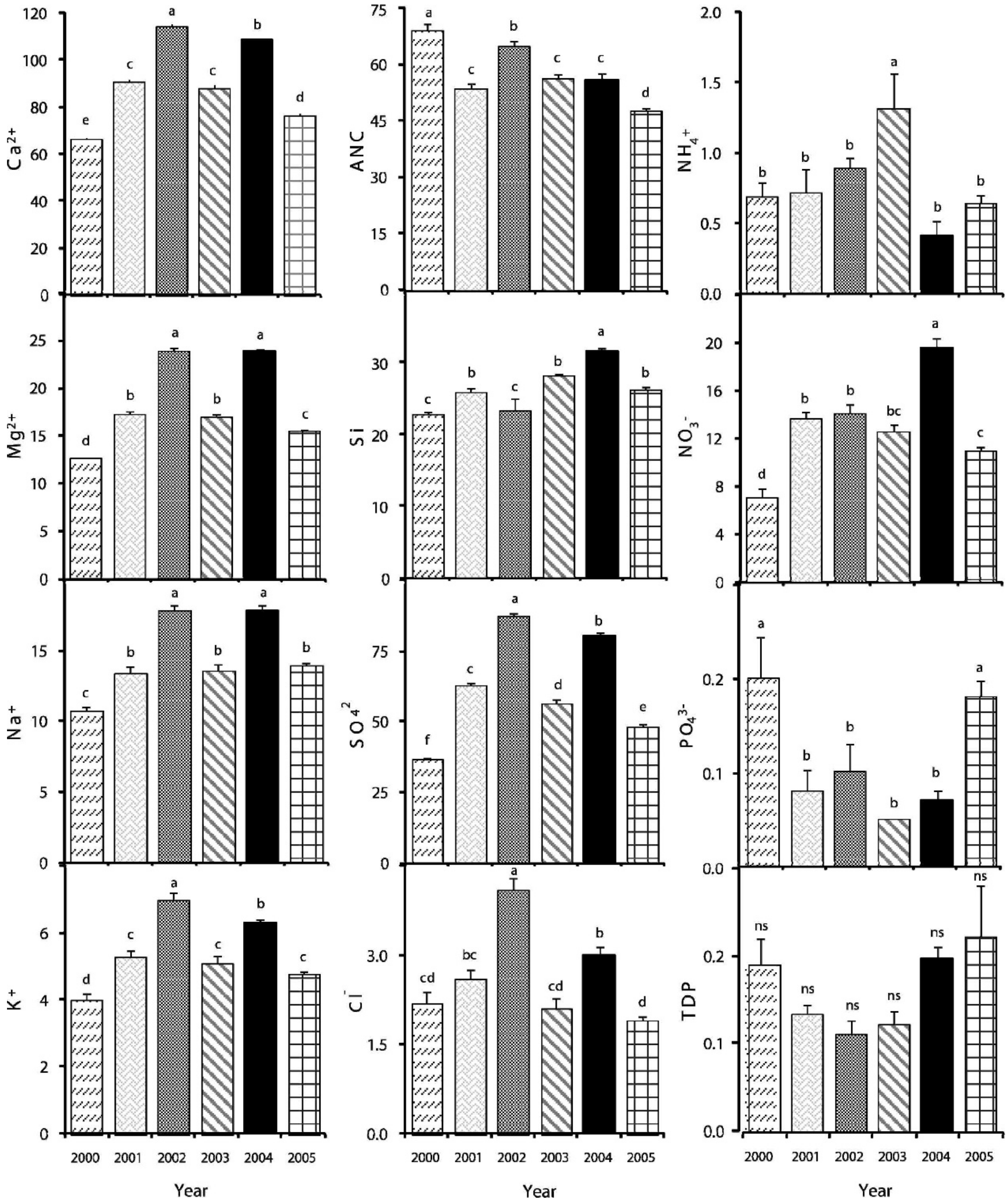

FIGURE 4. All-depths averaged (Mean + 1SE) Green Lake 4 chemical characteristics, 2000–2005. Differences among years were tested with a one-way ANOVA followed by the Student-Newman Keuls post-hoc test: those differences significant at $p < 0.05$ are indicated with lower case letters, with "ns" indicating no significant difference among years. (Units for all parameters in μeq L^{-1} except for Si and TDP = μmol L^{-1}). Acronyms for the environmental characteristics are included in Table 1.

post-drought years of 2003–2005 had significantly greater algal biovolume at $\alpha = 0.05$ than the regional-scale drought years of 2000–2002. This increase in biovolume mainly reflects the increase in abundance of taxa in the chrysophyte, chlorophyte, and haptophyte divisions. Calculations of Shannon-Wiener Diversity Index (H′) for each year indicate that phytoplankton diversity was significantly higher in 2001 and 2002 (2.01 $\pm$ 0.08 and 2.04 $\pm$ 0.10, respectively) than in 2003, but was not significantly different from H′ in 2000, 2004, or 2005 (Flanagan, 2007).

Detailed analyses of several genera highlight the observed patterns at higher taxonomic levels (Fig. 8). *Chrysococcus* sp. was the major species which accounted for the post-drought increase in biovolume of Chrysophyta (Fig. 8A). The biovolume of the chlorophyte *Chlorococcum* sp. also was greatest in 2003 and 2004 (Fig. 8B). Another chlorophyte, *Chlamydomonas* sp., thrived only during 2005 (Fig. 8C). Finally, the chlorophyte *Ankyra* sp. was abundant only during the summer of the extreme 2002 drought (Fig. 8D). Likewise, the diatom *Synedra* sp. was also a dominant

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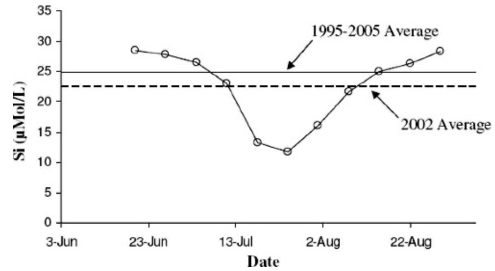

FIGURE 5. Silica concentrations measured at the outlet to Green Lake 4 during the 2002 sampling season. Also shown are the average silica concentrations for the 2002 ice-free sampling season and the average for the 10 year period from 1995 to 2005 ice-free sampling seasons.

algal species only throughout the summer of 2002 (Fig. 8E), with biovolumes exceeding those in any other year by more than a thousandfold. The abundance of *Plagioselmis* sp., a cryptomonad, remained relatively consistent throughout the study (Fig. 8F).

A principal components analysis of biovolume-weighted abundance data for all sampling depths and dates was performed to examine the relationships among algal species. In the PCA biplot of the GL4 phytoplankton data (Fig. 9), Axes 1 and 2 together accounted for 39% of the variance in community composition. Results of the ANOVA tests on the PCA scores indicate significant interannual differences in the phytoplankton community composition on the first two axes ($p < 0.0001$). Axis 1 clearly separated the regional scale drought years (2000–2002) from the post-drought years (2003–2005). The 2002 algal assemblage was associated with high abundance of *Synedra* sp. and *Ankyra* sp. In general, the drought years were associated with low abundance of *Chrysococcus* sp. and *Chlorococcum* sp. The second axis distinguished the community in 2002 from 2000–2001, the first years of the regional scale drought, and separates the communities in the post-drought years. The lake stratification was greatest in 2002, but even during this year, the species composition did not significantly differ among the sampled depths based on ANOVAs of the species scores for the first 2 axes.

The relationship between environmental variables and phytoplankton species composition was investigated using RDA. The species scores, fit for the first two RDA axes, total fraction of the variance explained, and the total variance explained are shown in Table 4. The first two RDA axes were both significant and explained 16% of the variance in the species data. The forward selection process identified six significant variables (ANC, NO_3^-, SO_4^{2-}, Cl^-, NH_4^+, K^+). Based on the variance partitioning these variables could individually explain 3.3, 5.8, 2.2, 4.0, 2.4, and 2.3%, respectively, of the total variance. The correlation triplot depicts the relationships among these variables and selected phytoplankton taxa (Fig. 10). The first RDA axis explained 10.3% of the variance ($\lambda_1 = 0.103$; $p = 0.001$) and the second RDA axis explained 6.1% of the variance ($\lambda_1 = 0.061$; $p = 0.001$). The first axis represents a gradient from higher acid neutralizing capacity and chloride concentrations in the positive direction and higher nitrate concentrations in the negative direction. The second RDA axis is most highly correlated with sulfate and potassium concentrations. The taxa most strongly associated with the first axis were *Synedra* sp. and *Chrysococcus* sp. *Synedra* sp. and *Ankyra* sp. appear to define the 2002 assemblage, while *Chrysococcus* sp. is negatively associated with Axis 1 and aligns with 2003. The 2002 assemblage is identified as having almost no overlap with those from the other years. Furthermore, during the summers, when the lake was the most strongly stratified (2000, 2002, and 2004; Fig. 3), the epilimnetic samples (surface and 3 m) had significantly greater scores ($p < 0.05$) on Axis 2 than the hypolimnetic samples (9 m). During summers when the lake was weakly stratified, there was not a consistent epilimnetic vs. hypolimnetic trend with respect to Axis 2.

Discussion

PHYTOPLANKTON COMMUNITY RESPONSE TO EXTREME DROUGHT

This study of Green Lake 4 began in the summer of 2000, the third year of a 5-year regional drought. The final year of the drought, 2002, was an extreme event, corresponding to the lowest

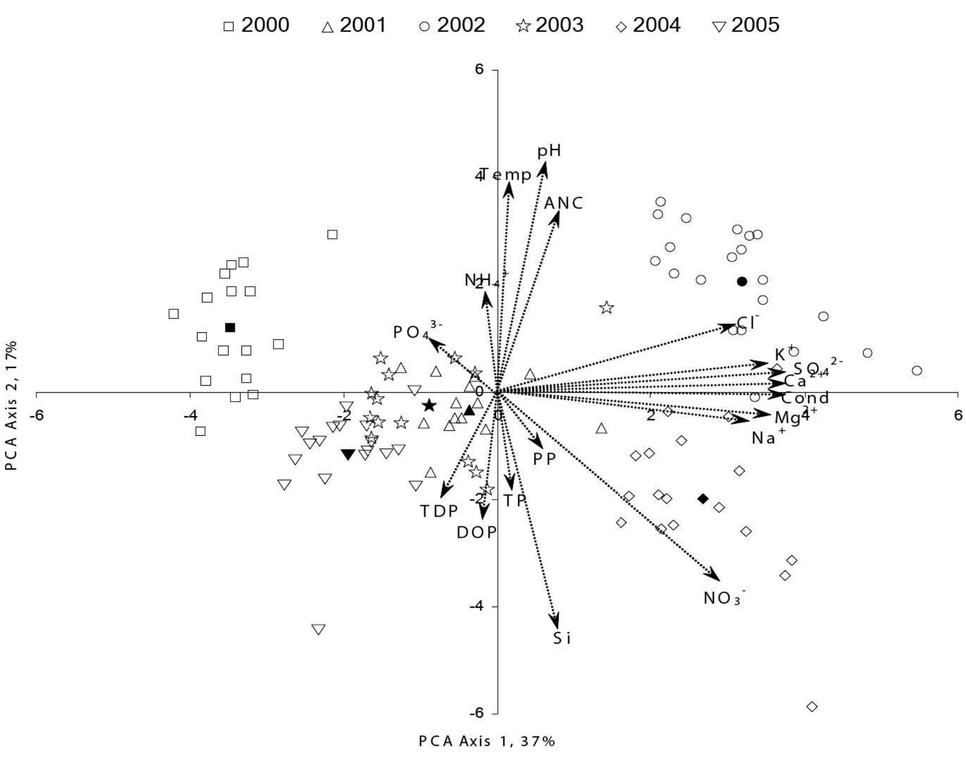

FIGURE 6. Biplot of the first two axes of a principal components analysis of the environmental variables which explained 54% of the variance. Solid symbols are the annual means. Arrows represent the correlations of the environmental variables with the two axes. Acronyms for the environmental characteristics are included in Table 1.

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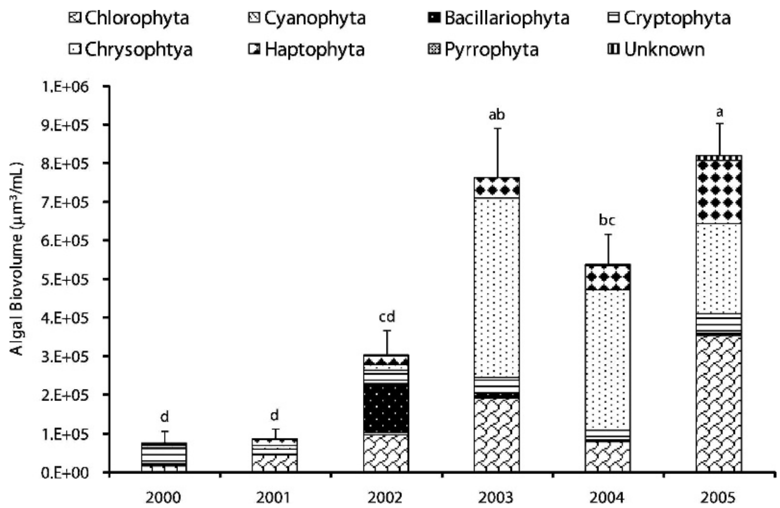

FIGURE 7. Total algal biomass as biovolume-weighted abundance (Mean + 1SE) for each division in each year, Green Lake 4, 2000–2005. Differences among years were tested with a one-way ANOVA followed by the Student-Newman Keuls post-hoc test: those differences significant at $p < 0.05$ are indicated with lower case letters.

annual precipitation in the 110-year-long climate record for the Colorado Rocky Mountains. The physical and chemical conditions in Green Lake 4 in 2002 were strongly influenced by the drought conditions in the watershed. In 2002, the discharge from the lake outlet was the lowest in 23 years of hydrologic monitoring. The highest values for pH, conductivity, and acid neutralizing capacity also occurred in 2002, along with the highest concentrations of major cations (i.e., Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}) and anions (i.e., Cl^{-}, SO_4^{2-}). Associated with the 2002 drought was an increase in summer air temperature of almost 1 °C. The drought conditions and the warmer summer air temperatures were amplified in the lake, causing an earlier ice-out by one month and an increase in summer surface water temperatures to 14 °C, over 3 °C greater than observed in other years of the study. The post-drought years were typified by higher precipitation and discharge, cooler water temperatures, and decreased concentrations of major ions. This decrease in major ion concentrations can likely be attributed to changes in the hydrology of the system at the catchment scale. For example, Ca^{2+} and SO_4^{2-} concentrations entering surface waters from a rock glacier in the Green Lakes Valley were approximately four times greater during the regional-scale drought years examined in this study as compared to earlier years (Williams et al., 2006).

The changes in the summer phytoplankton community during the 2002 drought were prominent, with two otherwise uncommon algal species becoming dominant. These algal species were *Synedra* sp. (Bacillariophyta) and *Ankyra* sp (Chlorophyta). The most dramatic increase in abundance was for *Synedra* sp. This diatom was extremely rare or undetected in the first two years of the study and in the prior study of a sediment core by Waters (1999). Of diatoms found in the sediment core of Green Lake 4, *Synedra* sp. composed less than 1% of the total diatom abundance at any given depth. Moreover, data from sediment traps deployed in the lake confirmed that the dominant species in the water column are reflected in those species found in the sediment core. The growth of *Synedra* sp. in 2002 was sufficient to deplete the concentrations

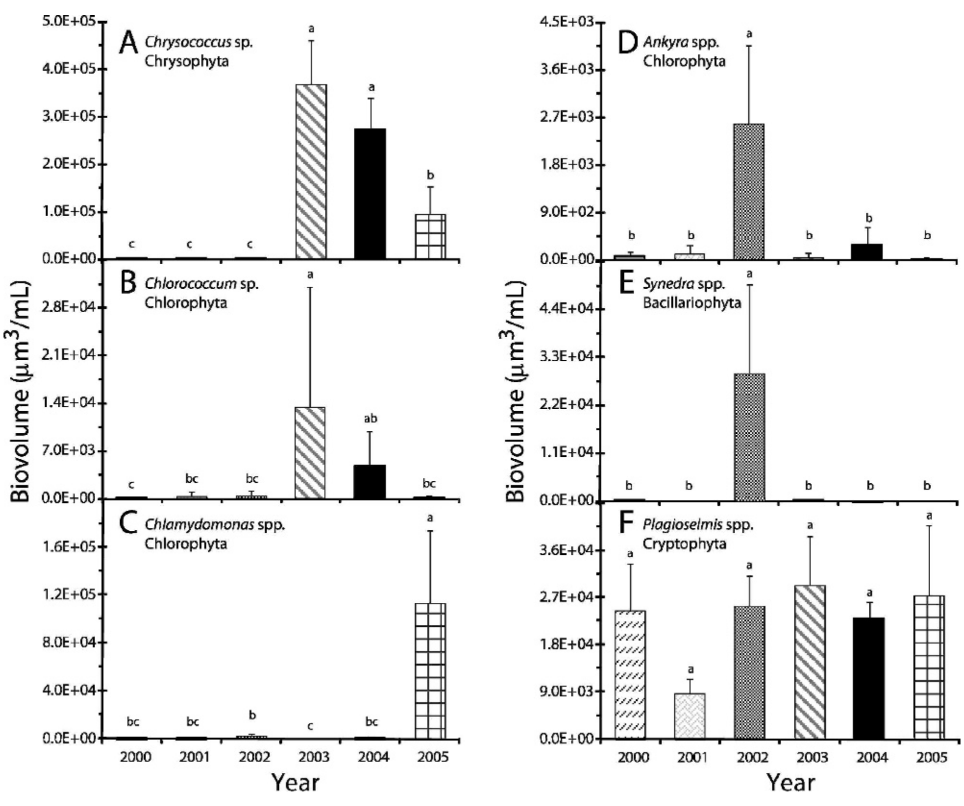

FIGURE 8. Average biovolume-weighted abundance (Mean + 1SE) of selected Green Lake 4 phytoplankton species, 2000–2005. Differences among years for each taxon were tested with a one-way ANOVA followed by the Student-Newman Keuls post-hoc test: those differences significant at $p < 0.05$ are indicated with lower case letters.

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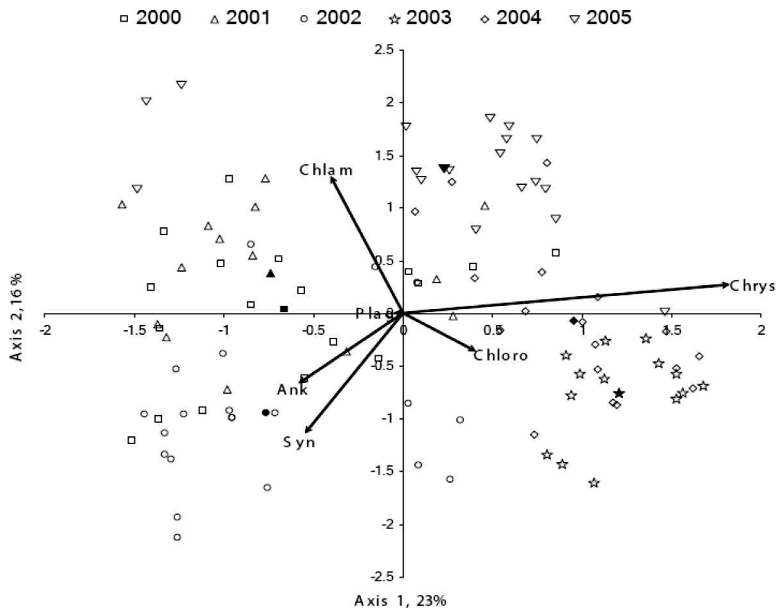

FIGURE 9. Biplot of the first two axes of a principal components analysis (PCA) of Green Lake 4 phytoplankton community composition based on biovolume-weighted abundance, 2000–2005, explaining 39% of the variance. Solid symbols represent the annual means. The arrows represent the correlations of the six indicator species with the first two PCA axes. Taxon names indicated by acronyms are given in Table 2.

of dissolved silica as the summer progressed, which was not observed in any other year. Although it has been noted that diatoms generally exhibit the greatest tolerance to warm temperatures (Reynolds, 1984), the increased temperatures were not identified in the statistical analyses as a significant driver contributing to the dominance by *Synedra* sp. Another distinctive feature of 2002 was the high hypolimnetic chlorophyll *a* concentrations, a finding consistent with the deep chlorophyll maximum observed in oligotrophic alpine lakes of the Beartooth Mountains, Montana/Wyoming (Saros et al., 2005).

The post-drought phytoplankton community was likewise distinctive. Firstly, populations of *Synedra* sp. and *Ankyra* sp. decreased to low levels in the year immediately after the 2002 drought and their abundance remained quite low throughout the post-drought period. Furthermore, a sustained increase in abundance of Chrysophyta, especially *Chrysococcus* sp., accounted for significantly greater algal biovolume concentrations in the post-drought period (Fig. 8). Because of the general adaptation of Chrysophyta to low temperatures (Roijackers, 1986), the cooler conditions may have contributed to the dominance of the phytoplankton by *Chrysococcus* sp. in the post-drought period.

These observations complement those of other researchers who have found a response in phytoplankton community composition of alpine lakes to changes in climate-related parameters. McMaster and Schindler (2005) found that the length of the ice-free season, water temperature, pH, and conductivity were all associated with interannual variability in phytoplankton communities in alpine ponds of Banff National Park, Canada. In greenhouse warming experiments in fishless alpine ponds, Strecker et al. (2004) demonstrated that warming had a significant time-dependent effect on phytoplankton community composition, in part reflecting the emergence of resting stages from pond sediments.

In these studies, as well as in this study of Green Lake 4, it is inherently difficult to separate the drought-related effects of

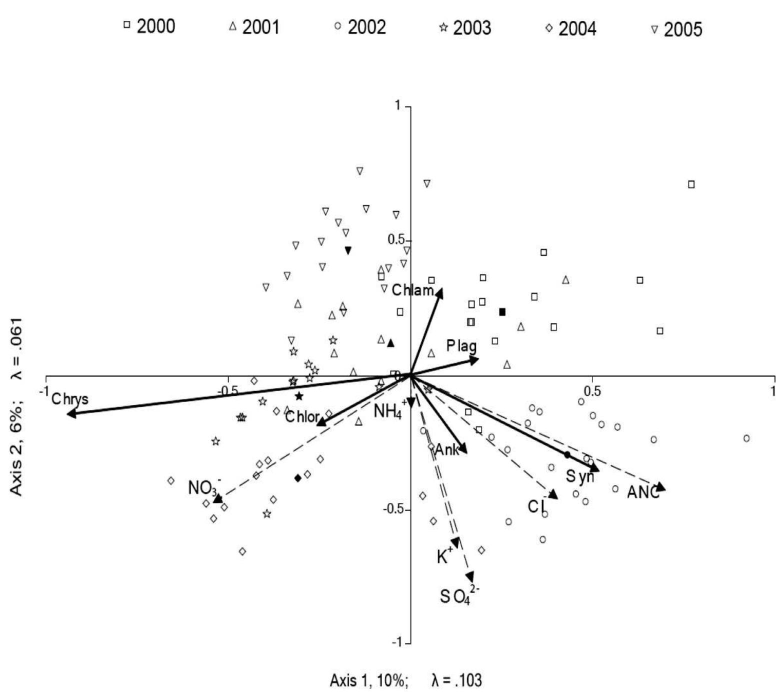

FIGURE 10. Correlation triplot based on redundancy analysis (RDA) depicting the influence of selected environmental variables on Green Lake 4 phytoplankton community data, 2000–2005. Axis 1 and Axis 2 cumulatively account for 16% of the variation in phytoplankton community composition. Solid arrows represent the correlations of the indicator species and dashed arrows represent the correlations of the environmental variables with the two RDA axes. Solid symbols represent the means for a given year. Names indicated by acronyms are given in Tables 1 and 2.

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TABLE 4

Redundancy analysis (RDA) output for all phytoplankton taxa. The species scores and fit for the first two RDA axes are presented along with the total fraction of variance explained by the RDA model and the total variance.

Species	Axis 1		Axis 2		Variance explained	Total variance
	Score	Fit	Score	Fit		
***Rhabdoderma* sp.**	0.14	0.02	–0.47	0.26	0.33	1.06
Cyanophyte spp.	0.02	0.01	0.08	0.15	0.21	0.06
***Dinobryon* sp.**	−0.04	0.00	0.30	0.09	0.13	1.25
***Raphidocelis* sp.**	0.10	0.01	−0.21	0.05	0.14	1.08
***Synedra* sp.**	0.52	0.21	−0.36	0.10	0.35	1.58
***Fragilaria* sp.**	−0.08	0.02	−0.08	0.02	0.17	0.43
***Chromulina* sp.**	0.32	0.13	0.18	0.04	0.25	0.96
Bacillariophyte spp.	−0.16	0.05	−0.06	0.01	0.11	0.59
Pyrrophyte spp.	0.02	0.01	0.03	0.01	0.07	0.11
Chlorophyte spp.	−0.04	0.00	0.13	0.03	0.04	0.67
Unknown	0.16	0.03	0.31	0.11	0.25	1.07
***Chrysococcus* sp.**	−0.94	0.36	−0.14	0.01	0.37	3.06
***Chlorococcum* sp.**	−0.25	0.04	−0.19	0.02	0.12	1.96
***Scenedesmus/Chrysochromulina* sp.**	−0.10	0.06	0.02	0.00	0.11	0.22
***Ankyra* sp.**	0.16	0.02	−0.30	0.09	0.14	1.22
***Chlamydomonas* sp.**	0.08	0.00	0.32	0.06	0.17	1.99
***Chlorella* sp.**	0.11	0.06	−0.05	0.01	0.14	0.23
***Plagioselmis* sp.**	0.19	0.09	0.06	0.01	0.24	0.47

increased hydraulic residence time, changes in water quality, and increases in water temperature as the phytoplankton community composition changes through a summer. The effect of increased hydraulic residence time may be greatest during snowmelt at the beginning of summer, when an alpine lake essentially becomes a wide place in the stream and species require rapid growth rates to persist in the lake (McKnight et. al, 1990), whereas the effects of higher water temperatures may be greatest in late summer. Moreover, phytoplankton communities may be influenced by the interactive effects of temperature and hydraulic residence time on finer scale mixing regimes in the epilimnion (Hauer et al., 1997; Lotter and Bigler, 2000; Battarbee et al., 2002; Anneville et al., 2005). Finally, the higher degree of stratification in 2002 may have indirectly influenced the species distribution by influencing variables such as light penetration and zooplankton grazing rates.

INTERPRETATION OF STATISTICAL RELATIONSHIPS

Taken as a whole, the statistical analyses of the environmental and phytoplankton species data serve to emphasize the distinct effects of the extreme drought of 2002 on the physical, chemical, and biological characteristics in Green Lake 4. The environmental conditions in the lake in 2002 were unique among the six years studied with high concentrations of major cations and anions (except for silica), as well as high temperatures. However, there is little evidence in the water chemistry of the regional drought that was occurring. Nor was there any suggestion of a major change in water quality after the 2002 drought. In addition, the concentrations of nitrogen and phosphorus exhibited relatively little significant interannual variability with the exception of the high ammonium concentrations in 2003 and high nitrate concentrations in 2004. It has been shown that reduced hydraulic residence time can act to increase internal loading of nutrients (Rippey et al., 1997). However, the fact that an increase in nutrient concentrations in Green Lake 4 did not occur in 2002 in concert with the increased residence time is likely due to the relatively low residence times in Green Lake 4 (maximum mean of 21.4 days).

The phytoplankton community was unique during the year of extreme drought. While some taxa, such as *Plagioselmis* sp. showed little consistent trend over the six years of the study, two interesting patterns stood out. First, the abundance of two taxa, *Synedra* sp. and *Ankyra* sp., increased by several orders of magnitude in 2002 and decreased just as quickly by the following year. However, the regional drought years (2000–2002) and the post-drought years (2003–2005) were separated along the first axis of the species PCA. This distinction was exemplified by the strong relationships of *Chrysococcus* sp. on this axis. In addition, the total algal biovolume increased dramatically in the post-drought years. While this record is relatively short, it appears that a large shift occurred in the phytoplankton community composition and biomass in response to the drought.

The measured environmental variables explained a significant portion of the phytoplankton species variance. Similar to the unconstrained ordination, the first RDA axis distinguished the early (2000–2002) and late (2003–2005) years of the study. The result that during summers years when the lake was stratified, the second axis of the RDA separated the epilimnetic samples from the hypolimentic samples suggests that light penetration and/or temperature may play a role in determining community composition. The taxa associated with the drought, *Synedra* sp. and *Ankyra* sp., were highly correlated with ANC, SO_4^{2-}, Cl^-, and K^+, whereas the taxa which increased in abundance post-drought, *Chrysococcus* sp. and *Chlorococcum* sp., were strongly correlated with NO_3^-. These patterns were similar to the *a posteriori* analysis of the species PCA suggesting that the environmental variables are explaining real variability in the community data. Thus, the statistical analyses support the conclusion that the environmental conditions of the extreme drought could explain some of the change in the structure of the phytoplankton community. Specifically, results of the RDA suggest that water quality parameters are as important, if not more so, than physical conditions as drivers of phytoplankton community response. Further, one important aspect of the function of the phytoplankton community, specifically the uptake of dissolved silica from the lake water by diatoms, was also much more pronounced during the extreme drought than during the other years of the study. The environmental conditions of the summer of 2002 may have surpassed a threshold for the dominant species of the phytoplank-

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ton community of Green Lake 4, allowing a few of the previously rare species, such as *Synedra* sp., to become established.

Although the statistical analysis of the monitoring data presented here does not provide an explanation for the post-drought increase in algal biovolume, the general increase in nutrient concentrations and the correlation of the abundance of *Chrysococcus* sp. and *Chlorococcum* sp. with NO_3^- in the RDA suggest a possible connection with drought-related changes in hydrologic flowpaths in the alpine watershed. Drought has the potential to influence surface water hydrochemistry through groundwater/surface water interactions, and through changes in source waters and flow paths (Brække, 1981; Williams et al., 1996). Additionally, variations in the relative contributions of snowmelt and groundwater directly affect surface hydrochemistry. For example, Williams and Melack (1997) observed that the beginning of snowmelt runoff after antecedent dry periods commonly produced elevated water chemistry concentrations.

SYNERGISTIC INTERACTIONS

In alpine lakes, the response of the phytoplankton community to climate-driven conditions may be amplified by synergistic interactions with other drivers of environmental change. Atmospheric nitrogen deposition at Niwot Ridge is presently increasing at a rate of 0.3 kg N ha^{-1} yr^{-1} (Williams and Tonnessen, 2000). This sustained nitrogen deposition can affect the stoichiometry of the lake ecosystem by inducing or accentuating phytoplankton P limitation and thus resulting in high N:P and C:P ratios in phytoplankton biomass (Sterner and Elser, 2002). Such stoichiometric shifts may create ultra P-limited conditions, especially in otherwise low nutrient lakes such as Green Lake 4. Furthermore, this altered state could eliminate algal species that cannot survive in severely P-limiting conditions, while elevated phytoplankton C:P ratios could propagate beyond the level of primary producers to impair zooplankton because high dietary C:P ratios can result in direct zooplankton P-limitation (Sterner and Elser, 2002). The higher biovolume of the post-drought years could possibly reflect a response to a moderation of phosphorus limitation by the phytoplankton. If there was a change in groundwater/surface water interactions caused by the drought, such conditions could increase the flux of phosphorus to the lakes from mineral weathering in shallow groundwater. Thus, this study suggests that watershed-scale changes following drought may also have an indirect and sustained effect on the phytoplankton community, prolonging the response to extreme drought.

Conclusions

Changes in phytoplankton communities in alpine lakes can offer clues as to how these ecosystems may respond to projected climate changes in the Rocky Mountain region. The driving mechanisms of phytoplankton species succession are related to seasonal changes in the physical and chemical environment. These changes interact to influence varied growth and loss rates among the algal species, resulting in differences in community composition. We found that the extreme drought in 2002 was associated with a distinctive phytoplankton community dominated by previously rare species and that this change in the phytoplankton community was related mainly to chemical changes, as opposed to physical changes, in the lake environment. Following the 2002 drought, two species of Chlorophyta became dominant and this change was associated with increases in nitrate concentrations, which are in part controlled by atmospheric nitrogen deposition from anthropogenic sources. These results are relevant to water resource management. Firstly, the identification of *Synedra* sp. as a potential bioindicator for drought in Green Lake 4 may be useful in interpreting lake sediment diatoms records for past drought conditions. Secondly, identification of phytoplankton community responses to transitions to a less oligotrophic state driven by climatic and anthropogenic changes will be useful to water resource managers as stresses on pristine high quality water sources increase.

Acknowledgments

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