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Paleolimnological records of nitrogen deposition in shallow, high-elevation lakes of Grand Teton National Park, Wyoming, U.S.A.

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Abstract

Reactive nitrogen (Nr) from anthropogenic sources has been altering ecosystem function in lakes of the Rocky Mountains, other regions of western North America, and the Arctic over recent decades. The response of biota in shallow lakes to atmospheric deposition of Nr, however, has not been considered. Benthic algae are dominant in shallow, high-elevation lakes and are less sensitive to nutrient inputs than planktonic algae. Because the benthic substrate is typically more nutrient rich than the water column, shallow lakes are not expected to show evidence of anthropogenic Nr. In this study, we assessed sedimentary evidence for regional Nr deposition, sediment chronology, and the nature of algal community response in five shallow, high-elevation lakes in Grand Teton National Park (GRTE). Over 140 diatom taxa were identified from the sediments, with a relatively high species richness of taxa characteristic of oligotrophic conditions. The diatom assemblages were dominated by benthic taxa, especially motile taxa. The GRTE lakes demonstrate assemblage-wide shifts in diatoms, including the following: (1) synchronous and significant assemblage changes centered on ca. A.D. 1960; (2) pre-1960 assemblages differed significantly from post-1960 assemblages; (3) pre-1960 diatom assemblages fluctuated randomly, whereas post-1960 assemblages showed directional change; and (4) changes in $\delta^{15}N$ signatures were correlated with diatom community composition. These results demonstrate recent changes in shallow high-elevation lakes that are most correlated with anthropogenic Nr. It is also possible, however, that the combined effect of Nr deposition and warming is accelerating species shifts in benthic diatoms. While uncertainties remain about the potential synergy of Nr deposition and warming, this study adds shallow lakes to the growing list of impacted high-elevation localities in western North America.

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Introduction

Lake sediments record direct evidence of atmospheric deposition of reactive nitrogen (Nr) across the northern hemisphere (Baron et al., 2000; Wolfe et al., 2001; Holtgrieve et al., 2011; Kopáček and Posch, 2011; Wolfe et al., 2013). In western North America, Nr is deposited primarily as nitrate (NO_3^-) and ammonium (NH_4^+), which alters surface water chemistry and induces a distinctive suite of shifts in species composition, particularly diatom species composition (Burns, 2003; Fenn et al., 2003a, 2003b; Porter and Johnson, 2007; Kissman et al., 2013). The release of Nr to the biosphere during the past 150 years has escalated due to increased combustion of fossil fuels, as well as the production and application of synthetic N fertilizers (Vitousek et al., 1997; Holtgrieve et al., 2011). Nitrogen is frequently a limiting nutrient for primary producers, and as a result, inputs in excess of natural supply may induce changes to species composition, biodiversity, community dynamics, and nutrient cycling in both aquatic and terrestrial ecosystems. Chronic deposition of anthropogenic Nr to oligotrophic lakes of the northern hemisphere has altered nutrient dynamics primarily by exacerbating phosphorus (P) limitation (Elser et al., 2009a, 2009b).

High-elevation lakes of western North America are vulnerable to both acidification and eutrophication from Nr introduced through atmospheric deposition (Seastedt et al., 2004; Baron et al., 2011; Nanus et al., 2009; Sheibley et al., 2014). Annual precipitation is dominated by snow, and orographic effects cause precipitation to increase with altitude (Barry, 1973), leading to higher rates of Nr deposition with increasing elevation (Williams and Tonnessen, 2000). High-elevation lakes are typically oligotrophic and generally occupy poorly buffered catchments characterized by sparsely or unvegetated talus, poorly developed soils, and exposed bedrock. Catchment vegetation is sparse, allowing inorganic nutrients to be released to surface waters, particularly during spring snowmelt (Williams et al., 2009). The hydrology of high-elevation lakes is dominated by spring snowmelt, which can deliver an accumulated pulse of atmospheric pollutants. Glacial meltwater further contributes both inorganic solutes and nutrients (Baron et al., 2009; Saros et al., 2010b; Montross et al., 2013).

The Teton Mountain Range is steep and rugged, with many peaks over 3000 m a.s.l. and over 100 high-elevation lakes formed in glacially scoured basins. Typically, deep lakes are selected for paleolimnological reconstruction, but many of the deep lakes of the Tetons are subject to avalanche debris on the frozen surface during winter. Inorganic debris is then deposited onto the soft sediments with the melting of ice-cover. Such debris not only makes sediment coring difficult, it compromises the integrity of the sediment record.

Alternatively, shallow lakes are common in high elevations in the Rocky Mountains (Pennak, 1969; Hall and Herrmann, 1980). Shallow lakes, however, have not been considered explicitly with respect to atmospheric deposition of Nr. The physical and chemical properties of shallow lakes presumably dictate that their biota respond in an alternate manner to input of Nr than the biota of deeper high-elevation lakes. Indeed, shallow lakes of temperate zones are an

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archetype for alternate stable states, dependent upon nutrient loading (Cattaneo, 1987; Wetzel, 2001; Scheffer and van Nes, 2007; Cantonati and Lowe, 2014). In low nutrient conditions, shallow lakes are highly transparent with abundant submerged macrophytes, while in high nutrient conditions, shallow lakes become turbid and macrophytes disappear. In addition to the characteristics of shallow lakes (e.g., reduced thermal stratification, exposure to wind mixing, resuspension of sediments), high-elevation shallow lakes possess unique features. For example, the water column and parts of the sediments may be frozen for a large part of the year. During the period of ice-cover, nutrient concentrations increase in the water column as a result of freeze concentration (Spaulding et al., 1993). High-elevation lakes receive greater ultraviolet radiation, which inhibits planktonic photosynthesis (Vinebrooke and Leavitt, 1999), or favors particular species (Bothwell et al., 1993). While phytoplankton are inhibited by ultraviolet radiation, motile epipelic species are able to migrate into surface sediments to avoid damaging radiation (Vinebrooke and Leavitt, 1999). Furthermore, compared to deeper high-elevation lakes, shallow high-elevation lakes are subject to greater warming by light penetration (Strecker et al., 2004).

Throughout western North America, diatoms serve as indicators of biotic integrity and have been utilized to define thresholds of environmental change in deep lakes (Wolfe et al., 2001, 2003; Saros et al., 2003; Baron, 2006; Arnett et al., 2012; Brahney et al., 2014a; Sheibley et al., 2014; Hundey et al., 2014). In particular, two planktonic diatom species, *Asterionella formosa* Hassall and *Fragilaria crotonensis* Kitton, have been documented as nitrophilous in lakes of the Rocky Mountains (Saros et al., 2005b; Saros et al., 2010a). Although these diatoms are common in mesotrophic and eutrophic lakes globally, their increased presence in oligotrophic lakes is interpreted as a response to subtle nutrient enrichment occurring in response to relatively low Nr inputs. Diatoms have enabled the establishment of critical loads in aquatic ecosystems, defined as the threshold Nr deposition rate below which there is no discernible ecological effect (Porter and Johnson, 2007). This approach is particularly informative for evaluating and meeting management targets (Pardo et al., 2011). In high-elevation regions of western North America, diatom-based estimates of the Nr critical load are of the order of 1.5 kg N ha^{-1} yr^{-1} as wet deposition (Baron, 2006; Saros et al., 2010a), much lower than temperate ecosystems at lower altitudes (Nanus et al., 2012). The response of diatoms in shallow lakes to Nr has not been investigated, but we expect that the critical load for biotic response would be greater than in deep lakes.

Grand Teton National Park is proximal to several major Nr point sources, including the Snake River Valley of Idaho and northern Utah, where ammonia (NH_3) emissions from agriculture are sufficient to be detectable using infrared remote sensing (Clarisse et al., 2009). Other sources include oil and gas extraction industries to the east and south of GRTE (National Emissions Inventory, 2008; http://www.epa.gov/ttn/chief/net/2008inventory.html). Wet atmospheric Nr deposition in northwestern Wyoming and southern Montana has been assessed at Gypsum Creek (WY98, elevation 2428 m a.s.l.), Yellowstone National Park (WY08, elevation 1912 m a.s.l.), and Little Bighorn Battlefield National Monument (MT00, elevation 982 m a.s.l.) since the 1980s, as part of the National Atmospheric Deposition Program (NADP; http://nadp.sws.uiuc.edu/sites/sitemap.asp?state=wy). Mean annual Nr deposition rates spanning the water years 1984–2012 ranged 0.8–1.4 kg N ha^{-1} yr^{-1}, and all sites witness an increase in wet-deposition Nr deposition on the order of 0.02 kg N ha^{-1} yr^{-1}. Wet plus dry Nr deposition at the National Oceanic and Atmospheric Administration (NOAA) Climate Center on the east side of the Teton Range (elevation 1978 m a.s.l.) was estimated at 2.5 kg N ha^{-1} for the 2011 water year (Benedict et al., 2013a, 2013b). Deposition of Nr increases with elevation (Williams and Tonnessen, 2000) and because high-elevation watersheds offer little uptake of dissolved inorganic N, high-elevation lakes are subject to the maximum impact of anthropogenic Nr (Seastedt et al., 2004). Therefore, we expected the loads would be near 2.5 kg N ha^{-1} in the many shallow, high-elevation lakes of GRTE. In previous studies, lakes in GRTE were ranked based on sensitivity to acidification due to atmospheric deposition, with 36% of lakes predicted to be vulnerable (Nanus et al., 2003, 2005, 2009). The purpose of this study is to assess the lake-sediment based evidence for regional Nr deposition, its chronology, and the nature of algal community responses in five shallow, high-elevation lakes in GRTE.

Methods

STUDY SITES

Grand Teton National Park is located in northwestern Wyoming (Fig. 1) and is part of the Greater Yellowstone Ecosystem. The park is a designated Class I protected area. The Teton Mountain Range has many peaks over 3000 m in elevation, with more than 100 high-elevation lakes formed in glacially scoured basins last influenced by the late Pinedale glaciation 30,000 to 10,000 years ago (Love and Reed, 1968). The underlying geology is predominantly granite, gneiss, and schist, with veins of volcanic intrusions.

We obtained cores from five lakes (Table 1) based on suitability for recovery of sediment cores for paleolimnological reconstruction. The study lakes include Holly, Surprise, Amphitheater, Grizzly, and Whitebark Moraine Pond (unnamed on USGS maps) (Fig. 1). The lakes are located between 2800 and 3000 m a.s.l. and are small (1.1–4.9 ha surface area), situated in catchments ranging 16–114 ha in area (Table 1). All lakes were less than 10 m in depth. The secchi depth was equal to the maximum depth, or up to 3 m greater than the secchi depth. (Note the relation between secchi depth and euphotic depth is variable [Pennak, 1949; Tilzer, 1988], but by rough approximation, $Z_{eu} \approx 5\sqrt{Z_s}$). Whitebark Moraine Pond is a seepage lake and rooted macrophytes are present over the benthos. The other lakes are drainage lakes, with distinct surface water inlets and outlets. Grizzly and Holly Lakes were stocked in the early 20th century with Yellowstone cutthroat trout, *Oncorhynchus clarki bouvieri* (Hazzard, 1931; Stephens, 2007), and these populations are sustained by natural reproduction. The remaining lakes are fishless.

WATER CHEMISTRY

Lakes were sampled by inflatable raft during the ice-free months of July and August 2010. Each lake was surveyed with a depth finder to determine maximum depth. Samples for water chemistry were collected and secchi depth was measured at the central sampling location of each lake. Water samples were collected from three depths: surface (0.3 m), mid-depth (2–3 m), and deep (1 m from bottom) using a Van Dorn water sampler. Water was collected for dissolved ions, silica, pH, conductivity, and total phosphorus in unused DI-washed Nalgene high-density polyethylene (HDPE) bottles and kept refrigerated or frozen prior to analysis within a few days at the Kiowa Environmental Chemistry Laboratory (INSTAAR, University of Colorado, Boulder, Colorado). A portion of each sample was filtered immediately through prerinsed, precombusted 47-mm, 1.0-µm binder-free Whatman glass fiber fil-

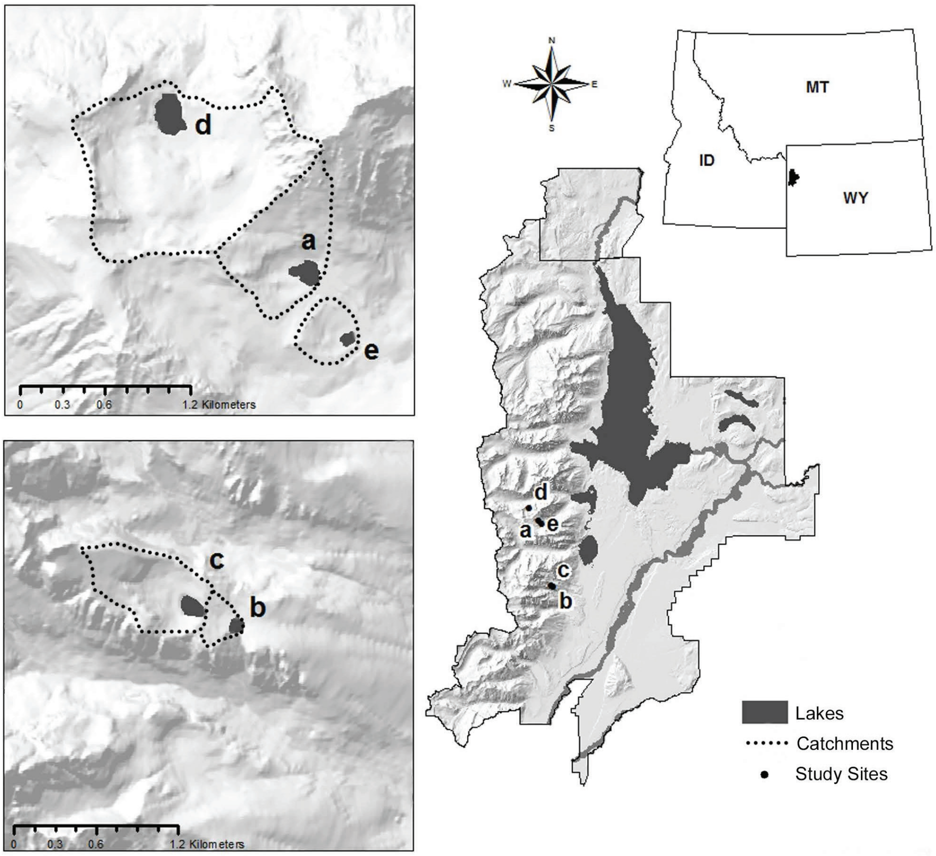

FIGURE 1. Map of Grand Teton National Park, Wyoming, showing the major park water bodies and five study lakes (a) Holly Lake, (b) Surprise Lake, (c) Amphitheater Lake, (d) Grizzly Lake, and (e) Whitebark Moraine Pond (unnamed on published maps), and their watersheds. Base map from U.S. Geological Survey digital data, NAD 1983, UTM Zone 12N.

ters GF/F for filtrate collection. A 100 mL aliquot of filtered sample was refrigerated at ~4 °C in an HDPE bottle for immediate analysis of NH_4^+ and later analysis of anions and cations. A 75 mL aliquot of unfiltered sample was refrigerated at ~4 °C in an HDPE bottle for pH, conductivity, acid-neutralizing capacity (ANC), and total phosphorus. A precombusted glass amber bottle with Teflon lid was used for collection of dissolved organic carbon (DOC) and total dissolved nitrogen.

Lab analyses for pH, conductivity, ANC, inorganic cations (Ca, Mg, Na, K, Li, Mn), nutrients (ammonium, nitrate, nitrite, silica, orthophosphate, and total phosphorus), and dissolved organic carbon were measured by the Kiowa Environmental Chemistry Laboratory using standard protocols (https://instaar.colorado.edu/research/labs-groups/kiowa-environmental-chemistry-laboratory).

CORING AND SEDIMENT CHRONOLOGY

Sediments were collected from the deepest point in each basin with a modified Kajak-Brinkhurst gravity-coring device (Glew, 1989), fitted with a 7.6-cm-diameter clear polycarbonate core tube. Upon visual examination of core stratigraphy and confirmation of an intact sediment-water interface, cores were extruded on site at increments of 0.25 cm from surface sediments to 10 cm, 0.5 cm increments from 10 to 20 cm, and 1 cm increments from 20 cm to the core base. Core sections were bagged in labeled Whirlpak bags and refrigerated until delivery to the Sediment Processing Lab (INSTAAR, University of Colorado, Boulder), where they were weighed, freeze-dried, and archived in glass vials. Bulk sediments were analyzed for moisture content (%H_2O), carbonate (%), organic matter (%), $\delta^{13}C$, C (µg C g^{-1} dry sediment), $\delta^{15}N$, N (µg N g^{-1} dry sediment), and P (µg P g^{-1} dry sediment).

Sieved (100 µm mesh) dry sediment subsamples of 0.1 to 5 g were used for radiometric dating using excess sediment ^{210}Pb activities determined by alpha spectrometry at MyCore Scientific Inc. (Dunrobin, Ontario, Canada). The constant rate of supply method (CRS) was used to model ages from excess ^{210}Pb activities (Appleby and Oldfield, 1978). Samples below the depth of unsupported ^{210}Pb were assigned provisional ages using linear interpolation. Sedimentation rates (g m^{-2} yr^{-1}) were calculated from the cumulative dry mass (g m^{-2}) multiplied by the decay constant (λ, yr^{-1}) divided by the supported sediment ^{210}Pb activity (Bq g^{-1}) derived from secular equilibrium with ^{210}Po.

SOFT ALGAE AND DIATOM ANALYSIS

Phytoplankton samples were collected from three water-column depths from each lake, as with water chemistry (above) and preserved with Lugol's solution. Subsamples were settled in Utermöhl chambers and examined using an inverted microscope for algal species composition. Diatom slide preparation was conducted using 5 mg dry sediment digested in 30% hydrogen peroxide and placed in a hot water bath for 2 days. Peroxidated slurries were rinsed with de-ionized water and centrifuged repeatedly (Renberg, 1990). A 0.4 to 1.0 mL aliquot of Polybead 4.5 µm polystyrene microspheres (concentration: 2.5 × 10^6 spheres mL^{-1}) was added to each digestion for calculation of diatom concentrations (Battarbee, 1973). Spiked slurries were pipetted onto glass cover slips, dried overnight, and mounted using Zrax resin. A minimum of 300

TABLE 1

Lake physical and chemical characteristics from ice-free sampling from July to August 2010 for five lakes in Grand Teton National Park, Wyoming. Water chemistry presented is the mean of three water column samples from the epilimnion (0.3 m), mid-depth (2–3 m), and hypolimnion (0.5 m above maximum depth). Fish status is based on Stephens (2007), when Yellowstone cutthroat trout were found in Grizzly and Holly Lakes. The drainage lakes possess surface water inlets and outlets, while the seepage lake (Whitebark Moraine Pond) lacks a surface water inlet or outlet.

Parameter	Holly Lake	Surprise Lake	Amphitheater Lake	Grizzly Lake	Whitebark Moraine Pond
Latitude (°N)	43.7927	43.7285	43.7297	43.8030	43.7884
Longitude (°W)	–110.7980	–110.7772	–110.7813	–110.8105	–110.7943
Elevation (m)	2870	2915	2957	2810	2801
Lake surface area (ha)	2.8	1.0	2.0	5.2	1.0
Watershed area (ha)	57	43	37	159	16
WA:SA	21	43	19	31	16
Lake type	drainage	drainage	drainage	drainage	seepage
Fish	yes	no	no	yes	no
Maximum depth (m)	8.5	7.0	8.5	7.6	3.7
Secchi depth (m)	5.7	7.0	7.6	5.5	3.7
TN (μmol L^{-1})	3.8	5.2	5.2	5.7	7.7
TP (μmol L^{-1})	0.113	0.097	0.078	0.079	0.155
TN:TP (molar)	33	54	67	72	50
pH	6.8	6.4	6.5	6.8	6.7
Conductivity (μS cm^{-1})	13.3	6.4	6.7	15.6	11.2
ANC (μeq L^{-1})	99	50	50	119	87
DOC (mg L^{-1})	0.59	0.79	0.57	0.51	1.78
NH_4^+ (μmol N L^{-1})	0.610	0.292	0.063	0.063	0.063
Ca^{2+} (μmol L^{-1})	36.3	15.2	16.0	48.4	30.6
Cl^- (μmol L^{-1})	2.7	3.0	2.3	2.2	2.4
NO_3^- (μmol N L^{-1})	0.01	0.01	1.68	1.77	0.01
SO_4^{2-} (μmol L^{-1})	10.6	3.3	3.1	10.6	7.4
PO_4 (μmol L^{-1})	0.022	0.017	0.030	0.022	0.027
Si (μmol L^{-1})	43.1	13.9	14.6	27.9	16.6

Notes: WA = watershed area, SA = lake surface area, TN = total nitrogen, TP = total phosphorus, ANC = acid neutralizing capacity, and DOC = dissolved organic carbon.

diatoms were enumerated under oil immersion at 1000× using an Olympus Vanox microscope equipped with differential interference contrast optics and a 1.3 NA objective. Diatom species identifications were based on several taxonomic sources (Patrick and Reimer, 1966, 1975; Krammer and Lange-Bertalot, 1985, 1986, 1988, 1991, 2000, 2004), in certain instances augmented by confirmations using scanning electron microscopy. Several of the taxa encountered are presented in detail with corresponding light and scanning electron micrographs (Spaulding et al., 2010).

SEDIMENT STABLE ISOTOPES

Sediment stable isotopic composition was measured on freeze-dried bulk sediment samples at the University of California–Davis Stable Isotope Facility. Stable isotopic ratios of C ($\delta^{13}C$) and N ($\delta^{15}N$) were analyzed with a PDZ Europa ANCA-GSL elemental analyzer interfaced with a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, U.K.). Percent elemental C and N were obtained simultaneously from the pyrolytic digestion, enabling the computation of sediment C/N molar ratios. Sediment $\delta^{13}C$ is expressed in ‰ relative to the Vienna PDB standard, whereas $\delta^{15}N$ is expressed in ‰ relative to air ($\delta^{15}N_{air}$ = 0‰). For both isotopic species, analytic reproducibility is of the order ±0.1‰. The $\delta^{13}C$ values in each sediment core were corrected for the Seuss effect, which is the modeled depletion of atmospheric $\delta^{13}C$ values due to accelerated rates of fossil fuel burning during industrialization (Keeling, 2003; Verburg, 2007).

DATA ANALYSIS

Diatom counts from each section were converted to relative frequencies (% of individual taxa relative to total diatom count) for graphing and data analysis. Diatom assemblage data were square-root transformed and subjected to indirect ordination using correspondence analysis (CA) with the Vegan Community Ecology Package (Version 2.0-10) of R (R Core Team, 2013). Relationships to sediment geochemical data (C, δ^{13}C, N, and δ^{15}N) were explored using constrained correspondence analysis (CCA). To further query the data, data were analyzed using PRIMER 6 software (Plymouth Marine Laboratory, U.K.). Species data were standarized, square-root transformed, and plotted using multidimensional scaling (MDS). The relative abundances over time, and their rankings, were identified in each sediment core using the BEST algorithm. BEST selects species that best explain a common pattern by maximizing a rank correlation between respective resemblance matrices. The statistical significance of diatom assemblage change within each core over time was tested using a priori groups (pre-1960 and post-1960) using the RELATE algorithm in PRIMER 6. The RELATE analysis tests the hypothesis of no relation between multivariate samples, the observed set of taxa and a random permutation of taxa. Results are expressed as Spearman's rank correlation (rho) and significance level, in which low *p*-values are random and high *p*-values are nonrandom.

Results

LAKE NUTRIENT STATUS

All lake waters were circumneutral with low conductivity, ionic strength and nutrient (N and P) concentrations (Table 1). Nutrients varied in total concentration and speciation between the lakes (Fig. 2). Total N (TN) concentrations ranged from 3.8 μmol L^{-1} in Holly Lake to 7.7 μmol L^{-1} in Whitebark Moraine Pond. The relative proportions of N species as NH_4^+, NO_3, particulate N (PN), and dissolved organic N (DON) also differed between the lakes (Fig. 2). For example, in Amphitheater Lake, NO_3^-, PN, and DON were present in nearly equal molar proportions. In Whitebark Moraine Pond, DON comprised most of the N pool, consistent with its hydrologic setting as a seepage lake. Total N concentrations varied more between lakes than TP concentrations, which occurred at consistently low concentrations (Table 1). The highest TP concentration was found in Whitebark Moraine Pond and comprised primarily dissolved organic P. The lowest TP concentrations occurred in Amphitheater Lake (Table 1), predominantly in the form of particulate, bound P.

Molar nutrient ratios allow evaluation of nutrient status and estimation of nutrient limitation, factors that are relevant in determining potential for biotic response to increasing deposition of Nr. Molar TN:TP ratios ranged from 33 to 115 (Table 1, Fig. 3). According to accepted classification systems (Guildford and Hecky, 2000; Elser et al., 2009a, 2009b), TN:TP molar ratios greater than 50 are suggestive of P limitation. Using this metric, all lakes except Holly were P-limited. The log DIN:TP (on a mass basis) is an alternate predictor, with log DIN:TP greater than 3.4 representing the threshold for P limitation (Bergström, 2010). According to this metric, all lakes except Whitebark Moraine Pond and Surprise Lake are P limited.

SEDIMENT CHRONOLOGY, GEOCHEMISTRY, AND STABLE ISOTOPES

Sediment data (Table 2) are summarized for each lake (Figs. 4–8), showing the diatom taxa with the greatest change in species composition, or Nr deposition indicator species (if present), downcore sample scores on the first axis of correspondence analysis (CA1), N (μg g^{-1}), δ^{15}N, molar ratio of carbon to nitrogen (C:N), and CRS age model. The CRS ^{210}Pb year 1960 is marked with a horizontal dotted line in each figure.

The CRS ^{210}Pb age models for each of the study lakes are robust (Figs. 4–8). Percent carbonate is low for all lakes, as expected for granitic watersheds. Whitebark Moraine Pond has the greatest percent organic matter. Sediment concentrations of C, N, and P are in the ranges 724–2554 μg C g^{-1}, 44–310 μg N g^{-1}, and 289–1817 μg P g^{-1}, respectively. Sharp increases in sediment N concentrations occur after ca. 1960 in the Holly and Amphitheatre Lake cores, concurrent with decreases in C:N. The bulk N concentration in sediments increases only slightly in Grizzly Lake and negligibly in Surprise and Whitebark Moraine Lakes. The mean bulk δ^{13}C signature in all sediments (Seuss-effect corrected values) ranged from –26.72‰ to –22.64‰ (Table 2). These values are within the range expected of terrestrial soil organic matter, suggesting that allochthonous inputs drive the C budget of these oligotrophic lakes (Boutton, 1991). Bulk δ^{15}N signature, however, became depleted by a mean of 2.2‰ across all lakes over from the oldest sediments to the most recently deposited. Bulk δ^{15}N values fluctuated between 2.6‰ and 1.7‰ prior to 1850, after which they declined linearly to a value of 0.05‰ around the year 2000. The oldest dates obtained from the other four lakes were between 1850 and 1865. Bulk δ^{15}N signatures for

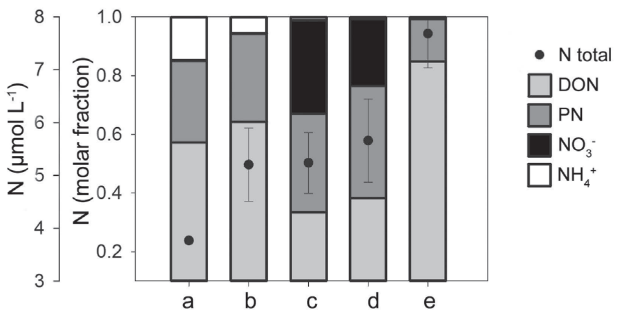

FIGURE 2. Nitrogen speciation for (a) Holly, (b) Surprise, (c) Amphitheater, and (d) Grizzly Lakes, and (e) Whitebark Moraine Pond. Total nitrogen (TN) is given by black circles, whereas bars indicate proportions of dissolved organic nitrogen (DON), particulate nitrogen (PN), nitrate (NO_3^-), and ammonia (NH_4^+).

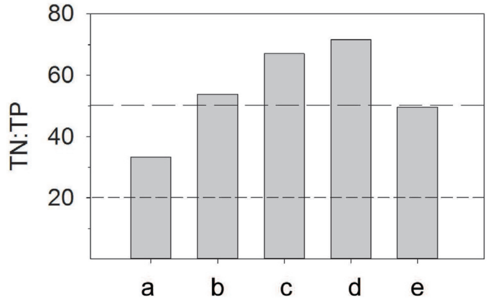

FIGURE 3. Molar ratio of total nitrogen (TN) to total phosphorus (TP) in lake water, with thresholds for nutrient deficiency (Guildford and Hecky, 2000). Below the threshold ratio of 20 (short dashed line) phytoplankton is predicted to be deficient in N. Above a threshold ratio of 50 (long dashed line) phytoplankton is deficient in P. At intermediate molar ratios, either N or P can be deficient, or co-limitation may occur. Lakes are abbreviated: (a) Holly Lake, (b) Surprise Lake, (c) Amphitheater Lake, (d) Grizzly Lake, and (e) Whitebark Moraine Pond.

TABLE 2

Summary sediment geochemistry (mean and standard deviation) for all five lakes. Moisture content (H_2O), carbonate, and organic matter are expressed in percent of dry mass. Sedimentation is presented as a rate (g m^{-2} yr^{-1}). Sediment $\delta^{13}C$ is expressed in ‰ relative to the Vienna PDB standard, and $\delta^{15}N$ is expressed in ‰ relative to air ($\delta^{15}N_{air}$ = 0‰). Concentration of carbon (C), nitrogen (N), and phosphorus (P) are reported in µg g^{-1}. Note that the high sedimentation rate in Holly Lake includes clastic material of varying size classes deposited in the sediments, potentially from avalanche debris.

	Holly Lake	Surprise Lake	Amphitheater Lake	Grizzly Lake	Whitebark Moraine Pond
H_2O	50.9 ± 8.5	83.7 ± 2.7	74.1 ± 6.1	73.0 ± 7.6	89.8 ± 1.3
Carbonate	4.8 ± 2.3	5.1 ± 3.0	1.6 ± 1.0	5.2 ± 2.1	2.5 ± 0.8
Organic Matter	7.4 ± 2.6	17.1 ± 2.6	10.5 ± 3.4	10.1 ± 1.3	23.5 ± 3.7
Sedimentation	46.4 ± 50.9	10.5 ± 1.2	15.1 ± 6.1	9.3 ± 3.8	8.4 ± 2.5
$\delta^{13}C$	–23.5 ± 0.3	–25.6 ± 0.4	–25.9 ± 0.4	–24.6 ± 0.3	–23.7 ± 0.5
$\delta^{15}N$	1.62 ± 1.05	1.42 ± 0.73	1.27 ± 1.40	1.40 ± 0.94	0.57 ± 0.76
C	1870 ± 460	1430 ± 270	1500 ± 260	1720 ± 240	159.0 ± 340
N	196 ± 56	123 ± 20	150 ± 37	160 ± 36	144 ± 28
P	859 ± 398	499 ± 92	622 ± 272	591 ± 98	821 ± 318

the oldest sediments of these lakes varied from 1.2‰ in Whitebark Moraine to 2.8‰ in Holly. The progression from heavier to lighter bulk $\delta^{15}N$ signatures in Whitebark Moraine and Surprise was similar to that from Grizzly beginning about 1920 to present, although there was not a strong inflection point over the ~160 year record. The bulk $\delta^{15}N$ signatures for Holly and Amphitheater also declined from the oldest sediments to 2010, but the rate of depletion increased after ca. 1970 (Figs 4–8). The depleted $\delta^{15}N$ signatures are greater in magnitude than concomitant increases in sediment N concentration.

ALGAL ASSEMBLAGES

Samples collected from the phytoplankton and preserved in Lugol's solution were composed primarily of chlorophytes, with few cyanobacteria (data not shown). No nitrogen fixing

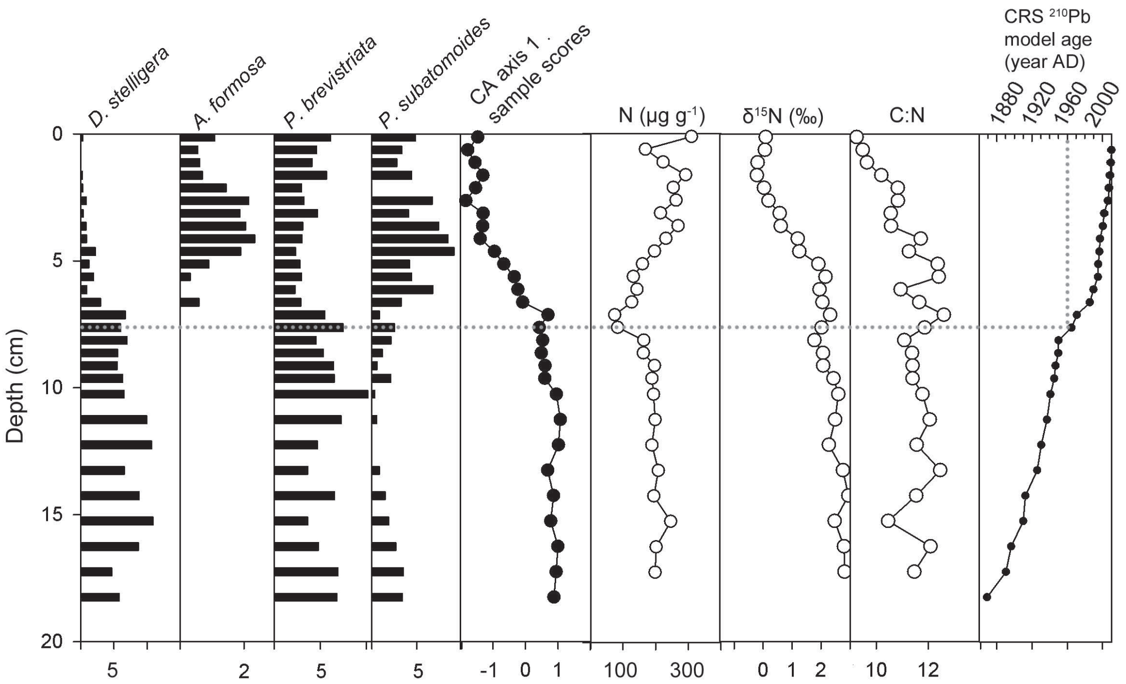

FIGURE 4. **Sediment core fossil diatom stratigraphies and geochemistry from Holly Lake. Horizontal bars of the relative abundance of fossil diatom taxa found in sediment cores with greatest change in species composition, including reactive nitrogen (Nr) deposition indicator species *Asterionella formosa*. Sediment profiles of the first correspondence axis (CA1) based on unconstrained ordination of species relative abundance, N (µg g^{-1}), $\delta^{15}N$, molar ratio of carbon to nitrogen (C:N), and constant rate of supply (CRS) age model. Unconstrained CCA explained 34% of the variance ($p < 0.005$) with an eigenvalue of 0.128 for CA1. The CRS ^{210}Pb year 1960 is marked with a dotted line.**

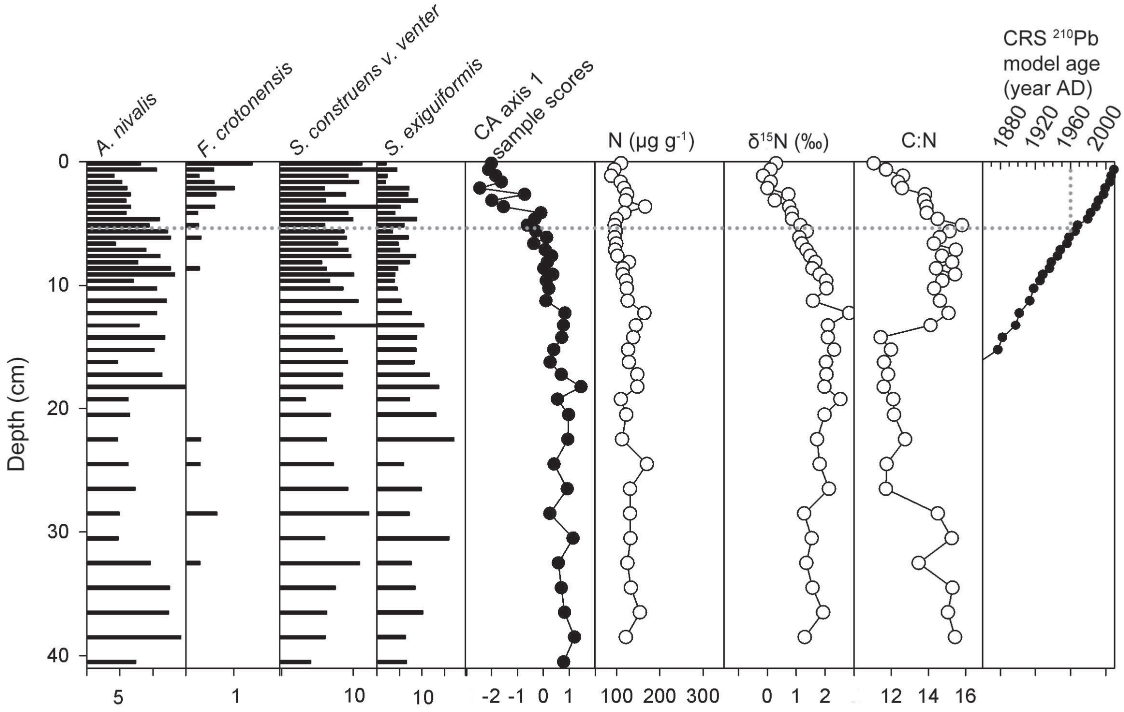

FIGURE 5. **Sediment core fossil diatom stratigraphies and geochemistry from Surprise Lake. Horizontal bars of the relative abundance of fossil diatom taxa found in sediment cores with greatest change in species composition, including Nr deposition indicator species *Fragilaria crotonensis*. Sediment profiles of the first correspondence axis (CA1) based on unconstrained ordination of species relative abundance, N (µg g^{-1}), $\delta^{15}N$, molar ratio of carbon to nitrogen (C:N), and CRS age model. Unconstrained CCA explained 61% of the variance ($p < 0.005$) with an eigenvalue of 0.059 for CA1. The year 1960 is marked with a dotted line.**

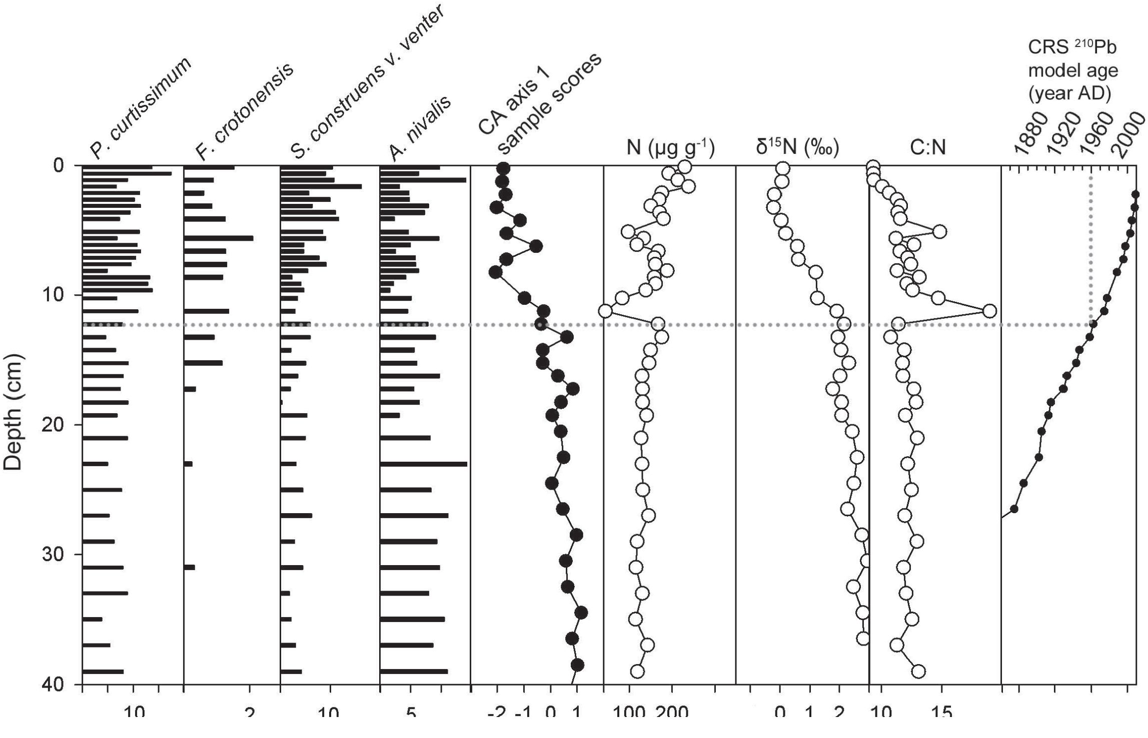

FIGURE 6. **Sediment core fossil diatom stratigraphies and geochemistry from Amphitheater Lake. Horizontal bars of the relative abundance of fossil diatom taxa found in sediment cores with greatest change in species composition, including Nr deposition indicator species *Fragilaria crotonensis*. Sediment profiles of the first correspondence axis (CA1) based on unconstrained ordination of species relative abundance, N (µg g^{-1}), $\delta^{15}N$, molar ratio of carbon to nitrogen (C:N), and CRS age model. Unconstrained CCA explained 33% of the variance ($p < 0.005$) with an eigenvalue of 0.039 for CA1. The year 1960 is marked with a dotted line.**

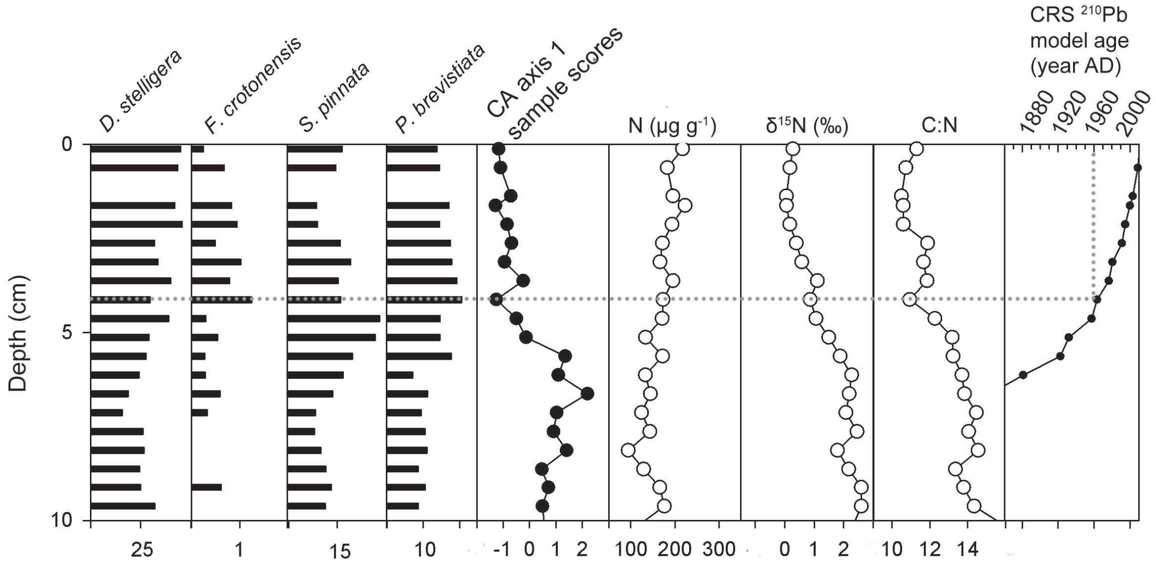

FIGURE 7. Sediment core fossil diatom stratigraphies and geochemistry from Grizzly Lake. Horizontal bars of the relative abundance of fossil diatom taxa found in sediment cores with greatest change in species composition. Sediment profiles of the first correspondence axis (CA1) based on unconstrained ordination of species relative abundance, N (µg g^{-1}), δ^{15}N, molar ratio of carbon to nitrogen (C:N), and CRS age model. Unconstrained CCA explained 25% of the variance ($p < 0.005$) with an eigenvalue of 0.036 for CA1. The year 1960 is marked with a dotted line.

taxa were observed. Planktonic diatoms were present, but low in number at <1000 cells mL^{-1}, with *Discostella stelligera* (Cleve et Grunow) Houk et Klee in Grizzly Lake as the most abundant.

Over 140 diatom taxa were identified from the sediments, with a relatively high species richness of taxa characteristic of oligotrophic conditions. The diatom assemblages are dominated

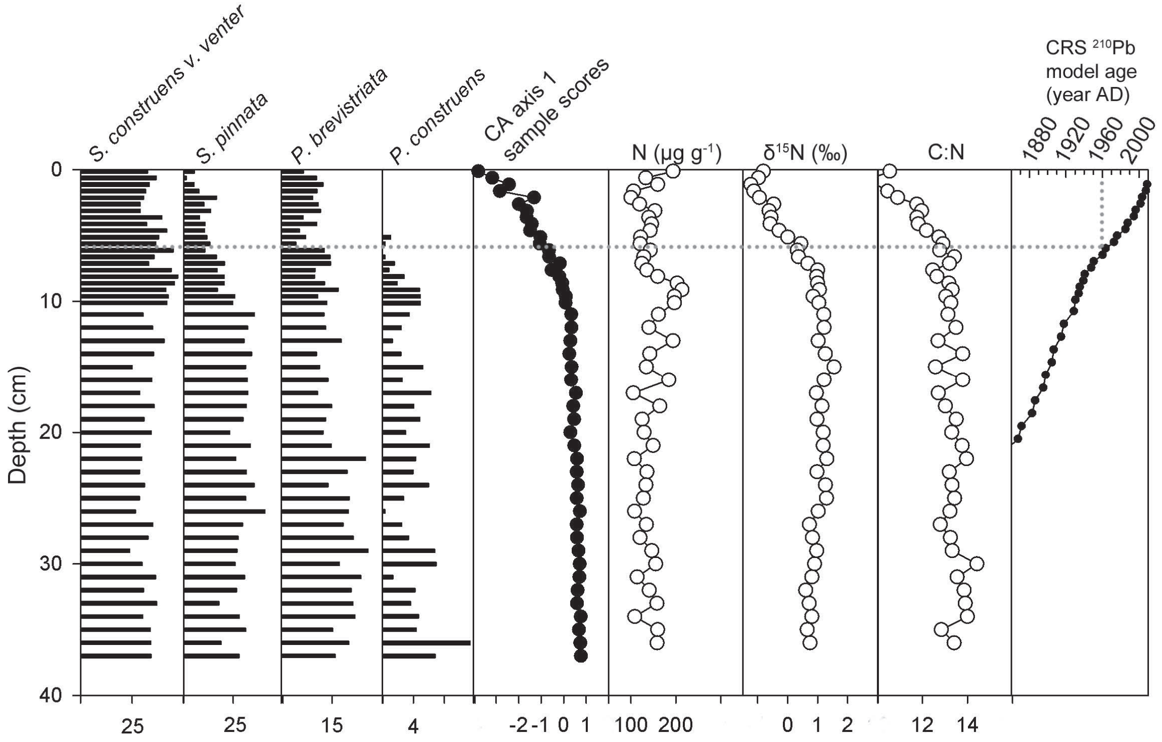

FIGURE 8. Sediment core fossil diatom stratigraphies and geochemistry from Whitebark Moraine Pond. Vertical bar of the relative abundance of fossil diatom taxa found in sediment cores with greatest change in species composition. Sediment profiles of first correspondence axis (CA1), unconstrained ordination of species relative abundance, N (µg g^{-1}), δ^{15}N, molar ratio of carbon to nitrogen (C:N), and CRS age model. Unconstrained CCA explained 36% of the variance ($p < 0.015$) with an eigenvalue of 0.155 for CA1. The year 1960 is marked with a dotted line.

by benthic taxa, especially motile taxa (Table 3). The planktonic mesotrophic marker taxon *A. formosa* became more prevalent in recent decades in Holly Lake. The change in relative abundance, however, was relatively low, reaching a maximum abundance of 3%. Concomitant with the increase of *A. formosa* was a decrease in *D. stelligera*, from over 10% relative abundance to below detection in sediments. A second planktonic, mesotrophic marker, *Fragilaria crotonensis,* increased in recent decades in Surprise and Amphitheater Lakes, but here too, the change was relatively muted, and never exceeded 2%. *Fragilaria crotonensis* was present in other lake sediments, but in trace amounts (Table 3) that lacked robust temporal trends. The taxonomic and temporal structure of these

TABLE 3

Mean relative frequencies of the most common diatom taxa, with taxonomic authorship, identified in the sediments of the study lakes. Taxa that are predominantly planktonic are indicated in bold; motile taxa are indicated by "*."

Taxon	Holly	Surprise	Amphitheater	Grizzly	Whitebark Moraine
*_Achnanthidium minutissimum_ (Kützing) Czarnecki	0.9	0.2	0.3	0.2	0.2
Aulacoseira ambigua (Grunow) Simonsen	2.2	2.1	0.7	0.3	0.1
A. nivalis (W. Smith) English et Potapova	0.1	8.7	6.9	0.2	0.8
Discostella stelligera (Cleve et Grunow) Houk et Klee	4.4	0.0	0.1	31.4	0.0
*_Encyonema minutum_ (Hilse) Mann	0.7	1.2	0.4	0.9	1.2
*_E. graclloides_ Krammer	0.1	1.7	0.8	0.3	0.7
*_E. rostratum_ Krammer	0.0	1.9	1.3	0.1	0.1
*_Eolimna minima_ (Grunow) Lange-Bertalot	0.4	1.3	0.4	0.2	1.8
*_E. subminuscula_ (Manguin) Moser et al.	2.2	2.8	3.3	0.7	0.9
*_Fallacia indifferens_ (Hustedt) Mann	0.1	1.2	1.4	0.5	0.5
Fragilaria crotonensis Kitton	0.2	0.2	0.4	0.5	0.0
*_Navicula digitulus_ Hustedt	0.9	1.9	1.5	1.5	0.4
*_N. leptostriata_ Jorgensen	0.4	0.7	0.2	0.1	0.7
*_N. schmassmanni_ Hustedt	2.1	1.0	1.4	2.2	0.0
*_Nitzschia bulnheimiana_ (Rabenhorst) H.L. Smith	0.3	0.0	0.0	0.2	0.7
*_Nupela fennica_ (Hustedt) Lange-Bertalot	0.0	0.1	0.1	1.6	0.1
*_N. vitiosa_ (Schimanski) Siver et Hamilton	1.4	0.1	0.7	0.2	0.1
*_Pinnularia microstauron_ var. _nonfasciata_ Krammer	1.2	5.6	4.5	1.4	0.8
*_Psammothidium curtissimum_ (Carter) Aboal et al.	2.8	4.8	8.8	2.5	0.7
*_P. daonense_ (Lange-Bertalot) Lange-Bertalot	0.7	4.9	8.0	0.8	0.3
*_P. didymum_ (Hustedt) Bukhtiyarova et Round	1.6	0.0	0.0	0.3	0.0
*_P. helveticum_ (Hustedt) Bukhtiyarova et Round	0.5	1.1	1.7	0.9	0.3
*_P. levanderi_ (Hustedt) Bukhtiyarova et Round	0.7	1.9	0.1	0.6	0.2
*_P. subatomoides_ (Hustedt) Bukhtiyarova et Round	4.1	4.5	7.2	4.6	0.6
*_Pseudostaurosira brevistriata_ (Grunow) Williams et Round	1.3	0.2	0.1	13.4	11.9
*_P. pseudoconstruens_ (Marciniak) Williams et al. al.Round	2.1	0.0	0.0	0.3	2.9
*_Sellaphora disjuncta_ (Hustedt) Mann	1.3	0.0	0.0	0.7	0.2
*_S. laevissima_ (Kützing) Mann	0.8	0.4	0.2	0.5	1.2
*_S. pupula_ (Kützing) Mereschkowsky	1.3	1.5	1.5	0.3	0.3
*_S. seminulum_ (Grunow) Mann	3.6	5.4	3.6	2.3	0.7
Stauroforma exiguiformis (Lange-Bertalot) Flower et al.	0.8	7.2	2.6	0.4	1.0
*_Stauroneis neohyalina_ Lange-Bertalot et Krammer	0.1	1.0	1.2	0.2	0.2
Staurosira brevistriata (Grunow) Williams et Round	13.3	0.0	0.0	0.7	2.3
S. construens var. _venter_ (Ehrenberg) Hamilton	7.7	12.8	5.9	0.4	34.1
Staurosirella oldenburgiana (Hustedt) Morales	2.6	0.0	0.0	0.3	0.2
S. pinnata (Ehrenberg) Williams et Round	15.0	0.1	0.0	14.6	22.5

TABLE 4

Diatom taxa and their ranking, from highest to lowest, in influence to assemblage change over time was determined using the BEST algorithm. The BEST analysis selects species that best explain a pattern by maximizing a rank correlation between respective resemblance matrices. Grizzly Lake and Whitebark Moraine Pond had the fewest diatom taxa that drove assemblage change; their rankings are shown here. The other lakes (Holly, Surprise, and Amphitheater) had fifteen taxa, or more, contributing to assemblage change.

Taxon rank	Grizzly	Whitebark Moraine
1	*Discostella stelligera*	*Staurosira construens*
2	*Staurosirella pinnata*	*Staurosira construens* var. *venter*
3	*Pseudostaurosira brevistriata*	*Staurosirella pinnata*
4	*Psammothidium subatomoides*	*Pseudostaurosira brevistriata*
5	*Psammothidium curtissimum*	
6	*Navicula seminulum*	
7	*Psammothidium helveticum*	

changes is similar to those observed elsewhere in deeper lakes of the Rocky Mountains, but to a lesser extent (Wolfe et al., 2003; Saros et al., 2005b).

Diatom assemblage changes in Surprise and Amphitheater Lakes and Whitebark Moraine Pond were nearly exclusively benthic taxa (Figs. 5, 6, and 8). For example, in Whitebark Moraine Pond, *Staurosirella pinnata* (Ehrenberg) Williams et Round and *Pseudostaurosira brevistriata* (Grunow) Williams et Round decreased in relative abundance in recent decades. Other shifts were more subtle and only apparent when the entire assemblage was taken into account through unconstrained correspondence analysis (CA). The first axis sample scores of the CA reflect temporal variation in species composition (Figs. 4–8). Not only does the diatom composition of each lake show distinct temporal change, but the assemblages change near, or prior to, 1960 in all of the lakes.

The taxa that changed in relative abundance over time, however, differed among lakes (Table 4). The changes in assemblage were attributed to 4 taxa in Whitebark Moraine Pond, 7 taxa in Grizzly Lake, 15 taxa in Holly Lake, and >15 taxa in Surprise and Amphitheater Lakes. The only species that decreased post-1960 in both Grizzly and Whitebark Moraine Pond were *P. brevistriata* and *S. pinnata.* In summary, the shifts in species composition were attributed to a number of taxa, and those shifts were not similar across lakes. This response differs from the response of deeper lakes in the presence of increased Nr, in which species shifts are generally among the same species, such as *A. formosa*. Furthermore, shifts in species abundance (Table 4) or replacement (Figs. 4–8) do not support the idea that sediment compaction in older sediments is responsible for the temporal changes.

TABLE 5

Summary of analyses using the RELATE test. Diatom assemblages from each lake were separated a priori into pre- and post-1960 populations and analyzed for random versus non-random changes in distribution. Results are expressed as Spearman's rank correlation (ρ) and significance level (*p* value), with high significance levels ($p < 0.005$) indicating random distributions. Significant directional changes are shown in bold.

Lake	ρ	*p* value
Holly pre-1960	0.658	0.001
Holly post-1960	**0.116**	**0.159**
Surprise pre-1960	0.325	0.001
Surprise post-1960	**0.215**	**0.051**
Amphitheater pre-1960	0.464	0.001
Amphitheater post-1960	**0.727**	**0.029**
Grizzly pre-1960	0.402	0.001
Grizzly post-1960	**0.241**	**0.147**
Whitebark Moraine pre-1960	0.323	0.001
Whitebark Moraine post-1960	0.478	0.001

Within each lake record, the statistical significance of assemblage change (based on the first correspondence axis) over time was tested using a priori selected groups (pre-1960 and post-1960). In all lakes except Whitebark Moraine Pond, pre-1960 assemblages differed significantly from post-1960 assemblages (Table 5, Fig. 9). Prior to 1960, algal assemblages fluctuated in a statistically random fashion (based on the PRIMER RELATE function). Post-1960, algal assemblages exhibited significant directional change. Whitebark Moraine Pond was an exception, in that assemblage shifts were not significant at the 1960 break point. The lack of significance is likely due to assemblage changes that began prior to 1960 (Fig. 8). The first CA axis was also evaluated using cluster analysis to examine natural break points in community composition. Such break points were present in all lakes, but none was statistically significant.

The $\delta^{15}N$ signatures were most correlated with diatom community composition, explaining 2.9%–11.3% of the variance (Table 6). The relationship was statistically significant in Holly, Amphitheater, Grizzly, and Whitebark Moraine Lakes. The second strongest correlation was between N concentration and diatom community composition, explaining 2.2%–5.2% of the variance (Table 6).

Discussion

Benthic algae are less sensitive to nutrient inputs than planktonic algae, and we expected that changes in sediment diatoms in shallow lakes might not show evidence of deposition of atmospheric Nr. The GRTE lakes did, however, demonstrate assemblage-wide shifts in diatom assemblage, as evidenced by the following:

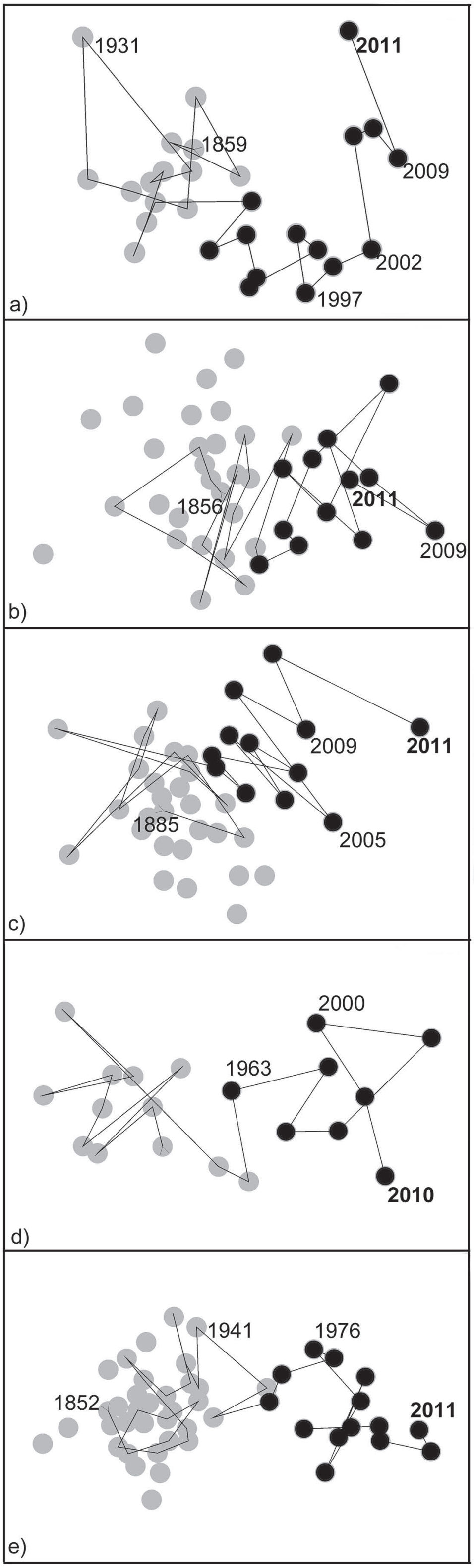

FIGURE 9. Multidimensional scaling (MDS) of the sediment core fossil diatom assemblage data, showing change over time of the five study lakes, (a) Holly Lake, (b) Surprise Lake, (c) Amphitheater Lake, (d) Grizzly Lake, and (e) Whitebark Moraine Pond. Years (2010 or 2011) in bold font marks the upper, most recent section of the core. Core sections are joined in chronologic order, with points prior to 1850 unmarked because of limits of CRS ^{210}Pb. Core sections prior to 1960 are shown by gray circles; core sections post 1960 are shown by black circles.

TABLE 6

Summary of CCA results constraining diatom assemblages to sediment δ^{15}N and N concentration. Results are expressed as % variance explained by δ^{15}N ‰ and N, significance level (*p*), and number of samples (*n*). Significance levels (*p* < 0.005) are shown in bold.

Lake	δ^{15}N	*p*	N	*p*	*n*
Holly	11.3	**0.005**	2.98	**0.001**	28
Surprise	2.90	0.015	0.01	0.400	48
Amphitheater	5.20	**0.005**	3.00	0.050	38
Grizzly	6.88	**0.005**	5.20	**0.005**	20
Whitebark Moraine	4.80	**0.005**	2.20	**0.005**	40

(1) significant assemblage changes centered on ca. 1960, (2) pre-1960 assemblages differed significantly from post-1960 assemblages (Whitebark Moraine Pond is an exception, likely because the assemblages show change prior to 1960), (3) pre-1960 diatom assemblages fluctuated randomly, whereas post-1960 assemblages showed directional change, (4) changes in δ^{15}N signatures were correlated with diatom community composition in Holly, Amphitheater, Grizzly, and Whitebark Moraine Lakes.

Multiple physical factors create bias toward the dominance of benthic primary production in shallow high-elevation lakes. Incident light is available to diatoms growing in littoral zones (benthic areas above the light compensation depth) because of the high water transparency. Dissolved and particulate organic matter is greater in the sediments than in the water column, so that cells in close contact with sediments are less likely to be nutrient limited than planktonic cells (Saros et al., 2005a, 2005b). Furthermore, plankton may be at a distinct disadvantage, especially when dissolved organic carbon concentrations are low and minimally absorb damaging ultraviolet radiation. Ultraviolet radiation inhibits growth (Vinebrooke and Leavitt, 1999), creating more transparent waters and favoring benthic diatoms that can escape ultraviolet radiation by migrating within the surface sediments.

Despite the fact that benthic algae are less sensitive to nutrient inputs, our results indicate biotic response of shallow lakes to deposition of atmospheric Nr, as registered by N isotopic depletion. The sediments show depletion of δ^{15}N by a mean of 2.2‰ across all lakes, and may reflect a combination of (1) changing atmospheric acidity, (2) diagenesis, and (3) accelerated Nr deposition across both urban and remote regions of the northern hemisphere (Hobbs et al., 2010; Holtgrieve et al., 2011; Benedict et al., 2013a; Wolfe et al., 2013; Geng et al., 2014). First, although high-elevation Teton lakes are vulnerable to acidification by Nr introduced through atmospheric deposition (Nanus et al., 2009), neither the water chemistry (Table 1) nor diatom species shifts are indicative of acidification. Greenland ice core records suggest that around 1850, an equilibrium shift in gas-particle partitioning of atmospheric nitrate occurred. This, rather than direct deposition of N species to remote Greenland, was due to increases in industrial sulfur and nitric oxide emissions in the northern hemisphere (Geng et al., 2014). Second, diagenetic processes within lake sediments typically alter the primary atmospheric isotopic signals (Lehmann, 2002; Enders et al., 2008). A model to account for the diagenetic effect on sedimentary lake δ^{15}N was applied to Holly Lake, demonstrating a strong correlation between the measured and modeled δ^{15}N (Brahney et al., 2014b). We therefore conclude that diagenesis did not influence the timing or direction of the isotopic signal in these lakes. Third, $\delta^{15}N$ signatures were most correlated with diatom community composition, with statistically significant relationships in Holly, Amphitheater, Grizzly, and Whitebark Moraine Lakes. Grizzly Lake's sediments, much older than 1850, begin to show a trend of linear depletion of $\delta^{15}N$ near 1850. The other four lakes show a similar depletion, but since the cores are younger, we cannot tell when the bulk signatures began to change. The rate of depletion for two lakes, Holly and Amphitheater, increases again between ca. 1970–1980 (Figs. 4 and 6), and may reflect increased atmospheric N deposition from regional agricultural or industrial sources (Holtgrieve et al., 2011; Benedict et al., 2013b). Holly and Amphitheater have the lowest watershed area to lake area ratio of all the study lakes, possibly unmasking atmospheric deposition signals that are attenuated in catchments with a greater proportion of soils and vegetation.

We are not able to discount the effect of climatic warming on GRTE lakes, especially because diatom response to warming has been documented, particularly across the Arctic (Douglas et al., 1994; Smol et al., 2005). Warming is likely to be greater in shallow lakes than in deeper lakes, especially during the brief ice-free summer season. A trend in rising temperatures, decline in precipitation, and increase in drought frequency have been documented in Wyoming (Mote et al., 2005). An increased relative abundance of a planktonic taxon, *D. stelligera,* has been attributed to climate warming in Arctic and boreal lakes (Rühland et al., 2008), while its near disappearance has been attributed to atmospheric metal pollution (Moser et al., 2010). Such variable responses of a species to differing environmental change reinforce the designation of *D. stelligera* as sensitive to environmental disturbance. The relation of *D. stelligera* relative abundance to lake nitrate concentration was indistinguishable from *A. formosa* in other Rocky Mountain lakes (Arnett et al., 2012). The proximate cause of the near disappearance of *D. stelligera* in recent decades in Holly Lake is unclear, although others (Arnett et al., 2012) confirmed that *D. stelligera* and *A. formosa* did not co-dominate in oligotrophic lakes, a pattern we also observed in shallow lakes. Instead, their relative abundances were inversely related.

Fish introductions could potentially influence species composition, $\delta^{15}N$, and C:N sediment trends. The introduction of fish can alter lake P concentrations and cycling (Parker et al., 2001). Holly and Grizzly Lakes are known to have been stocked with fish, but there is no documentation for the other lakes. Nevertheless, all lakes share the same trend in depleted $\delta^{15}N$, C:N ratios, and diatom community composition over time. Although we are not able to rule out the influence of fish on long-term species composition, we conclude that there is little support for the presence of fish impacting the $\delta^{15}N$ signatures.

Only Holly Lake appeared to be limited by N based on water chemistry, but water column solute chemistry is a poor index of the nutrient environment available to benthic diatoms. Furthermore, water chemistry values were based on samples collected in late summer, and N values typically reach maximum values during spring snowmelt. Nevertheless, the increase of *A. formosa* in the Holly Lake sediment record is commensurate with declines in C:N ratios, suggestive that greater planktonic Nr availability may have stimulated an increase in this taxon. Similarities favor planktonic algal productivity in Holly and Grizzly Lakes: both have higher water column Si than the other lakes, and the secchi depths are shallower than the lake bottom, suggesting benthic algal growth might be limited at depths deeper than about 5.5 m. In deeper lakes, benthic species are exposed to low light intensities, and may be in fact shaded by increases in phytoplankton driven by eutrophication.

It is possible that a combination of warming and N deposition could affect benthic diatoms through altered trophic level interactions (Thompson et al., 2008), habitat disturbance, and altered water transparency. Of all the study lakes, Whitebark Moraine Pond experienced the greatest relative change in diatom species assemblage, and the shift (decline of the first CA axis) began prior to other lakes. Whitebark Moraine Pond is a small lake (1 ha) and the shallowest (3.7 m) of the study lakes. It has the greatest potential for warming by absorbance of heat by the lake sediments, particularly during the summer months. Given the outlook for greater warming, the lakes will likely experience more ice-free days and warmer summer water temperatures. Synergy between warming temperatures and increased Nr deposition would be expected to accelerate primary production, favoring the accelerated C fixation and lower C:N, further altering benthic diatom species composition.

Conclusions

Shallow high-elevation lakes of GRTE contain large littoral zones, which are typically areas of high productivity and biodiversity (Cantonati and Lowe, 2014). Benthic diatoms in the littoral zone tend to be limited by light, rather than nutrients (Vadeboncoeur et al., 2001), which is likely the reason for a muted or indirect response to the nutrient status of the water column. Therefore, among lakes vulnerable to atmospheric deposition of Nr, shallow lakes are the least likely sites we expect to see biotic changes. Yet, benthic diatom assemblages are altered in GRTE lakes near 1960, in association with depletion of $\delta^{15}N$. It is also possible, however, that the combined effect of Nr deposition and warming accelerates the response of species shifts in benthic diatoms in shallow lakes. This study did not address the potential synergy of Nr deposition and warming, yet the combined effects may provide part of the explanation for the unexpected response by benthic diatoms. While uncertainties remain about the potential synergy of Nr deposition and warming, this study adds shallow lakes to the growing list of impacted high-elevation localities in western North America.

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