

Recent changes in production in oligotrophic Uinta Mountain lakes, Utah, identified using paleolimnology

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Abstract

We use multiple proxies from lake sediment records of six remote alpine lakes in the Uinta Mountains, Utah, to investigate primary production and potential drivers of changes in trophic status over the last two centuries. Chlorophyll *a*, chlorophyll *a* flux, and percentage of organic matter (determined by loss on ignition) increase beginning in the mid-20th century in five of the six alpine study lakes, indicating increasing production. These changes tend to coincide with decreasing sedimentary $\delta^{15}\text{N}$ and increasing abundance of the nitrophilous diatom *Asterionella formosa*. An earlier, more subtle change in diatom community composition and $\delta^{15}\text{N}$ indicates that human activities prior to 1950 had measurable effects on these lake ecosystems, although no corresponding increase in primary production was observed at this time. Multiple factors can lead to increased primary production at alpine sites, but the evidence presented shows that enhanced atmospheric deposition of nitrogen and phosphorus explain the recent, more prominent increase in production. Although previous research has suggested that alpine lakes are nitrogen limited, our results suggest nutrient limitation varies spatially and temporally, and is complex in these oligotrophic systems. This and other factors, such as catchment characteristics, will affect the sensitivity of a lake to atmospheric deposition–fertilizing effects. The changes observed show that remote lakes are vulnerable to long-distance transport of nutrients, and that the risk of eutrophication could be intensified by increased nutrient inputs from expanding mining, fossil fuel combustion, and agriculture and by rapid warming predicted for the southwest.

In this study, we investigate the potential drivers of changing primary production since the 19th century in alpine lakes in the Uinta Mountains, Utah. Because phosphorus (P) and nitrogen (N) are the elements that most often limit freshwater production, changes in inputs of N or P can alter ecosystem processes, reduce biodiversity, and lead to surface-water eutrophication (Vitousek et al. 1997). Although few symptoms of eutrophication have been reported for Uinta Mountain lakes, the rapid industrial, agricultural, and urban expansion occurring upwind of the Uinta Mountains along the Wasatch Front may put Uinta Mountain lakes at risk of enhanced deposition of nutrients, in particular fixed N species (NO_3^- and NH_4^+) and P, which are delivered mainly by precipitation and dust, respectively.

In the last century, humans have drastically increased the amount of biologically available N (NO_3^- and NH_4^+) on a global scale, largely via synthetic fertilizer use, fossil fuel burning, intensive animal husbandry, and the cultivation of leguminous crops (Vitousek et al. 1997). Records maintained by the National Atmospheric Deposition Program National Trends Network (NADP NTN; <http://nadp.sws.uiuc.edu/ntn/>) for the U.S.A. show that on a national scale, areas with the greatest wet deposition of NO_3^- and NH_4^+ generally coincide with areas of high population density and intensive agriculture. In these areas, runoff from fields and urban areas, sewage, and industrial effluent tend to be much greater sources of N to aquatic systems than

atmospheric deposition. In contrast, in remote alpine sites, atmospherically derived N makes up a larger proportion of anthropogenic N inputs, as many of the other sources are absent. High-resolution modeling of N deposition that combines NADP NTN records with United States Geological Survey (USGS) annual snowpack surveys and precipitation models reveals that remote high-elevation sites have some of the highest levels of atmospheric nitrate deposition in the western U.S. (Nanus et al. 2012). Elevated atmospheric N deposition resulting from N volatilized from farmer fields and feedlots or from fossil fuel combustion has been linked to subtle ecological changes in alpine, arctic, boreal, and temperate sites in the Northern Hemisphere (Holtgrieve et al. 2011).

Although it is evident that recent values of $\delta^{15}\text{N}$ in lake sediments are decreasing in a variety of remote aquatic systems (Holtgrieve et al. 2011), there are still uncertainties regarding the influence of factors other than enhanced atmospheric N deposition on primary production in dilute alpine systems (Catalan et al. 2013). For example, P has been given relatively little attention in these environments, even though particulate P in dust can contribute substantial amounts to an alpine lake (Psenner 1999). Recent increases in P loading to Emerald Lake, Sierra Nevada Mountains, California, have been attributed to atmospheric deposition of organophosphate pesticide or aeolian transport of dust from the San Joaquin Valley (Sickman et al. 2003). Climate warming, local grazing, and fish stocking can influence primary production and result in changes in $\delta^{15}\text{N}$; diagenesis of organic matter can also mimic some of the

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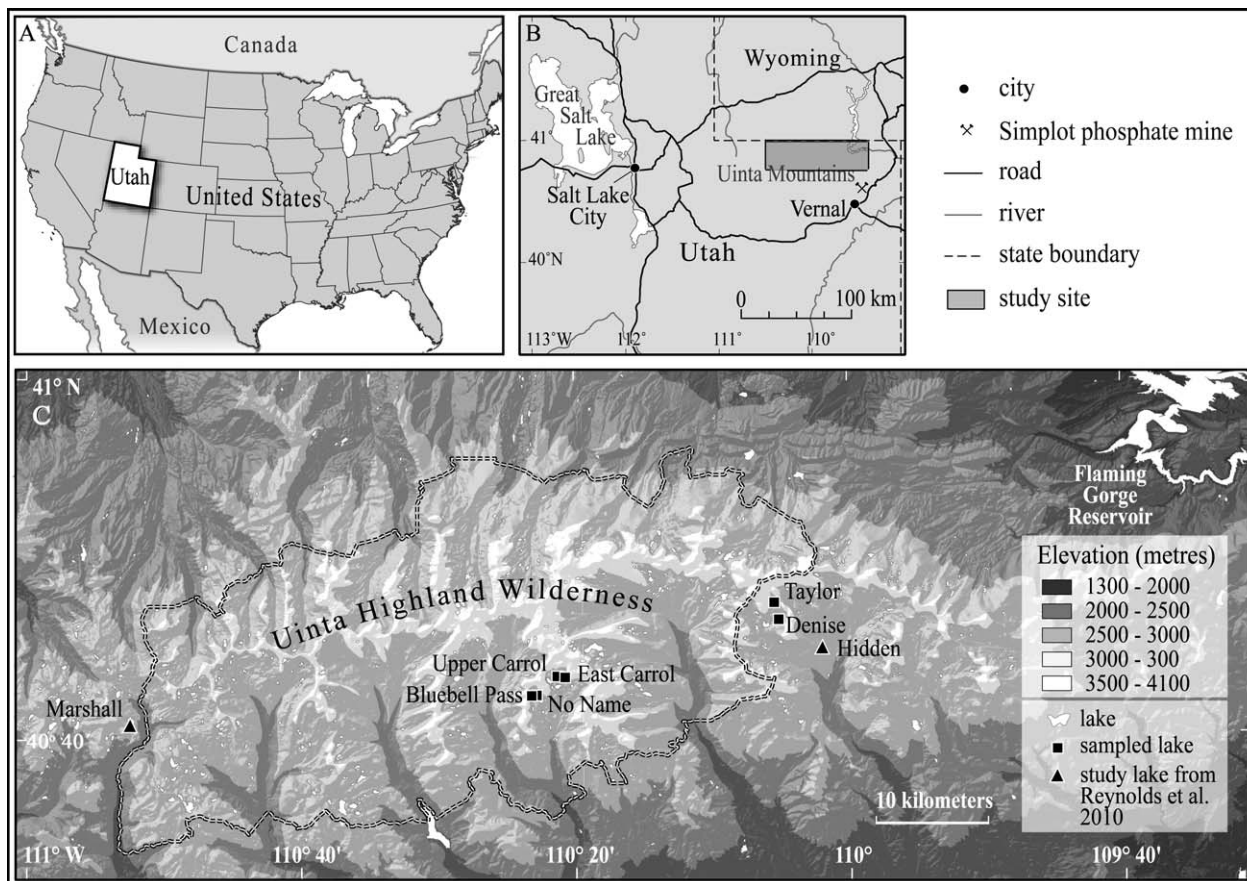


Fig. 1. Map of northeastern Utah showing (A) the location of Utah in the U.S., (B) the location of the Uinta Mountains in northeastern Utah, and (C) the topography of the Uinta Mountains with the locations of the six study lakes and Hidden and Marshall Lakes.

geochemical changes expected with increasing primary production. To mitigate the confounding influence of diagenetic effects, we employ a multiproxy approach with independent proxies of production, including spectral analysis of sedimentary chlorophyll *a* (Chl *a*) that tracks both primary and degraded chlorophyll (Michelutti et al. 2005).

Alpine environments have several characteristics that make them sensitive to changes in nutrient inputs. (1) Some alpine environments are subject to greater atmospheric deposition than low-lying areas at similar latitudes because of orographic precipitation, higher wind speeds, and increased cloud presence (Lovett 1994). (2) Snowmelt-dominated hydrology, combined with low biological N demand in spring, leads to seasonal spikes in surface-water NO_3^- and NH_4^+ concentrations (Campbell et al. 2000). (3) Short growing seasons, minimal vegetation, and steep slopes limit N retention in the terrestrial environment (Campbell et al. 2000).

Because the Uinta Mountains have no NADP NTN sites, limited lake water monitoring records, and only short-term snow water chemistry records (< 5 yr), we collected and analyzed lake sediment cores from six high-elevation Uinta Mountain lakes. A set of geochemical and biological proxies was analyzed to explore for and evaluate

potential causes of recent primary production changes in these alpine environments. The percentage of organic matter (determined by loss on ignition), along with Chl *a*, can be a useful indicator of primary production. Stable isotopic ratios of organic matter N ($^{15}\text{N}:^{14}\text{N}$) provide evidence for changing N sources and cycling, and are useful for comparison with previous research. Stable isotopic ratios of organic matter carbon ($^{13}\text{C}:^{12}\text{C}$) contribute to our understanding of changes in primary production. Carbon (C):N ratios are used to evaluate the relative proportions of algal versus terrestrial organic matter contributions to the lake (Meyers and Ishiwatari 1993). Diatoms have been selected as a biological proxy based on their sensitivity to changing nutrients (Hall and Smol 2001) and expected strong response to increased N availability.

Methods

Study area—The Uinta Mountains are an east–west trending mountain range that reaches elevations over 4000 m above sea level (a.s.l.), and stretches 200 km across the northeastern part of Utah (40° – 41° north, 109° – 111° west) to northwestern Colorado (Fig. 1). The mountain range contains hundreds of lakes and has minimal exposure to direct human activity, making it ideal for investigating

Table 1. Summary characteristics of the six study lakes. Secchi depths are averages of single measurements taken in 2007 and 2008. Chl *a* values are averaged from water samples taken in 2007–2009, 2011, and 2012. Temperature, pH, specific conductivity, and dissolved oxygen were measured at 0.5 m intervals for each lake, at the deepest part of the lake, which allowed us to determine whether or not the lakes were stratified. Trophic status was determined by comparison of Secchi depth, TP, TN, and Chl *a* values to those listed in table 13–18 of Wetzel (2001). Oligo, oligotrophic; meso, mesotrophic.

Lake name	Latitude (°N)	Longitude (°W)	Elevation (m a.s.l.)	Lake depth (m)	Stratifies	Secchi depth (m)	Trophic status
Denise	40.77	110.09	3399	2.4	no	>2.4	oligo
Taylor	40.79	110.09	3414	9.7	yes	3.4	oligo–meso
Upper Carrol	40.72	110.35	3395	13.8	yes	4.7	oligo–meso
East Carrol	40.72	110.35	3423	5.5	no	3.3	oligo–meso
No Name	40.71	110.38	3355	5.4	no	>5.4	oligo
Bluebell Pass	40.70	110.39	3342	7.7	yes	2.1	oligo–meso

nutrient inputs and lake response. The geology is primarily quartzite, sandstone, and shale. Model results combining NADP NTN and snow chemistry data indicate that the highest elevations of the Uinta Mountains receive 0.02–0.03 kg km⁻² inorganic N annually, and exceed critical loads of N deposition (Nanus et al. 2012). Inorganic N deposition in the Uinta Mountains is higher than in most low-lying areas of the western U.S., but similar to other high-elevation regions such as the Colorado Front Range, which receives 0.02–0.04 kg km⁻² inorganic N annually (Nanus et al. 2012).

Six high-elevation (> 3000 m a.s.l.) lakes were selected for this study in order to detect variability in lake responses. Consideration of other catchment features (e.g., vegetation cover, type of vegetation, seepage lake or not), when available, were useful here. The lakes, with Utah Department of Wildlife Resources codes in parentheses, are Denise (WR-9), Taylor (WR-8), Upper Carrol (X-18), East Carrol (X-21), No Name (X-26), and Bluebell Pass (X-25; Table 1). Lakes were selected to maximize differences in other catchment features.

Water chemistry—Water samples were obtained from each lake in late July and early August of 2007–2010. Water samples were collected in pre-cleaned polyethylene Nalgene® bottles from the deepest part of the lake, 0.5 m below the surface, and were kept cool in the field (~ 1–3 d) until they were returned to the Ashley National Forest in Vernal, Utah. The water samples were used for nutrient analysis (nitrite + nitrate, nitrite, ammonium, phosphate, total P [TP], and total N [TN]) and filtered for Chl *a*. The samples were frozen immediately after filtering and sent to Chesapeake Biological Laboratory in Maryland for analyses. The Chesapeake Biological Laboratory protocols are available from <http://nasl.cbl.umces.edu/>. Trophic status was determined by comparison of Secchi depth, TP, TN, and Chl *a* values to those reported in tables 13–18 of Wetzel (2001). At the time of sampling temperatures were recorded at 0.5 m intervals at the deepest part of the lake to determine whether the lake was thermally stratified.

Sediment coring—Lake sediment cores between 25 and 50 cm in length with an undisturbed sediment–water interface were obtained from the deepest part of each lake during the summers of 2006 (Taylor and Denise Lakes) and

2007 (East Carrol, Upper Carrol, No Name, and Bluebell Pass Lakes) using a Kajak-Brinkman gravity corer fitted with a plastic coring tube of 6.5 cm inner diameter. Lake sediments were extruded on site and were subsampled at 0.5 cm contiguous intervals, except at depths greater than 20 cm in Taylor and Denise Lakes, which were subsampled at 1 cm intervals. The subsamples were stored in Whirlpak® bags in dark conditions at 4°C at the Lakes and Reservoir Systems Research Facility at the University of Western Ontario, London, Ontario, Canada.

Chronology—Lake sediments were dated using ²¹⁰Pb (half-life = 22.26 yr) techniques (Appleby 2001) on 15 dried and ground samples per lake between 0 and 22 cm core depth. Samples were initially analyzed using α -spectrometric measurements of ²¹⁰Po, a decay product of ²¹⁰Pb, at MyCore Scientific in Deep River, Canada (Cornett et al. 1984). The ²¹⁰Pb ages were calculated using the constant rate of supply (CRS) model, in which lake sediments are assumed to be receiving a constant input of unsupported ²¹⁰Pb from the atmosphere (Appleby 2001) and the background (supported ²¹⁰Pb) was determined as the average of the constant ²¹⁰Pb concentrations in the three to five deepest sections of the core. The supported ²¹⁰Pb concentrations in these cores are higher than in some other areas because the rocks in the study area are enriched in uranium and radium. The errors on the dates in the oldest sediment layers were large (27–418 yr; Fig. 2); to verify these dates, γ spectrometry was used for two lakes (Taylor and East Carrol). Gamma spectrometry can provide a more accurate determination of background (supported) ²¹⁰Pb in this type of lake (Appleby 2001), and therefore reduce errors, allowing us to confirm the α -spectrometric dates. The γ -spectrometric technique also provides an independent verification of the ²¹⁰Pb dates by the simultaneous analysis of ¹³⁷Cs, an artificial radioisotope produced by nuclear weapons testing, which peaked in 1963. These measurements were made at the Paleoecological Environmental Assessment and Research Laboratory (PEARL) at Queen's University, Canada. Dates were calculated using the Binford package (Jeziorski and Thienpont 2010) for the R software environment (R Development Core Team 2011).

Lake production measures—Loss on ignition was performed on every centimeter of the six lake sediment cores

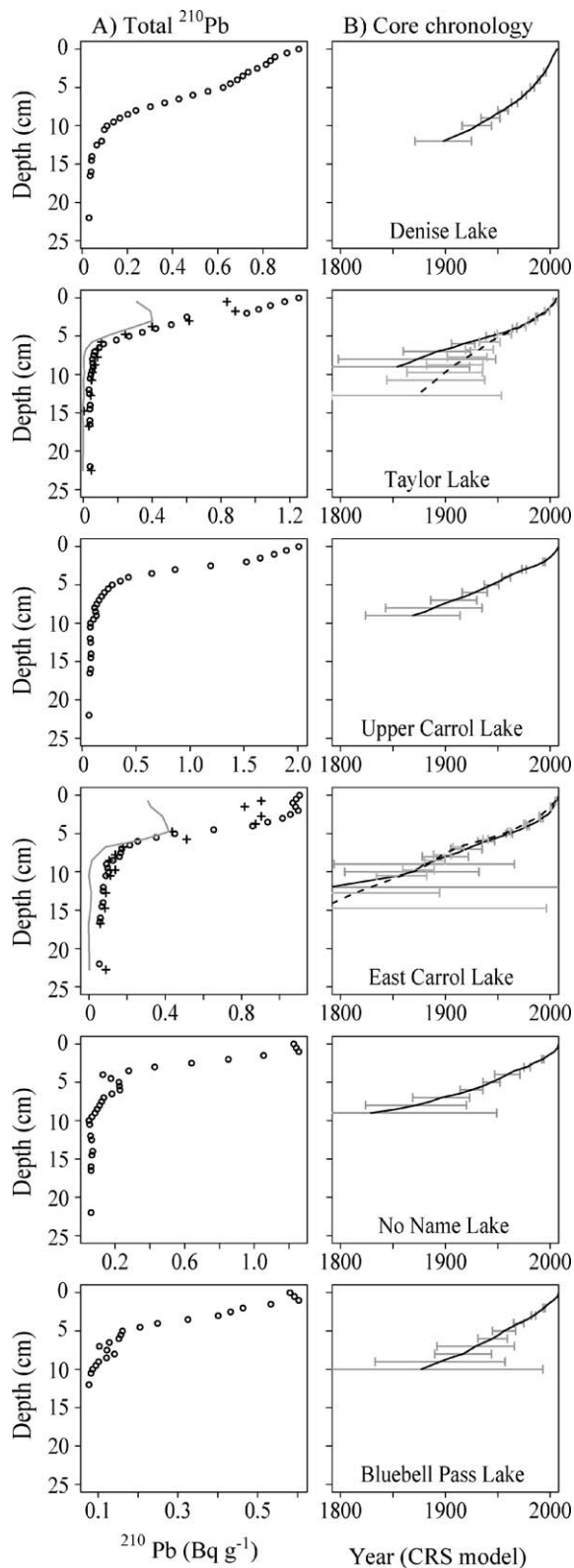


Fig. 2. (A) Total ^{210}Pb activities from the six study lakes using α spectrometry performed at MyCore Scientific (open circles) and γ spectrometry performed at PEARL (crosses). ^{137}Cs , measured using γ spectrometry at PEARL, is represented by the gray line. (B) Core chronology based on the CRS model from α spectrometry at MyCore (black line) and γ spectrometry

following the methods in Dean (1974). The concentrations of sedimentary Chl *a* + its derivatives were inferred for every centimeter of the six lake sediment cores using visible reflectance spectroscopy at PEARL. This technique takes advantage of the spectral signal of preserved Chl *a* and its diagenetic products, pheophytin *a* and pheophorbide *a*, in lake sediments as detailed in Michelutti et al. (2005). Hereafter, Chl *a* refers to this group of pigments plus its derivatives. Briefly, sediments were freeze-dried and sieved to eliminate material $> 125 \mu\text{m}$, thus preventing water content and grain size from affecting the spectral signal. Sediment reflectance spectra were measured between 400 and 1100 nm at 2 nm intervals using a Model 6500 series Rapid Content Analyzer (FOSS Near Infrared Systems), which provides the output of percentage absorbance as an average of 32 scans. Chl *a* concentrations were determined based on its strong linear correlation to the area under the curve of the absorption peak between 650 and 700 nm. Chl *a* flux rates were calculated on the dated portions of the cores to take into account the influence of sedimentation rate on Chl *a* concentrations.

Sediment geochemistry—Prior to isotopic analysis, rotating anode powder x-ray diffraction was used to test for the presence of carbonate in the samples. None was detected (detection limit = 0.5%), thus ensuring that only organic C contributed to the measured $^{13}\text{C}:^{12}\text{C}$ ratio. Stable isotope results are reported in parts per thousand (‰) using δ notation:

$$\delta_{\text{P}} = \frac{(R_{\text{P}} - R_{\text{std}})}{R_{\text{std}}}$$

where R is the $^{15}\text{N}:^{14}\text{N}$ or $^{13}\text{C}:^{12}\text{C}$ ratio of the sample (P) and standard (std), respectively, for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Measured $\delta^{13}\text{C}$ values dated from A.D. 1700 and after were corrected for the Suess effect (the decrease in $\delta^{13}\text{C}$ of the atmosphere resulting from the release of CO_2 with low ^{13}C content by fossil fuel burning and deforestation) following the polynomial correction factor described by Verburg (2007). Samples were freeze-dried and homogenized with a mortar and pestle to a consistent ($< 125 \mu\text{m}$) grain size. The stable isotopic compositions of N and C were analyzed using a Costech Elemental Combustion System connected to a Thermo Finnigan Delta^{PLUS} XL mass spectrometer. Sample $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were calibrated to Vienna Peedee belemnite and ambient air, respectively, using L-glutamic acid reference materials USGS40 (accepted: $\delta^{13}\text{C} = -26.39\text{‰}$, $\delta^{15}\text{N} = -4.52\text{‰}$) and USGS41 (accepted: $\delta^{13}\text{C} = +37.63\text{‰}$, $\delta^{15}\text{N} = +47.6\text{‰}$), both from the USGS (Qi et al. 2003). In addition, internal keratin and International Atomic Energy Agency (IAEA-N-2) ammonium sulfate standards were analyzed to monitor analytical precision and accuracy. A $\delta^{13}\text{C}$ value of $-23.99\text{‰} \pm 0.08\text{‰}$ was obtained for 10 analyses of the internal keratin standard, which compares well with its average value of -24.04‰ .

←

performed at PEARL (dashed line). Error bars represent 1 SD above and below the date.

Table 2. Summary of nutrient measurements of study lake water samples and N:P relationships. Bold text represents N limitation, italic text represents uncertain limitation, and underlined text represents P limitation.

Lake	Date	DIN ($\mu\text{g L}^{-1}$)	TN ($\mu\text{g L}^{-1}$)	TP ($\mu\text{g L}^{-1}$)	DIN:TP mass ratio*	TN:TP mass ratio†	TN:TP molar ratio‡	Chl <i>a</i> in water ($\mu\text{g L}^{-1}$)
Denise	Jul 2011	—	230	9.5	—	<u>24.2</u>	<u>53.5</u>	—
Denise	Jun 2012	10.8	150	13.2	0.8	<u>11.4</u>	<u>25.7</u>	4.4
Denise	Sep 2012	12.7	470	29.3	0.4	<i>16.0</i>	35.5	3.8
Taylor	Jul 2011	139.0	240	15.4	<u>9.0</u>	<i>15.6</i>	<i>34.5</i>	1.0
Taylor	Sep 2011	28.0	210	11.0	<u>2.5</u>	<u>19.1</u>	<u>42.2</u>	3.1
Taylor	Jun 2012	17.0	190	18.5	0.9	<u>10.3</u>	<u>22.7</u>	7.0
Taylor	Sep 2012	9.7	220	10.8	0.9	<u>20.4</u>	<u>45.0</u>	1.5
Upper Carrol	May 2012	28.3	270	16.4	<i>1.7</i>	<u>16.5</u>	<i>36.4</i>	3.8
East Carrol	May 2012	28.0	130	6.7	<u>4.2</u>	<u>19.4</u>	<u>42.9</u>	1.1
No Name	May 2012	18.3	180	9.1	<u>2.0</u>	<u>19.8</u>	<u>43.7</u>	2.4
Bluebell Pass	May 2012	12.0	180	8.0	1.5	<u>22.5</u>	<u>49.8</u>	2.9

* Limitation thresholds are taken from Bergström (2010).

† Limitation thresholds are taken from Downing and McCauley (1992) and Sakamoto (1966).

‡ Limitation thresholds are taken from Guildford and Hecky (2000).

Sample reproducibility was $\pm 0.09\%$ for $\delta^{13}\text{C}$ (standard deviation [SD], $n = 5$). A $\delta^{15}\text{N}$ value of $+6.29\% \pm 0.13\%$ (SD, $n = 11$) was obtained for an internal keratin standard, which compares well with its average value of $+6.36\%$. A $\delta^{15}\text{N}$ value of $+20.44\% \pm 0.01\%$ ($n = 2$) was obtained for IAEA-N-2, which compared well with its accepted value of $+20.3\%$. Sample reproducibility was $\pm 0.04\%$ for $\delta^{15}\text{N}$ (SD, $n = 5$).

Organic C and TN contents were determined using a Fisons 1108 elemental analyzer. These results were used to calculate atomic C:N ratios. Sample reproducibility was ± 0.33 for % C (SD, $n = 9$) and ± 0.02 for % N (SD, $n = 9$). The C:N ratio, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ were measured on samples every 5 cm, with more samples analyzed in sections of the core in which the percentage of organic matter changed more rapidly. The powder x-ray diffraction, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, % C, and % N analyses were carried out at the Laboratory for Stable Isotope Science at the University of Western Ontario, Canada.

Diatoms—Diatom analysis was performed on samples every centimeter for the top 10 cm, and then every 2–3 cm below that point. Approximately 1 cm³ subsamples were treated with a 50:50 molar weight solution of nitric and sulfuric acid to digest organic matter. After 24 h the samples were heated to 80°C for 2 h. Treated samples were rinsed a minimum of 10 times (at least 24 h between washes) with distilled water until neutrality was reached, and then mounted onto slides using a high-refractive (refractive index = 1.65–1.7) mounting medium. For each sample a minimum of 500 diatom valves were identified and counted using a Leica E-600 light microscope outfitted with differential interference contrast optics and at 1000X magnification. A Retiga® 2000 Fast 1394 digital camera was used to facilitate identification. Principal components analysis (PCA) was used to identify relationships among diatom species and the presence of trends in the diatom stratigraphies. PCA was carried out on samples appearing in at least three samples with at least 1% relative frequency in one lake. By plotting the first axis sample scores

stratigraphically, changes in diatom fossil assemblages could be compared easily to other paleoindicators. The statistical significance of each first axis was tested using the broken stick method (Jackson 1993).

Results

Water chemistry—The six study lakes are oligotrophic or on the boundary between oligotrophic and mesotrophic (Table 1), as determined by TP, TN, Chl *a*, and Secchi depth values (Tables 1 and 2). The lake with the highest springtime measures of TN and TP is Upper Carrol Lake. The limiting nutrient for each lake is difficult to identify regardless of the method used because the ratios are often values that could indicate either N or P limitation (Table 2). Downing and McCauley (1992) suggest that N limitation is more common in lakes with TN:TP ≤ 14 (mass ratio), whereas lakes with TN:TP > 17 (mass ratio) tend to be P limited (Sakamoto 1966). Using water chemistry data from lakes and oceans, Guildford and Hecky (2000) found that N deficiency is likely at TN:TP < 20 (molar) and P deficiency at TN:TP > 50 (molar). Because TN can contain a large proportion of biologically unavailable N (e.g., 34%–97% at the six study lakes), Bergström (2010) suggests that the TN:TP ratio may not be a realistic indicator of limiting nutrients, and that the dissolved inorganic N (DIN):TP ratio is a better predictor of limiting nutrient conditions in oligotrophic lakes. DIN:TP ≤ 1.5 likely indicates N-limited lakes, whereas DIN:TP ≥ 3.4 likely shows P-limited lakes (Bergström 2010). Based on our data, some lakes are N limited and some are P limited; others lie between the thresholds for N and P limitation (Table 2). These results also show that there is likely temporal variation in nutrient limitation. For example, the DIN:TP ratio indicates that Taylor Lake is P limited in summer 2011, uncertain or shifting between N and P limitation in fall 2011, and N limited in spring 2012 (Table 2).

Chronology—The total ²¹⁰Pb activity of the six lakes decreases predictably with depth, allowing for the development

of robust CRS chronologies (Fig. 2). Background ^{210}Pb was reached within 9–12 cm in each of the six lakes, indicating average sedimentation rates of 0.5–1 mm yr⁻¹. The dating models developed using α and γ spectrometry for East Carrol Lake are strikingly similar (Fig. 2). Cesium-137 peaks at 1961 ± 1.3 yr, which coincides with the peak of nuclear bomb testing in 1963. The ^{137}Cs peak in Taylor Lake occurs at the CRS-derived age of 1976 ± 3.25 yr. However, samples were measured for ^{137}Cs only at every other half centimeter in this section of the Taylor Lake core. At this resolution, peak ^{137}Cs could be off by a decade in either direction. Despite the larger errors for dates determined from deeper intervals using α spectrometry, there is no statistical difference between dates attained by α and λ spectrometry, given the measurement errors. For consistency among lakes, all dates presented hereafter are based on the CRS depth–age curves using the dates obtained by α spectrometry. In the absence of terrestrial organic material suitable for ^{14}C dating, the ^{210}Pb dating models were extended using linear regression ($R^2 > 0.95$ for all six lakes), and give basal dates ranging from A.D. 1187 at No Name Lake (at 42.5 cm depth) to A.D. 1671 at Bluebell Pass Lake (at 25.75 cm depth). These extrapolations provide a historical context for the observed post-~ 1850 trends, although the pre-1850 dates are considered with caution, as basal ^{210}Pb sedimentation rates tend to be systematically overestimated compared to models that include ^{14}C dates (Cooke et al. 2010).

Lake production indicators—In five of the six lakes (East Carrol, No Name, Taylor Lake, Denise, and Bluebell Pass Lakes) the Chl *a* and percentage of organic matter are relatively constant from the beginning of the record until 1940–1960, when production progressively increases (Fig. 3). By comparison, Upper Carrol Lake exhibits a gradual increase in Chl *a* and percentage organic matter throughout the record. The Chl *a* flux illustrates the primary production trend without the influence of sediment accumulation rate on concentration, and reveals that all but Upper Carrol Lake experienced increased production in the surface sediments (Fig. 3).

The C:N ratios at Denise Lake decrease over the duration of the record from ~ 14 to ~ 9. In the other lakes, C:N ratios are relatively constant at ~ 10–14 (depending on the lake) until ~ 1950, at which time they decrease to < 10, except at Upper Carrol Lake, in which C:N remains at pre-1955 values.

N and C isotopic compositions of organic matter—The N isotopic compositions in all but Denise Lake remain constant in the earlier parts of the records. Beginning around the mid-1850s, $\delta^{15}\text{N}$ begins to decrease in all of the lakes except No Name. A sharper decrease follows in the last ~ 60–70 yr (decreases of up to 3‰) in all lakes, including No Name (Fig. 3). Upper Carrol Lake is the exception to this trend, as the decrease in $\delta^{15}\text{N}$ remains relatively gradual after 1940 for a total shift of only ~ 1‰.

The Suss-corrected $\delta^{13}\text{C}$ range between -31‰ and -21‰ is within the typical range for lake sediment containing organic matter dominated by aquatic primary

producers (Finlay and Kendall 2007). The $\delta^{13}\text{C}$ recorded for Upper Carrol Lake (-31‰) is lower compared to the other sites (-26‰ to -21‰). In Denise, Taylor, and No Name Lakes, $\delta^{13}\text{C}$ gradually increases by 1‰ or 2‰ over the entire record, whereas for Upper Carrol, East Carrol, and Bluebell Lake, $\delta^{13}\text{C}$ is fairly constant throughout the cores.

Diatoms—Four of the six study lakes (Denise, Taylor, East Carrol, and Bluebell Pass Lakes) show comparable timing of changes (Fig. 4). Diatom sample scores on the first PCA axis show that the initial change in diatom community composition occurs in the mid-1800s and is approximately coincident with the start of the $\delta^{15}\text{N}$ decrease. Although the timing of the changes is markedly similar between lakes, the direction of change varies. The most consistent change occurring in the four lakes is an increase in nitrophilous *Asterionella formosa*. In three of the lakes (Denise, Taylor and Bluebell Pass) the change in diatom community composition is characterized by an increase in PCA axis 1 scores and in planktonic diatoms, mainly *A. formosa*, but in Denise Lake also small *Cyclotella* species (including *Cyclotella stelligera*, *Cyclotella pseudostelligera*, *Cyclotella atomus*, and *Cyclotella ocellata*), *Fragilaria tenera*, and the tycho planktonic *Fragilaria capucina* var. *gracilis*. In Denise Lake positive PCA axis 1 scores also indicate a shift from small, benthic *Fragilaria* to small *Achnanthes* and *Navicula* species. In East Carrol Lake, although the percentage of planktonic diatoms decreases, PCA axis 1 scores shows that there is a shift within the planktonic diatom community from mainly *Aulacoseira* and *Cyclotella* species to *A. formosa*, *F. capucina* var. *gracilis*, and *F. tenera*. In Upper Carrol Lake, although the PCA score data appear noisy, there is almost no change in diatom community composition and *A. formosa* is a dominant species throughout. In No Name Lake there is a distinct and rapid change in diatom community composition at the same time Chl *a* increases and a subtle change at the same time as the $\delta^{15}\text{N}$ decreases. As the PCA scores indicate, these changes are distinctly different from the other lakes and are characterized by a decrease in planktonic diatoms, first *Aulacoseira* species and then *Cyclotella* species, and an increase in small, benthic *Fragilaria* species, first *Fragilaria pinnata* and small *Navicula* species, and then dramatically *Fragilaria constricta* var. *venter*.

Discussion

We show that high alpine lakes in the Uinta Mountains experienced a recent increase in production in all but Upper Carrol Lake as documented by the increases in Chl *a* and percentage of organic matter beginning between 1940 and 1960. Low C:N ratios indicate that the increase in organic matter is likely algal, as C:N ratios < 10 are observed post-1950 in five of six lakes. The C:N ratios from 10 to 20 (as is seen before 1950 at these sites) indicate either a mixed source of algae, aquatic macrophytes, and terrestrial material (Meyers and Ishiwatari 1993) or algal growth under N-limiting conditions (Hecky et al. 1993). The

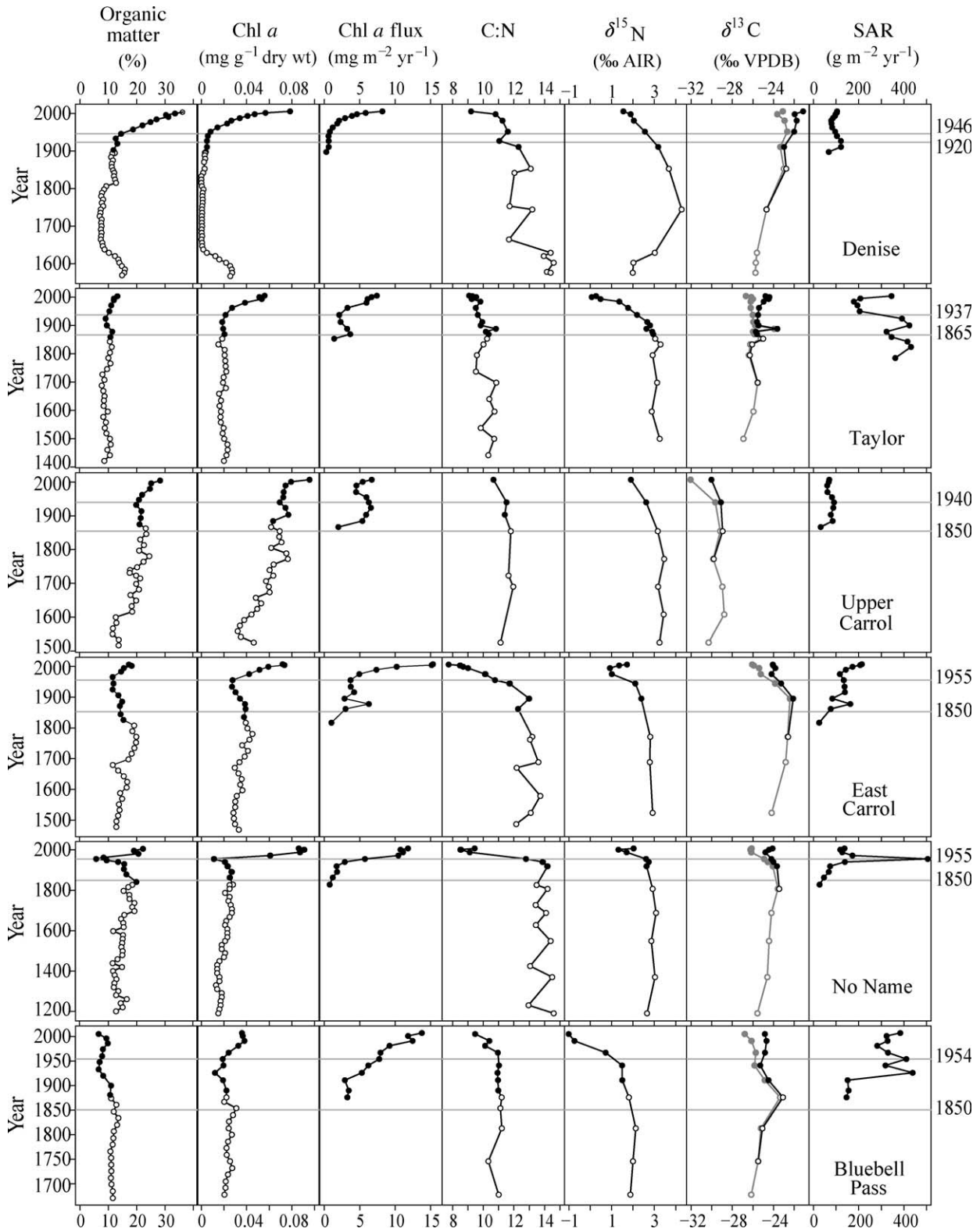


Fig. 3. Key biogeochemical data for Denise, Taylor, Upper Carrol, East Carrol, No Name, and Bluebell Pass Lake sediment cores. Filled circles represent data constrained by the ²¹⁰Pb dated section of the cores, whereas open circles represent data for which chronology was established by fitting a linear regression to the dates and extending below the ²¹⁰Pb dated section. Sediment accumulation rate (SAR) is calculated from the ²¹⁰Pb activity data and is therefore limited to the ²¹⁰Pb dated section of each core. Chl *a* flux is calculated as the product of Chl *a* and SAR. Measured δ¹³C is shown in gray, whereas Suess-corrected δ¹³C (applied only to years after 1700) is shown in black. dry wt, dry weight.

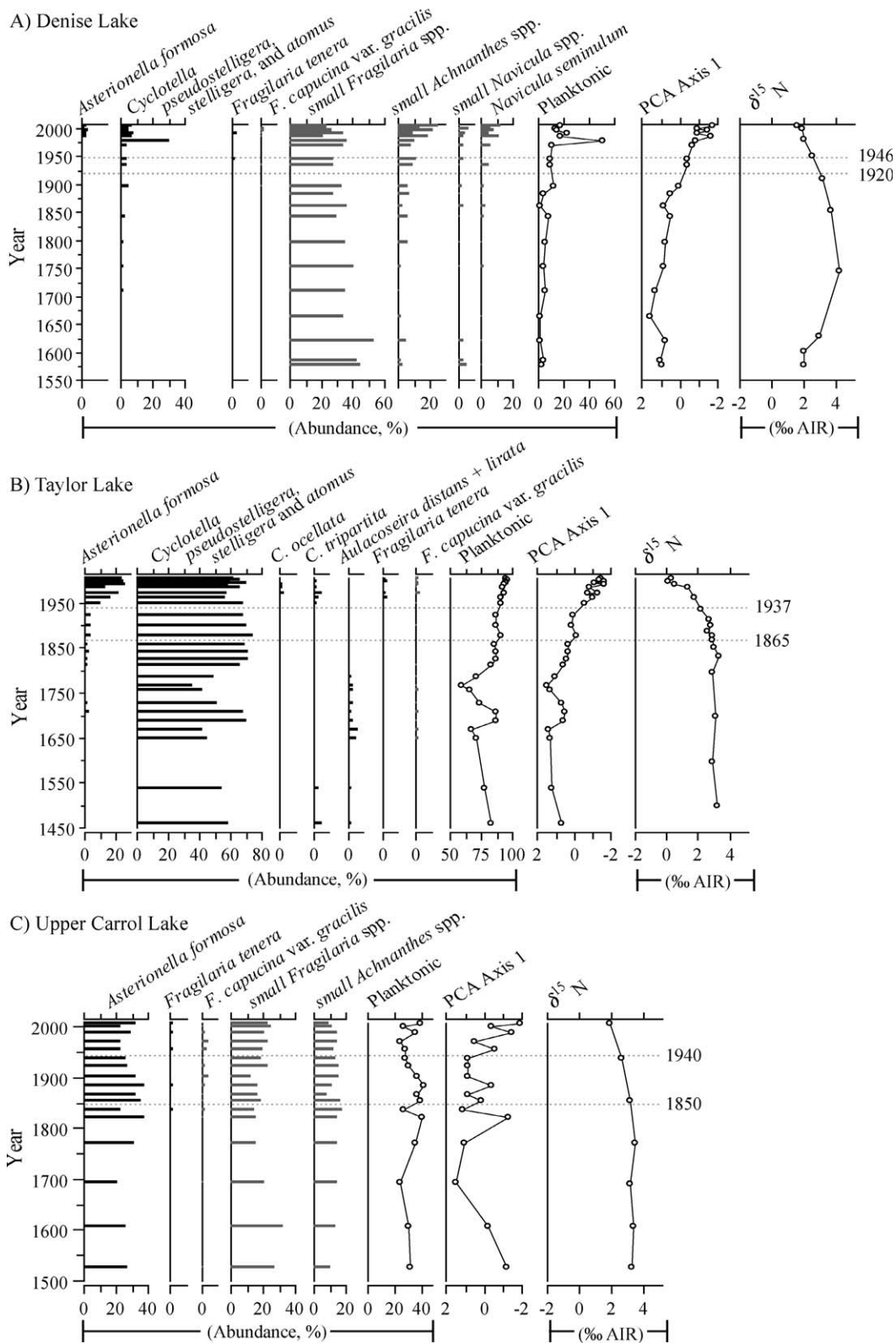


Fig. 4. Abundances (%) of dominant diatom taxa and groups of taxa are divided into planktonic (black bars) and benthic (gray bars) species. Percentages of planktonic diatoms and PCA axis 1 sample scores are compared to $\delta^{15}N$, which is considered a proxy for N deposition for each of the six lakes. On each plot the upper horizontal gray dotted line indicates the main change in Chl *a*, which occurred ~ 1950, and the lower horizontal indicates when $\delta^{15}N$ became greater than mean presettlement (pre-1850) values.

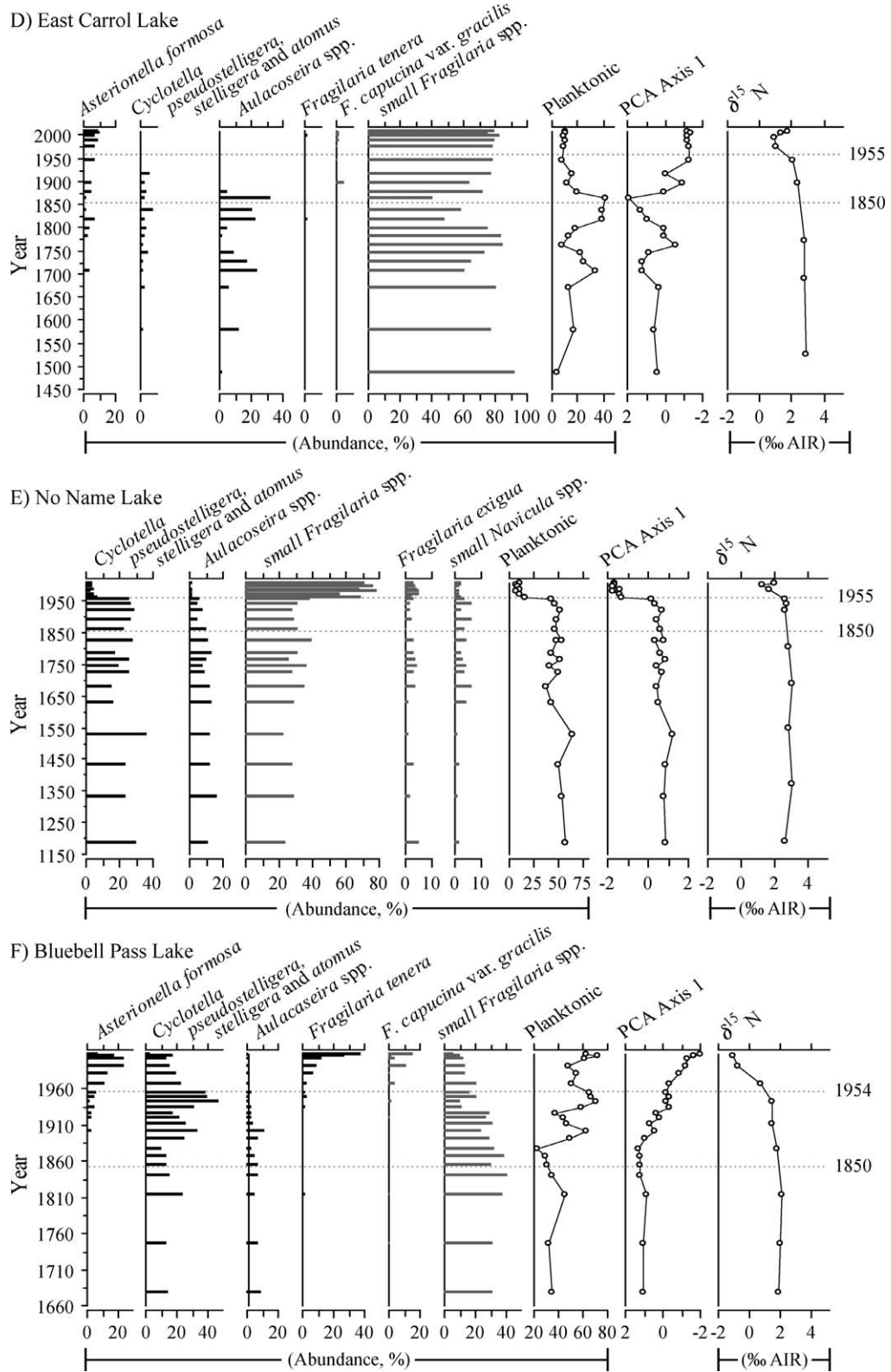


Fig. 4. Continued.

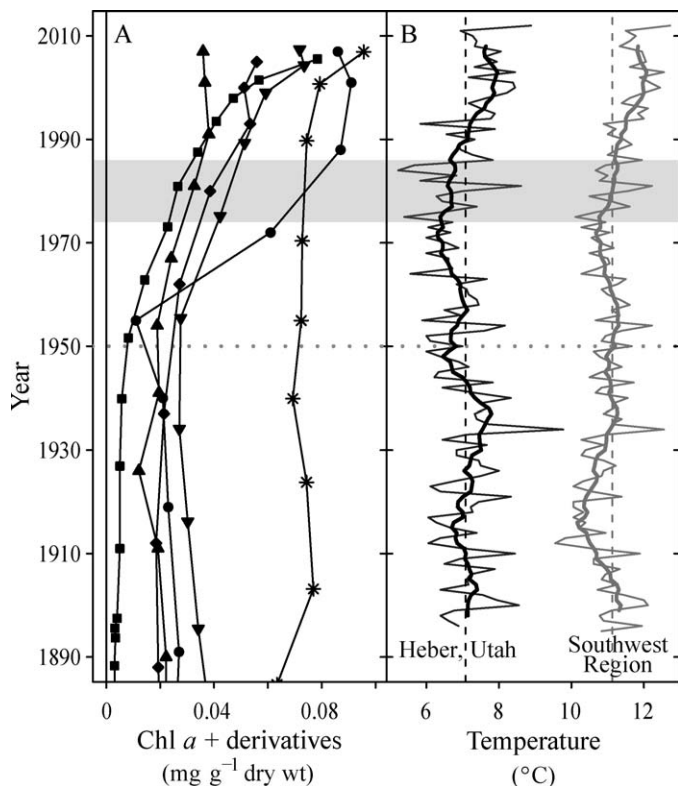


Fig. 5. (A) Chl *a* + derivatives for study lakes with the beginning of increased production marked by the gray dotted line. (B) Mean annual temperature for Heber, Utah, and for the southwest region of the United States, which shows similar trends to winter and summer mean temperatures. The thick lines are 9 yr running means and the dashed vertical lines are mean temperatures for the entire record. The gray horizontal band indicates the beginning of modern climate warming in the southwestern United States and at Heber. Fully adjusted monthly mean temperature data have been obtained from the U.S. Historical Climatology Network at the Carbon Dioxide Information Analysis Center, <http://cdiac.ornl.gov/epubs/ndp/uschn/uschn.html/> (Heber) and National Climatic Data Center, National Oceanic and Atmospheric Administration, <http://www.ncdc.noaa.gov/cag/time-series/us> (Southwest Region of the United States).

increasing Chl *a* flux in all five lakes demonstrates that the rise in primary production is independent of sedimentation rate. An increase in primary production generally results in progressively higher $\delta^{13}\text{C}$, given that algae preferentially utilize ^{12}C and subsequently draw the lighter isotope out of the photic zone (Hollander and McKenzie 1991). Trends in the Suess-corrected $\delta^{13}\text{C}$ vary between lakes from slightly decreasing to slightly increasing, and therefore do not suggest a strong influence of productivity on C isotope composition. It is possible that the effects of increasing primary production on $\delta^{13}\text{C}$ are being offset by other ecological changes. For example, Wang et al. (2013) suggested that decreasing $\delta^{13}\text{C}$ despite increasing production at a maar lake in China was linked to shifts from benthic to planktonic diatoms. In order to test for this possibility, $\delta^{13}\text{C}$ for individual algal and diatom taxa would need to be determined for Uinta Mountain lakes.

Decreasing $\delta^{15}\text{N}$ accompany the trends of increasing lake production. Initial and relatively subtle decreases in $\delta^{15}\text{N}$ began prior to the changes in lake production, in the mid-1800s, in all lakes except No Name Lake. The most prominent decrease in $\delta^{15}\text{N}$, however, is synchronous with changes in primary production in the mid-1900s. This major change is evident in all six lakes.

Although diagenesis of organic matter should also be taken into account as a possible explanation for the observed trends, we consider it unlikely. (1) Diagenesis is expected to result in downcore decreases in Chl *a* and percentage organics (Meyers and Lallier-Verges 1999). However, the sedimentary Chl *a* measurements used in this research include the spectral signal for Chl *a* and its diagenetic products, pheophytin *a* and pheophorbide *a* (Michelutti et al. 2005), and therefore track both primary and degraded Chl *a* products. (2) Although C:N ratios would be expected to increase down core during diagenesis because of selective degradation of N-rich organic compounds, the opposite diagenetic effect has been demonstrated for oligotrophic lakes (Meyers and Lallier-Verges 1999). (3) The Uinta Mountain sediment cores exhibit decreasing $\delta^{15}\text{N}$ toward the core tops (Fig. 3), which is opposite to the downward depletion of ^{15}N expected within a typical diagenetic profile (Galman et al. 2009). (4) Diagenetic effects are generally expected to result in increased $\delta^{13}\text{C}$ downcore in the most recent 5–10 yr of sediment (Galman et al. 2009), whereas the trends in the Uinta sediment $\delta^{13}\text{C}$ are inconsistently expressed in the upper portion of the cores.

Given that the recorded increases in lake production are real, what is causing this change in these remote lakes? Recent climate warming has been linked to enhanced primary production in arctic environments (Michelutti et al. 2005) and to altered community compositions of diatoms in alpine, arctic, and temperate sites in North America (Rühland et al. 2008). Alpine habitats are more sensitive to warming relative to low-lying regions at similar latitudes (Beniston 2003), and the western U.S. is warming at a faster rate than the world average (Saunders et al. 2008, <http://www.nrdc.org/globalwarming/west/west.pdf>). The mechanisms by which warming could result in enhanced production in oligotrophic ecosystems include lengthening the ice-free season and growing season, changes in thermal properties, enhanced nutrient cycling, increasing nutrients in the catchment, and increasing lake water residence time (Rühland et al. 2008). The changes in diatom community composition in four (Denise, Taylor, East Carrol, and Bluebell Pass Lakes) of the six lakes are similar to diatom community composition changes described by others in response to warming temperatures (Rühland et al. 2008). However, the timing of warming and changes in the recorded proxies are not synchronous (Fig. 5). The longest and most complete temperature record that is located close (~ 120 km) to the study area in Heber, Utah, shows steadily increasing mean annual, summer (June, July, and August), and winter (December, January, and February) temperatures beginning in the mid-1980s, which is typical timing when compared to the regional trend for the western U.S. (Saunders et al.

2008, <http://www.nrdc.org/globalwarming/west/west.pdf>). This warming trend postdates the changes observed in Chl *a* for these sites, suggesting that warming was not the main trigger for enhanced lacustrine primary production at these sites. Our findings, however, do not rule out climate as a contributing factor to increased primary production, particularly since the 1980s and into the future when the rate of warming is anticipated to accelerate (Saunders et al. 2008, <http://www.nrdc.org/globalwarming/west/west.pdf>).

Increased lake production can be caused by human disturbance within the catchment, which results in increased transfer of nutrients from the catchment to the aquatic system (Hall and Smol 2001). In the Uinta Mountains, humans have had relatively little direct effect on the landscape, with the exception of changes resulting from grazing. Grazing can alter species composition, disrupt nutrient cycling, reduce litter cover, compact soils, reduce infiltration, increase runoff, and increase soil erosion, and through these mechanisms increase production in aquatic systems. Although records are intermittent, sheep grazing was common practice in the Uinta Mountains by 1890, and many areas are still grazed by sheep and cattle. Grazing in both the Dry Gulch and Whiterocks River allotments (which together encompass all six study lakes) is likely to have peaked in the 1920s or 1930s (U.S. Forest Service 1947 unpubl.). Expected increases in erosion at these lakes would be recorded by an increase in the percentage of inorganics from the catchment that would presumably spike with peak grazing and then subside as grazing became less intense and the catchments recovered. However, the organic content does not exhibit any trends consistent with such a history (Fig. 3). If grazing resulted in increased transport of nutrients to the lake from manure, production should have been greatest in the 1930s and $\delta^{15}\text{N}$ should have increased moderately, as livestock manure typically has $\delta^{15}\text{N}$ of $\sim +9\text{‰}$ (Bateman and Kelly 2007). In contrast, primary production is low during peak grazing and the $\delta^{15}\text{N}$ decrease, indicating that local free-range grazing is not directly responsible for changes in primary production.

Another anthropogenic perturbation that could lead to increased lake production is fish stocking. Fish stocking can result in increased primary production by changing patterns of herbivory and reintroduction of benthic nutrient sources to pelagic communities (Schindler et al. 2001). The timing of fish stocking probably coincides with increased production in Uinta Mountain lakes. Although some lakes in Utah were stocked prior to the 1950s, it was done on horseback (Hallows 2009 unpubl.); this made it unlikely for remote Uinta Mountain alpine lakes to have been stocked until aircraft were used beginning in the late 1950s. Fish stocking records indicate that No Name, Bluebell Pass, East Carrol, Upper Carrol, and probably Taylor and Denise Lakes were stocked as early as 1958 (Rabe 1968) with either cutthroat trout (*Oncorhynchus clarkii*) or brook trout (*Salvelinus fontinalis*) (Utah Division of Wildlife Resources unpubl.). Fish sampling surveys from 1978 at East Carrol, Upper Carrol, No Name, and Bluebell Pass Lakes indicate no natural fish populations, and that stocked fish were not reproducing (Utah Division of Wildlife Resources 1978 unpubl.). The $\delta^{15}\text{N}$ decrease with

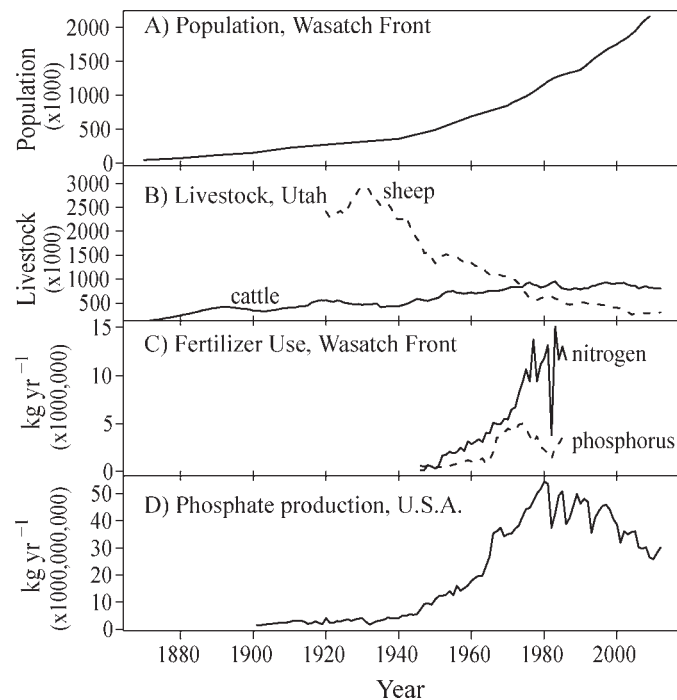


Fig. 6. Trends in potential supply of N and P to the Uinta Mountains. Data have been obtained from the following sources: (A) Population in the Wasatch Front (Davis, Salt Lake, Weber, Box Elder, and Utah Counties; United States Census Bureau, <http://www.census.gov/popest/data/historical/index.html>; University of Virginia, Geospatial and Statistical Data Center 2004, <http://mapserver.lib.virginia.edu/collections/>). (B) Livestock in Utah State (United States Department of Agriculture, National Agricultural Statistics Service, <http://quickstats.nass.usda.gov/>). (C) N and P fertilizer use in the Wasatch Front (Davis, Salt Lake, Weber, Box Elder, and Utah Counties; Alexander and Smith 1990). (D) Production of phosphate rock in the United States (U.S. Geological Survey 2014, <http://minerals.usgs.gov/minerals/pubs/historical-statistics/>).

increasing lake production is opposite to what is expected with fish stocking. Fish stocking is expected to cause an increase in $\delta^{15}\text{N}$ (Gasirowski and Sienkiewicz 2013). Organic matter $\delta^{15}\text{N}$ typically increases by $\sim 3\text{‰}$ – 4‰ with each trophic level of the lake food web (Minagawa and Eitaro 1984), so the repeated introduction of fish to these lakes over the last 50 yr should result in ^{15}N enrichment of the lakes (Gasirowski and Sienkiewicz 2013). Fish undernourishment, as has been reported in Bluebell Pass Lake (Rabe 1968) and No Name and East Carrol Lakes (Utah Division of Wildlife Resources 1978 unpubl.), can result in further increases in $\delta^{15}\text{N}$ (Adams and Sterner 2000). Therefore, the trends in $\delta^{15}\text{N}$ indicate that fish stocking is unlikely to have been the triggering factor for changes in primary production despite similar timing.

The timing of the production changes illustrated by Chl *a* and organic matter contents at five of the six Uinta Mountain study lakes coincides with the rise of intensive agriculture and rapid population growth upwind at the Wasatch Front, both of which are associated with the increase in fossil fuel combustion and the use of synthetic N fertilizers produced via the Haber-Bosch process (Fig. 6).

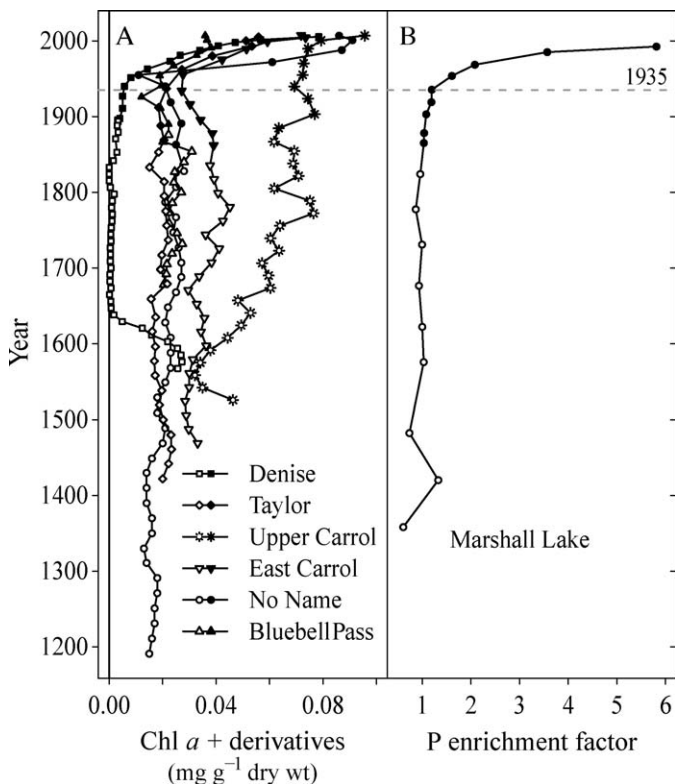


Fig. 7. (A) Chl *a* + derivatives for each of the six study lakes compared to the (B) P enrichment factor for Marshall Lake, Uinta Mountains (Reynolds et al. 2010). Data with solid symbols are constrained by ^{210}Pb dates, whereas open symbols are extended below the ^{210}Pb -dated section by fitting a linear regression to the dates. The gray dotted line at 1935 represents the point in time after which P became elevated above background levels.

These activities increase the availability of fixed N, and result in enhanced atmospheric N deposition. The recent increase in the percentage of nitrophilous *A. formosa* in Denise, Taylor, East Carrol, and Bluebell Pass Lakes' sediment cores is also consistent with increased fixed N availability, particularly in alpine environments (Saros et al. 2005). Although the increase in *A. formosa* at Denise Lake appears small, we consider the increase ecologically significant because this taxon would not typically prefer a lake as shallow as Denise (2.4 m) and was near absent prior to ~ 1950. The decrease in $\delta^{15}\text{N}$ observed for the lakes examined here is consistent with a change in the source of fixed N. Bateman and Kelly (2007) report mean $\delta^{15}\text{N}$ of $+0.2 \pm 1.9\text{‰}$ for synthetic N fertilizer, which is sufficiently low for atmospheric transport to produce the observed decrease in N isotopic compositions. Enhanced fossil fuel combustion related to population growth and industrial expansion could also have contributed to the observed pattern in N isotopic compositions, given that nitrates derived from fossil fuel combustion typically have low $\delta^{15}\text{N}$ (-10‰ to $+5\text{‰}$; Finlay and Kendall 2007).

Although the recent (~ 1950) increase in lake primary production is the most prominent change observed in these sediment records, four of the lakes (Denise, Taylor, East Carrol, and Bluebell Pass) indicate an earlier, subtler shift.

From approximately 1850, $\delta^{15}\text{N}$ decreases, and PCA scores and *A. formosa* abundance increase, suggesting an increase in nutrient delivery. This change predates local grazing activity and fish stocking, and shows no relation to temperature. We suspect these changes may result from an initial increase in land clearance in the southwest and mining activities after the settlement of the Wasatch Front in 1847 (Reynolds et al. 2010). Grazing along the Wasatch Front could have produced a supply of excess nutrients to these high alpine sites, similar to the changes observed in the San Juan Mountains in the late 19th century (Neff et al. 2008). NO_x from smelting associated with local mining at this time could also have contributed to these relatively subtle paleolimnological changes.

Decreasing $\delta^{15}\text{N}$ concomitant with increasing production indicates atmospheric N deposition–fertilizing effects, but what was the role of P? Researchers have suggested that alpine lakes are ultimately N limited (Williams et al. 1996) or co-limited by N and P (Baron et al. 2000). However, enhanced anthropogenic N deposition can also result in a shift to P limitation (Arnett et al. 2012). Shifting N:P ratios and corresponding changes in the limiting nutrient imply that P via eolian transport of dust from intensive livestock grazing and fertilizer use or mining (Neff et al. 2008; Reynolds et al. 2010) could contribute to enhanced primary production at times. Focusing only on N inputs may be an oversimplification in this environment.

Although the natural P cycle does not have a significant atmospheric component, the recent increase in phosphate mining and phosphate fertilizer use has resulted in greater atmospheric transport of P. A study of the sediments from Marshall Lake and Hidden Lake, Uinta Mountains, illustrated that P has become increasingly elevated since 1950, which is attributed to atmospheric dust fallout from intensive agricultural activity (Reynolds et al. 2010). This timing coincides with the increase in primary production at the Uinta Mountain study sites (Fig. 7) and with the rise in phosphate use in the Wasatch Front and overall phosphate production in the U.S. (Fig. 6). Phosphate in Uinta Mountain dust samples is elevated relative to the underlying bedrock; the higher P contents have been attributed to either nearby phosphate mining based on the presence of apatite in dust or agricultural intensification based on elevated soil and fertilizer minerals like calcium, sodium, and cadmium (Squire 2012).

Our data show that lake production is increasing because of atmospheric deposition of nutrients, but are there other consequences of atmospheric deposition fertilization for remote alpine lake ecosystems? Although all lakes show decreasing $\delta^{15}\text{N}$, the PCAs indicate that only four lakes show comparable shifts in diatom species composition, which mirror the decreasing $\delta^{15}\text{N}$ and are linked to atmospheric deposition of N and P. The change in diatom community composition predates the change in algal production, which is not surprising owing to the subtle changes in atmospheric deposition indicated by the early decreases in $\delta^{15}\text{N}$ and the sensitivity of diatoms to nutrient concentrations (Hall and Smol 2001). The change in diatom community composition beginning around 1850 shows changes in both the benthic and planktonic communities,

and would be expected to have bottom-up consequences on lake ecosystems. Upper Carrol Lake records virtually no change in lake production or diatom community composition, and No Name Lake records changes in diatom community composition that could be described to be opposite to the other lakes. In Upper Carrol Lake the lack of response may be the result of naturally elevated nutrient levels. This is supported by continuously high Chl *a* concentrations and percentages of *A. formosa* (Fig. 4). Upper Carrol Lake differs from the other five lakes because it is surrounded by a wide (tens to hundreds of meters), relatively flat, and well-vegetated expanse that includes marshy areas; mosses; grasses; sedges, particularly *Carex aquatilis*; and abundant shrubs, including *Salix planifolia* (shrub willow) and *Betula glandulosa* (dwarf birch), which could naturally lead to elevated nutrient concentrations (Pathak et al. 2012). In fact, Table 2 shows that springtime concentrations of both TN and TP are generally greatest in Upper Carrol Lake.

At No Name Lake, although the trends in Chl *a* and $\delta^{15}\text{N}$ are similar to those in the other lakes, the change in diatom community composition is markedly different. The rapid decrease in planktonic diatoms and increase in pioneering, benthic taxa in the mid-1900s is indicative of a different forcing mechanism, probably a local catchment disturbance (e.g., a landslide), that has overridden some changes that might have occurred because of atmospheric pollution. Evidence for a local catchment disturbance includes a concomitant and rapid decrease in the percentage of organics from about 15% to 5% and the occurrence of a distinct millimeter-scale, pale-colored layer in otherwise brown sediments. Pioneering diatoms, such as *F. construens* var. *venter*, increase dramatically at this time. A landslide could “reset” an alpine lake ecosystem to conditions similar to those at its origin, allowing these small benthic pioneering diatoms to rapidly expand. There is, however, evidence that this lake was different from the others even before the mid-1900s. Subtle changes in diatom community composition recorded by PCA scores and coincident with the decrease in $\delta^{15}\text{N}$ suggests a unique response regardless of the catchment disturbance. The reason for this difference is unclear, but might be related to this lake being the only surficially closed basin with lake level changes on the order of meters observed over a decade of field work.

The studied Uinta Mountain lake sites are critical bellwethers for environmental change, as they record an increase in production in the last 60 yr that adds to evidence that long-distance transport of nutrients is causing detectable changes in lake ecosystems. Although evidence of more serious effects of eutrophication (e.g., algal blooms) has only rarely been reported (K. Moser unpubl.) in the Uinta Mountains, we can already detect subtle shifts in ecosystem functioning. By studying several lake sites, we have shown that not all high-elevation lakes are responding equally to increased nutrient deposition. The present study indicates that enhanced N and P deposition may both be important factors in increasing primary production in Uinta Mountain lakes. This result is of critical timing as populations, fossil fuel combustion, and agricultural

activities are increasing, and new phosphate mines and mine expansion near Vernal, Utah, are under consideration. Increasing primary production may also be exacerbated by future warming. In western North America temperatures are anticipated to increase by $\sim 2.0^\circ\text{C}$ – 5.8°C by the end of the 21st century (Saunders et al. 2008, <http://www.nrdc.org/globalwarming/west/west.pdf>), and warmer temperatures have been linked to increased algal production (Smol et al. 2005). A strong correlation between changes in arctic limnic ecosystem functioning and structure and warming temperature has been reported (Smol et al. 2005). Such changes may have been delayed in the western U.S. because temperatures have only recently begun to rise in this region (fig. 5, Saunders et al. 2008, <http://www.nrdc.org/globalwarming/west/west.pdf>). Previous nutrient inputs may only serve to compound the effects of future warming. In other words, the effects of warming on alpine regions that might be anticipated from research on arctic lakes, where nutrient delivery has been smaller, may not yet be realized.

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