

Rapid communication

Anthropogenic nitrogen deposition induces rapid ecological changes in alpine lakes of the Colorado Front Range (USA)

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Abstract

Recent sediments from two alpine lakes (> 3300 m asl) in the Colorado Front Range (USA) register marked and near-synchronous changes that are believed to represent ecological responses to enhanced atmospheric deposition of fixed nitrogen from anthropogenic sources. Directional shifts in sediment proxies include greater representations of mesotrophic diatoms and increasingly depleted $\delta^{15}\text{N}$ values. These trends are particularly pronounced since ~ 1950, and appear to chronicle lake responses to excess N derived from agricultural and industrial sources to the east. The rate and magnitude of recent ecological changes far exceed the context of natural variability, as inferred from comparative analyses of a long core capturing the entire 14,000-year postglacial history of one of the lakes. Nitrogen deposition to these seemingly pristine natural areas has resulted in subtle but detectable limnological changes that likely represent the beginning of a stronger response to nitrogen enrichment.

Introduction

The global nitrogen cycle is being dramatically altered by human activities (Vitousek et al., 1997). Enhanced deposition of reactive nitrogen from anthropogenic emissions (primarily NO_3^- and NH_3) has resulted in conditions of nitrogen saturation in many northern hemisphere forest ecosystems (Durka et al., 1994; Fenn et al., 1998). Excess nitrogen is also evident from alpine areas proximal to regions of industrial, urban, and agricultural growth (Williams et al., 1996). In the Colorado Front Range, which lies immediately west of the rapidly-expanding Denver-Fort Collins urban axis, ongoing water quality monitoring efforts indicate recent increases in surface water NO_3^- concentrations (Caine, 1995; Baron & Caine, 2000). However, because N fluxes in these alpine basins are highest during the nival melt period (May-June), a time when most catchment biomass remains dormant (Baron & Campbell,

1997), direct evidence that terrestrial communities have been altered by increased N availability has been inconclusive to date. Baron et al. (1994) predicted moderate increases of tundra primary productivity as the most likely consequence to current rates of N deposition, which are in the range of 3–5 kg N ha⁻¹ yr⁻¹. These rates are significantly lower than those reported from more severely impacted regions, such as parts of New England (≥ 10 kg N ha⁻¹ yr⁻¹; Fenn et al., 1997).

Our hypothesis is that aquatic algae, including diatoms, should be among the first group of organisms to respond to greater N availability, given their high sensitivity to changes in resource allocation (Interlandi & Kilham, 1998). In addition, diatom standing crop is typically high during the spring snow-melt period characterized by elevated limnetic NO_3^- fluxes (McKnight et al., 1990), when N released from the snowpack transits rapidly through the ecosystem with minimal terrestrial uptake.

Materials and methods

The sediment records are from Sky Pond (40°16'–42" N, 105°40'06" W; 3322 m asl) and Lake Louise (40°30'28" N, 105°37'13" W; 3360 m asl), two small lakes (surface areas < 5 ha; Z_{\max} < 8 m) immediately east of the Continental Divide in Rocky Mountain National Park, Colorado. Both lakes are situated at the alpine treeline and occupy cirques formed during the last glaciation (late Pinedale) in Precambrian crystalline lithologies. Although Sky Pond has been stocked successfully with salmonids since the 1920's, Lake Louise is fishless. Whereas Sky Pond is frequented by hikers during the summer months, Lake Louise is significantly more remote and consequently more seldom visited by tourists. Seasonally-averaged mean NO_3^- and NH_4^+ concentrations in Sky Pond are 1.20 mg L⁻¹ and 48 µg L⁻¹, respectively, and 1.03 mg L⁻¹ and 31 µg L⁻¹ in Lake Louise. Concentrations of PO_4^{2-} are consistently < 10 µg L⁻¹ in both lakes. Average lake-water pH and conductivity are 6.70 and 13.3 µS cm⁻¹ for Sky Pond, and 6.89 and 19.6 µS cm⁻¹ for Lake Louise.

Recent sediments were obtained in 1997 with a modified Kajak-Brinkhurst gravity corer that captures the mud-water interface intact (Glew, 1989), and extruded in continuous 0.5 cm increments in the field. The cores were dated using sediment ²¹⁰Pb activity determined by α -spectroscopy, to which the constant rate of supply (CRS) model has been applied (Appleby & Oldfield, 1978). Down-core profiles of sediment ²¹⁰Pb activity decrease progressively to supported (background) levels, verifying the stratigraphic integrity of the cores, despite their homogenous visual appearance (olive silt gyttja).

Diatom analyses followed standard methods for the preparation and enumeration of microscope slides (Battarbee, 1986). At least 400 diatom valves were counted from each slide at 1000× under oil immersion, and thereafter converted to relative frequencies. Sediment $\delta^{15}\text{N}$ measurements were conducted in order to assess changes in the biogeochemistry of N within the lake basins. Sediment $\delta^{15}\text{N}$ was determined by isotope ratio mass spectrometry (IRMS) on combusted and cryogenically-purified samples (Fry et al., 1992). The reproducibility of $\delta^{15}\text{N}$ measurements is $\pm 0.1\%$. Sediment Pb concentrations are used to independently confirm the arrival of anthropogenic emissions to the lakes via atmospheric deposition. Concentrations of Pb in sediments were determined by X-ray fluorescence (Rh source).

In order to assess purely natural pre-historic limnological variability, samples were also analyzed from the upper 325 of a 377 cm percussion core from Sky Pond, described in detail by Menounos & Reasoner (1997). The lower 50 cm of this core is biologically-sterile glacial diamicton, indicating that the entire history of the lake is captured. Five accelerator mass spectrometry (AMS) ¹⁴C dates constrain the chronology of the long core. These were obtained on insect fragments, conifer needles, and humic acids extracted from bulk sediment (Menounos & Reasoner, 1997).

Results

Diatoms

Stratigraphic profiles of the dominant diatoms from the Sky Pond and Lake Louise gravity cores are illustrated in Figure 1. Before ~1900, diatom assemblages in both lakes were dominated by *Aulacoseira distans* (Ehr.) Simonsen, *A. perglabra* (Oestr.) Haworth, *Fragilaria pinnata* Ehr., *F. construens* var. *venter* (Ehr.) Grun., and various small *Achnanthes* spp. (*A. levanderi* Hust., *A. saccula* Carter, *A. oestrupii* (Cleve-Euler) Hust., *A. laterostrata* Hust., *A. helvetica* (Hust.) Lange-Bertalot, and *A. minutissima* (Kütz.)). This is a typical flora of oligotrophic Rocky Mountain lakes. The mesotrophic planktonic taxa *Asterionella formosa* Hassal and *Fragilaria crotonensis* Kitton became common elements within diatom assemblages of the 1900–1950 interval. Both of these taxa are present in trace frequencies in older sediments, implying that their observed increases were environmentally stimulated, and not the consequence of recent algal colonization events. Subsequently, between 1950 and 1970, *A. formosa* became the dominant diatom in both lakes (Figure 1). *Asterionella formosa* is an opportunistic alga that responds rapidly to disturbance and nutrient enrichment. For example, it is often among the first diatoms to follow human settlement and agriculture in the catchments of European lakes (Renberg et al., 1993; Anderson et al., 1995; Reavie & Smol, 2001). Moreover, the growth of *A. formosa* and *F. crotonensis* has been accelerated, respectively, by in-lake nitrogen additions (McKnight et al., 1990) and laboratory culturing experiments (Interlandi & Kilham, 1998).

Nitrogen isotopes and Pb concentrations

In both gravity cores, sediment $\delta^{15}\text{N}$ values are stable between 4 and 5‰ prior to ~1900, but begin to decrease

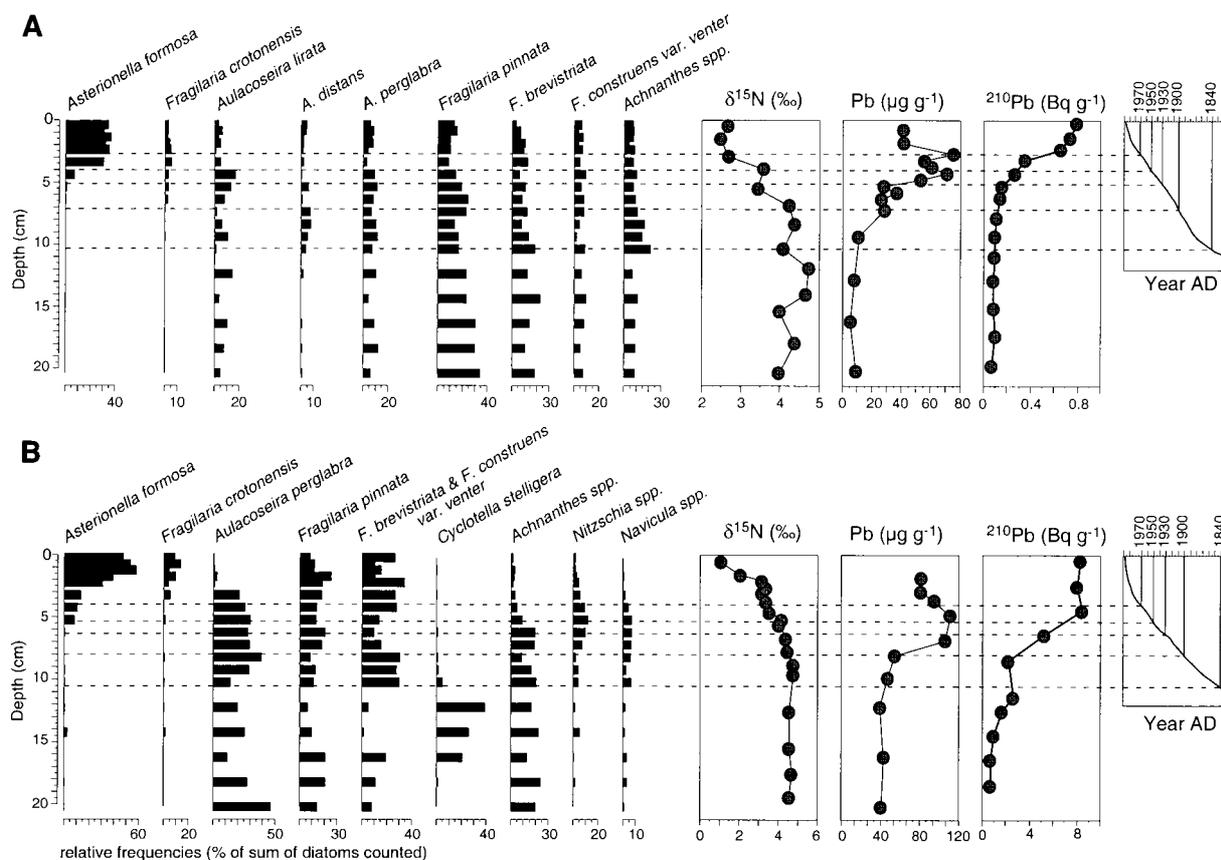


Figure 1. Stratigraphies of the relative frequencies of dominant diatom taxa, sediment $\delta^{15}\text{N}$, Pb concentrations, and ^{210}Pb activities from the upper 20 cm of the gravity cores from Sky Pond (A) and Lake Louise (B). Depth-age relationships shown on the right represent CRS age models applied to the ^{210}Pb data.

shortly thereafter, by about 1‰ in the first half of the 20th century (Figure 1). The trend towards lighter isotopic values accelerated after ~ 1950, with further depletions of 1.0 and 2.5‰ in Sky Pond and Lake Louise, respectively. Although sediment diagenetic transformations could potentially be invoked to account for the observed $\delta^{15}\text{N}$ stratigraphic trends, several recent investigations have demonstrated that sediment $\delta^{15}\text{N}$ is a faithful recorder of the isotopic composition of the overlying water column (Brenner et al., 1999; Teranes & Bernasconi, 2000). We submit that the sediment isotopic trends from Sky Pond and Lake Louise primarily reflect ever-augmenting additions of isotopically-depleted N compounds transported atmospherically from areas east of the Colorado Front Range. Nitrogen oxide emissions from automobiles and electricity-generating plants have increased greatly in the western United States since ~ 1940 (Gschwandtner et al., 1985). These sources produce NO_x with $\delta^{15}\text{N}$ values ranging

from -7 to +12‰ (Heaton, 1990; Shanley et al., 1998), with further fractionation possible during atmospheric transport and wet deposition. Although data from the Colorado Front Range are sparse, $\delta^{15}\text{N}$ measurements from NO_3^- in high elevation precipitation samples range from -2 to +6‰ (Kendall et al., 1995). The highly variable character of $\delta^{15}\text{N}$ values associated with fossil fuels suggests that this is not the sole contributor to the observed trends of directional decreases in sediment $\delta^{15}\text{N}$. We note that fertilizer NH_3 and NO_x typically have $\delta^{15}\text{N}$ of $\sim 0 \pm 3\text{‰}$, whereas NH_3 emissions from confined animal feeding operations range from -15 to -9‰ (Macko & Ostom, 1994; Shanley et al., 1998). Ever-increasing contributions from these latter sources are therefore entirely compatible with progressively lighter sediment isotopic values (Figure 1).

Stratigraphic trends of sediment Pb concentrations from both lakes (Figure 1) preserve pre-1930 Pb increases associated with widespread mining and smelt-

ing activities in the Rocky Mountains and the Denver region (Baron et al., 1985). Thereafter, sediment [Pb] largely reflects regional leaded gasoline use, which is confirmed by decreases since the 1970's from the abandonment of Pb additives to gasoline. These trends indicate that automotive pollution, which may also influence sediment $\delta^{15}\text{N}$, consistently attains the elevations of the study sites. However, the decoupling of Pb and $\delta^{15}\text{N}$ profiles after ~ 1970 strongly implies that the source of N deposition to the lakes is considerably broader than automotive NO_x . This agrees well with the suggestion that agricultural sources of N deposition are playing an increasingly dominant biogeochemical role for the area under consideration.

Natural range of variability

The natural, pre-industrial variability of sediment proxies is assessed by 46 diatom and 28 $\delta^{15}\text{N}$ analyses from the 14,000-year percussion core from Sky Pond. Large diatom floral changes characterized the lake's early ontogeny, as the ecosystem progressed from a barren deglacial state to one in which alpine tundra became well-established in the catchment. Sediments from this interval are dominated alternately by *Pinnularia* spp. (*P. biceps* Greg. and *P. nodosa* (Ehr.) W. Sm. and small alkaliphilous *Fragilaria* spp. The genera *Aulacoseira*, *Achnanthes*, and *Navicula* expanded after 10,000 years before present. Diatom assemblages from the long and short cores from Sky Pond have been compared objectively using Rate of Change Analysis (Jacobson & Grimm, 1986), in which a measure of dissimilarity between stratigraphically successive samples is normalized to the time interval separating the deposition of each (Figure 2). We used the Manhattan metric distance as the measure of between-sample dissimilarity ($\text{MMd}_{ij} = \sum_k |x_{ik} - x_{jk}|$, where x_{ik} and x_{jk} are the relative frequencies of taxon k in successive samples i and j), and the radiometric age constraints for the short and long cores (CRS ^{210}Pb and calibrated AMS ^{14}C years, respectively). The results indicate, as expected, that the highest rates of naturally-mediated change occurred in the early stages of lake ontogeny. However, even the highest rates of change expressed by natural edaphic, climatic, or limnological processes are overshadowed by those of recent decades, which we attribute to anthropogenic N deposition. Sediment $\delta^{15}\text{N}$ measurements from the Sky Pond long core illustrate that the amplitude of natural $\delta^{15}\text{N}$ variability is no greater than that expressed by the trend of the last few decades (~ 2‰), but that, importantly, never in the past 14,000

years did sediment $\delta^{15}\text{N}$ values become as severely depleted as they are at present (Figure 2).

Discussion

The post-1950 period of rapid sediment isotopic and diatom shifts corresponds with intensifications of agricultural practices, animal husbandry, and population growth in adjacent regions to the east of the Colorado Front Range (Figure 3). Widespread implementation of the Haber-Bosch process in the manufacture of commercial N fertilizers began after 1950, leading to massive introductions of synthetic N to cultivated soils (Smil, 1997). In the 10 counties east of the Front Range, cattle numbers in confined feeding operations rose from 1.4–3.7 million head between 1940 and 1973, whereas human population increased from 713,000 to 2.4 million between 1950 and 1995. Although the resulting increase in the rate of deposition of reactive N to adjacent mountains is currently less than half of maximum values measured in the eastern USA, it is nonetheless sufficient to induce substantial changes in the structure of algal communities, and shift sediment nitrogen isotopic signatures to reflect augmented anthropogenic contributions. However, no diatom evidence for lake acidification is recorded, although acidification has been predicted as an eventual consequence of sustained elevated $[\text{NO}_3^-]$ (Kling & Grant, 1984).

We deduce the principal source of N-deposition to be east of the Front Range, since surface water $[\text{NO}_3^-]$ decreases progressively westward of the Continental Divide (Landers et al., 1986; Eilers et al., 1987). Therefore, because the dominant pattern of atmospheric circulation over the Colorado Front Range is westerly (Pacific) flow, a strong case is made for the potency of episodic upslope (easterly) deposition generated by convective heating on the plains. Despite representing a secondary air mass trajectory, easterly flow nonetheless appears fully capable of transporting pollution originating in the Denver-Fort Collins axis to elevations > 3300 m. Sky Pond and Lake Louise are significantly higher than the previously suggested altitudinal limit of anthropogenic deposition by upslope air-mass trajectories (Sievering et al., 1996).

Despite being located on federally protected lands, our study sites can no longer be considered pristine, given the accelerated ecological changes manifested over recent decades. The longer-term paleolimnological record demonstrates that these marked shifts are unprecedented in the context of naturally-mediated ecologi-

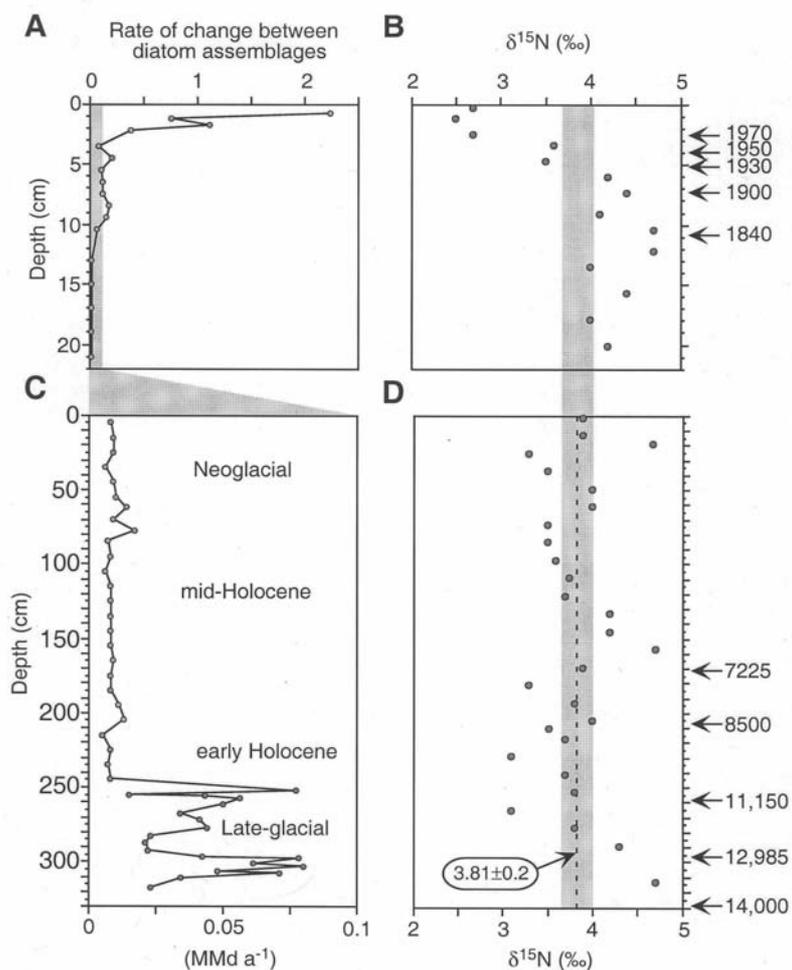


Figure 2. Comparison of diatom and sediment $\delta^{15}\text{N}$ data from the short (A, B) and long (C, D) cores from Sky Pond. Diatom relative frequencies in both cores have been converted to a rate of change measure, using the Manhattan metric distance (MMd_i) as the between-sample dissimilarity, normalized to the interpolated time elapsed between the deposition of stratigraphically adjacent samples. Note the change of scales for the rate of change results between (A) and (C). For the corresponding sediment $\delta^{15}\text{N}$ values, the shaded envelope indicates the mean $\pm 1\sigma$ for measurements from the pre-industrial sediments of the long core ($n = 28$). Arrows indicate radiometric ages (^{210}Pb CRS and calibrated AMS ^{14}C).

cal variability. Alpine catchments in the western United States should therefore be viewed as highly susceptible to anthropogenic modifications of the nitrogen cycle. The ecological sensitivity and rapid response to disturbance of diatom communities suggest that they represent a particularly useful group of early-warning indicators for potentially more profound ecological reorganizations. Oligotrophic lakes have been shown to respond synergistically to compounded anthropogenic stressors (Schindler et al., 1996), implying that the future resilience of remote lakes to other impacts, such as climate change, may already be reduced. This raises concerns about the future trajectories of alpine

lakes, since enhanced nitrogenous emissions, whether viewed at regional or global scales, are unlikely to be soon diminished.

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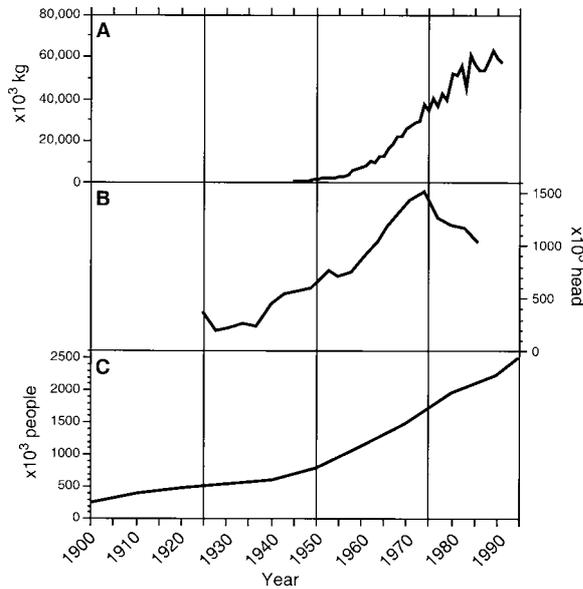


Figure 3. Compilations of available historical records for (A) annual nitrogen fertilizer use, (B) heads of cattle, and (C) human population in the ten counties of Colorado adjacent to the Front Range. The data are compiled from Alexander & Smith (1990) and census data for the following counties: Adams, Arapahoe, Boulder, Douglas, Jefferson, Larimer, Logan, Morgan, Washington, and Weld.

the long core from Sky Pond, as well as A. Mosier, P. Matson, J. Sachs and E. Steig for discussions at various stages of preparation.

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