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Research paper

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Abstract

Understanding effects of recent climate warming and changes in catchment conditions on nutrient cycling and the biology of shallow subarctic lakes is necessary to predict their evolution. Here, we use multiple analytical methods on sediment cores to identify effects of change in catchment conditions on nutrient availability and biotic assemblages in two subarctic lakes on the Seward Peninsula (Alaska, USA). We compare limnological and biotic responses to flooding and expansion of a thermokarst lake basin (late 1950s), increased shrub growth in the catchment of another lake (since the mid-1980s), and regional warming (since the late 1970s). Among these three environmental drivers, the largest biotic responses occurred because of flooding and expansion of the thermokarst lake. An increase in the nitrogen isotope composition and decline in organic carbon isotope composition in sediments are interpreted to reflect an elevated supply of dissolved inorganic carbon and nitrogen. This was associated with significant shifts in composition of chironomid and diatom assemblages. In contrast, increases in particulate organic carbon and nitrogen from enhanced shrub growth had less influence on the biota. Declines in cold-water biotic indicators typical of warming lakes in Arctic regions occurred several decades after catchment-induced changes to the nutrient supply in both systems. This indicates that initial lake catchment condition may mediate lake-specific changes in nutrient cycling and aquatic productivity within regions undergoing warming.

Keywords

catchment condition, climate warming, environmental change, paleolimnology, trophic systems

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Introduction

Shallow lakes in subarctic and Arctic regions provide critical habitat for wildlife but are predicted to be among the most sensitive freshwater ecosystems to climate change and human activities. Recent accelerated permafrost thawing, for example, has resulted in substantial loss in water surface area and complete drainage in many high-latitude regions (e.g. Smith et al., 2005; Yoshikawa and Hinzman, 2003). With little buffering capacity, shallow lakes are highly susceptible to limnological and biotic change (Lim et al., 2005; Medeiros et al., 2012), and detailed study of these phenomena have implications beyond a sentinel role for detecting climate warming. For example, changes in catchment supply of nutrients on aquatic production are likely to be important (Fritz and Anderson, 2013). Yet, there is little known of the expected decadal-scale limnological and ecological transitions associated with such catchment processes at high latitudes.

Changes in catchment conditions as a consequence of a warming climate have the potential to alter the limnology of subarctic and Arctic lakes (Jorgenson et al., 2006; Lantz and Kokelj, 2008; Osterkamp and Romanovsky, 1999). For example, geochemical modification of soils as a result of thawing permafrost influences the input of dissolved and particulate substances to Arctic lakes (Lantz and Kokelj, 2008), which often have low ionic concentrations because of limited groundwater contributions (Lim et al., 2005). Kokelj et al. (2009) found that retrogressive thaw slumps lead to elevated ionic concentrations and water clarity in comparison with undisturbed lakes in the western Canadian Arctic. The increase in water clarity is likely because of the sedimentation and flocculation of organic materials, which Mesquita et al. (2010) have shown to cause increased macrophyte production. Lougheed et al. (2011) also noted that aquatic macrophyte biomass has increased in Alaskan lakes since the 1970s. The input of organic-rich sediments from thawing permafrost may also affect lake nutrient cycling (Bowden et al., 2008; Thompson et al., 2012), which is known to regulate macrophyte biomass and production in wet-sedge tundra (Shaver et al.,

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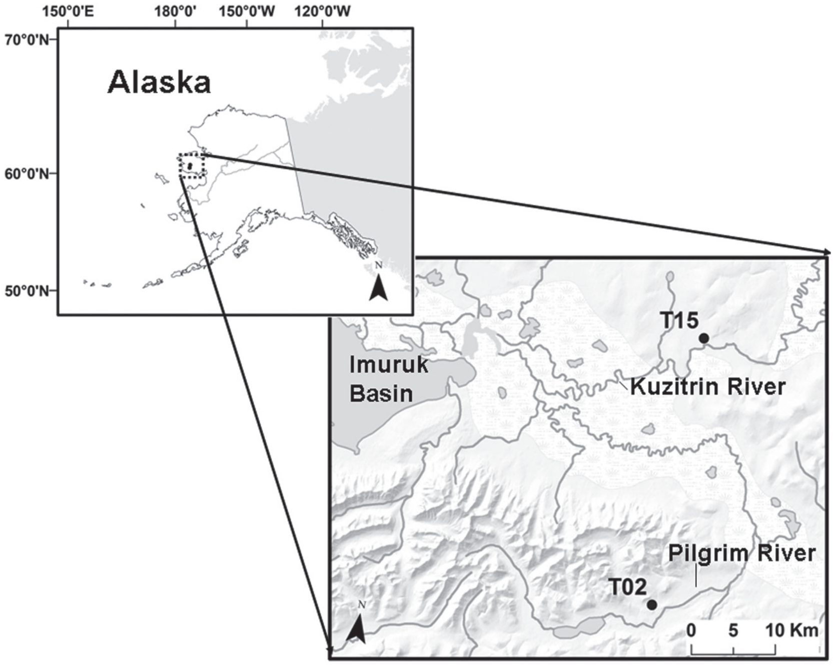

Figure 1. Location of Lakes T02 and T15, Seward Peninsula, Alaska.

1998). Consequently, greater nutrient availability and increased benthic habitat and biomass may result in significant alteration of aquatic trophic systems (Mesquita et al., 2010).

The degradation of permafrost under warmer temperatures is expected to enhance the development of woody vegetation, particularly in the discontinuous permafrost zone (Lloyd et al., 2003; Nicholas and Hinkel, 1996; Rovansek et al., 1996). Terrestrial net production is low in tundra environments because of poorly drained soils with a limited supply of available nutrients (Waelbroeck et al., 1997). However, permafrost degradation improves drainage (Woo et al., 1992), which promotes the growth of woody shrubs (Myers-Smith et al., 2011). Shaver et al. (1992) noted that warmer temperatures stimulate the growth of vegetation and sequestration of nitrogen. For example, dwarf birch (*Betula nana*) is able to elongate its shoots in response to higher air temperatures and nitrogen availability (Myers-Smith et al., 2011). The increased growth of shrubs in catchment areas of lakes can alter a number of ecosystem processes, including surface reflectance and energy flux (Chapin et al., 2005), fire regimes (Mack et al., 2011), organic matter delivery to lakes and nutrient exchange (Cornelissen et al., 2007), nitrogen mineralization and fixation feedbacks (Buckeridge et al., 2010), and the net carbon balance (Mack et al., 2004). Previous studies of Holocene-scale climate transitions have identified associated biotic responses to dissolved organic carbon concentrations that increased with the establishment of terrestrial vegetation (Fallu et al., 2005; Pienitz et al., 1999). However, there has been less focus on nutrient loading to aquatic ecosystems as a consequence of recent increases in shrub density in subarctic lake catchments.

Recent expansion of tall woody shrubs in the 1980s has been documented on the Seward Peninsula in response to increased air temperature (Lloyd et al., 2002; Silapaswan et al., 2001). Jones et al. (2011a) have also reported that a majority of thermokarst systems have expanded since the 1950s, and several lakes have experienced lateral drainage in recent years. Human activities, such as road construction, also have the potential to affect lake catchments in permafrost regions. The Seward Peninsula has a road network of over 480 km in length; in some cases, thermokarst basins have been bisected by roads. Thus, this region serves as an area where changes in, and consequences of, the delivery of particulate and dissolved substances to lakes resulting from catchment modifications can be examined.

Changes in nutrient availability in lakes because of altered catchment conditions may develop over time scales that are difficult to capture with routine limnological measurements. Alternatively, examination of information preserved in sediment cores from subarctic and Arctic lakes has been used extensively to characterize the ecological reorganization of aquatic food webs in response to a warmer climate (e.g. Quinlan et al., 2005; Rühland et al., 2013). Here, we address key questions about how lake nutrient conditions and aquatic biota are responding to altered catchment conditions in a subarctic area undergoing environmental change. These include (1) what effect do disturbances to catchment condition, such as thermokarst expansion, have on a lake's nutrient balance and biotic assemblages; (2) similarly, what is the effect of enhanced shrub development within lake catchments; and (3) do catchment-driven changes in lake nutrient conditions and biotic assemblages differ from those driven by warming? We measured organic carbon and nitrogen elemental and isotope composition and determined diatom and chironomid assemblages on radiometrically dated sediment cores to identify the responses of nutrient regimes and biota in two lakes on the Seward Peninsula whose catchment conditions have recently changed. At one lake, we also measured cellulose oxygen isotope composition to reconstruct past hydrological conditions. Study lakes include 'Lake T15' (informal name), a thermokarst basin, which has undergone recent flooding and shoreline erosion, and 'Lake T02' (informal name), which has experienced substantial shrub growth within its catchment during the past few decades. Although there is widespread recognition of direct influences of temperature on subarctic aquatic ecosystems, we focus on understanding the role of changing catchment condition on lake nutrients, productivity, and biotic assemblages.

Study sites

The Seward Peninsula is the eastern remnant of the Bering Strait land bridge in northwestern Alaska (Figure 1). The study region is characterized by upland tundra; the treeline is 50–60 km southeast of the study lakes. Elevation ranges from sea level to 1437 m a.s.l., with the majority of the landscape below 600 m a.s.l. Most of the peninsula is underlain by Quaternary basaltic flows, with granite, schist, and schistose limestone. Discontinuous permafrost extends from 15–50 m below the surface (Hinzman et al.,

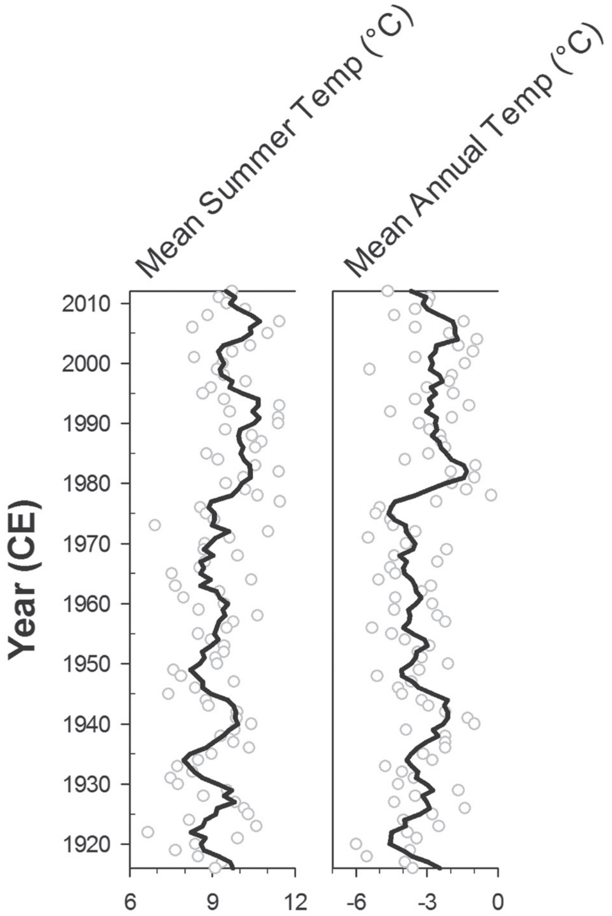

Figure 2. Observed temperature and trends from 1910–2011 from the Nome, AK, climate station (NOAA 2013 – http://pafg.arh.noaa.gov/). Solid lines indicate 5-year running mean.

2005). Mountainous areas receive twice the snowfall of lower elevations and the average snowpack near the study sites is about 82 cm. Climate records for the town of Nome (25–30 km south of the study sites) indicate a step-shift increase of approximately 2.0°C in mean annual and summer temperatures in the late 1970s (Figure 2).

Lake T15 (65°13.9554′N, 164°49.3920′W) is the largest remaining fragment of a once larger thermokarst pond (Figure 1). Outflow from the lake drains into the Kuzitrin River. A road was constructed through the former thermokarst basin in the late 1950s. Historical photographs also reveal an increase in lake surface area beginning after 1950 (Figure 3a). Lake T02 (64°56.54′N, 164°50.60′W) is a closed-drainage basin on a moraine boulder field and is also adjacent to a road constructed in the late 1950s (Figures 1 and 3b). The moraine was formed by the lobate terminus of the Crater Creek glacier (>40,000 BP) (Kaufman and Calkin, 1988). The lake basin and nearby terrain show evidence of pronounced shrub expansion and growth since 1972 (Figure 3b). The margins of the lake are now surrounded by tall shrubs (mainly *Betula nana* and *Salix glauca*). Both lakes are oligotrophic and relatively dilute, but nutrients, dissolved inorganic and organic carbon, ions, and some metals are higher in Lake T15 than in Lake T02 based on water samples collected in mid-summer 2011 (Table 1).

Material and methods

Field methods

Sediment cores were recovered on 5 August 2011 from lakes T02 (12.5-cm long) and T15 (10.5-cm long) from a central location within each lake using an Uwitec gravity corer (8.4-cm diameter) deployed from a boat. The cores were collected from water depths of 4.1 and 3.2 m at lakes T02 and T15, respectively. Each core was extruded in the field and sectioned into 0.5-cm intervals. The upper ~2 cm of sediment cores contained coarse organic flocculent material underlain by massive organic mud. Sediment samples were stored in Whirl-Pak® bags and kept cool (4°C) and dark until processed.

Laboratory methods

Sediments were analyzed for their percent organic matter (%OM) and carbonate content (expressed as percentage of dry sediment mass) at 0.5-cm intervals by measuring the weight loss-on-ignition (LOI) following sequential combustion of dried sediment at 550°C and 950°C (Heiri et al., 2001).

The chronology of each sediment core was established using the Constant Rate of Supply (CRS) model based on measurements of the activities of ^{210}Pb and ^{226}Ra (inferred from the mean of ^{214}Bi and ^{214}Pb activities) on each 0.5-cm interval, following methods outlined in Appleby (2001) and procedures described in MacDonald et al. (2012). Sediment samples were also measured for ^{137}Cs, but because of apparent migration, these data could not be used to identify the 1963 (peak fallout) stratigraphic horizon.

Geochemical analysis. Both cores were analyzed for bulk organic carbon and nitrogen elemental and isotope composition following methods described in Wolfe et al. (2001). Each 0.5-cm interval was treated with 10% HCl in a 60°C water bath to remove carbonates and rinsed with de-ionized water repeatedly until a neutral pH was reached. Samples were sieved at 500 µm to remove coarse debris, and subsamples of the fine fraction were weighed and analyzed for organic carbon and nitrogen elemental and isotope composition using an elemental analyzer interfaced with a continuous-flow isotope-ratio mass spectrometer at the University of Waterloo Environmental Isotope Laboratory. C:N ratios are reported as weight ratios. Isotope results are reported in δ notation as per mil (‰) relative to Vienna Pee Dee Belemnite (VPDB) for carbon isotope composition and relative to atmospheric nitrogen (AIR) for nitrogen isotope composition. Analytical uncertainties are ±0.06‰ for carbon isotope composition and ±0.09‰ for nitrogen isotope composition based on repeated analyses of samples.

Since there were signs of evaporation (high-water marks) along the rocky margins of Lake T02, cellulose oxygen isotope analysis was conducted to reconstruct past hydrological conditions following techniques described by Wolfe et al. (2001). The fine fraction of sediments already processed for organic carbon and nitrogen elemental and isotope analysis (see above steps) was processed further to remove non-cellulose fractions with the use of bleaching, solvent extraction, alkaline hydrolysis, and oxyhydroxide leaching. The freeze-drying process separated the remaining minerogenic fraction, making density separation using sodium polytungstate unnecessary. Subsamples of freeze-dried cellulose concentrate were submitted to the University of Waterloo Environmental Isotope Laboratory to determine oxygen isotope composition by high-temperature pyrolysis using a continuous-flow isotope-ratio mass spectrometer. Some intervals had insufficient cellulose for analysis. Data are reported as δ values, representing deviations in per mil (‰) from the Vienna Standard Mean Ocean Water (VSMOW). Analytical uncertainty is estimated at ±0.5‰. Lake water δ^{18}O was inferred using a cellulose-water fractionation factor of 1.028 (Wolfe et al., 2001).

Biological analysis. Every 0.5-cm interval for both sediment cores were processed for subfossil chironomid head capsules, which were enumerated from sediments washed through nested 212- and 106-µm mesh sieves following Medeiros and Quinlan (2011). A minimum of at least 50 head capsules were enumerated

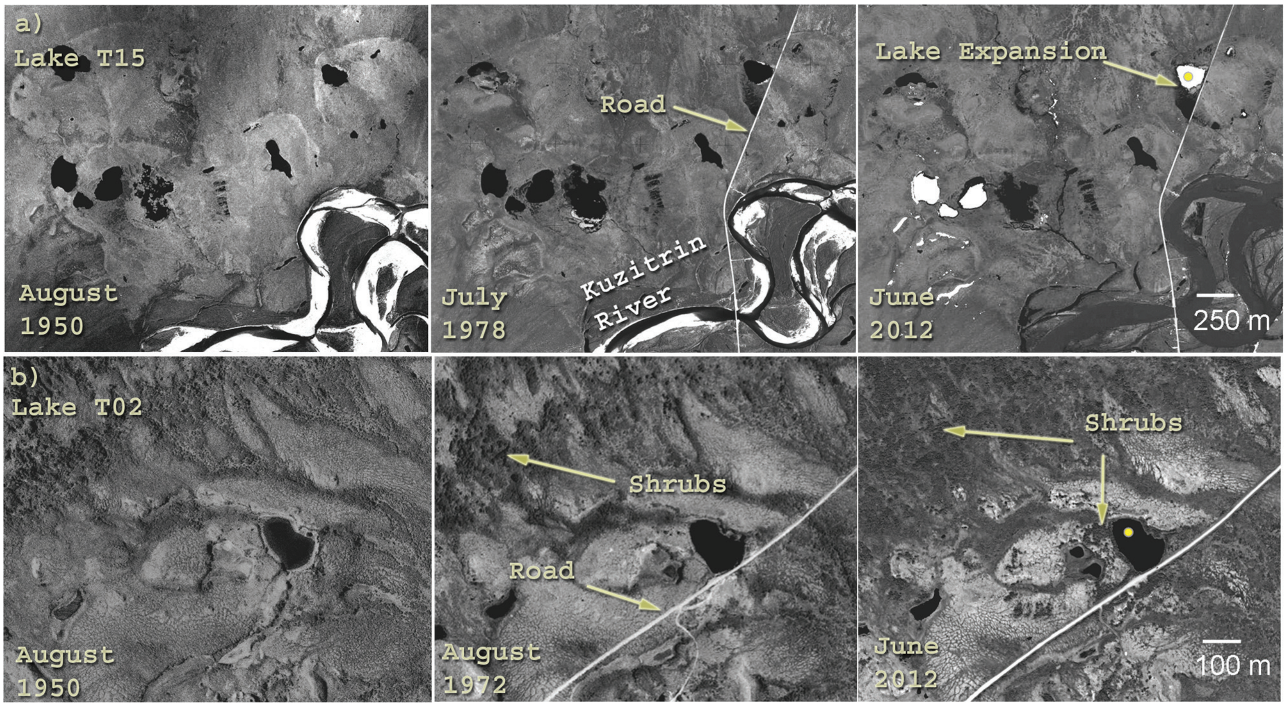

Figure 3. Historical images of the study lakes on the Seward Peninsula (coring locations indicated): (a) Lake T15 is adjacent to a road constructed in the late 1950s. Evidence of lake expansion is apparent in the 1978 and 2012 photos and (b) the catchment of Lake T02 has undergone considerable expansion of shrubs since 1972. The lake is also adjacent to a road constructed in the late 1950s.

Table 1. Water chemistry of lakes T15 and T02 collected in the field (5 August 2011) and analyzed by the Canadian Centre for Inland Waters National Laboratory for Environmental Testing using protocols outlined in the Analytic Methods Manual of Environment Canada (Environment Canada, 1994).

	T15	T02
Elevation (m)	91	184
Area (ha)	2.89	1.17
Temp (°C)	15	16
Depth (m)	3.2	4.1
CHLA (μm/L)	0.9	2.3
TN (μm/L)	593	344
TP (μm/L)	8.9	4.5
DOC (mg/L)	18.7	6.5
DIC (mg/L)	7.2	2.6
POC (μm/L)	530	467
PON (μm/L)	50	50
Cl (mg/L)	2.1	1.8
SO_4 (mg/L)	0.3	1.5
Ca (mg/L)	7.0	2.9
Mg (mg/L)	1.4	0.5
K (mg/L)	0.08	1.85
Na (mg/L)	3.4	1.1
SiO_2 (mg/L)	6.7	0.05
Al (mg/L)	52.1	60.8
Ba (mg/L)	6.8	2.9
Cu (mg/L)	0.51	0.9
Fe (mg/L)	385	47
Mn (mg/L)	18.9	3.0
Mo (mg/L)	0.13	0.06
Ni (mg/L)	1.94	0.78
Pb (mg/L)	0.03	0.06
Rb (mg/L)	0.27	3.4
Sr (mg/L)	24.2	8.6
Zn (mg/L)	2.5	1.3

(Quinlan and Smol, 2001), mounted onto glass slides, and identified at 400–1000× magnification to the best taxonomic resolution possible based on Oliver and Roussel (1983), Wiederholm (1983), Rieradevall and Brooks (2001), Brooks et al. (2007), Medeiros and Quinlan (2011), and Stur and Ekrem (2011). The relative abundance of each taxon was calculated as the percent of total identifiable midges and was Hellinger-transformed for numerical analyses.

To prepare samples for analysis of diatom assemblages, well-mixed subsamples of wet sediment from each 0.5-cm interval for both sediment cores were placed into 15 mL centrifuge tubes and digested in a mixture of equal parts concentrated nitric and sulfuric acid (50:50 by volume) to remove the organic matrix, following standard methods described in Battarbee et al. (2001). Samples were allowed to digest in a hot water bath (85°C) for at least 8 h. After cooling, diatoms were allowed to settle for 24 h, and the acids were removed by siphoning off the upper 2/3 of the supernatant, followed by dilution with distilled water. Rinses with distilled water, followed by a 24-h period to allow diatoms to settle, were repeated until the pH of the supernatant was the same as the distilled water. Once acid residues were removed, we added a measured volume of a microsphere solution to estimate the abundance of diatoms in the samples. The diatom slurries were mounted on slides in four dilutions per sample using Naphrax® mounting medium. A minimum of 300 diatom valves per sample were enumerated and identified to species level using a Zeiss microscope with differential interference contrast optics at 1000× magnification. Taxonomic identifications were based on Krammer and Lange-Bertalot (1986–1991) and Lavoie et al. (2008). The diatom data were expressed as taxon relative abundances of the total diatom sum, and as total abundance of diatoms calculated from use of microspheres following methods described in Battarbee and Kneen (1982).

Numerical analysis. Trends in geochemnical parameters were identified through a breakpoint analysis, where generalized linear models with piecewise linear relationships were estimated with a fixed number of breakpoints according to methods outlined by Muggeo (2008). Stratigraphic intervals were defined independently for both chironomids and diatoms using a constrained cluster analysis with incremental sum of squares partitioning (CONISS) and a squared chord-distance dissimilarity coefficient (Gordon and Birks, 1972). The number of significant zones was determined by comparing the dispersion of the hierarchical classification with that obtained from a broken stick model (Bennett, 1996). All analyses were performed in the R statistical language with use of the Rioja and segmented libraries. Because of a large number of rare taxa, only taxa with a minimum abundance of 2% abundance or greater, and present in at least two samples, were retained in the analyses (Quinlan and Smol, 2001; Rühland and Smol, 2005).

Results

Sediment core chronologies

Total ^{210}Pb activity for Lake T15 generally declines from the top of the core to 4.0-cm depth, where there is a stepwise decrease from 115 to 50 Bq/kg (Figure 4a). Below 4 cm depth, total ^{210}Pb activity continues to decline and approaches supported ^{210}Pb (i.e. ^{226}Ra) activity at 8.0-cm depth (23 Bq/kg). A basal CRS modeled ^{210}Pb date of 1922 (10.5 cm) was determined with an estimated mean sampling resolution of 4.5 years. Errors (2 SD units) of the CRS modeled ^{210}Pb dates range from 0.12 to 10.52 years (average = 3.5 years). An average dry mass sedimentation rate of 157 g/m^2/yr was estimated with two large peaks at ~1961 (301 g/m^2/yr) and ~1934 (380 g/m^2/yr) (Figure 4b).

Radiometric analysis of Lake T02 determined that total ^{210}Pb activity declined exponentially from 380 Bq/kg at the top of the core to 100 Bq/kg at 12.0-cm depth (Figure 4c). Total ^{210}Pb activities were not observed to reach supported ^{210}Pb levels of 78 Bq/kg (^{226}Ra). To correct for this, the Constant Flux to Constant Sedimentation model (Appleby, 2001) was used to estimate the quantity of missing ^{210}Pb inventory, which was then incorporated into the CRS model. A basal CRS modeled ^{210}Pb date of 1916 (12.5 cm) was determined with an estimated mean sampling resolution of 4.6 years. Errors (2 SD units) of the CRS modeled ^{210}Pb dates range from 0.25 to 13.18 years (average = 3.3 years). An estimated average sedimentation rate (Figure 4d) of 231 g/m^2/yr was determined with two peaks at ~1971 (382 g/m^2/yr) and ~1950 (372 g/m^2/yr).

Geochemical and biological stratigraphy

Lake T15: thermokarst basin. Breakpoint analysis identified a stratigraphic change in geochemical data at 1964 ± 3.3 years (Figure 5). The lower geostratigraphic zone (~1920 to 1964) is characterized by decreasing trends in %OM (40–32%), %C_{org} (21–18%), %N (1.2–1.0%), C:N (18.5–16.5), and $\delta^{13}C_{org}$ (−29.2‰ to −30.0‰), whereas δ^{15}N values generally increased (0.2–0.8‰). In the upper geostratigraphic zone, trends reversed and increased for %OM (32–37%), %C_{org} (18–20%), and %N (1.0–1.2%), whereas similar trends are maintained for C:N (16.5–15.5), $\delta^{13}C_{org}$ (−30.0‰ to −30.5‰), and δ^{15}N (0.8–1.5‰).

A total of 60 chironomid taxa (per sample average = 24) were identified in the Lake T15 sediment core. Concentrations of chironomids (head capsules per gram dry weight (HC/g DW)) increased from 420 to over 2000 HC/g DW in uppermost sediments (Figure 6). Three biostratigraphic zones were delineated by the constrained cluster analysis of chironomid assemblages, with stratigraphic shifts at ~1959 and ~1985. Prior to ~1959, assemblages were dominated by *Sergentia, Limnophyes, Procladius*, and *Tanytarsus heliomesonyctios* (previously referred to as *Corynocera oliveri*; Stur and Ekrem, 2011). The biostratigraphic zone from 1959 to 1985 represented a transition period, with *Corynocera ambigua* increasing from <10% of the chironomid community prior to ~1959 to >45%. This interval was also marked by a reduction in *Zalutschia lingulata pauca, Limnophyes, Paratanytarsus*, and *Sergentia*. The most recent biostratigraphic zone (~1985–present) was dominated by *Corynocera ambigua*, which represents >50% of the chironomid assemblage and is also characterized by declines in *Tanytarsus heliomesonyctios*, and *Psectrocladius sordidellus*-type, and small increases in *Zalutschia zalutschicola* and *Microtendipes*.

The diatom flora of the Lake T15 sediment core consisted of a total of 57 taxa representing 17 genera. Assemblages largely consisted of small benthic Fragilariaceae taxa (e.g. *Staurosirella pinnata, Staurosira construens* var. *venter*, and *Pseudostaurosira brevistriata*; Figure 7). Diatom concentrations were high and decreased during the past two decades with values ranging from a maximum of 2.35 × 10^8 to 9.05 × 10^6 valves/g in uppermost sediments. The constrained cluster analysis of diatom assemblages indicated two stratigraphic shifts at ~1952 and ~1985. Prior to ~1952, assemblages were dominated by *Aulacoseira alpigena, Staurosira construens* var. *venter*, and *Pseudostaurosira brevistriata*. Between ~1952 and ~1985, the benthic diatom *Staurosirella pinnata* increased from <5% to >10% of the diatom assemblage, whereas *Aulacoseira alpigena* decreased by >5%. Recent decades (~1985–2011) were represented by an overall stabilization of dominant taxa and subtle increases (2%) of *Achnanthes marginulata* and *Navicula pupula*.

Lake T02: shrub basin. Breakpoint analysis identified a stratigraphic change in geochemical indicators at ~1980 ± 3.7 years (Figure 8). The lower geostratigraphic interval (~1920–1980) is characterized by relatively constant values for %OM (~14%), %C_{org} (~6%), and %N (~0.6%), and increasing values for C:N (10.5 to 11.0) and $\delta^{13}C_{org}$ (−27.0‰ to −26.5‰). δ^{15}N values were mostly constant (~2.5‰) except for a decrease to 1.6‰ at ~1930 and an increase to 3.0‰ at ~1983. Although the $\delta^{18}O_{lw}$ profile is lower resolution, values averaged about −20‰ with a peak at ~1970 (−15‰). At ~1980, several of the geochemical parameters abruptly increased, including %OM (14–16%), %C_{org} (6.0–7.5%), and %N (0.5–0.7%). These parameters continued to increase gradually to the top of the record. C:N (~11.5) and $\delta^{18}O_{lw}$ (−14‰) were also higher after ~1980. In contrast, decreasing trends are evident for $\delta^{13}C_{org}$ (−26.5‰ to −27.4‰) and δ^{15}N (2.5‰–2.0‰) after ~1980.

The Lake T02 sediment core contained 48 chironomid taxa (per sample average = 16). Concentrations of head capsules per gram dry weight of sediment decreased from 225 HC/g DW at ~1916 to a low of 90 HC/g DW at ~1970, and then increased to a high of 315 HC/g DW in recent sediment intervals (Figure 9). Three biostratigraphic zones were delineated by the constrained cluster analysis of chironomid assemblages, marked by transitions at ~1970 and ~1999. Prior to ~1970, assemblages contained high relative abundances of cold-water adapted taxa common to Arctic regions, such as *Heterotrissocladius, Micropsectra insignilobus*-type, and *Parakiefferiella nigra*-type. The period between ~1970 and ~1999 was marked by a reduction of *Stictochironomus* type B (average 12–5%) and an increase in *Procladius* (1–3%), *Monodiamesa* (<1% to 3%), *Protanypus* (<1% to 3%), *Parakiefferiella nigra*-type (4–11%), *Tanytarsus mendax*-type (<1% to 6%), *Zalutschia lingulata pauca* (average 5–11%), and *Corynoneura arctica*-type (<1% to 8%). This was followed by a reduction of *Heterotrissocladius* (30–10%), *Parakiefferiella nigra*-type (11–2%), and a marked increase (11% to >30%) in *Zalutschia lingulata pauca* in recent sediments (~1999–2011).

Diatom assemblages were relatively species-rich in the sediment core from Lake T02, with a total of 85 diatom taxa representing 30 genera. Assemblages were composed predominantly of benthic taxa with the exception of a high relative abundance of tychoplanktonic *Aulacoseira alpigena* (Figure 10). Diatom concentrations were high

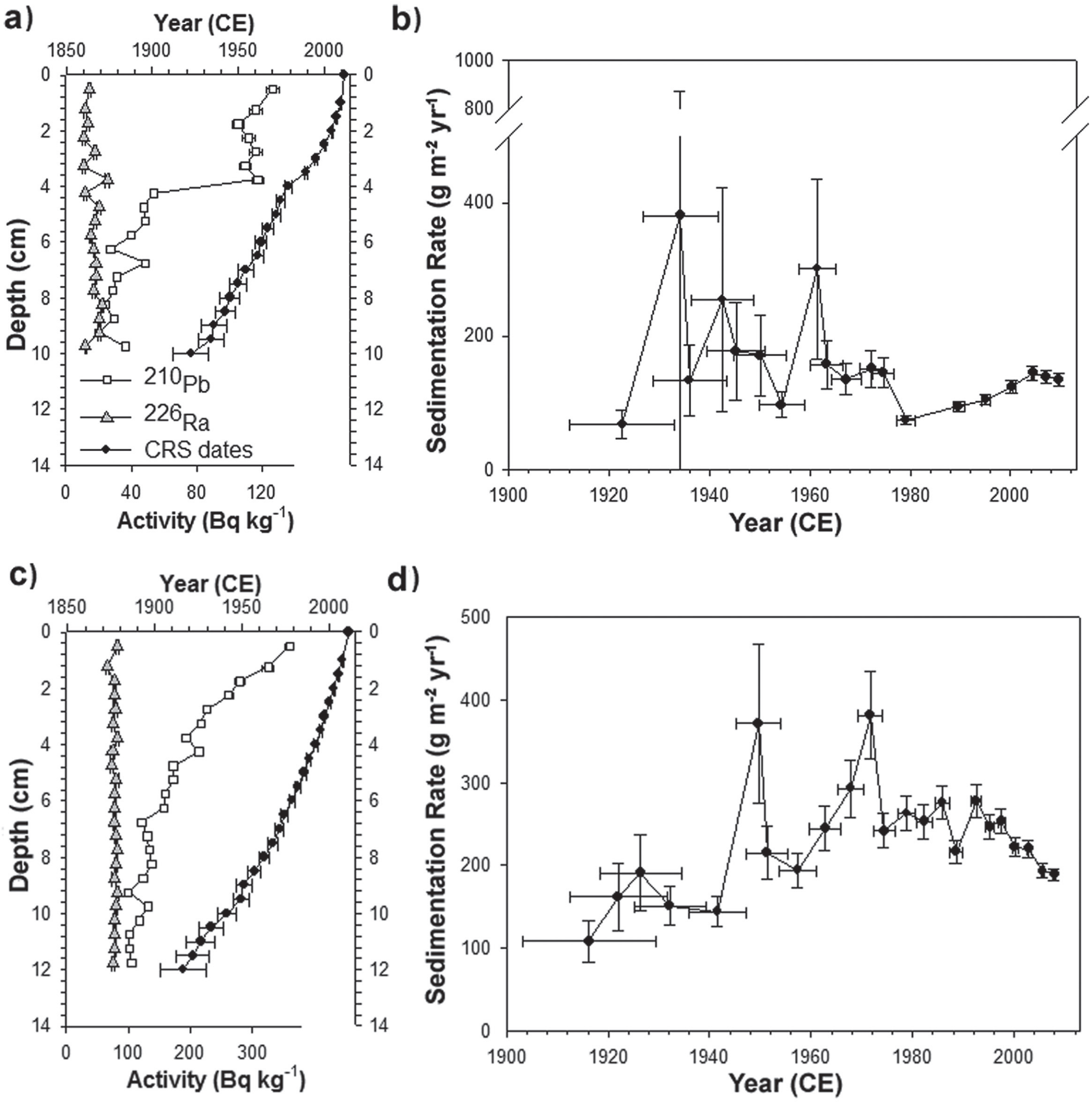

Figure 4. (a) ^{210}Pb activity profiles and age–depth relation, (b) estimated dry mass sedimentation rate versus estimated sediment age for Lake T15, (c) ^{210}Pb activity profiles and age–depth relation, and (d) estimated dry mass sedimentation rate versus estimated sediment age for Lake T02.
CRS: Constant Rate of Supply.

prior to 1965 (average = 1.36×10^7 valves/g) and exhibited a slight decrease in the past two decades (average = 2.62×10^6 valves/g). Three biostratigraphic zones were determined through the independent constrained cluster analysis, with transition dates at ~1972 and ~2001. Prior to ~1972, diatom assemblages were primarily represented by *Aulacoseira alpigena, Cyclotella pseudostelligera, Staurosirella pinnata*, and *Fragilaria microstriata*. A substantial decrease in planktonic *Cyclotella pseudostelligera* (average 15–5%) and marked increase in *Aulacoseira alpigena* (25–38%) and *Hippodonta hungarica* (from <1.0% to 5% average) at ~1972 define the first prominent shift in diatom assemblages. Increasing abundances of *Aulacoseira alpigena* persisted until ~2001 when their abundances experienced a sharp decline at ~2000 (from 38% to 19%), which also corresponds with an increase in the abundance of *Staurosirella pinnata* (3–10%).

Discussion

Lake T15: thermokarst basin

In the earliest part of the sediment record (1920s) of Lake T15, high %OM, %C$_{org}$, and %N suggest relatively high productivity. This interpretation is also supported by high δ^{13}C$_{org}$ values, which occur because of productivity-driven ^{13}C-enrichment of dissolved inorganic carbon (Meyers and Teranes, 2001). C:N ratios are high, which is often interpreted as a reflection of input of terrestrial organic matter (Meyers and Teranes, 2001). However, δ^{15}N values are close to 0‰, suggesting that aquatic productivity may have occurred under nitrogen-limiting conditions, which can also lead to high C:N ratios (Talbot and Lærdal, 2000). During the next several decades until the 1960s, a decline in %OM, %C$_{org}$, %N, and δ^{13}C$_{org}$ suggests decreasing aquatic productivity, and declining C:N ratios suggest lower nitrogen demand. The 1960s marked a major shift in aquatic productivity, from a system limited by nitrogen and a decreasing trend in aquatic production, to conditions where increasing %OM, %C$_{org}$, %N, δ^{15}N, and declining C:N ratios suggest increasing nitrogen availability and aquatic productivity. Unlike the earliest part of the record, these trends correspond with low δ^{13}C$_{org}$, high δ^{15}N, and low C:N ratios, which can be explained by an increase in the supply of soil-derived ^{13}C-depleted dissolved inorganic carbon and ^{15}N-enriched dissolved inorganic nitrogen entering the lake.

The shift in production in the 1960s interpreted from the sediment geochemistry closely corresponds to changes in the assemblages of both chironomids and diatoms. Prior to the

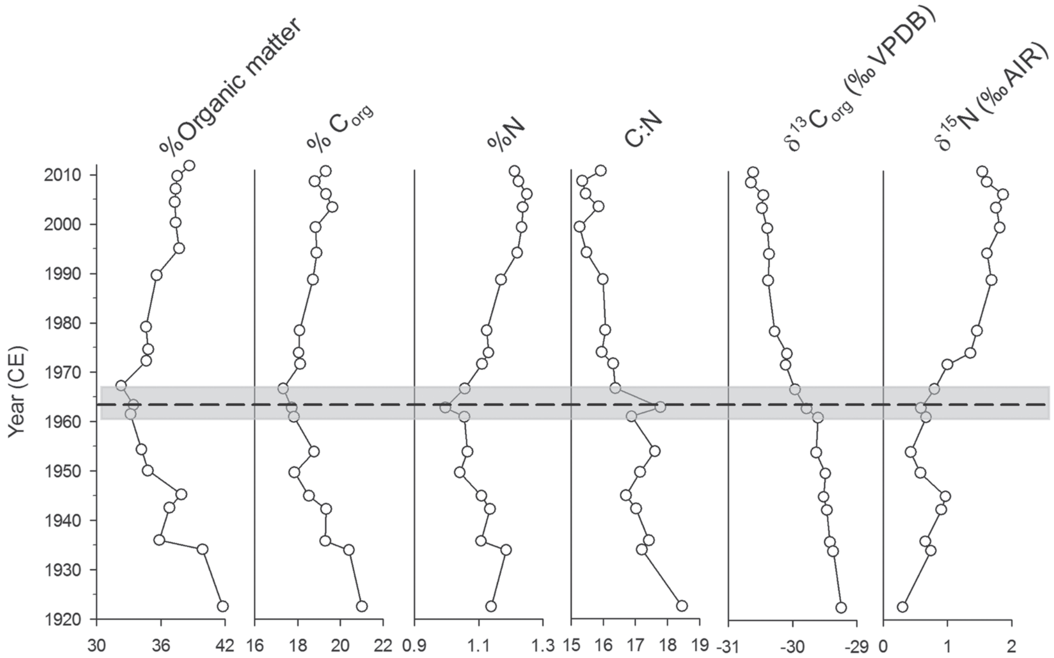

Figure 5. Geochemical stratigraphy for Lake T15 versus ^{210}Pb estimated age. Dashed line indicates stratigraphic change based on breakpoint analysis (1964 ± 3.3 years).
VPDB: Vienna Pee Dee Belemnite; AIR: atmospheric nitrogen.

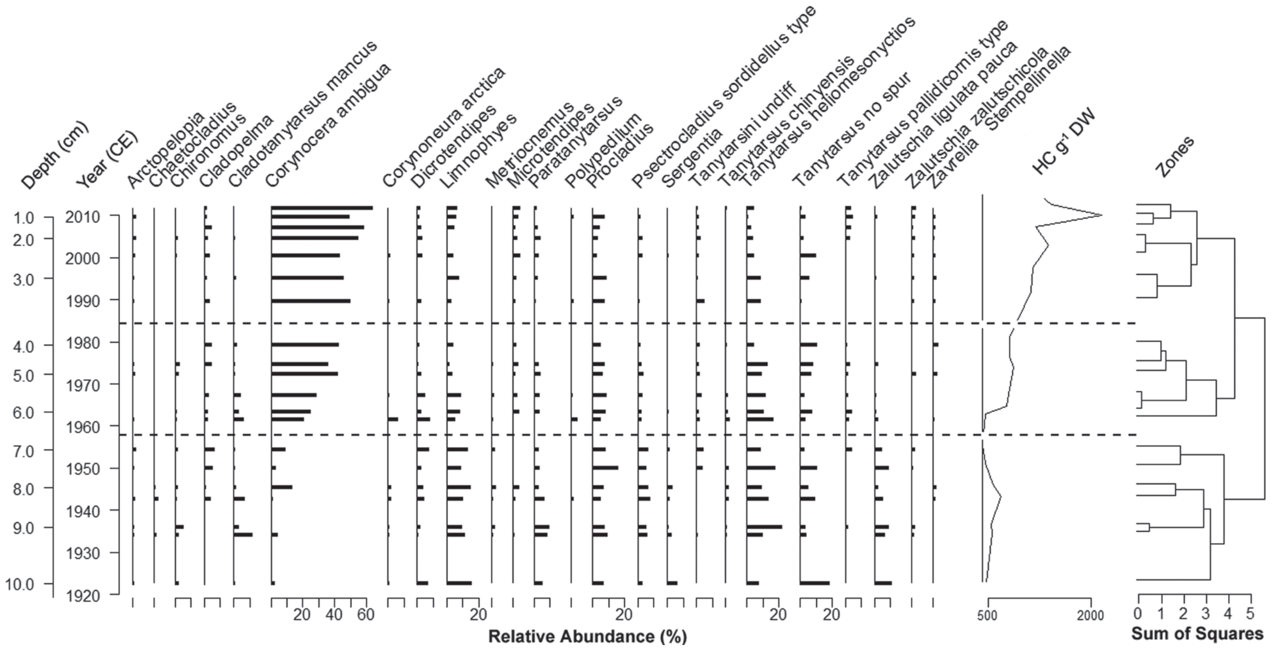

Figure 6. Relative abundance (%) of selected chironomid taxa from the core of Lake T15 plotted versus ^{210}Pb estimated age. Concentrations of chironomids (head capsules per gram dry weight) are included. Stratigraphic zones delineate significant changes in the chironomid assemblage as determined using constrained incremental sum of squares.

1960s, the assemblages were diverse and represented by relatively high abundances of cold-water adapted chironomids and acidophilus diatom taxa. A decline in the abundance of acidophilus taxa (e.g. *Zalutschia lingulata pauca, Aulacoseira alpigena*) and a large increase in the abundance of *Corynocera ambigua* in the 1960s correspond with the increase in δ^{15}N and decline in $\delta^{13}C_{org}$. This was followed by an increase in small, benthic, alkaliphilus *Fragilaria* species, suggesting increasing alkalinity after ~1960.

Although climate is usually considered the primary driver of aquatic ecosystem dynamics in subarctic and Arctic regions, the earliest stratigraphic changes observed in Lake T15 occurred decades before the post-1970 period of observed summer warming. Road construction in the remnants of the larger lake basin during the late 1950s likely caused flooding and expansion of the lake margins (visible from aerial photographs; see Figure 3a). The erosion of bank materials following the disruption of the thermokarst basin likely increased the supply of dissolved nutrients to the lake as well as its alkalinity. MacDonald et al. (2012) also noted that increases in lake sediment δ^{15}N values may be a result of ^{15}N-enriched nitrate leaching from soils of active thermokarst systems. An increase in dissolved nutrients promoting robust

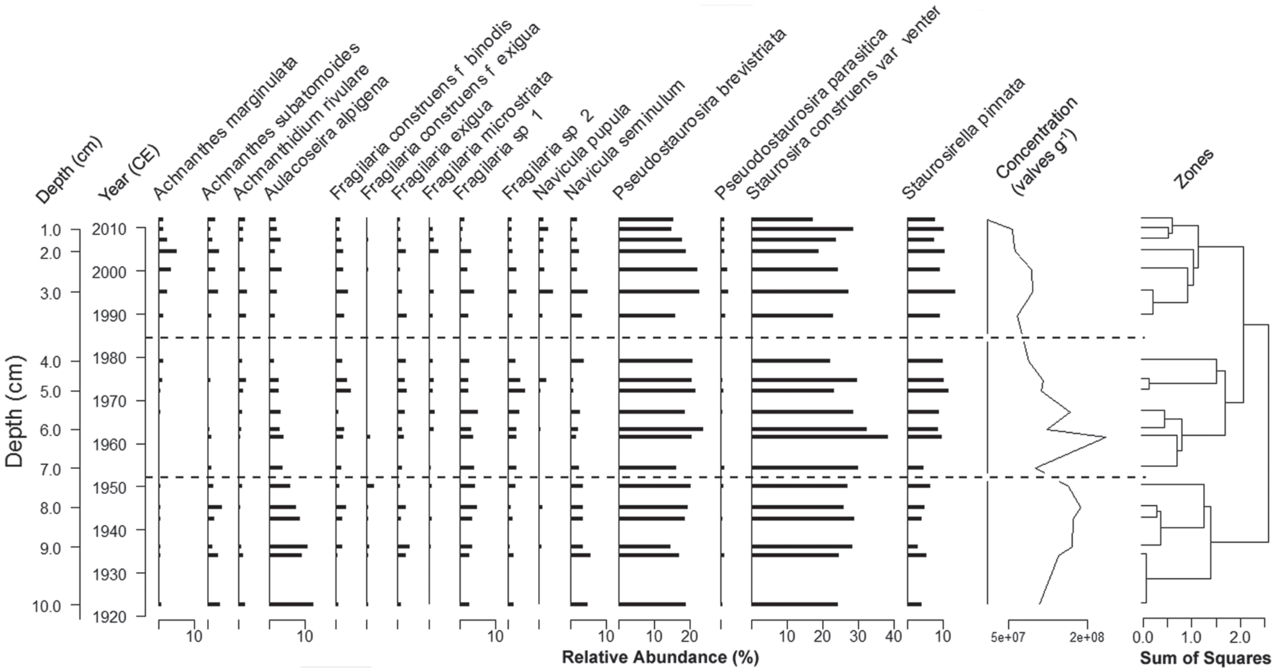

Figure 7. Relative abundance (%) of selected diatom taxa from the core of Lake T15 plotted versus ^{210}Pb estimated age. Concentration of diatoms (valves/g) are included. Stratigraphic zones delineate significant changes in the chironomid assemblage as determined using constrained incremental sum of squares.

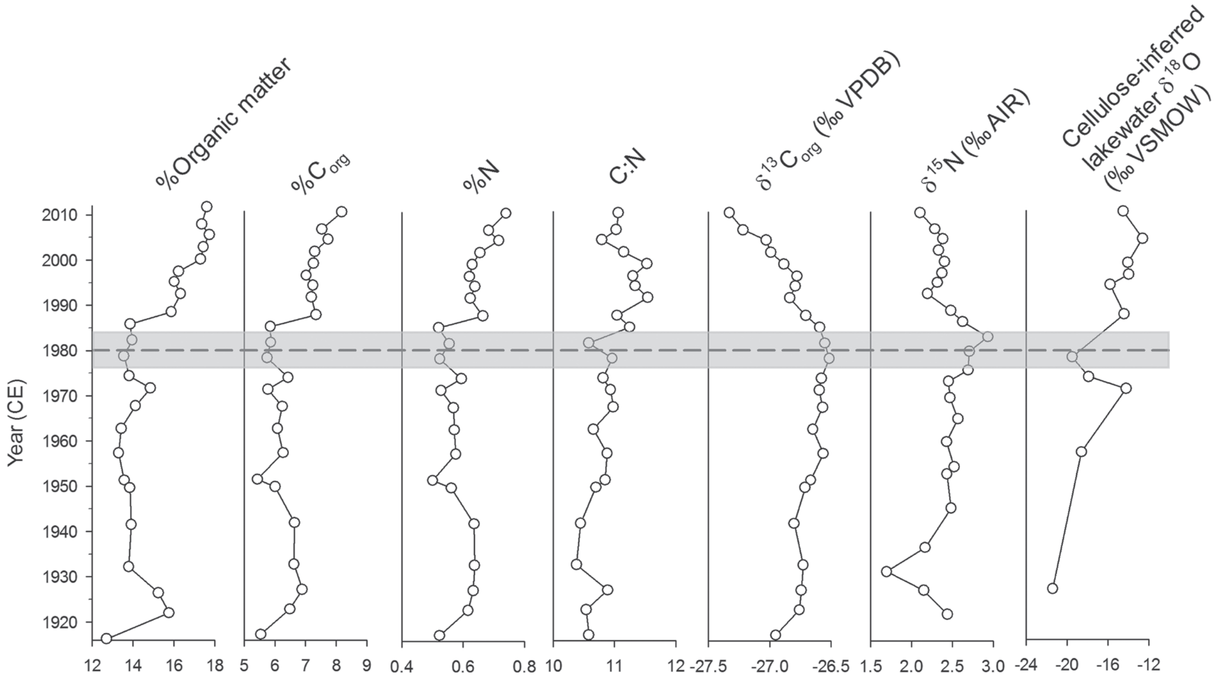

Figure 8. Geochemical stratigraphy for Lake T02 versus ^{210}Pb estimated age. Dashed line indicates stratigraphic change based on breakpoint analysis (1980 ± 3.7 years).
VPDB: Vienna Pee Dee Belemnite; AIR: atmospheric nitrogen; VSMOW: Vienna Standard Mean Ocean Water.

growth of macrophytes in the benthic zone (e.g. Kufel and Kufel, 2002; Mesquita et al., 2010) may have contributed to the large shift in *Corynocera ambigua* ~1960. After 1960, the decrease in acidophilus diatoms (e.g. *Aulacoseira alpigena*) suggests an increase in lake-water pH associated with the input of dissolved inorganic carbon.

The second major shift in biotic assemblages occurred ~1985 and is characterized by the reduction of cold-water indicator chironomid taxa (*Tanytarsus heliomesonyctios*) and increases in epiphytic diatoms (*Achnanthes marginulata, Achnanthidium rivulare*, and *Navicula pupula*). This suggests warmer water temperatures and the development of aquatic macrophytes, which aligns with the increase in temperature in the Nome meteorological record (Figure 2).

Lake T02: shrub basin

From the early part of the record until the 1980s, low C:N ratios and high δ^{15}N values suggest aquatic production occurred under conditions where there was an ample supply of nitrogen. A slight increasing trend in $\delta^{13}C_{org}$ and δ^{15}N suggests a small increase in aquatic production during this stratigraphic interval. After ~1980,

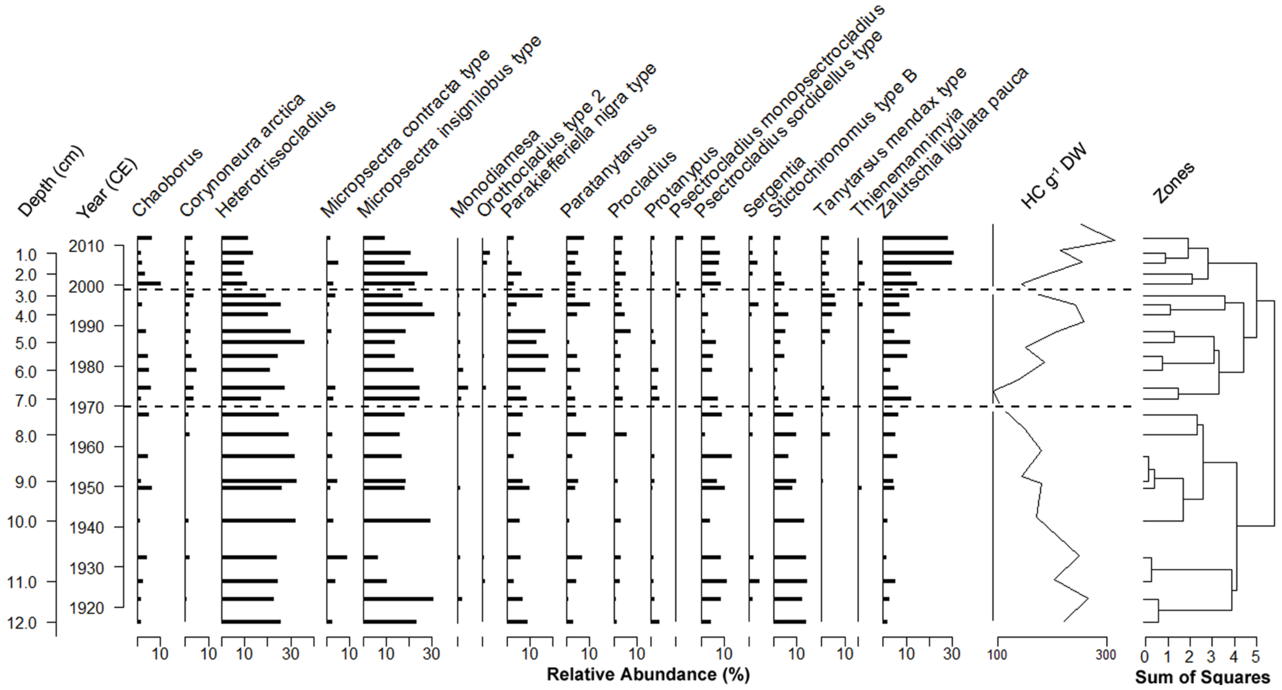

Figure 9. Relative abundance (%) of selected chironomid taxa from the core of Lake T02 plotted versus ^{210}Pb estimated age. Concentrations of chironomids (head capsules per gram dry weight) are included. Stratigraphic zones delineate significant changes in the chironomid assemblage as determined using constrained incremental sum of squares.

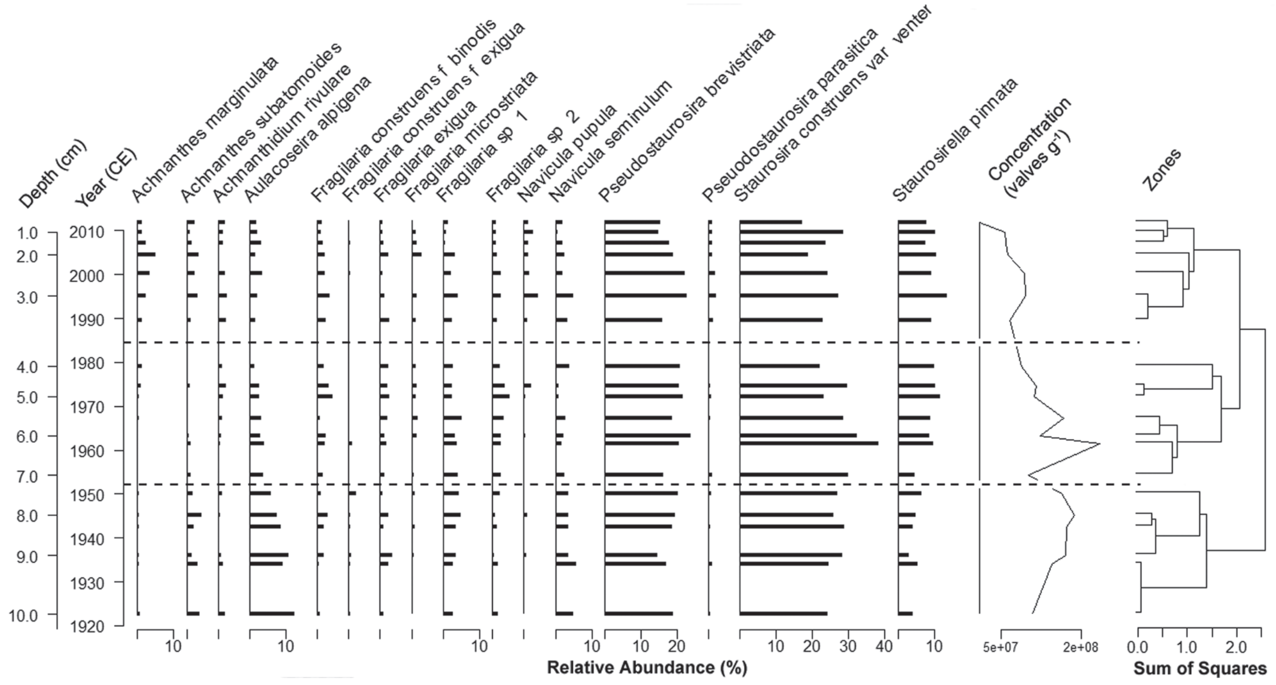

Figure 10. Relative abundance (%) of selected diatom taxa from the core of Lake T02 plotted versus ^{210}Pb estimated age. Concentration of diatoms (valves g^{-1}) are included. Stratigraphic zones delineate significant changes in the chironomid assemblage as determined using constrained incremental sum of squares.

when the breakpoint analysis indicated that there was a significant shift in the geochemical record, C:N ratios increase slightly and δ^{15}N remains >2‰. This suggests a small increase in terrestrial particulate organic matter input to Lake T02, which may also explain the shift to lower $\delta^{13}C_{org}$ values. The increase in %OM, %C_{org}, and %N may also reflect increases in terrestrial particulate organic matter deposition and/or increases in aquatic production. Although an increase in isotopically enriched terrestrial-derived cellulose could also explain the inferred increase in $\delta^{18}O_{lw}$, biotic evidence discussed below is consistent with evaporative lake-level drawdown.

Prior to ~1970, chironomid assemblages were represented by mainly cold-water adapted stenothermic taxa. An increase in the chironomid *Zalutschia lingulata pauca* and the diatom *Aulacoseira alpigena* following ~1970 may indicate an increase in humic conditions for Lake T02. This may be due to increasing terrestrially derived particulate organic matter input, as suggested by the small rise in C:N ratios. Increases in epiphytic diatoms, such as *Hippodonta hungarica* (Pavlov et al., 2013), and littoral chironomids (e.g. *Corynoneura arctica*) may also be because of greater input of terrestrially derived organic matter, which is known to enhance growth of the epilithon (Bunting et al., 2010; Perren et al., 2012; Vinebrooke and Leavitt, 1998). In addition, a decrease in the diatom *Cyclotella pseudostelligera* and chironomid *Stictochironomus* type B, beginning in the early 1970s, suggests a decline in deep water habitat. These changes are consistent with evidence of increasing evaporative isotopic enrichment at this time. Subsequently, large reductions of cold-water stenothermic chironomids (e.g. *Heterotrissocladius, Parakiefferiella nigra*) at ~2000 indicate reduced lake-levels and/or increases in water temperature.

We attribute the geochemical and biotic changes in the 1970–1980s to lake-level drawdown and a transition from a rocky catchment to a vegetated catchment composed of large shrubs (Figure 3b). Unlike in the record of Lake T15, there is little evidence to suggest that road construction in the late 1950s influenced the geochemical or biological record in Lake T02.

Importance of local catchment processes versus regional climate

The lake sediment records serve as a 'natural experiment' that document 20th century increases in the supply of dissolved nutrients and particulate organic matter from changes in catchment conditions, as well as a regional climate signal. Increased temperatures in subarctic and Arctic regions are known to increase the thickness of the active layer, enhance microbial activity, and subsequently increase particulate and dissolved organic carbon from the landscape to lakes (Fritz and Anderson, 2013; Hobbie et al., 2002). However, while temperature was found to have an important role in driving biotic responses (e.g. declines in cold-water indicators ~1985 for Lake T15; ~1999 for Lake T02), our results indicate changes in catchment conditions that increased terrestrial sources of dissolved inorganic carbon and nitrogen altered the Lake T15 trophic system. Notably, the significant shift observed in both diatom and chironomid assemblages in the mid–late 1950s of Lake T15, which we attribute to increasing supply of dissolved inorganic carbon and nitrogen to the lake, preceded the recent increase in temperature by several decades. Jones et al. (2011a) noted that a majority of thermokarst lakes in the northern Seward Peninsula have expanded since the 1950s, and Jones et al. (2011b) reported elevated nitrogen export from thawing permafrost. Thus, increased dissolved inorganic carbon and nitrogen input to thermokarst lakes undergoing warming may generate similar large-scale shifts in biotic assemblages as observed in Lake T15.

The relative magnitude of change in diatoms and chironomids associated with the increase in supply of nutrients in the 1960s at Lake T15 was prominent compared with the responses observed to the increases in temperature in the late 1970s. The increased availability of nutrients, and likely change in periphytic habitat, increased the abundance of chironomids but reduced the overall diversity. While the overall diversity of diatoms increased, there was a shift toward benthic taxa. This increase in benthic taxa is the opposite pattern observed by Rühland et al. (2013), who attributed increases in diversity and abundances of multiple indicators as a direct consequence of warming. This contrast may reflect the complexity of biotic responses in lakes experiencing changes in catchment condition in warming environments.

Shrubs are predicted to expand into much of the previously barren-ground tundra landscape of the Seward Peninsula (Pearson et al., 2013), which will undoubtedly alter local hydrological and biophysical processes (Fritz and Anderson, 2013). While chironomid assemblages were observed to shift in the 1970s in Lake T02, noteworthy declines in planktonic diatoms (especially *Cyclotella*) and increases in littoral chironomids are likely attributable to habitat responses to lake-level drawdown. The increase in shrub cover of the catchment of Lake T02 led to an increase in particulate organic matter input to the lake in the 1980s, but the biotic response was less prominent than the biotic responses to changes in the lake margin of Lake T15. Evidently, the increase in particulate organic carbon and nitrogen from enhanced shrubbery had less influence on biota at Lake T02 compared with increases in the supply of dissolved nutrients at Lake T15.

Conclusion

A paleolimnological approach applied to subarctic Alaskan lakes undergoing ecological transition was able to distinguish the relative roles of late 20th century catchment and climate changes on nutrient conditions and lake productivity. Changes to nutrient cycling in lake catchments frequency coincides with increases in temperature. However, the sediment records of Lakes T15 and T02 show that biotic assemblages can have varied responses. The shift in production in the 1960s for Lake T15, related to increasing supply of dissolved inorganic carbon and nitrogen from flooding and expansion of the thermokarst basin, led to major shifts in chironomid and diatom assemblages. This preceded the recent increase in temperature by decades, which also led to an increase in lake productivity. In contrast, the increase in shrub cover in the catchment of Lake T02 corresponded to increases in particulate organic matter input to the lake in the 1980s, but this had less influence on chironomid and diatom assemblages than the response of Lake T15 to changes in catchment condition. Large reductions of cold-water stenothermic chironomids in the Lake T02 sediment record did not occur until ~1999 and are likely associated with warming.

Our findings strongly suggest that biotic assemblages of subarctic aquatic systems can be influenced by both climate and catchment processes. This contrasts with other studies in the high-Arctic Archipelago where paleolimnological evidence showed no biotic response to anthropogenic introduction of nutrients until air temperatures surpassed a threshold (Antoniades et al., 2011). Additional paleolimnological studies at sites across the subarctic and Arctic, with emphasis on comparing biotic assemblages and isotope geochemistry, may elucidate the relationships between catchment-related nutrient cycling and lake productivity in areas undergoing warming. Understanding how catchment-related nutrient flux affects biotic assemblages is complex, but necessary to anticipate aquatic ecosystem responses to ongoing environmental change.

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