# Diatom assemblage response to Iroquoian and Euro-Canadian eutrophication of Crawford Lake, Ontario, Canada

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**Abstract** Diatom and geochemical data from Crawford Lake, Ontario, have been used to document limnological responses to periods of cultural disturbance resulting from native Iroquoian occupation of the watershed (1268–1486 AD) and Euro-Canadian agriculture and deforestation (1867 AD–present). Here, we further develop the high-resolution nature of the Crawford Lake sediment record to examine the physical, chemical and biological aspects of limnological response to human disturbances in the lake catchment area with exceptional detail. We report detailed diatom abundance and flux data for individual taxa from Crawford Lake, and further describe the relationship between assemblage composition and environmental conditions using canonical correspondence analysis (CCA). Diatom assemblage data are used to calculate diatom inferred-total phosphorus (DI-TP) concentrations for the past ~1,000 years. We also examine the diatom community response during and after periods of disturbance by Iroquoian and Euro-Canadian populations, and compare this response to existing geochemical proxies of lake production and new elemental geochemical indicators of catchment area erosion. In particular, we explore the differing limnological response to the two distinct periods of cultural eutrophication and examine the limnological processes that occurred during the period of low (or no) human activity (1487–1866 AD), when geochemical indicators of lake production recovered to pre-disturbance conditions, but diatom assemblages notably did not. Our results illustrate the highly susceptible nature of diatom

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communities to periods of anthropogenic disturbance, and emphasize that ecological indicators (such as diatom assemblages) should be included with other proxies (such as nutrient concentrations and physical characteristics) when assessing disturbance and recovery in lake systems.

## Introduction

Cultural eutrophication in lakes, the process by which humans stimulate algal productivity by elevating nutrient inputs, continues to rank as one of the most common water quality problems in the world (Smith 2003). Increased urbanization, sewage disposal and intensive agriculture during the past century have noticeably affected the nutrient state of lakes and their ecology. Starting in the 1970s, countries in Europe, North America, and other industrialized regions began efforts to significantly reduce nutrient loading to lacustrine systems in order to reduce or reverse the effects of cultural eutrophication. While the process and causes of eutrophication have been studied extensively, empirical models of the recovery phase are necessarily limited by having only a few decades of observations (see Jeppesen et al. 2003). Paleolimnological studies provide important tools which can be used to augment short, observed records of recovery with additional data regarding the speed of recovery, the magnitude of disturbance, and the nature of baseline conditions in the watershed.

Paleolimnological and archeological data show that humans have been modifying lakes and surrounding lands for many centuries or millennia (Renberg et al. 1993; Ohlendorf et al. 2003; Douglas et al. 2004; Miettinen et al. 2005). These studies have emphasized the long-lasting effects of settlement and land-use changes upon lacustrine ecosystems, and generally document large-scale changes in lacustrine ecology coincident with increased human population, agriculture, and industry (Garrison and Fitzgerald 2005;

Wolin and Stoermer 2005). Given intense eutrophication and modification of lakes and reservoirs during the 20th century, and recent efforts to restore such systems to pre-disturbance conditions, a systematic understanding of the chemical, physical and biological processes during and after periods of cultural disturbances is highly applicable to modern watershed management practices and procedures.

Recently, a detailed study of a ~1,000-year sediment record from Crawford Lake (43°28′ N, 79°57′ W), Ontario, Canada documented the complex limnological responses to periods of cultural disturbance from the start of native Iroquoian occupation of the watershed (1268–1486 AD) through Euro-Canadian agriculture and deforestation to the present (Ekdahl et al. 2004). Crawford Lake is a small (2.5 ha), deep (24 m) body of water located approximately 1 km west of the Niagara Escarpment (Fig. 1). Crawford Lake sediments consist of carbonate-rich varves that have been dated by varve counting and radiocarbon methods back to 932 AD (Ekdahl et al. 2004 and references therein). Based on pollen, diatom, and geochemical data, several workers have divided the history of Crawford Lake into 4 zones: the pre-Iroquoian (prior to 1268 AD), Iroquoian (1268–1486 AD), post-Iroquoian (1487–1866 AD), and Canadian (1867 AD to present) (Fig. 2; Byrne and McAndrews 1975; McAndrews and Boyko-Diakonow 1989; Ekdahl et al. 2004). Pre-Iroquoian sediments lack preserved varves. The Iroquoian zone is marked by the appearance of cultigen pollen, well-preserved varved sediments, increasing mass accumulation rates (MAR) of $CaCO_3$ and organic carbon, a decrease in organic matter C/N ratios, and an increase in $\delta^{13}C_{CaCO3}$ values (Fig. 2). These data reflect elevated photosynthetic algal production and a change in the water column redox state caused by increased nutrient delivery related to Iroquoian land-use practices (Ekdahl et al. 2004). The highest interpreted rates of productivity coincide with the two periods of Iroquoian village construction. Details of the Iroquoian settlements, population sizes and agricultural activities can be found in Finlayson (1998) and Warrick (2000).

The beginning of the post-Iroquoian zone is placed at 1487 AD based on the disappearance of

Fig. 1 Location of Crawford Lake, Ontario, Canada. Dashed contours in lake bathymetry indicate 15 and 24 meters water depth, and X shows the location of cores taken in 2001. The nearest weather station, located in the town of Milton, is approximately 4 km ENE of Crawford Lake. Bathymetry modified from McAndrews and Boyko-Diakonow (1989)
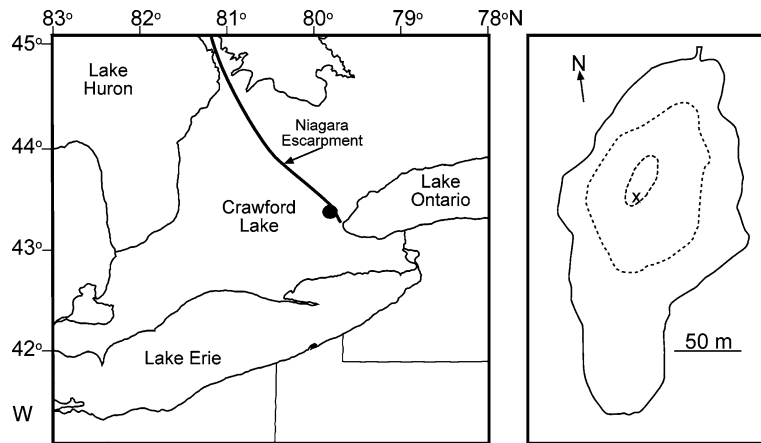


cultigen pollen (Ekdahl et al. 2004). As Iroquoian activity in the watershed diminished, the CaCO$_3$ MAR, organic carbon MAR, and $\delta^{13}C_{CaCO3}$ values returned to near pre-Iroquoian levels; however, organic C/N ratios remained low and well-preserved varves (albeit thinner) persisted though this time interval (Fig. 2). The Canadian zone begins at 1867 AD and is marked by darker brownish-black sediments containing thick varves and by increased accumulations of charcoal, ragweed pollen (*Ambrosia*), and Poaceae pollen (McAndrews and Boyko-Diakonow 1989; Clark

and Royall 1995). CaCO$_3$ and organic carbon MARs increased during the Canadian zone, while organic C/N ratios decreased; $\delta^{13}C_{CaCO3}$ values did not change appreciably (Ekdahl et al. 2004; Fig. 2).

The study by Ekdahl et al. (2004) revealed complex changes in diatom assemblages during and after the two periods of cultural disturbance. During the post-Iroquoian period (1486–1867 AD), geochemical proxies largely indicated a relatively rapid return to pre-disturbance oligotrophic conditions, whereas diatom flora persisted
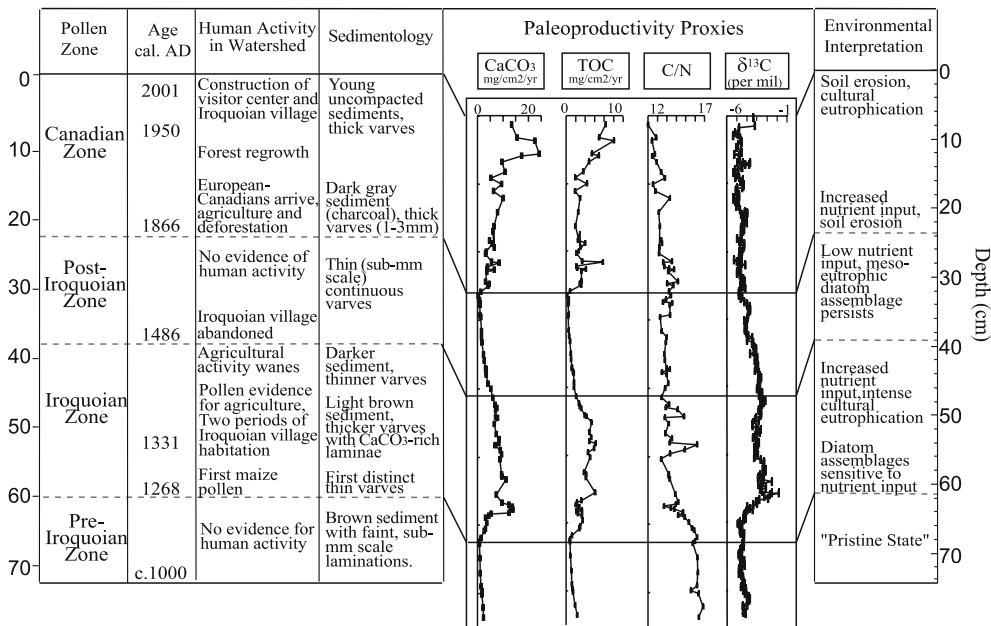


Fig. 2 Summary diagram outlining the history of Crawford Lake for the past ~1,000 years (Boyko-Diakanow 1979; Rybak and Dickman 1988; Ekdahl et al. 2004)

in a meso-eutrophic assemblage (dominated by *Fragilaria crotonensis*, *Synedra nana*, and *Cyclotella michiganiana*) indicative of continually elevated nutrient concentrations. On one hand, these data may be consistent with previous studies that have suggested that algal assemblages can be more responsive than geochemical proxies to changing nutrient conditions, and that a gradual return to pre-disturbance lake conditions does not necessarily lead to the re-establishment of pre-disturbance aquatic communities (Stoermer et al. 1996; Dokulil and Teubner 2005). Alternatively, limnological processes including weakening of lake meromixis and/or seasonal variability related to climate change might better explain the data. Diatom assemblages also responded to the second period of anthropogenic disturbance, when (starting in 1867 AD) Euro-Canadian agricultural activities significantly increased lake production but had comparatively less impact on diatom assemblages than the initial Iroquoian disturbance.

The goal of this paper is to combine new empirical data, multivariate statistical analysis, and modeled nutrient values to carefully examine the complex limnological processes during and after two well-documented periods of cultural disturbance in the Crawford Lake watershed. Additionally, we present water chemistry profiles to describe the current state of meromixis in the lake and sediment geochemical indicators to document catchment area erosion by Iroquoian and Euro-Canadian populations. This new study of Crawford Lake sediments illustrates the importance of paleolimnological studies in describing true baseline conditions in anthropogenically modified lake systems, and further demonstrates the usefulness of a multi-proxy approach to more accurately assess the degree of disturbance and lake recovery.

## Methods

Three freeze cores, ranging from 70 to 85 cm in length, were collected from near the deepest point of Crawford Lake (~24 m) in June 2001. Carbon isotope data are from core CL-F01, which was sampled into individual years from 2001 to 1867 AD (0–26 cm core depth). Samples were taken every 0.2 cm for the remainder of the core. Diatoms, ^{14}C dates, and all other geochemical proxies are from CL-F02, which was sampled at 0.2 cm intervals for the entire core. A 65 cm-long gravity core, dated by correlation to the depth–age model established on the freeze core, was used to determine sediment elemental compositions and bulk density. Bulk sediment concentrations of Al, Na, K, Ti, and Fe were determined by ICP-MS at the USGS Earth Surface Processes lab in Denver, Colorado. Development of the core chronology is described in Ekdahl et al. (2004).

Water chemistry measurements are from water samples taken in June 2001, when the lake was thermally stratified. Temperature, dissolved oxygen and specific conductivity measurements were made in situ. For all other analyses, samples were recovered at discrete depths with a van Dorn style bottle. Water pH was measured on-shore immediately after the samples were collected with electrodes calibrated to standard solutions of pH 4 and 7. The remaining water was filtered through 0.2 μm glass filters into vials for subsequent laboratory analyses in the Experimental and Aqueous Geochemistry Laboratory at the University of Michigan. Dissolved inorganic carbon (DIC) data are from analyses performed by coulometric titration on a UIC Carbon Coulometer 5011, on fixed ($CuCl_2$) 50 ml aliquots, with a precision of ±1%. Aliquots for cations (Na, Ca, Fe, Mn) and Si were preserved with trace metal grade nitric acid and measured on a Leeman Labs Inc. Plasma Spec ICP-AES 2.5 with a precision of ±1%. Anions (Cl, $SO_4$, $NO_3$) were measured on a Dionex 4000I series ion chromograph with a precision of ±1%. Diatom slide preparation followed standard procedures (Stoermer et al. 1995), where prepared sample was settled onto cover slips of a known area (Battarbee 1973). A minimum of 500 diatom valves was counted at 1250× magnification under oil immersion. Diatom fragments were counted in quartiles, allowing for a highly accurate calculation of diatom accumulation rate (DAR). Texts used for diatom identification are Krammer and Lange-Bertalot (1986–1991), Patrick and Reimer (1966), and Stoermer and Yang (1971).

Multivariate statistics were calculated with CANOCO v. 4.0 (ter Braak and Šmilauer 1998).

The first axis of an exploratory detrended correspondence analysis (DCA), with a gradient length of 3.35 standard deviations, indicated that statistical techniques suited for unimodal assemblages are appropriate for Crawford Lake. We use canonical correspondence analysis (CCA), which relates individual samples and corresponding environmental variables. CCA is a multivariate ordination and regression technique that is useful when analyzing a large number of taxa and environmental variables that potentially influence species abundance (ter Braak 1986). Diatom species present in greater than 3% relative abundance in at least one sample were included in the analysis. Taxa that comprised greater than 3% of the total diatom assemblage in less than 3 samples were downweighted relative to more abundant diatoms. While downweighting slightly increased the eigenvalues for the first two canonical axes, the overall environmental-sample trends were similar in both unweighted (not shown) and weighted CCAs.

Diatom inferred total phosphorus (DI-TP) values were calculated using the program $C^2$ (Juggins 2003), and are based upon a 64-lake diatom-lake chemistry calibration set for Southern Ontario developed by Reavie and Smol (2001). Reavie and Smol (2001) identified 5 lakes as statistical outliers, leaving a total of 59 lakes in their calibration set; the same number of lakes is used here. The model establishes diatom phosphorus optima using measured values of spring phosphorus concentrations in the lake chemistry calibration set; Crawford Lake phosphorus concentrations are extrapolated based on the weighted species optima and the diatom assemblages at discrete depths in the sediment core. Spring total phosphorus levels ranged from 4 to 54 µg l$^{-1}$ in the calibration set, which includes oligotrophic to eutrophic bodies of water.

## Results and discussion

### Water chemistry

Water chemistry changes with depth document the chemical, biological and physical properties of the lake. The mixolimnion (0 – ~10 m depth) is characterized by higher pH and $O_2$ concentrations, reflecting seasonal photosynthesis (Fig. 3). The mixolimnion exhibits low concentrations/values of Si, Ca, DIC, Fe, Mn, and specific conductance due to the biological activity of diatoms (decreased Si) and other algal species. Elevated values of $SO_4^{-2}$ and $NO_3^-$ in the stagnant, non-circulating monimolimnion (~10+ m depth) reflect the incorporation in reduction–oxidation reactions. A large increase in the specific conductance in the monimolimnion reflects the accumulation of dissolved solids in the bottom waters of the lake.

Concentrations of chloride (Cl$^-$), a highly soluble, mobile, conservative ion in freshwater systems, decreases with depth in the Crawford Lake water column (Fig. 3). Cl$^-$ is recognized as a ubiquitous contaminate in groundwater and surface waters in Southern Canada due to the use of road salts (NaCl, CaCl$_2$) for winter road maintenance (Williams et al. 1999). Thus, the elevated Cl$^-$ concentrations in the surface waters can be attributed to a relatively recent increase in anthropogenic inputs; lower Cl$^-$ concentrations in the bottom waters reflect pre-contaminated conditions. This offset in Cl$^-$ concentrations emphasizes the meromictic nature of the lake and suggests that the water column must not have mixed in at least the last few decades.

### Elemental data

Accumulation rates of Al, Na, K, Fe, and Ti are useful in estimating the influx of allochthonous siliciclastic material in Crawford Lake sediments. Accumulations of these elements are highest during the Iroquoian zone (60–35 cm gravity core depth) and again in the Canadian zone (from 20 cm to the top of the core). In the Crawford Lake watershed, siliciclastic material derives from glacial till deposits in the upland areas where soils are best developed. Thus, the two periods of increased siliciclastic material influx correlate to increased erosion rates as related to farming and deforestation. In the post-Iroquoian zone (approximately 20–35 cm in the gravity core), siliciclastic components disappear almost completely, suggesting that erosion rates were greatly

**Fig. 3** Water chemistry data from Crawford Lake, Ontario, Canada
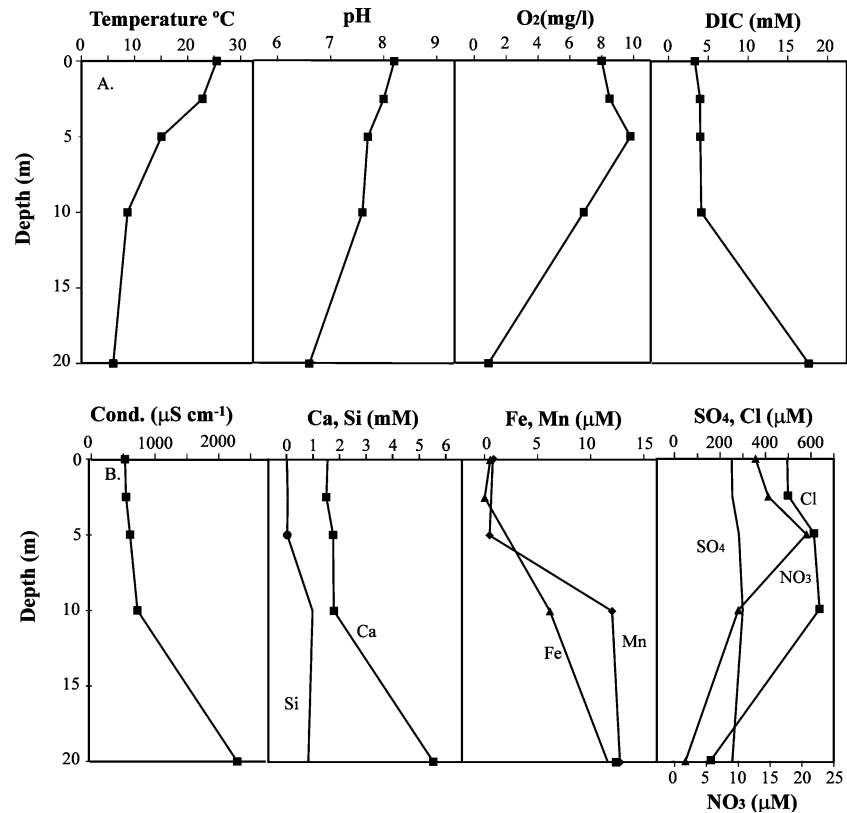


reduced soon after the Iroquois abandoned the watershed (Fig. 4).

Diatom stratigraphy and statistical analysis

Over 260 species of diatoms were identified in Crawford Lake sediments, with many in low concentrations. Modification of the pristine diatom assemblage by Iroquois occupation of the watershed, and subsequent changes in major diatom species related to abandonment of the watershed and settlement by Euro-Canadians, has been previously described (Ekdahl et al. 2004). Autecological data on diatom species were used to describe the nature of Iroquoian disturbance within the watershed. After an initial pulse of biologically derived nutrients resulted in an increase in *Stephanodiscus* (Stoermer et al. 1978) and decrease in *Cyclotella bodanica*, construction within the watershed increased soil run-off that further altered the diatom flora. The greatest period of disturbance in the watershed translates

to a peak in the relative abundance of *Asterionella formosa* (Ekdahl et al. 2004).

Diatoms present in greater than 3% abundance in one or more samples are plotted against age in Fig. 5. Species found in the post-disturbance zones generally indicate eutrophic to meso-eutrophic water conditions (Engstrom et al. 1985; Ramstack et al. 2003), further illustrating the transition from low-nutrient oligotrophic conditions characteristic of the pre-Iroquoian zone to nutrient-enriched waters following anthropogenic disturbance. The response of numerous rare taxa largely concurs with the documented response of more abundant species. Populations of small, centric, meso-eutrophic species *Cyclotella distinguenda*, *Cyclotella glomerata*, and *Cyclotella stelligeroides* were established rapidly in response to Iroquoian perturbation (1268–1486 AD); these species were not observed in the pre-disturbance zone, and comprise a significant proportion of the diatom flora following the initial perturbation. Numerous benthic taxa also appeared following
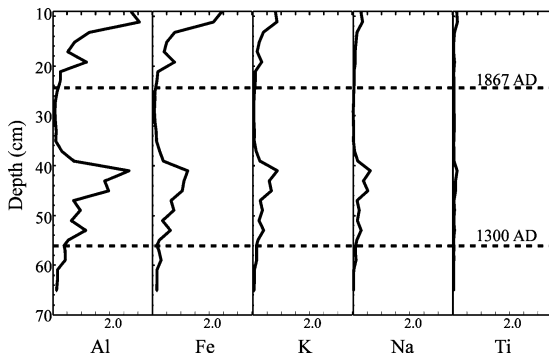
**Fig. 4** Elemental geochemical data for Al, Fe, K, Na, and Ti. Values are given as fluxes in mg cm$^{-2}$ year$^{-1}$

Iroquoian disturbance, including *Cymbella delicatula*, *Navicula radiosa*, and *Staurosira pinnata*. Other benthic species present in low abundance during the pre-Iroquoian zone (e.g., *Nitzschia* species, *Achnanthidium minutissimum*, and *Amphora libyca*) were more abundant following Iroquoian settlement. These benthic species persisted in higher abundance, relative to the pre-Iroquoian zone, throughout the remainder of the core.

We calculated absolute diatom flux (valves cm$^{-2}$ year$^{-1}$), or DAR, to compare diatom production before, during, and after the two periods of cultural eutrophication (Fig. 6). The extraordinary
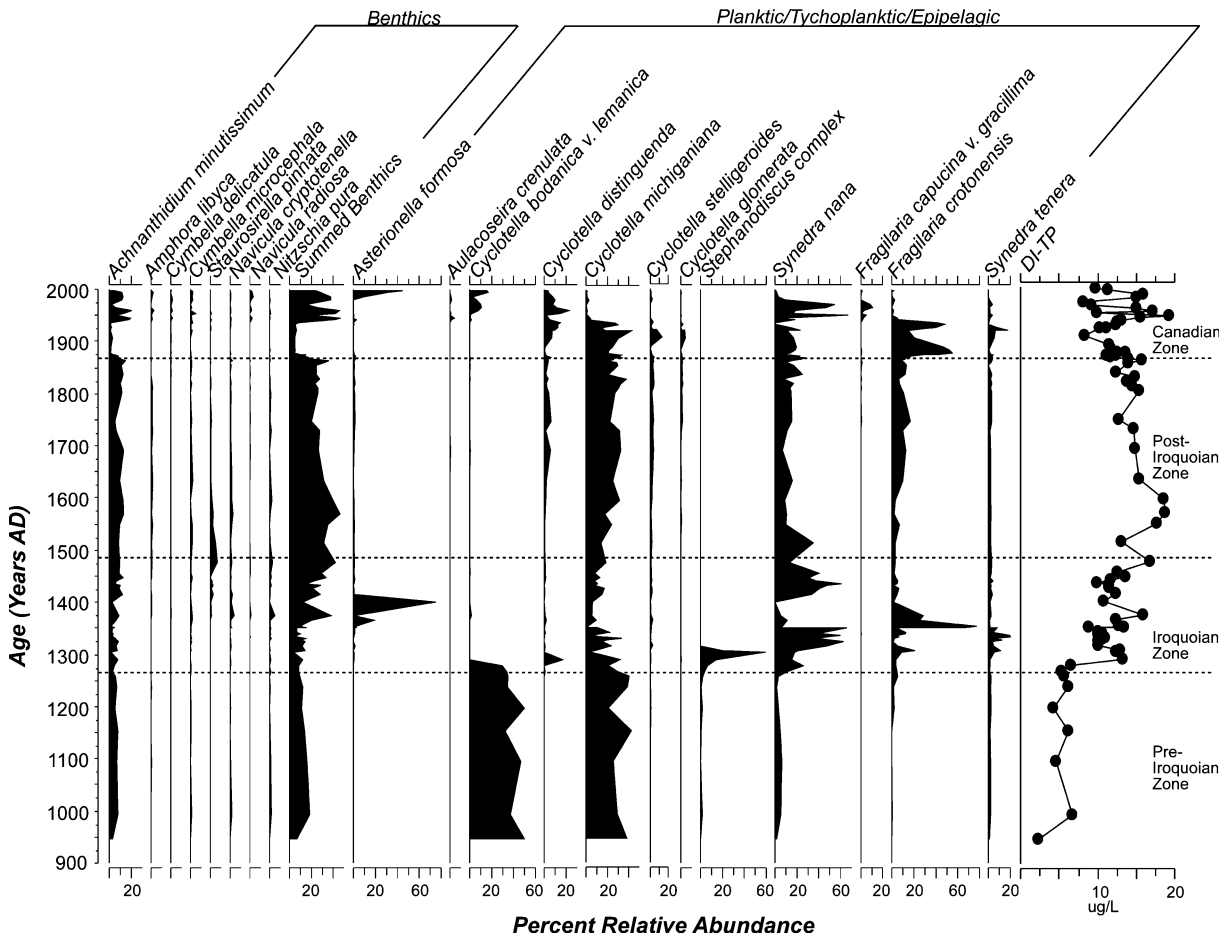


**Fig. 5** Crawford Lake diatom stratigraphy, 948–2001 AD, expressed as percentages of total diatom abundance. Species that comprise ≤3% in one or more samples are shown. Also shown are diatom inferred-total phosphorus (DI-TP) values. DI-TP values calculated using a weighted-averaging technique (Juggins 2003) based upon species-nutrient optima of modern diatoms from a 64-lake calibration set from southern Ontario (Reavie and Smol 2001)
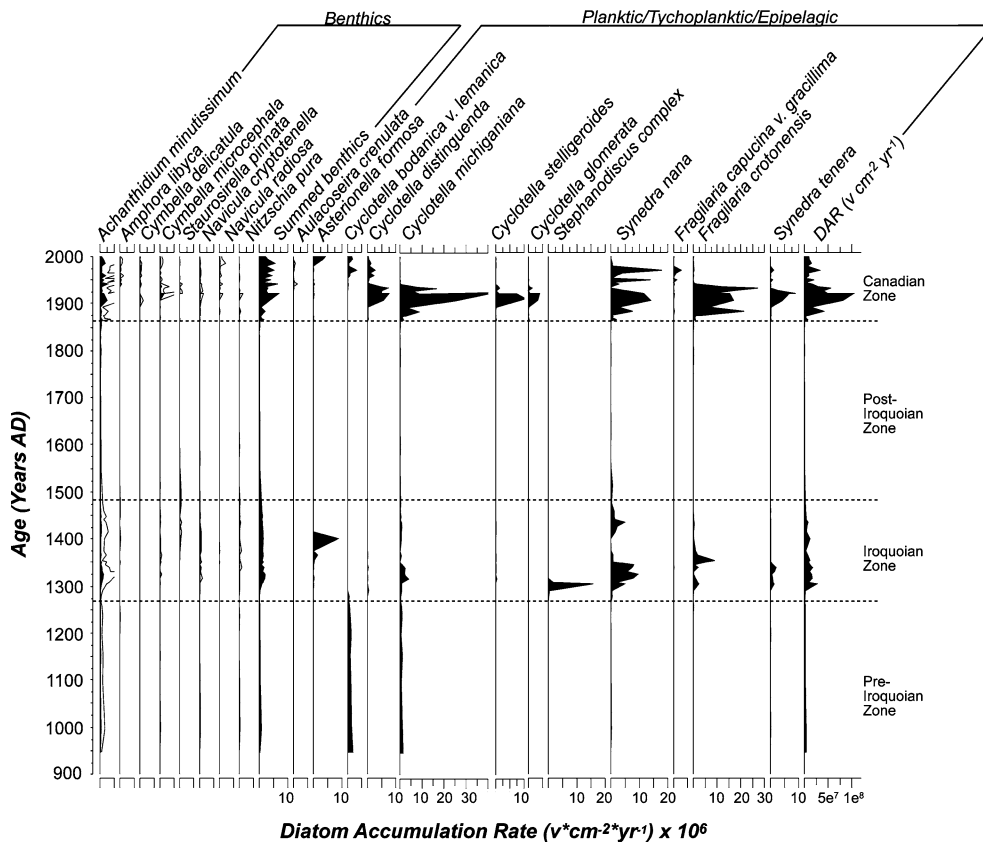
**Fig. 6** DARs for Crawford Lake, Ontario. Values in millions of valves cm$^{-2}$ year$^{-1}$. Unfilled outlines are 10× exaggerations. Species that comprise ≤3% in one or more samples are shown. Total DAR during the post-Iroquoian zone is in the hundreds of thousands, and is below the field of resolution in the diagrams

high-resolution dating of the varved Crawford Lake sediment core allows for very accurate calculations of sediment accumulation rates, and allows for the opportunity to compare diatom abundance data (Fig. 5) with diatom production rates (Fig. 6), and other geochemical indicators of paleoproductivity in the lake. In general, the DARs predictably illustrate significant increases in diatom production during the two periods of cultural eutrophication. Diatom productivity was relatively low during the pre-Iroquoian zone (average $2.9 \times 10^6$ v cm$^{-2}$ year$^{-1}$) and increased abruptly to an average $8.7 \times 10^6$ v cm$^{-2}$ year$^{-1}$ during the Iroquoian zone in response to increased nutrient availability (Fig. 6). Diatom productivity rapidly decreased during the post-Iroquoian zone (average $6.5 \times 10^5$ v cm$^{-2}$ year$^{-1}$) before increasing again in response to increased nutrient availability during the Euro-Canadian Zone (average $2.3 \times$

$10^7$ v cm$^{-2}$ year$^{-1}$; Fig. 6). Diatom productivity peaked in the 1920s, when diatom productivity rates were over $1 \times 10^8$ valves cm$^{-2}$ year$^{-1}$ (Fig. 6). The diatom accumulation data follows general trends of the geochemical proxy data suggesting reduced nutrient availability, and reduced whole lake productivity, during the post-Iroquoian zone. Together, these data lend further interest to interpretation of the diatom assemblages during the post-Iroquoian zone when meso-eutrophic species such as *Fragilaria crotonensis*, *Synedra nana*, *Achnanthidium minutissimum* and others continued to dominate the diatom flora.

Calculation of the DAR also provides insight on the observed decrease in percentage of benthic diatoms that immediately followed Euro-Canadian settlement (1867–1925 AD, see Fig. 5). In a previous investigation, this decrease in percentage of benthic diatoms was ascribed to changes in

light availability, suggesting that increased planktic diatoms prohibited benthic growth due to shading (Ekdahl et al. 2004). However, DAR data reveal a modest increase in benthic diatom productivity during this period (1867–1925 AD) and a very significant increase in planktic diatom productivity (Fig. 6). Thus, we can now accurately observe that the decrease in relative abundance of benthic diatoms at the start of the Euro-Canadian zone is simply an artifact of a very substantial increase in planktic diatom productivity, and is not indicative of reduced benthic diatom productivity overall. The above discussion emphasizes the usefulness of DARs in well-dated sediment sequences where accurate calculation of accumulation rates is possible.

The DAR data are also helpful in interpreting diatom response during the post-Iroquoian zone, when nutrient input decreased yet meso-eutrophic species continued to dominate the diatom flora. While the relative abundance data suggest continued nutrient availability for diatom production, the diatom accumulation data follow the trend of the geochemical production proxy data that show reduced nutrient availability, and reduced whole lake productivity, during the post-Iroquoian zone.

Statistical examination of the diatom and geochemical data sets more fully quantifies the rela-

tionship between diatom assemblages, changes in nutrient supply, and inferred lake trophic level. We used CCA to investigate the relationship between diatom assemblages, changes in nutrient supply, and inferred trophic level, and used the geochemical paleoproduction proxy data (CaCO$_3$, TOC, $\delta^{13}$C, and C/N ratio) to represent environmental variables. Sediment geochemistry and diatom sample intervals did not always overlap; therefore, the number of samples available for use in CCA analysis was reduced. In the CCA, we used geochemical data that were dated to within +2 years relative to the dated diatom material. We also used age, presence/absence of cultigen pollens (pollen indicating agricultural activity in the watershed), and biostratigraphic zone as additional environmental variables. Forward selection indicated that the percentage of variance described by biostratigraphic zone was not highly significant ($F$-test = 0.62, $P$ = 0.70 under a 499-run Monte–Carlo simulation), and is not plotted in the CCA biplot (Fig. 7). CCA axes 1 and 2 describe a cumulative 64% of the species–environment relationship ($\lambda_1$ = 0.261, $\lambda_2$ = 0.244).

The CCA indicates that changes in environmental conditions had a marked effect on the diatom assemblages. The major gradient in sample scores (Axis 1) is closely aligned with Age,
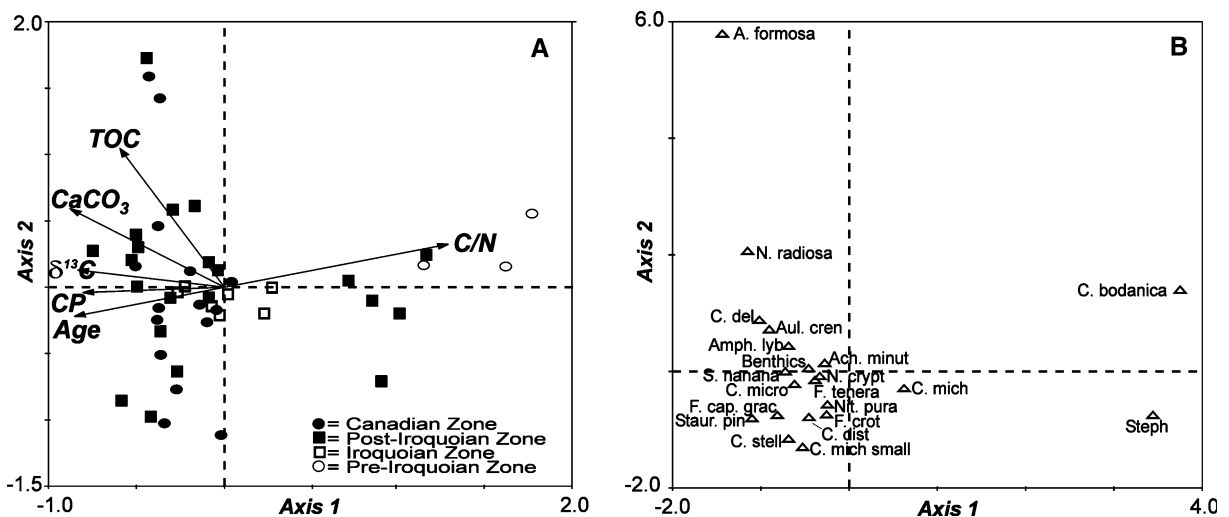


**Fig. 7** CCA for Crawford Lake diatoms and environmental variables (arrows). Sample scores (**a**) and species scores (**b**) are plotted against the first two canonical axes

C/N, cultigen pollen, and $\delta^{13}C$ (Fig. 7a), suggesting that changes in nutrient availability were a major forcing factor in diatom assemblage variability. Pre-Iroquoian, early Iroquoian, and post-Iroquoian samples with high C/N and low $\delta^{13}C$ values plot farthest to the right along axis 1. Most of the disturbance samples plot in the two left CCA quadrants. These samples represent the most recent three zones (Iroquoian through Canadian), with variability amongst these zones spread along axis 2. Samples from the Canadian zone are largely confined to the lower left quadrant, and grade from low-TOC and $CaCO_3$ samples, such as those found during the earliest and middle portions of the Canadian zone, to modern samples with high carbon accumulation rates found in the upper left quadrant near the heads of the environmental variables. Samples from the post-Iroquoian zone are concentrated near the origin. The results of the CCA indicate that axis 1 distinguishes between pre-settlement assemblages and those that exist after anthropogenic modification; axis 2 reflects changes since Iroquoian settlement.

Species scores are largely clustered in the lower left quadrant (Fig. 7b), reflecting the behavior of species that are strongly responsive to changes in water chemistry. *Asterionella formosa* plots in a region associated with high nutrient ($CaCO_3$ and TOC flux) levels. *Cyclotella bodanica* and *Stephanodiscus* species are highly correlated with C/N and Age; *C. bodanica* occurs in the oldest sediments with relatively high C/N values, indicating that this species is descriptive of oligotrophic conditions. Other planktic species, such as *Cyclotella stelligeroides* and *Cyclotella distinguenda*, are found in the lower left quadrant at the opposite end of the TOC and $CaCO_3$ vectors, indicating their affinity for meso-eutrophic conditions with moderately high water column nutrients. Many of the planktic diatoms are highly responsive to inferred changes in nutrients, while benthic diatoms that may obtain nutrients from their surrounding substrates (Lowe 1996; Vadeboncoeur et al. 2003) are not as sensitive to the wide fluctuations in nutrient availability. These results show that there are two main environmental gradients in the Crawford Lake diatom assemblages that represent the dominant eutrophication trends; a gradient representing Age, C/N ratio, and $\delta^{13}C$, and a second nutrient/productivity gradient as represented by TOC and $CaCO_3$.

## DI-TP concentrations

Transfer functions generated from large calibration sets are useful in extending limited water chemistry measurements and in reconstructing environmental changes that effect water chemistry (Birks et al. 1990). We used a calibration set developed by Reavie and Smol (2001), based on data from 64 lakes in Southern Ontario, to infer total phosphorus concentrations from our diatom record over the past ~1,000 years. The Reavie and Smol (2001) calibration set is particularly well-suited to application here, as it is comprised of lakes that are geographically, geologically and climatologically similar to Crawford Lake. A weighted-averaging transfer function generated with the program $C^2$ (Juggins 2003) was applied to the Crawford Lake fossil diatom data. The relationship between observed phosphorus levels and values from the weighted averaging calibration models is highly significant ($r^2 = 0.637$, root mean square error (RMSE) = 7.3 µg $l^{-1}$, $r^2_{boot} = 0.466$, $RMSE_{boot} = 10.0$ µg $l^{-1}$; both $r^2$ and $r^2_{boot}$ significant at $P < 0.01$; Reavie and Smol 2001).

Results of the Crawford Lake DI-TP reconstruction are shown against diatom relative abundance in Fig. 5. DI-TP concentrations are initially low (3 µg $l^{-1}$) in the pristine pre-Iroquoian zone, and increase abruptly to 12 µg $l^{-1}$ at the start of the Iroquoian zone (1268 AD). DI-TP values continue to increase throughout the Iroquoian zone to near 17 µg $l^{-1}$ by 1525 AD. DI-TP concentrations gradually decrease to 11 µg $l^{-1}$ by the end of the post-Iroquoian zone, yet remain elevated relative to pre-disturbance DI-TP concentrations. DI-TP values decrease immediately following the Euro-Canadian horizon. This is likely a function of the species composition of the calibration set, which moves away from benthic species with high TP optima towards small planktic centric diatoms (which, in this calibration set, have relatively low TP optima). DI-TP concentrations are highly variable during the Canadian zone but generally increase, reaching values

of 17 μg l$^{-1}$ during the 1950s–1980s. Modern DI-TP values are near 11 μg l$^{-1}$.

## Paleoproductivity, nutrient levels, and lake recovery

Although the effects of reduced nutrient input have been described for numerous lakes (Jeppesen et al. 2003), most direct observations are necessarily limited to a view of lake recovery over only the last few decades. Thus, the Crawford Lake record provides an opportunity to explore the response of a meromictic lake to nutrient reduction over a much longer time period. Here, we discuss the limnological response to the two periods of cultural eutrophication, and closely examine limnological processes that occurred during the period of low (or no) human activity (1487–1866 AD), when geochemical indicators of lake productivity show recovery to pre-disturbance conditions, but diatom assemblages and DI-TP concentrations do not.

There are several explanations for the disagreement between geochemical indicators of lake productivity and diatom assemblages. It is possible that the geochemistry proxies in Fig. 2 are not necessarily a straightforward measurement of whole-lake production (e.g., nutrient availability). While it is true that TOC and CaCO$_3$ abundance can be a function of preservation and source (Meyers and Teranes 2001), and that carbonate δ$^{13}$C values can be complicated by variations in microbial activity in the lake (Hollander and Smith 2001; Teranes and Bernasconi 2005), it is unlikely that all the geochemical indicators would be off so consistently and in the same direction. Diatom accumulation data (Fig. 6) follows the geochemical trends closely, further suggesting that the geochemical proxies record whole-lake production.

A second possible explanation for the disagreement is that the diatom transfer function used to estimate past trends in TP (the DI-TP concentrations) may not be well-suited (despite the ideal location and characteristics of the training set) for application to Crawford Lake and, as a result, may not provide accurate estimates. To assess the appropriateness of the cali-

bration set, we conducted a DCA between the Crawford Lake fossil diatom assemblage and the modern analogue assemblage. The results, plotted in Fig. 8, highlight some of the problems inherent in applying diatom-based inference models to down-core studies.

The calibration and fossil assemblages form two distinct groups in the DCA biplot, only overlapping along axis 2. However, axis 2 does capture a relatively high proportion of variance ($\lambda_1 = 0.3686$, 58% of total variance; $\lambda_2 = 0.119$, 17% of total variance), and appears to represent a carbon accumulation trend in the diatom data. Thus, the results of the DCA suggest that species differences between the calibration set and the Crawford Lake data may cause some small error in reconstructing past TP trends, but generally reassures that the DI-TP model should be capable of accurately interpreting large scale shifts in TP as based on the Crawford Lake diatom assemblages. We also note that the DI-TP concentrations capture the transition from a pristine to modified system very well, and generally reflect the overall diatom assemblage throughout the entire record (Fig. 5). Thus, we are left with the conclusion that the DI-TP does not recover to a pre-disturbance state during the ~400 years after the Iroquoian occupation simply because the diatom assemblages themselves do not recover to
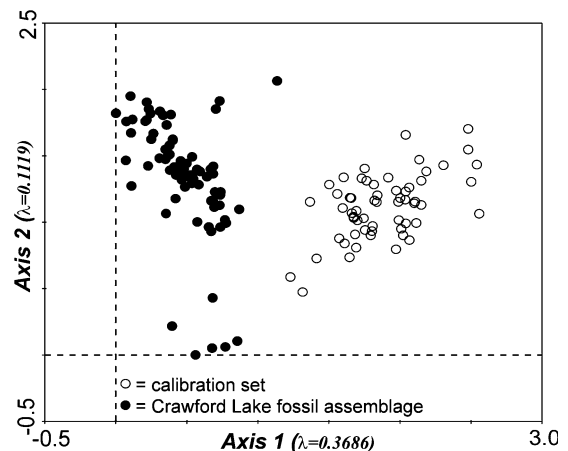


**Fig. 8** DCA of the Crawford Lake fossil diatom assemblages (solid circles) and calibration set lakes (open circles) from the 64-lake calibration set of Reavie and Smol (2001). In this DCA, both sets of samples were active, following the method of Laird et al. (1998)

the pre-disturbance assemblages observed in the pre-Iroquoian zone.

Given that trends in the geochemistry data are most likely accurate and that trends in the DI-TP data seem to accurately reflect the diatom assemblages, our discussion can turn to the possible mechanisms for maintaining a meso-eutrophic diatom community composition throughout the post-Iroquoian zone. One potential mechanism is that internal phosphorus recycling, which can maintain a relatively high level of aquatic productivity despite reduced nutrient load (Søndergaard et al. 2003), provided a seasonal elevated nutrient source for diatom productivity. In modern Crawford Lake, the impact of nutrient recycling is likely mitigated by the meromictic status of Crawford Lake. However, it is possible that the strength of the chemocline weakened during the post-Iroquoian zone. Weakening of this physical barrier, perhaps driven by changes in the strength of seasonal overturn arising from regional climate change, would allow for greater nutrient mixing, especially during times of the year when the lake would be more susceptible to overturn such as early spring and late fall. Consequently, nutrients in the monimolimnion could have more easily reached the overlying biologically active water column (e.g., Smol and Boucherle 1985), especially during periods of isothermal water temperatures. In this scenario the diatom assemblages and DI-TP values reflect conditions during very specific times of year, when spring or fall mixing supplied nutrients to the photic/oxic zone. However, the geochemical proxy signals would record time-averaged estimates of productivity and nutrient availability.

Although a seasonal weakening of meromixis in the lake provides a plausible mechanism for maintaining seasonally elevated nutrient levels to support the mesotrophic diatom assemblage, the mechanism does not agree that well with other sedimentological information. Continued varve preservation provides evidence for continued stratification and basin anoxia. Also, diatom accumulation data decreases rapidly to pre-disturbance levels during the post-Iroquois zone (Fig. 6), indicating low overall diatom production. Thus, we conclude that total primary production decreased quickly in response to reduced nutrient

input in the post-Iroquoian zone, whereas the diatom community assemblages were very slow to respond. Proxies for primary production, including diatom abundance (Fig. 6), responded very quickly to renewed nutrient availability at the Euro-Canadian horizon. In comparison, diatom *assemblages* did not change much during the transition from the post-Iroquoian Zone to the Euro-Canadian zone. Together the data show that, in terms of the ecological response to cultural modification, the initial perturbation appears to have been far more important than subsequent disturbances.

## Conclusions

Previous studies of Crawford Lake sediments have questioned whether Iroquoian impact on the surrounding ecosystem would have been great enough to significantly alter the environment (Campbell and McAndrews 1993; Campbell and Campbell 1994). The expanded data set and the modeled DI-TP values presented here largely confirm earlier studies (Ekdahl et al. 2004) in demonstrating that initial Iroquoian horticultural activity (1268–1486 AD) irreversibly altered nutrient dynamics, diatom community structure and lake circulation. In fact, in terms of diatom community structure, the initial perturbation by Iroquoian activities appears to have been far more important than the lake recovery period or subsequent disturbances.

Our combined dataset illustrates how ecological, geochemical and physical proxy data are best used in concert when examining the complex relationship between nutrient availability, lake primary production and ecological response. Additionally, this study illustrates the usefulness of paleolimnological studies in describing true baseline conditions in heavily modified watersheds, and carries implications for watershed management and lake restoration. We assert that a true assessment of pristine conditions should be made before complex and expensive restoration efforts begin, and should be used to assess the effectiveness of such effort. For good management practices, multi-proxy reconstructions that include both detailed geochemical and biological

data are needed to accurately detail pre-disturbance lake characteristics and to measure the effect of human settlement on lake water chemistry and ecology. Rather than a quick return to pristine or pre-disturbance lake conditions, recovery may be a long-term process requiring decades to centuries.

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