

January 2000

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Submitted July 16, 1998; accepted April 25, 1999.

Review paper

Nutrients as a link between ionic concentration/composition and diatom distributions in saline lakes

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Abstract

Diatom profiles in closed-basin lake sediments are commonly used to reconstruct climate change based on the observed correlations between salinity (ionic concentration) and modern diatom assemblages. Diatom assemblages are strongly correlated not only with salinity but also anion composition, with certain taxa characteristic of carbonate systems and others sulfate-dominated waters. Although strong correlations exist, the actual mechanisms behind these correlations are unknown. Here we briefly review the influence of salinity and ionic composition on nutrient dynamics in saline lakes and suggest that these interactions may drive shifts in diatom species composition along gradients of ionic concentration/composition. We discuss the influence of salinity and anion composition on nutrient availability, as well as on nutrient requirements and uptake by diatoms.

Keywords: saline lakes, diatom physiology, paleoclimate reconstruction, nutrients, brine composition

Introduction

Lakes are intricately tied to the climate system in that their water levels and chemical composition are a manifestation of the balance between hydrologic inputs (precipitation, stream inflow, surface runoff, groundwater inflow) and outputs (evaporation, stream outflow, groundwater seepage) (Mason *et al.*, 1994). In closed-basin lakes, without outflow, changes in the balance between precipitation and evaporation result in the concentration or dilution of lake-water and hence in changes in ionic concentration (salinity) and ionic composition. These hydrochemical changes in turn may affect the physiological response and thus the

species composition of the lake's biota, including that of diatoms.

Diatom species distributions are highly correlated with salinity (Blinn, 1993; Fritz *et al.*, 1993; Wilson *et al.*, 1994; Gasse *et al.*, 1995), and it is this correlation that forms the foundation for the use of diatoms as tools for climate reconstruction (Gasse *et al.*, 1987; Bradbury *et al.*, 1989; Fritz *et al.*, 1991; Metcalfe, 1995). Salinity is reconstructed from changes in the species composition of diatoms of known salinity optima, and then patterns of salinity change through time are used to infer changes in the balance between precipitation and evaporation. The statistical techniques used to reconstruct salinity from fossil dia-

toms do not assume that salinity itself is the primary cause of changes in species composition, but simply that salinity or some variable highly correlated with salinity is the driver of species shifts. However, if the cause of shifts in species composition over time is a variable correlated with salinity, rather than salinity itself, then there may be multiple environmental pathways or states that can produce a given change in species composition. Thus, unambiguous interpretation of fossil diatom records requires that the mechanisms relating diatoms to salinity change should be understood.

Diatom distribution is also correlated with anion balance (Blinn, 1993; Fritz *et al.*, 1993; Gasse *et al.*, 1995), with some taxa characteristic of carbonate-dominated brines and others sulfate-dominated systems. Significant alteration of brine composition in closed-basin lakes can occur via the precipitation of minerals during evaporative concentration, and thus diatom species composition may be altered by climate-driven changes in brine composition, as well as by changes in salinity (Eugster & Jones, 1979). Again the mechanisms relating species distributions and anion dominance are largely unknown.

Nutrient concentrations and ratios frequently control primary production and algal community structure in lacustrine systems (Likens, 1972; Kilham and Tilman, 1979; Kilham, 1982), and a review of the literature suggests that in saline lakes salinity and anion composition may influence nutrient availability to primary producers, as well as nutrient requirements and uptake by diatoms. Thus we propose that shifts in diatom species composition along gradients of ionic concentration and composition may be driven in part by nutrients. If nutrients influence diatom distributions along gradients of salinity and/or brine type, this may affect paleolimnological reconstructions in saline lakes. In North America, many salt lakes in semiarid regions are situated in agricultural areas and frequently have very high nitrogen and phosphorus concentrations (Cumming *et al.*, 1995; Hall *et al.*, 1999). Nutrient enrichment may expand the high end of a taxon's salinity tolerance range. For example, Fritz *et al.* (1993) observed that *Stephanodiscus parvus*, *S. hantzschii*, *S. minutulus*, and *Cyclostephanos dubius*, all typically freshwater taxa, could also be found in eutrophic hyposaline waters. Eutrophication may have expanded modern diatom distributions with respect to salinity, and this could potentially bias salinity reconstructions toward higher values. Thus, a greater understanding of the link between nutrients and the response of diatoms to ionic concentration/composition may enhance paleoclimate reconstructions.

Impact of total dissolved solids (TDS) and ionic composition on nutrient dynamics

Nutrient requirements and uptake

Certain diatoms, such as *Cyclotella meneghiniana*, produce amino acids such as proline in response to increased osmotic pressure (Schobert, 1974). The synthesis of these compounds results in the exertion of an equal or greater osmotic pressure intracellularly; higher external salinities demand greater production of these compounds. Because amino acids contain nitrogen, the stimulation of proline synthesis may affect algal requirements for this nutrient. Hence, as salinity increases, diatoms that synthesize proline or other amino acids as osmotic regulators should require more N. Interspecific differences in competitive abilities for N may then be a dominant factor in structuring the diatom community.

Silica utilization may also be affected by salinity, as Tuchman *et al.* (1984) found that *C. meneghiniana* exhibited lower frustule silica content with increasing salinity. In their experiment, cells were grown in NaCl concentrations ranging from 18–4,000 mg l⁻¹. Individuals in the higher salinity treatments had significantly less silica per cell and grew faster than individuals from the lower salinity treatments. The difference in silica content was not due to variation in frustule diameter but rather in frustule thickness. It is unknown whether the silica contents of other taxa vary with salinity or what the mechanism of influence is.

Ionic concentration and composition can influence nutrient transport across the cell membrane and hence nutrient uptake by algae. For instance, Bhattacharyya & Volcani (1980) showed that silicate uptake by the marine diatom *Nitzschia alba* is a sodium-dependent process, with the transport system being driven by a Na⁺ gradient maintained across the membrane by Na⁺, K⁺-ATPase. The authors found that as extracellular concentrations of Na⁺ increased, so did the uptake rate of silicate, leading them to hypothesize that silicate ions enter the cell in symport with Na⁺. This may explain the faster growth rates observed at higher salinities by Tuchman *et al.* (1984), as described above, if the enhanced Si uptake promotes cell division rather than greater silicification. In contrast, the addition of K⁺ did not stimulate silicate transport. For some algae, such as the green alga *Selenastrum capricornutum* and the blue-green alga *Microcystis aeruginosa*, P transport is also dependent on extracellular ions, again with Na⁺ promoting uptake and K⁺ inhibiting it (Mohleji & Verhoff, 1980). The influence of these ions on P transport in diatoms is unknown.

Sulfate may also affect nutrient uptake by diatoms, as this ion is a competitive inhibitor of molybdate (MoO_4^{-2}) assimilation. Cole *et al.* (1986) found that MoO_4^{-2} uptake by a freshwater phytoplankton assemblage declined with increasing sulfate concentration and/or $\text{SO}_4^{-2}:\text{MoO}_4^{-2}$ ratio. Molybdenum (Mo) is an essential trace element, as it is a component of enzymes involved in dinitrogen fixation and assimilatory nitrate reduction. Therefore, in terms of the availability of N to algae, both N_2 fixation and NO_3^- uptake require sufficient Mo, whereas this trace metal apparently has no impact on NH_4^+ assimilation. Thus, due to interspecific differences in the form of N assimilated, the availability of Mo may influence the composition of diatom assemblages. For instance, certain taxa (*e.g.* *Cyclotella cryptica*, *Nitzschia dissipata*, and *Nitzschia communis*) require NO_3^- as an N source, while others (*e.g.* *Chaetoceros muelleri*, *Phaeodactylum tricorutum*, and *Navicula acceptata*) are capable of using either NO_3^- or NH_4^+ (SERI, 1986; Tadros & Johansen, 1988). Thus, under high $\text{SO}_4^{-2}:\text{MoO}_4^{-2}$ ratios, ammonium users may be favored. It is interesting to note that the strain of *C. muelleri* mentioned above was isolated from the Salton Sea (California), a chloride-dominated system. In contrast, a strain isolated from East Devils Lake (North Dakota), a sulfate-dominated system, cannot grow on NO_3^- alone but grows well when supplied with NH_4^+ (Saros, unpublished data).

Nutrient cycling

Sulfate also plays a role in nutrient cycling in lakes and hence influences nutrient availability. As mentioned above, N_2 fixation requires sufficient Mo. Marino *et al.* (1990) found that the $\text{SO}_4^{-2}:\text{MoO}_4^{-2}$ ratio, not P concentration or N:P ratio, was the best predictor of the abundance of planktonic, N-fixing blue-green algae in 13 saline lakes in Alberta, with a decline in these blue-greens as the ratio increased. Through N-fixation, blue-green algae convert N from N_2 into forms usable by other algae, contributing anywhere from 0–82% of the total open water N budget (Schindler, 1977; Howarth *et al.*, 1988). Therefore, the presence of N-fixing cyanobacteria can raise N:P ratios. Systems with high $\text{SO}_4^{-2}:\text{MoO}_4^{-2}$ ratios tend to have low populations of these blue-green algae, possibly resulting in depressed N concentrations relative to P. This is one mechanism by which sulfate can lower the N:P ratio; it can also do so by raising P con-

centrations. Caraco *et al.* (1989) found that in a set of 23 aquatic systems, P release from sediments increased with sulfate concentration. In brackish and saline systems with high sulfate concentrations (ranging from 0.3–3.0 g l⁻¹), P immobilization by sediments tended to be low under both oxic and anoxic conditions. This may explain why primary production in high sulfate systems is often P sufficient (Bierhuizen and Prepas, 1985; Howarth, 1988), with low N:P ratios frequently found in these systems. In contrast, low sulfate/high bicarbonate lakes tend to exhibit high N:P ratios (Figure 1); primary production in these systems is often strongly correlated with total phosphorus (TP). As a relationship has been observed between N:P ratios and primary production in saline systems, it seems plausible that this ratio may also play a role in determining diatom community structure. To our knowledge, direct ordination analyses of diatom distributions in saline lakes have not included N:P ratios, but both Cumming *et al.* (1995) and Fritz (unpublished) have found that nutrient concentrations explain a significant fraction of variation in the species data. As depicted in Figure 2 for the Northern Great Plains (NGP) region (Fritz, unpublished), TP varies in a similar direction to % SO_4 and SO_4 , which is consistent with greater phosphorus release from sediments as SO_4 concentrations increase. Nitrogen data are unavailable for these systems, thus we are presently unable to explore interactions between N or N:P ratios and ionic parameters.

Conclusions

Salinity and ionic composition affect diatom ecology, both directly (*e.g.* via their influence on physiological processes) and indirectly (*e.g.* via their influence on biogeochemical cycles). However, the actual mechanisms by which these parameters influence diatom community structure in saline lakes are as yet undetermined. Of course, the ability to withstand osmotic pressure may fully explain the correlation between salinity and diatom distributions. However, given the above discussion, it seems plausible that nutrient dynamics may serve as a link between observed correlations between diatom assemblages and salinity or ionic composition. Further insight into the mechanisms behind these correlations should enhance our ability to reconstruct paleoclimate in arid and semiarid regions.

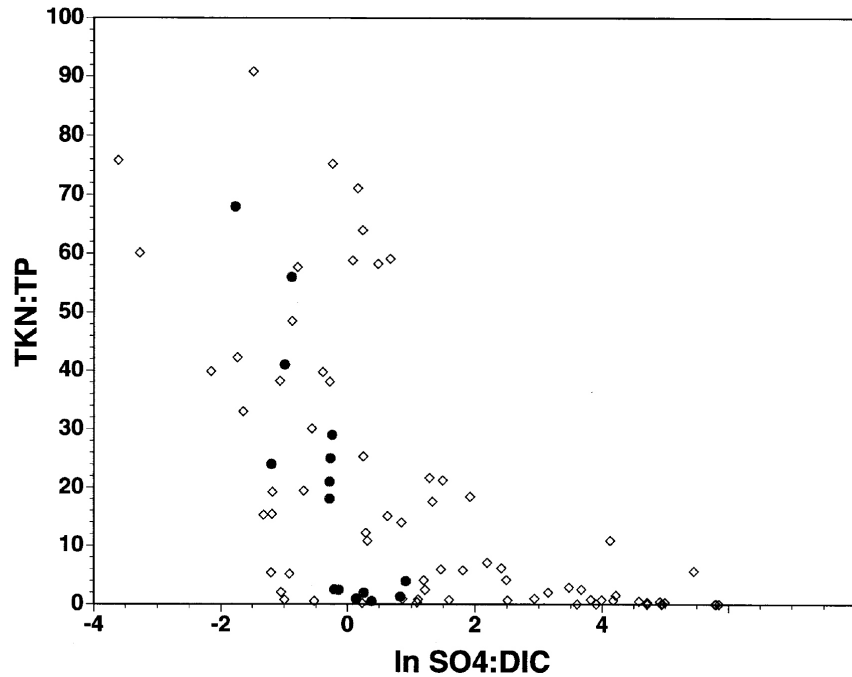


Figure 1. Plot of $\ln \text{SO}_4^{-2}:\text{HCO}_3$ vs. total Kjeldahl nitrogen (TKN):TP ratios for saline lakes in British Columbia (indicated by \diamond and based on data reported in Cumming *et al.*, 1995) and Alberta (indicated by \bullet and based on data reported in Bierhuizen & Prepas, 1985). TKN:TP ratios decline as sulfate becomes dominant (*i.e.* as $\ln \text{SO}_4^{-2}:\text{HCO}_3$ increases).

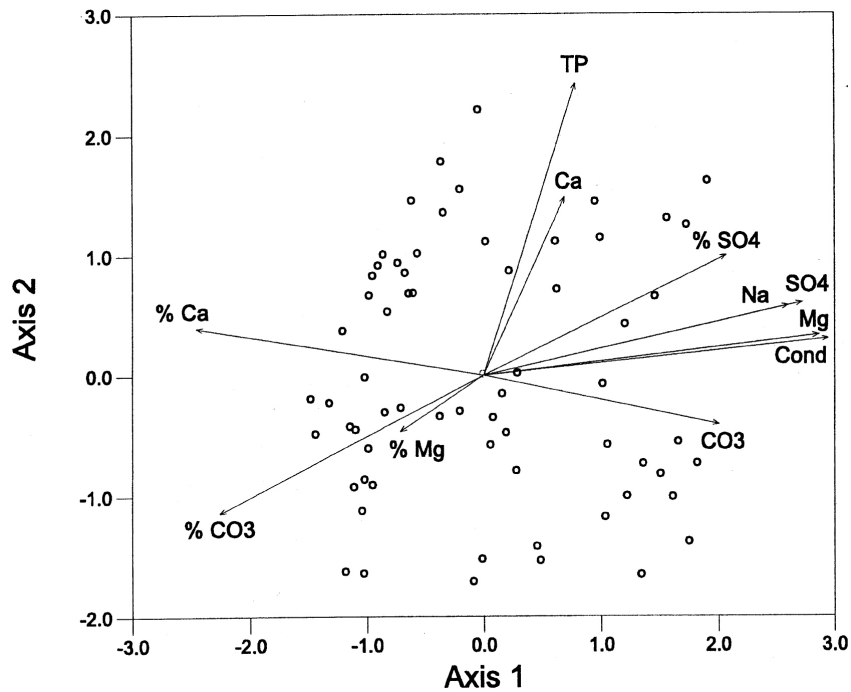


Figure 2. Results of canonical correspondence analysis (CCA) of relationship between diatom distributions and environmental variables in a suite of saline lakes in the Northern Great Plains (NGP). The data indicate that diatom distributions are highly correlated with conductivity, TP, and brine type. (From: Fritz *et al.*, 1993; unpublished).

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