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Sherilyn C. Fritz
University of Nebraska-Lincoln

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Sherilyn C. Fritz

University of Nebraska–Lincoln, Lincoln, NE, USA

Introduction

Diatoms are widely used to reconstruct past environments because of their sensitivity to a range of environmental variables. Among the variables that exert a strong influence on diatoms are ionic concentration, expressed as salinity or conductivity, and ionic composition. Because the ionic concentration and composition of inland water bodies is affected by changes in effective moisture (precipitation minus evaporation, P – E), changes in the abundance of diatom species that vary in their salinity tolerances provide a tool for the reconstruction of past climate.

The use of diatoms to infer changes in salinity driven by climate relies on settings where effective moisture variation is moderate to large and produces relatively large changes in lake salinity. These conditions are most common in semiarid and arid regions, where evaporative forcing is strong, and in topographically closed lakes where changes in P – E have the potential to concentrate or dilute dissolved salts. These conditions are widespread in the dry interiors of continents, in subtropical deserts, and in dry polar regions. Thus, diatom-inferred salinity can be used to reconstruct effective moisture from lake deposits in many regions of the globe.

In practice, the inference of climate from diatom-inferred salinity is complicated by the diverse controls on the hydrologic budgets of lakes and, occasionally, the accurate inference of salinity from diatoms may be obscured by other ecological influences. Nonetheless, diatom records have played a critical role in developing the understanding of the extent to which twentieth-century climate patterns are representative of long-term climate variation and of the patterns and controls on climate variability at decadal to orbital time scales.
Diatoms as Indicators of Salinity and Ion Composition

Salinity Classification of Diatoms
Diatoms have long been recognized as indicators of ionic concentration (salinity). Kolbe (1927), and subsequently Hustedt (1953), developed a system to classify diatoms according to their distribution in waters of varied salinity, the so-called halobion system. This system was primarily based on distributional patterns in sodium chloride (NaCl)-dominated marine and coastal environments, from marshes and estuaries receiving fresh surface runoff to the open ocean where salinity reaches ~35 g l⁻¹. Although this halobion classification was applied to lacustrine diatoms in the mid-1900s, it is not well suited for diatoms in continental lakes because of the much broader range of salinity and ion composition found there.

Studies to characterize the salinity ranges of lacustrine diatoms expanded in the 1970s and 1980s, when the potential to reconstruct past climate change from lake sediments became more broadly recognized (Ehrlich, 1978; Gasse, 1977). During the last few decades, studies of the distribution of diatoms relative to gradients of salinity and ion composition have been carried out on all the continents and in lakes from the high latitudes to the tropics and have fueled the use of diatoms as paleoclimatic indicators.

Diatoms occur in the full range of lakes from dilute freshwater to hypersaline brines (fig. 1), and classification schemes reflect this diversity of environments. One of the most commonly applied classification systems splits lakes and their associated diatom floras into freshwater (<0.5 g l⁻¹), subsaline (0.5–3.0 g l⁻¹), hyposaline (3.0–20 g l⁻¹), mesosaline (20–50 g l⁻¹), and hypersaline (>50 g l⁻¹) waters. Many species have distributional limits near the overlap of the subsaline and hyposaline ranges, and the diversity of taxa is low in mesosaline and hypersaline systems (Fritz et al., 2010b).
Figure 1. The salinity ranges (horizontal line) and salinity optima (dot) of selected diatom species from the Great Plains region of North America, generated from a survey of water chemistry and diatoms in the surface sediments of 66 regional lakes. Weighted averaging regression was used to calculate ranges and optima. Species are arranged from top to bottom in order of increasing salinity optima. Reproduced from Fritz SC, Juggins S, and Battarbee RW (1993) Diatom assemblages and ionic characterization of lakes in the northern Great Plains, N.A.: A tool for reconstructing past salinity and climate fluctuations. Canadian Journal of Fisheries and Aquatic Sciences 50: 1844–1856.

Although the distribution patterns of many diatoms are correlated with salinity, the mechanisms for this correlation are not well understood. Salinity imposes an osmotic gradient and hence an energetic cost on cells. At high salinity, diatoms manufacture proline or other osmolytes to deal with the osmotic gradient; many of these compounds are amino acids and rich in nitrogen. Thus, under high salinity, nutrient requirements may be higher (Saros and Fritz, 2000). Other compounds that are correlated with salinity gradients also may affect nutrient uptake by diatoms. For example, high concentrations of sulfate may interfere with molybdate uptake, a critical component of enzymes involved in nitrogen utilization. Many saline lakes in grasslands also have high dissolved organic carbon concentrations (DOC) and low chlorophyll relative to ambient nutrient concentrations (Salm et al., 2009). This suggests that DOC may form complexes with a critical nutrient that con-
trols primary production and thereby affects diatom productivity and species composition. Thus, several lines of evidence suggest that one of the major effects of changing salinity may be via its impact on nutrient availability, uptake, and requirements.

Diatoms also can be classified according to their distribution in waters of differing anion composition, and some species are characteristic of chloride, sulfate, or carbonate–bicarbonate-dominated waters (fig. 2). The reasons for differences in anion association also are unclear but are likely related partly to anion impacts on nutrient availability (Saros and Fritz, 2000). Shifts in anion composition of lacustrine systems can be indicative of changes in source waters, particularly groundwater, or of progressive changes in brine composition driven by climate.

Figure 2. Diatom-inferred cation composition (x-axis) and anion composition (y-axis) inferred from a series of diatom samples from sediment cores from 12 African lakes. Sediment samples from each of the 12 lakes are represented by a different symbol. A weighted average calibration model developed from over 300 modern lakes in Africa was used to reconstruct cation and anion composition from these sediment samples. The groups A0, A1, AII represent different combinations of lake water cation and anion dominance, as indicated in the figure. Subgroups 1–4 represent progressively increasing salinity within a given group. Reproduced from Gasse F (2002) Diatom-inferred salinity and carbonate oxygen isotopes in Holocene waterbodies of the western Sahara and Sahel (Africa). Quaternary Science Reviews 21: 737–767.

Quantitative Approaches for Salinity Reconstruction

Since the mid-1980s, transfer functions applied to fossil diatom assemblages have increasingly been used in paleoenvironmental studies to quantitatively reconstruct salinity, conductivity, or some other environmental variable of interest. These transfer functions are based on modern calibration data sets, which sample a group of contemporary lakes that span a salinity gradient and use these lakes to characterize the salinity range of diatom species and the so-called salinity optimum, the salinity at which each diatom species is most abundant (fig. 1). A variety of statistical techniques can be used to generate transfer
functions for the reconstruction of salinity or other environmental variables (Birks, 2010). The transfer function approach does not assume that salinity, or another reconstructed variable, is the proximate or physiological variable affecting diatom distribution, but simply that diatom distribution is highly correlated with salinity and that this relationship is stationary through time. In most cases, a regional transfer function cannot be independently tested by applying the function to a new group of lakes or by comparing a reconstruction from a sediment core with historic measurements of salinity from the same lake, although occasionally these sorts of data are available (e.g., Fritz, 1990). Therefore, statistical techniques for error estimation, such as bootstrapping or jack-knifing, are commonly used to evaluate transfer function performance (Birks, 2010; Fritz et al., 2010b).

Transfer functions for salinity reconstruction are effective in lakes that have undergone moderate to large fluctuations in salinity that exceed the standard error of prediction. Quantitative techniques also work best in systems where other water-chemistry variables that have a strong impact on diatoms, such as pH or nutrients, are less likely to show large changes over time. In theory, statistical approaches, such as variance partitioning, can account for the impact of multiple environmental influences on species distribution. In practice, however, modern data sets are constructed to optimize the environmental gradient of interest, in this case salinity, and other ecologically important variables may not be adequately accounted for. In these cases, the assumption that the relationship between species and salinity does not change with time may be invalid, such as has been demonstrated for diatom-based transfer functions for temperature (Bigler et al., 2002). Because of these issues, salinity reconstructions are most robust when they are corroborated by inferences from other proxies, such as ostracodes, chironomids, sedimentology, or sediment geochemistry (Aebly and Fritz, 2009; Gasse, 2002; Kropelin et al., 2008).

Quantitative reconstructions depend on having a modern calibration data set that accurately defines the environmental ranges and tolerances of diatom species. For most regions, the size of calibration data sets is less than 100 lakes, and although such a sample size can generate a statistically robust transfer function, it may not adequately capture the true optima of all taxa. In some regions, such as the tropical Andes, the density of modern samples is not yet sufficient to allow quantitative reconstructions, and the large number of apparently endemic species makes generalizations from the florals of other regions difficult. Finally, given the large range of environmental change in the past, some regions may no longer contain aquatic environments that are modern analogs for past environmental conditions. Thus, in Africa and Mexico, some of the dominant diatom taxa in fossil records do not occur in the modern flora (Gasse, 2002; Metcalfe et al., 2002), even given large spatially distributed modern data sets.

**Diatom Preservation in Saline Lakes**

Although diatoms are a common component of the algal community in lakes from low to high salinity, they are not always well preserved in sedimentary records. Diatom dissolution is highest in sodium carbonate solutions, where high pH (>9) enhances the dissociation of silicic acid, but dissolution also occurs in other salt solutions (Barker et al., 1994). Brines can induce the formation of diagenetic silicates (e.g., zeolites and smectite), leading to alteration or dissolution of diatom assemblages. These processes can alter not only total
diatom abundance in sediments, but also species composition because diatom species are differentially sensitive to dissolution and diagenesis (Barker et al., 1994; Ryves et al., 2001). In some cases, dissolution indices can be developed to correct for some of the bias imposed by taphonomic processes (Ryves et al., 2009).

**Lakes, Salinity, and Climate**
Climate affects the water budget of lakes via its influence on precipitation, surface evaporation, and groundwater flow. Shifts in a lake’s water balance, in turn, alter lake salinity through concentration or dilution of ions in solution. The magnitude of the climatic imprint depends on the morphometry of the lake and its drainage basin; both lake surface area and volume, for example, affect the degree to which precipitation or evaporation influence lake level and lake salinity. Overall, the best candidates for climate reconstruction from diatom-inferred salinity techniques are subsaline to hyposaline lakes in semiarid to arid climates because variations in precipitation and evaporation cause salinity changes that are sufficiently large to produce shifts in diatom species composition. The rate of lake response to climate is a product of the lake’s water residence time and the relative balance of surface flow relative to groundwater. In lakes where groundwater is a large component of the water budget, lake response is governed by the response time of the groundwater system, and short-term climatic change may have very little impact on the water and budget (Reed et al., 1999). Connection to a groundwater flow system also allows for loss of salts via subsurface outflow, whereas in a terminal basin (a basin without surface or subsurface outflow), salts build up over time.

Globally, subsaline and saline lakes outnumber freshwater lakes (Meybeck, 1995), and systems appropriate for paleoclimatic study are common in most of the regions of the world where water availability is limited. This includes the continental interiors of the Americas, Africa, Australia, and Eurasia, as well as the high-latitude regions of Antarctica and the Arctic. In the next section, examples of a range of lake systems are discussed in which diatom-inferred salinity has been used to infer paleoenvironmental and paleoclimatic history during the Quaternary.

**Quaternary Environmental History as Inferred from Diatoms**

**Quaternary Climate Variation at Orbital and Millennial Time Scales**
Shifts between freshwater and saline diatom taxa have been used effectively to infer moisture variation on orbital and millennial time scales in extant and former lake basins. In the Owens Lake basin in western North America (Bradbury, 1997), peaks in freshwater planktic diatoms and inferred deepwater conditions are broadly correlated with cold periods in the SPECMAP oxygen isotope record after ~400,000 years BP, when tectonic processes likely produced an increase in basin depth (fig. 3). Prior to that time, the evidence suggests that the basin was much shallower, and the correlation between intervals of increased planktic diatoms and cold climatic periods is not as strong. In Lake Titicaca in the tropical Andes, the increased abundance of freshwater planktic diatoms (fig. 4) indicates fresh overflowing conditions associated with increased precipitation, whereas benthic diatoms
and the saline planktic taxon, *Chaetoceros muelleri*, indicate periods when lake-level fell below the outlet and salinity built up. In this case, the wet intervals are coincident with global cold periods, including the Last Glacial Maximum, when cold temperatures reduced evaporation and high summer insolation and cold Atlantic Ocean sea-surface temperatures (SSTs) enhanced the South American summer monsoon. During the contrasting conditions of global interglacial periods, lake-level declines of up to 240 m (modern water depth is 285 m) were sufficient to more than double lake water salinity (Baker et al., 2001; Fritz et al., 2007); more discussion of the Lake Titicaca record is given in Mackay (this volume). Millennial-scale variations in lake level also are evident in Lake Titicaca and other lakes in the drainage basin and can be linked to climate variation in the North Atlantic region (Ekdahl et al., 2008; Fritz et al., 2010a). In Africa, massive reductions in lake level are evident during the late Pleistocene in the diatom record from Lake Malawai, as well as in other proxies analyzed in the same core (Stone et al., 2010). Similarly, a 50,000-year diatom record from Tanzania shows the influence of global temperature change on regional hydrology (Barker et al., 2003). Here changes in lake level and lake conductivity show a strong relationship to SST change in the SW Indian Ocean (fig. 5), which forces changes in the position of the intertropical convergence zone (ITCZ) and hence influences precipitation in the African tropics.

![Figure 3](image-url)

**Figure 3.** A comparison of the abundance of freshwater planktic diatoms in a drill core from Owens Lake, California compared with the SPECMAP δ¹⁸O record of global temperature change – high isotopic values represent global cold periods, whereas depleted values are warm periods. The δ¹⁸O record from a calcite vein at Devils Hole, Wyoming also
provides a chronology of temperature change; in this case with more depleted (smaller) values representing colder periods. The relative proportion of diatoms in each sample was calculated using a standard sample count of 300 diatom valves. In a few samples with very high diatom concentrations, more than 300 valves were counted and thus percentages exceed 100%. Reproduced from Bradbury JP (1997) A diatom-based palaeohydrologic record of climate change for the past 800 k.y. from Owens Lake, California. *Geological Society of America, Special Paper* 317: 99–112.

Figure 4. The diatom stratigraphy of the last ~30,000 years from Lake Titicaca, Bolivia-Peru. The dominance of freshwater planktic diatoms is inferred to represent times when the lake was fresh and overflowing, whereas benthic (*Pseudostaurosira zelleri* and other taxa) and saline (*Chaetoceros muelleri*) diatoms dominate when the lake-level fell below the outlet threshold (see Baker et al., 2001 for additional information).
Figure 5. The diatom stratigraphy of Lake Massoko, Tanzania compared with insolation and sea-surface temperature forcing. The detrended correspondence axis (DCA) scores summarize the patterns of change in the diatom species assemblage – samples with high DCA axis 1 scores are samples with high diatom-inferred conductivity and represent times of lowered P – E, an inference that is corroborated by pollen data. Reproduced from Barker P, Williamson D, Gasse F, and Gibert E (2003) Climatic and volcanic forcing revealed in a 50,000-year diatom record from Lake Massoko, Tanzania. Quaternary Research 60: 368–376.

Late-Glacial and Holocene Climate Change
Changes in salinity inferred from diatom records have played a prominent role in documenting hydrologic changes in the late-glacial period through the Holocene, particularly in the Americas and Africas. In northern Mexico and the Great Basin of the southwestern United States, diatom records suggest that the late-glacial period was wet as a result of the southerly displacement of the westerly storm tracks, followed by drying in the early to mid-Holocene as the storm tracks moved northward (Bradbury et al., 2001; Metcalfe et al., 2002). In central Mexico, the opposite climate pattern is evident, with a dry late-glacial period because of a southward displacement of the ITCZ and a reduction in trade wind sources of moisture. Holocene salinity and moisture patterns across Mexico are spatially complex, as a result of the differential influence of rising sea level, dating uncertainties, and increasing human impact on the landscape in the late Holocene (Metcalfe et al., 2000).

In Africa, diatom analysis has been instrumental in documenting massive precipitation changes during the late Quaternary, including the greening of the Sahara and Sahel in the early to middle Holocene (Gasse, 2002). At Bougdouma in Niger, for example, shifts between alkiliphilous benthic diatoms and freshwater planktic species suggest fluctuating water levels following the last period of glaciation (fig. 6). Stable wet conditions developed in the early Holocene (~10,300 years BP), followed by drying after 7,300 years BP, a trend
that is widespread throughout the Sahara and Sahel. Several wet pulses that produced a rising water table interrupted the drying trend, but conductivity and inferred aridity increased after 3,800 years BP, with desiccation of the basin during the last 1,000 years. These trends reflect variation in monsoon intensity across northwest Africa, but regional differences in the timing of lake salinity change reflect differences in the rate of response of different linked aquifer–lake systems.

Figure 6. The (a) diatom stratigraphy of Bougdouma in southern Niger and (b) various water-chemistry variables inferred from the diatom stratigraphy using transfer functions (lower figure). The cationic and anionic ratios are defined in figure 2. The assemblages defined on the right-hand part of the figure (A0, AI, AII) represent the inferred cation and anion water types as defined in figure 2. Reproduced from Gasse F (2002) Diatom-inferred salinity and carbonate oxygen isotopes in Holocene waterbodies of the western Sahara and Sahel (Africa). Quaternary Science Reviews 21: 737–767.

The impacts of groundwater on lake response to climate have been highlighted in several paleolimnological studies. In some lakes of the Ethiopian Rift Valley, diatom-inferred water chemistry does not show patterns of salinity change that would be predicted based
on independent evidence for precipitation variation (Telford et al., 1999). For example, an interval of high diatom-inferred conductivity from Lake Awassa corresponds with strand lines in an adjacent basin that document a contemporaneous interval of high precipitation (fig. 7). Increased inputs of saline groundwater to one lake but not the other are the likely explanation. Similarly, a karst lake in the Konya Basin of Turkey showed little change in diatom-inferred conductivity during the late Pleistocene, probably because of relatively constant inflow of fresh groundwater, whereas a neighboring lake with limited groundwater flow showed evidence of changes in conductivity and lake level indicative of changes in effective moisture (Reed et al., 1999).


Complex salinity responses to climate change also are evident in intermittently meromictic lakes in West Greenland. Here, the amplitude of salinity variation is apparently affected by the stability of stratification, producing a nonlinear response of lake salinity to climate change (Aebly and Fritz, 2009; McGowan et al., 2003). In some intervals, increased diatom-inferred salinity correlates with evidence of increased precipitation from
paleo-shorelines. Complex groundwater interactions are unlikely in this region because of permafrost. In this setting, the observed response likely resulted from the coalescence of a freshwater lake with a lake of higher salinity during times of increased precipitation or from the reworking of shoreline salt deposits as lake level rose.

The use of diatom-inferred salinity to infer changes in effective moisture also can be affected by the sensitivity of diatom assemblages to changes in salinity driven by climate. At high salinity, diatom diversity is commonly quite low, and the ecological tolerances of many high-salinity taxa are broad. Thus, species composition may not change as salinity changes. At Moon Lake, North Dakota, USA, for example, diatom-inferred salinity is very high during the mid-Holocene (fig. 8), indicative of the dry climate that was characteristic of the mid-latitudes of North America. But, the low variability in mid-Holocene diatom-inferred salinity probably results because changes in salinity caused by precipitation variation are not sufficiently large to change the composition of the diatom assemblage (Laird et al., 1996).

Figure 8. The diatom-inferred salinity of Moon Lake, North Dakota, USA during the last ~12,000 years (Laird et al., 1996).

Diatom records from the North American Great Plains also provide an example of the use of diatom-inferred salinity to evaluate natural drought variation and the degree to which the twentieth century climate patterns are representative of the natural variability of climate. Records from a suite of lakes in the United States and the Canadian prairies clearly show that droughts equivalent in magnitude to the Dust Bowl droughts of the 1930s
and 1940s were recurrent during the last millennium or two (Laird et al., 2003). These records also suggest that drought was more prolonged in the recent past than during the twentieth century; some droughts apparently persisted for a century or more. One of the major difficulties with these high-resolution records, however, is in the correlation of the pattern of change among multiple sites; the errors associated with a radiocarbon chronology prohibit a clear correlation of changes at multidecadal scales. Even directional shifts that are persistent can be difficult to interpret in climatic terms. Thus, a major shift at the onset of Little Ice Age about 800 years BP is manifested as an increase in salinity at one site and a decrease at another nearby lake (fig. 9), and it is unclear whether the differences reflect a sharp climatic gradient, or whether they are more likely due to differing hydrological responses to the same climatic forcing (Fritz et al., 2000).

**Figure 9.** Diatom-inferred salinity spanning the last ~2,000 years of two lakes in North Dakota, USA that are within 200 km of one another. The right-hand panel shows the deviation from the long-term mean salinity. Note that Moon Lake became fresher at ~AD 1200, whereas Coldwater Lake becomes saltier at about the same time (Fritz et al., 2000).

**Conclusions**

The use of diatoms to infer past moisture variation in continental settings has increased greatly during the last two decades, and appropriate basins are widespread in semiarid and arid regions worldwide. In these regions, lacustrine records often provide the best archives of long-term continental climate variation. Although some lakes in extremely dry climates may have discontinuous sedimentary records, in many basins, sedimentation rates are sufficiently rapid to allow the sedimentary record to be resolved at a subdecadal scale.
Although more studies are needed on how salinity and other ecologically important variables interact to influence diatoms, in many settings knowledge of diatom ecological tolerances is sufficient to enable robust reconstructions of qualitative changes in lake salinity. In some regions, calibration data sets have been developed to allow quantitative salinity reconstructions that are reasonably good at identifying the direction and relative magnitude of salinity change. In general, salinity change can be reconstructed from diatom assemblages with a high degree of confidence.

The inference of climate from salinity change is considerably more difficult, because of the potentially complex series of influences on the hydrologic budget of individual lakes. Although many of the issues involved in disentangling climate from biological and geochemical records are recognized (Fritz, 2008), more frequent application of modeling and empirical studies to quantify their potential impact in individual sites or regions would improve many paleolimnological interpretations. The tandem use of other proxies can help to constrain environmental interpretation from diatom records, although in some cases, reconciliation of apparently divergent inferences is not clear. Such cases also point to the need for more frequent integration of paleolimnology with modern process studies and modeling efforts. Overall the number of lacustrine records is still relatively limited, particularly at high temporal resolution and for periods much older than the Last Glacial Maximum. Thus, although the diatom paleoclimatology field has expanded in recent years, there is still a considerable distance to travel to unravel the patterns of environmental change across space and time, and the hierarchy of factors that produce them.

References


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