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Tracking Holocene Climatic Change with Aquatic Biota from Lake Sediments: Case Studies of Commonly Used Numerical Techniques

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Abstract

It is now widely recognized that reliable long-term climatic data are required to evaluate the impact of human activities on climate. Lake-sediment records are an important source of such paleoclimatic information, on timescales from years to millennia. However, unequivocal interpretation of biological climate-proxy data preserved in lake sediments can be very challenging. Here we review the different numerical approaches that are used to evaluate the sensitivity and reliability of species assemblages of aquatic biota (algae and invertebrates) extracted from lake-sediment records as proxies of past climatic conditions. The most common techniques used to assess this relationship between these proxies and climate include calibration functions that model the relationship across modern lake environments between species composition in the indicator group and particular climate-influenced aspects of their aquatic habitat, and assessments of the main directions of variation in species composition in relation to independent climatic data. Other statistical techniques, such as variation partitioning analysis, are used to assess the relative importance of climate versus other factors in influencing limnological changes seen in the sedimentary record. These techniques show that in climate-sensitive lake systems, the sedimentary remains of aquatic biota can be sensitive and trustworthy proxies, permitting quantitative reconstructions of past climatic conditions with high temporal resolution.

Keywords: Calibration functions, Chironomids, Climatic change, Diatoms, Invertebrates, Modern analogues, Ordination, Paleoclimate, Rate-of-change analysis, Reconstruction validation, Variation partitioning

Introduction

With recent concerns about global change, the need for reliable long-term paleoclimatic data is now universally recognized by governments and international organizations. Such records are necessary to provide information on the magnitude and patterns of past climatic change against which recent changes can be assessed. Furthermore, prognoses of future climatic conditions will be enhanced when we better understand the temporal and spatial patterns of natural climatic variability.

Historically, a great amount of information on long-term climatic variability has been provided by reconstructions of past vegetation changes from pollen and plant macrofossils preserved in lake sediments (e.g., Webb 1986; Prentice et al. 1991) and from studies applying geomorphological, sedimentological, and biostratigraphical methods to transects of sediment cores to reconstruct changes in water level (e.g., Harrison and Digerfeldt 1993). However, as noted by many authors (e.g., Ritchie 1987), pollen-based studies have certain limitations, which include the inability to identify many pollen taxa below the family level; the broad dispersal of many windblown pollen grains; the differential response of various tree species to climatic change associated with variation in topography, soils, life-cycle characteristics, and anthropogenic factors; and the general scarcity of pollen and macrofossils in some environments (e.g., regions at high altitudes and/or latitudes). None-the-less, contributions from palynological and lake-level studies have elucidated the broad-scale temporal and spatial template of climatic change in many regions, and in some regions have the potential to provide records of climatically-driven vegetation change with high temporal resolution (e.g., Clark et al. 2002; Lamb et al. 2003; Gajewski 2008; Kröpelin et al. 2008; St. Jacques et al. 2008a, 2008b).

Many lakes exhibit physical, chemical, and/or biological responses to changes in climatic conditions, and evidence of these changes are often preserved in their sediment record (Battarbee 2000; Smol and Cumming 2000; Fritz 2008). Analyses of the remains of aquatic algae (e.g., diatoms, chrysophytes, pigments) and invertebrates (e.g., chironomids, cladocerans, ostracods) in sediment cores from such climatically-sensitive lakes can potentially provide records of climatic and environmental change at a higher resolution than most palynological and many lake-level studies. Enhanced sensitivity of aquatic biological indicators (proxies) to environmental change is due to our ability to identify many of these organisms to species level, their short life-span, and their fast dispersal, which guarantees rapid colonization of newly available habitat and thus avoids significant lags in their response to climatic change. Thus, examination of changes in the species

composition of aquatic biota in sediment cores can provide valuable insights into how climatic conditions have varied in the past that may not be readily apparent from terrestrial indicators. However, the relative importance of climatic change can be complex, even in apparently simple aquatic systems (e.g., Anderson et al. 2008; Fritz 2008).

In this chapter, we provide an overview of the different numerical techniques that have been used to study the linkages between changes in biotic assemblages preserved in lake sediments and climatic change during the Holocene. It is important to note that these approaches are simply tools that are useful to assess, simplify, and visualize past environmental changes in a repeatable and somewhat objective manner. Many studies make limited use of numerical approaches but still yield valuable insights into past climatic conditions (e.g., Baker et al. 2001; Bennett et al. 2001; Dean 2002; Dean et al. 2002; Spooner et al. 2002). Finally, although the focus of this chapter is on approaches that have been used to interpret climatic signals in fossil assemblages of lake biota, equally important paleoclimatic information is derived from physical (e.g., Lamoureux 2000; Noon et al. 2001; Dean et al. 2002; Pienitz et al. 2009) and geochemical proxies (e.g., Dean 2002; Tierney et al. 2008; Pienitz et al. 2009; Toney et al. 2010). The latter increasingly include stable-isotope signatures extracted from lake biota, such as ostracods (e.g., von Grafenstein et al. 1999), chironomids (e.g., Verbruggen et al. 2010), and diatoms (e.g., Hernandez et al. 2010).

Biological Proxies of Past Climatic Conditions

Proxy data based on biotic assemblages preserved in lake sediments have long been known to be sensitive and reliable indicators of past climatic change, because of the strong influence of temperature and rainfall variations on the structure and function of their aquatic habitats. Lake characteristics that are sensitive to climatic changes can be both physical (e.g., temperature, ice cover, lake depth, river discharge, mixing regime, light transparency) and chemical (e.g., changes in alkalinity, pH, nutrients, salinity) (e.g., Walker et al. 1991; Walker 1995; Vinebrooke et al. 1998; Korhola 1999; Battarbee 2000; Smol and Cumming 2000; Korhola and Rautio 2001; Brodersen and Anderson 2002; Fritz 2008; Lotter et al. 2010; Wolin and Stone 2010). However, establishing an unequivocal connection of these limnological changes to climate is often difficult. The challenge is to demonstrate that the biotic proxy indicators are connected to climate in a systematic, predictable fashion. In some systems, this is exceedingly difficult because of the non-linear responses of the limnological system to climatic change and subsequent sedimentological complications, such as variable sedimentation rates and/or mixing (Verschuren 1999a, 1999b). Such complexities are related to basin hydrology, as well as to the physical, chemical, and biological characteristics of individual lake basins (Smol and Cumming 2000; Schwalb and Dean 2002; Fritz 2008). Additionally, because different groups of biological proxies have different life-

history strategies, changes in climate that influence aquatic systems can impact various proxies in different ways (Battarbee et al. 2002a; Heegaard et al. 2006). Therefore, it is not surprising that the response of different lakes, and of different proxies within a single lake, to climatic change can vary tremendously (Smol and Cumming 2000; Fritz 2008).

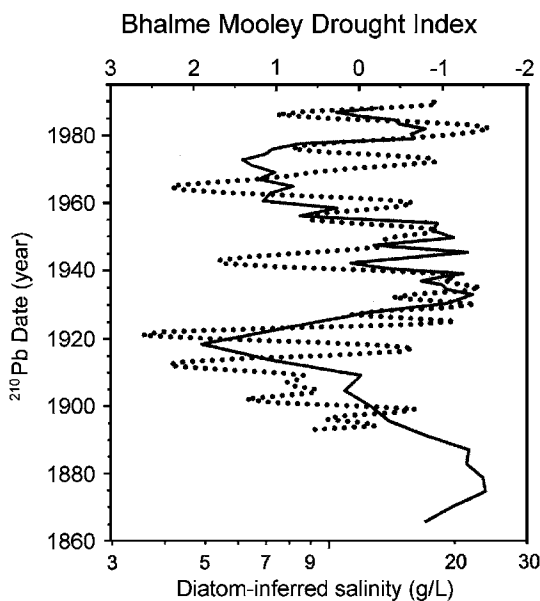
Successful paleoclimatic interpretation of in-lake biological proxies depends on a good understanding of the climatic response of a lake to changes in climate. Not surprisingly, selecting and then demonstrating the climatic sensitivity of a site is not a simple procedure. Smol and Cumming (2000) identified lakes that are thought to be especially sensitive. These include lakes from high latitudes, lakes that are close to ecotonal boundaries (e.g., near tree-line, near the forest-prairie boundary), and lakes in arid to semi-arid regions with limited groundwater inputs and, ideally, large catchments (i.e., amplifier lakes: Olaka et al. 2010). In addition to geographical position, sites sensitive to climatic changes can be identified from measurements of limnological change (e.g., changes in lake-water chemistry, transparency, declines in water levels, and/or changes in salinity) and from instrumental and/or historical records (Fritz 1990; Schindler et al. 1996; Verschuren 1996, 2003; Webster et al. 2000; Doran et al. 2002). However, data of sufficient duration and frequency are relatively rare, even in populated regions. Additional information on the hydrological responsiveness to changes in climatic conditions can be obtained by careful examination of temporal sequences of aerial photographs and satellite images (Donovan et al. 2002; Smith et al. 2005).

Once climate-sensitive lakes have been identified, it is becoming increasingly common to assess the strength of the climatic impact on biological proxies or inferred limnological variables in the sediment record by comparison of the proxy records with instrumental meteorological data (temperature, precipitation, drought indices), historical data of lake response to climate (e.g., lake-level changes, chemical constituents), or with independent evidence of climatic change (e.g., documentary, other paleoclimatic proxies). These comparisons may involve simple visual matching of pattern similarities in the paleolimnological and meteorological records, calculation of correlation coefficients between lake and climatic variables, or using multivariate numerical methods (e.g., variation partitioning: Borcard et al. 1992; Legendre and Birks 2012: ch. 8).

Comparison of Inferred Limnological Variables and Instrumental Climate Data

In arid to sub-humid regions, long-term (decade-scale and longer) variations in the balance of rainfall and evaporation can drive significant changes in lake level, which in turn may influence the physical, chemical, and biological environment of lakes to the extent that their signatures are recorded in the sedimentary record (Fritz 1996). In other regions, the influence of temperature is evident in the sedimentary record, either directly or indirectly, via changes in catchment

Figure 1. Diatom-inferred salinity estimates from Moon Lake (North Dakota, USA) (*solid line*) compared to a smoothed Bhalme-Mooley Drought Index (*dotted line*) based on nearby instrumental precipitation records over the last 100 years; $r = 0.49$, $p < 0.01$. (Modified from Laird et al. 1998a.)



hydrology, vegetation, ice cover, or mixing regimes. One way to validate proxy-based climatic inferences is to compare quantitatively or qualitatively the proxy-based reconstructions of environmental change (e.g., lake-water salinity, lake level, temperature) in the recent past with historical time-series of instrumental meteorological data. To date, the majority of such direct, quantitative comparisons have used approaches based on calibration functions (see Juggins and Birks 2012: ch. 14).

To evaluate the climatic sensitivity of Moon Lake (Northern Great Plains, USA), Laird et al. (1996a) assessed the correlation between diatom-inferred (DI) salinity through time in a ^{210}Pb -dated sediment core and instrumental time-series of effective moisture (precipitation minus evapotranspiration or ET). Diatom-inferred salinity showed major increases coincident with the major droughts of the 1930s and the 1890s, with a statistically significant relationship between DI salinity and effective moisture (Laird et al. 1996a). Because ET can be difficult to estimate, Laird et al. (1998a) replaced estimates of effective moisture with the Bhalme and Mooley drought index (BMDI), derived from nearby precipitation records (Figure 1). The BMDI was chosen as a measure of drought, because it is based on precipitation records from local stations, as opposed to regional precipitation averages used in some other indices, such as the Palmer Drought Severity Index. In this analysis, the BMDI was smoothed using a four-point Fourier transform filter to achieve approximately equal time resolution between the sediment record and the instrumental data. A modest correlation between diatom-inferred salinity and BMDI (Figure 1) can be attributed to several factors, including the low time resolution in core data from before 1940, the further distance of the meteorological station from the lake for the early instrumental period, and limnological changes that are potentially attributable to settlement and agricultural

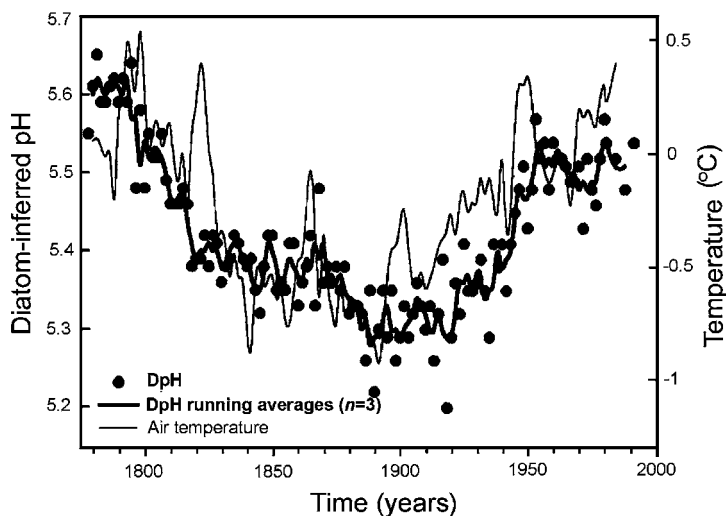


Figure 2. Diatom-inferred lake-water pH from Schwarzsee ob Sölden in the Austrian Alps since ~1780 compared with smoothed annual mean air temperature from 20 regional weather stations; $r = 0.68$, $p < 0.001$. (From Sommaruga-Wögrath et al. 1997, with permission.)

practices that may have impacted lake chemistry independent of climate since the early 1900s. Comparison of the Moon Lake record with regionally recognized climatic anomalies prior to the instrumental record (e.g., a tree-ring inferred wet period from 1825 to 1838 and the extreme 1890s drought) suggest, however, that the diatom-inferred salinity record does capture the general drought trends characteristic for the Northern Great Plains (Laird et al. 1996a, 1998a, 1998b). Consequently, this site was chosen to reconstruct drought intensity, duration, and frequency throughout the Holocene at both centennial and sub-decadal scales (Laird et al. 1996a, 1996b, 1998a, 1998b).

In a study from a mountain lake in the Austrian Alps, comparison between diatom-inferred pH and instrumental air temperature between 1778 and 1991 revealed a significant positive correlation ($r = 0.68$, $p < 0.001$) (Figure 2) (Sommaruga-Wögrath et al. 1997), suggesting that diatoms may be an important proxy of past temperatures. In two other alpine lakes, diatom-inferred pH and temperature were correlated during the entire 19th century, but the relationship weakened during the 20th century with the onset of acidic deposition (Psenner and Schmidt 1992). The mechanism that produced the pH increases during warming events and declines during cooler periods is likely to be related to changes in the duration and extent of ice-cover because these would alter light, temperature, and nutrient regimes, all of which affect diatom production and could influence in-lake production of alkalinity, as well as lake-water pH (Sommaruga-Wögrath et al. 1997). Periods of prolonged ice-cover would also reduce CO_2 exchange with the atmosphere and temporarily eliminate atmospheric inputs of base cations into the lake (Psenner and Schmidt 1992), both of which would affect the acid-base status in poorly-buffered lakes.

Bigler and Hall (2003) and Larocque and Hall (2003) compared chironomid and diatom-inferred mean-July air temperatures from northern Swedish sediment cores over the last century to measured values from nearby meteorological stations. In all four lakes studied, chironomid-inferred July temperatures were significantly but weakly correlated to the instrumental record ($r = 0.35\text{--}0.39$). The relationship between diatom-inferred and instrumental July temperatures was weaker, and no correlation coefficients or levels of significance were reported.

Many studies have validated climate proxies through a qualitative comparison of reconstructed environmental change to historically documented changes in climatically-sensitive limnological variables, an approach first used in comparisons of diatom-inferred salinity and ostracod trace-metal content with documented changes in the depth and salinity of Devils Lake (Northern Great Plains, USA) (Fritz 1990; Engstrom and Nelson 1991). One particular series of studies (Verschuren 1999a, 1999b, 2001; Verschuren et al. 1999a, 1999b, 2000a) investigated the sedimentological, geochemical, and biological signatures of climatically driven lake-level changes in a system of four contrasting lakes in the Eastern Rift Valley of Kenya, which because of their hydrological inter-connectedness have a common recorded lake-level history spanning the last 120 years (Verschuren 1996). Together these studies illustrate the complexity of chemical and biological responses to climatically-driven changes in water balance at sub-decadal time scales (Verschuren et al. 1999a, 1999b, 2000a), and how the signatures of this response in the sediment record are affected by sedimentation dynamics and taphonomy (Verschuren 1999a; Verschuren et al. 1999a). For example, although reconstructed salinity and lake-level changes in Lake Oloidien displayed the expected inverse relationship, this was modulated by delayed dilution of residual salts following a modest lake-level rise in the late 1950s and early 1960s (Figure 3) (Verschuren et al. 2000a). In nearby Lake Sonachi, diatoms quickly responded to a major 1890s lake-level rise which created stable density stratification of the water column. In the sediment record, however, their response is delayed by almost a decade because previously buried shallow-water diatoms are re-deposited in deep-water sediments during the transgression (Verschuren et al. 1999b). In the three main groups of aquatic invertebrates present (ostracods, cladocerans, chironomids), only some species responded directly to salinity change (via the physiological impact of osmotic stress). Most species responded more strongly to substrate changes associated with the lake-level change itself or to changes in the distribution of aquatic vegetation (Verschuren et al. 2000a). While lake depth, salinity, and substrate quality are all important factors in structuring aquatic invertebrate communities, it is sobering to realize that at the time-resolution of many modern paleoclimatic studies, the intuitive co-variation between these factors can be strongly modulated by transient system dynamics. None-the-less, invertebrate communities do remain useful proxies of past hydrological change, particularly in combination with diatoms and non-biological climatic proxies. Other qualitative studies (e.g., Legesse et al. 2002) have used both biological and sedimentological proxies to reveal fluctuations in water depth and salinity that are broadly consistent with available instrumental and historical records.

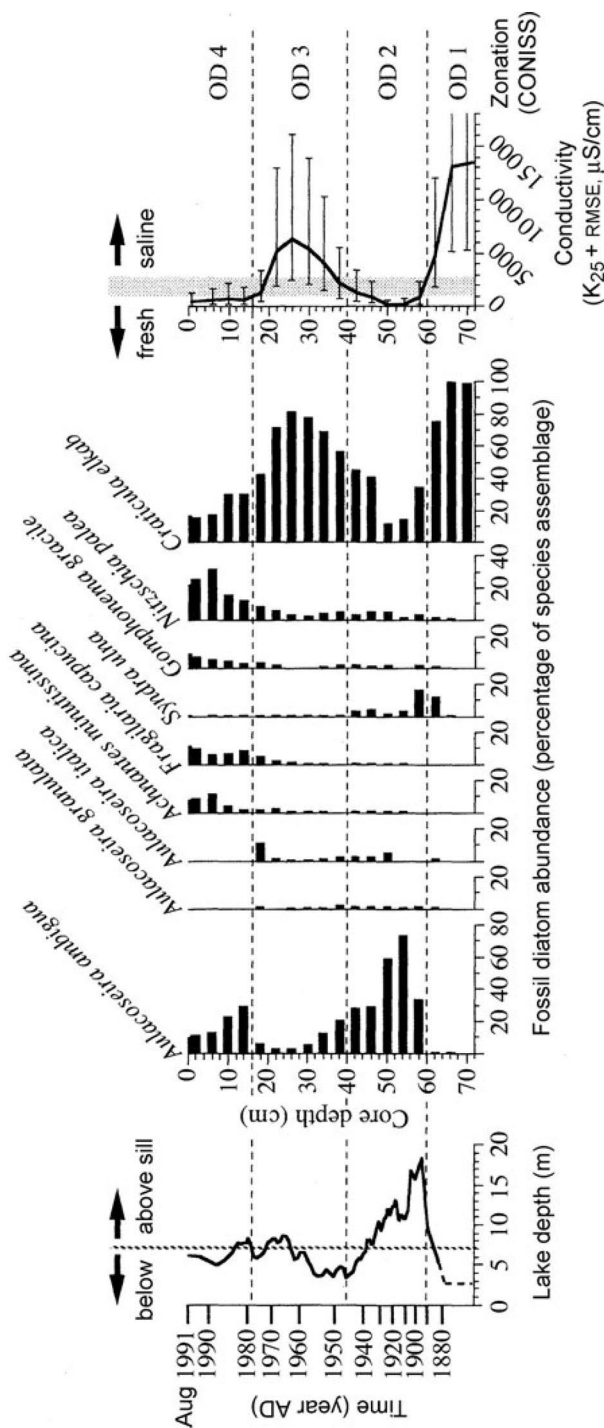


Figure 3. Changes in dominant diatom taxa and diatom-inferred conductivity in Lake Oloiden (Kenya) since ~AD 1860 compared with the instrumental lake-level record. "Below/above sill" refers to the elevation of the sill between the hydrologically-closed Lake Oloiden and the nearby hydrologically-open Lake Naivasha. When the two lakes are confluent at high lake-level (~AD 1885–1938, and much of the period 1963–1984), exchange of water between them removes dissolved salts from Lake Oloiden. (From Verschuren et al. 2000a; with permission.)

Although direct comparison of paleoclimatic reconstructions with meteorological data has yielded many valuable insights into the response of specific lakes to climatic variation, other approaches may be used. These include comparisons between the main directions of variation in fossil assemblages and instrumental climatic records (Sorvari et al. 2002), the use of variation partitioning to assess the role of climate in proxy records over the instrumental period (Lotter and Birks 1997; Hall et al. 1999; Quinlan et al. 2002), and comparisons of within-lake proxy records with independent estimates of climatic change (Anderson et al. 1996, 2008; Stager et al. 1997; Cumming et al. 2002; Wolfe 2003; Enache and Cumming 2009; Stone et al. 2011).

Direct Comparison of Biological Data to Instrumental Climatic Data

Ordination techniques (see Legendre and Birks 2012: ch. 8) are now widely used to quantify and summarize the main directions of variation in biological assemblages (Cumming and Moser 2007), which can then be correlated directly to instrumental climatic records. For example, Sorvari et al. (2002) examined the relationship between species-composition changes in the diatom communities of five lakes with varying characteristics in Finnish Lapland over the last 200 years using principal component analysis (PCA), a common ordination technique (Figure 4). The PCA sample scores from each lake record were highly correlated to each other ($r = 0.74\text{--}0.95$), as well as being significantly correlated to instrumen-

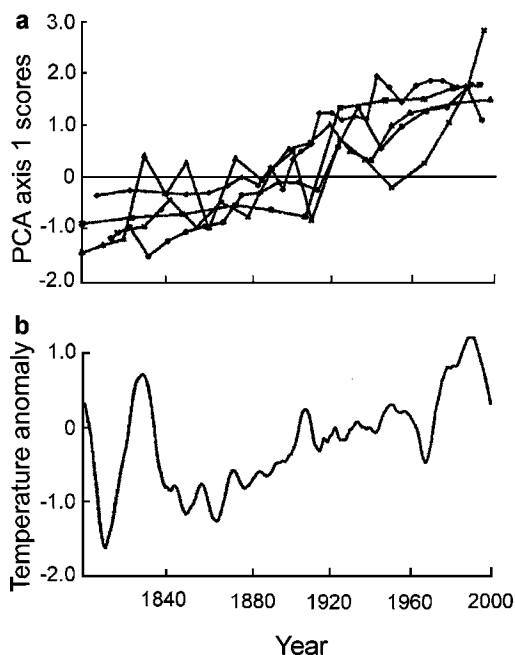


Figure 4. (a) Trends in principal component analysis (PCA) axis-1 sample scores of fossil diatom floras in five lakes from Finnish Lapland over the last 200 years in relation to (b) smoothed spring temperature anomalies ($^{\circ}\text{C}$). (Modified from Sorvari et al. 2002.)

tal records of yearly temperature ($r = 0.39\text{--}0.62$ in three of the five lakes investigated). Interestingly, the highest correlations ($r = 0.52\text{--}0.70$) were between the main direction of variation in the diatom assemblages and spring temperatures. Sorvari et al. (2002) suggested that the strong coherence of sedimentary signatures in these five lakes, and their significant correlation with temperature change over the last ~200 years, indicate that diatom floras did indeed respond to regional temperature rise, possibly through decreased ice-cover, a longer growing-season, or enhanced thermal stratification. This example illustrates that arctic as well as alpine lakes are sensitive locations to search for ecosystem changes in response to recent climatic change (Battarbee et al. 2002a; Heiri and Lotter 2005; Smol et al. 2005; Lotter et al. 2010). The response of these systems to climate is not limited to direct temperature influences, but may also include responses to changes in physical and chemical aspects of the aquatic environment, which themselves are affected by changes in temperature or precipitation. For example, such changes may include the duration of ice-cover, microhabitat availability, and changes in dissolved organic carbon (DOC) or acid-base status (Smol and Cumming 2000; Smol and Douglas 2007; Lotter et al. 2010).

In a large interdisciplinary study involving seven European high-elevation lakes, the Mountain Lake Research (MOLAR) project, researchers sought to establish links between various biotic and abiotic proxies in lake sediments and instrumental temperature records (summarized by Battarbee et al. 2002a). The biological proxy indicators included assemblages of diatoms, chrysophytes, chironomids, and cladocerans. Potential explanatory variables included: mean summer temperature (June to August and July to September), mean winter temperature (December to February), an index of continentality (difference between June to August and December to February), and mean annual temperature (average of all 12 months). Because instrumental data series directly linked to these remote high-elevation sites were not long enough for comparison with core data, homogenized lowland air-temperature records were transformed to values appropriate for each high-elevation site using the contemporary relationship between lowland temperatures and recently established on-site automatic weather stations (Agusti-Panareda and Thompson 2002). Prior to regression analysis, the variation in each of the biotic proxy data-sets was numerically reduced to its main direction of variation by calculating sample scores along PCA axes, following a square-root transformation of the species percent-abundance data. Correlations between the main direction of variation in the biological data and the instrumental records were very low, with few clear or consistent patterns. The highest correlations were found using the greatest smoothing of the instrumental data, suggesting that the biological proxy data may capture only the broadest, long-term changes in these records. Planktonic diatom assemblages (at most sites) and chrysophytes and chironomids (at a few sites) showed the highest correlation with the instrumental data (Battarbee et al. 2002b; Koinig et al. 2002). The generally weak correlations were mainly attributed to inaccurate dating and/or the limited sensitivity of some proxies to modest recent climatic forcing, as well

as confounding forcing factors, such as air pollution and earthquakes, at some sites. These results are perhaps not surprising, because different species thrive at different locations within the lake as well as at different times in the season (e.g., Interlandi et al. 1999; Bradbury et al. 2002; Catalan et al. 2002). Consequently, the use of yearly averages or average temperature in any given season will likely fail to represent accurately the ecological characteristics of some of the species to temperature. The low correlations found in this study in comparison to the five sites in Finnish Lapland may also suggest that the lakes in the MOLAR project were not as sensitive to recent climatic changes or that the degree of climatic change has been less in the MOLAR lakes in comparison to those in Lapland. Continued investigation of the response of varied proxies and European lakes to climate is ongoing in the large interdisciplinary European Millennium Project (e.g., von Gunten et al. 2008), which is focused on reconstructing regional climates of the last 1000 years.

Assessing the Influence of Climate on Lake History Using Variation Partitioning and Linear Mixed-Effects Models

Variation partitioning analysis (VPA) has been used increasingly to assess the relative influence of climate versus other factors in driving limnological changes reconstructed from the sedimentary record. Variation partitioning (Borcard et al. 1992; Legendre and Birks 2012: ch. 8; Lotter and Anderson 2012: ch. 18; Simpson and Hall 2012: ch. 19) uses direct gradient analysis or canonical ordination to estimate which fraction of the total variation in assemblage composition can be explained by specific categories of measured environmental variables, and which fraction is shared between different categories of variables. For example, Lotter (1998) used VPA to estimate the amount of variance in diatom data from a 100+-year varved sediment record from Baldeggersee (Switzerland) that could be explained independently by trophic state and climate (also see Lotter and Anderson 2012: ch. 18). The variation in the diatom data was partitioned into: (i) variation due to changes in lake trophic state only (modeled by measured and extrapolated total phosphorus, lake restoration, and their interaction); (ii) variation due to climatic change only (modeled by mean spring air temperatures); (iii) covariation between (i) and (ii); and (iv) variation unexplained by the model. Because of strong temporal autocorrelation in the data, the effect of time was removed prior to the statistical analyses. Trophic state and climate together accounted for only 14.2% of the total variation in the diatom data ($p = 0.01$), with 12.6% being explained by trophic state ($p = 0.06$), and only 1.1% by climate ($p = 0.08$). Hence, Lotter (1998) concluded that changes in climatic variables were relatively unimportant in comparison with trophic-state variables in explaining changes in the diatom assemblages. Lotter and Birks (1997) used a similar approach to disentangle the relative importance of trophic state and climate on varve thickness in the same lake. Heiri and Lotter (2005) used variance partitioning to examine the influence of co-variation between sum-

mer temperature and trophic state on calibration-function development in the Swiss Alps. Their analyses suggest that independent calibration functions can be developed for diatoms and benthic cladocerans but caution should be used in interpreting total phosphorus (TP) reconstructions from chironomids.

Hall et al. (1999) used VPA to determine how much of the down-core variation in diatom, pigment, and chironomid assemblages from Pasqua Lake (Saskatchewan, Canada) could be accounted for solely by climate (C), resource-use (R), urbanization (U), and by covariations between them (i.e., CR, CU, RU, and CRU). Hall et al. (1999) performed separate VPAs on the percent abundances of diatoms and chironomids and a 3-year running mean of pigment concentrations for periods beginning in 1890, 1920, 1950, and 1970, so that the relative importance of climate, resource-use, and urbanization on the biological records could be evaluated through time. All categories, both independently and in combination, explained significant amounts of variation in the biological data, although their relative importance depended on the fossil group and the period considered. Changes in urban population, sewage characteristics, livestock biomass, crop area, and temperature and precipitation proved to be consistently important explanatory variables in the history of this lake (Hall et al. 1999). However, the most consistently important explanatory variable was resource-use, accounting for between 14% and 25% of the variation in the fossil assemblages according to the VPAs. Variation attributable solely to climate was consistently low (between 4% and 10%), but the covariation between climate and resource-use and urbanization (CR, CU, or CRU) were typically quite large, at times accounting for more than 50% of the total variation. In a similar study from the Canadian prairies involving eight lakes, Quinlan et al. (2002) found that VPA identified climate (specifically winter temperature) as the category that accounted for the largest amount of variation in past chironomid assemblages (on average ~25%), whereas changes in resource-use and urbanization only accounted for ~7% and ~4% of variation, respectively. In summary, one of the benefits of VPA is that it potentially allows the relative importance of competing influences to be evaluated and quantified (Birks 1998).

Eggermont et al. (2010a) assessed whether the Rwenzori mountain lakes (Uganda/DR Congo) are sensitive to climate-driven environmental change of the same order of magnitude as that expected to result from current and future anthropogenic global warming. This was done by comparing the species assemblages of larval chironomid remains deposited recently in lake sediments with those deposited at the base of the short cores (dated to within or shortly after the Little Ice Age) in 16 lakes. Chironomid-based temperature reconstructions were made using temperature-inference models (Eggermont et al. 2010b) with calibration functions based on weighted averaging, weighted-averaging partial least squares, or a weighted modern analogue technique (see Juggins and Birks 2012: ch. 14; Simpson 2012: ch. 15). Excluding one atypical mid-elevation lake, Eggermont et al. (2010a) found a three-to-one ratio of sites with inferred warming against inferred cooling. The chironomid-inferred temperature changes mostly fell within the error range of the inference models, but a generalized lin-

ear mixed-effects analysis (SAS Inc. 2004; Birks 2012: ch. 11) of the combined result nevertheless indicated significantly warmer mean annual air temperature (on average $+0.38 \pm 0.11^{\circ}\text{C}$) at present compared to between ~85 and ~645 years ago. This result was independent of whether lakes were located in glaciated or non-glaciated Rwenzori catchments, and of basal core age, suggesting that at least part of the signal is due to relatively recent, anthropogenic warming.

Qualitative Validation of Biological Proxies Using Independent Evidence of Climatic Change

Support for the climatic sensitivity of lake systems is not limited to comparisons with instrumental and other historical data. Lake response to climate also can be assessed by comparisons (qualitative or quantitative) of in-lake climate-proxy indicators with other known climatic proxies. For example, Pienitz et al. (1999) assessed changes in diatom species composition in a sediment core from Queen's Lake (Northwest Territories, Canada), located north of the tree-line. Sharp increases in the abundances of black spruce (*Picea mariana*) pollen and sediment organic matter between ~5000 and 3000 years ago (Figure 5), in conjunction with isotopic changes, strongly suggested regional climatic warming during this interval (MacDonald et al. 1993; Wolfe et al. 1996). Coincident with these changes were abrupt changes in both the concentration and species composition of diatoms in the sediment profiles (Figure 5). By using a diatom-based calibration function for dissolved organic carbon (DOC), developed from a regional surface-sediment calibration-set (Pienitz et al. 1995), Pienitz et al. (1999) showed that the diatom changes were consistent with changes in lake-water transparency caused by changes in soils as trees moved into the watershed during climatic warming.

Another example of palynological data being used to support inferences of past changes in diatom species composition comes from Lake Victoria, East Africa (Stager et al. 1997). In this study, changes in diatom species composition over the last ~14,000 years were summarized into two main directions of variation by correspondence analysis (CA) (see Legendre and Birks 2012) (Figure 6). The two main directions of variation were interpreted to represent relative water column stability (or conversely mixing, an index of wind strength) and the ratio of precipitation to evaporation (or effective moisture, assumed to be reflected in lake depth) based on the known habitat requirements of the dominant diatom species found in the fossil record. In conjunction with pollen records of past changes in terrestrial vegetation within the Lake Victoria catchment from an earlier study from a nearby location (Kendall 1969), the diatom data permitted the delimitation of four major periods of limnological/climatic change over the past 14,000 years: (1) a period of aridity, from ~13,400 to 11,400 cal year. BP, represented by extremely high abundances of *Fragilaria* and other benthic diatoms coincident with the abundant occurrence of grass pollen and phytoliths; (2) an early-Holocene humid phase characterized by high abundances of

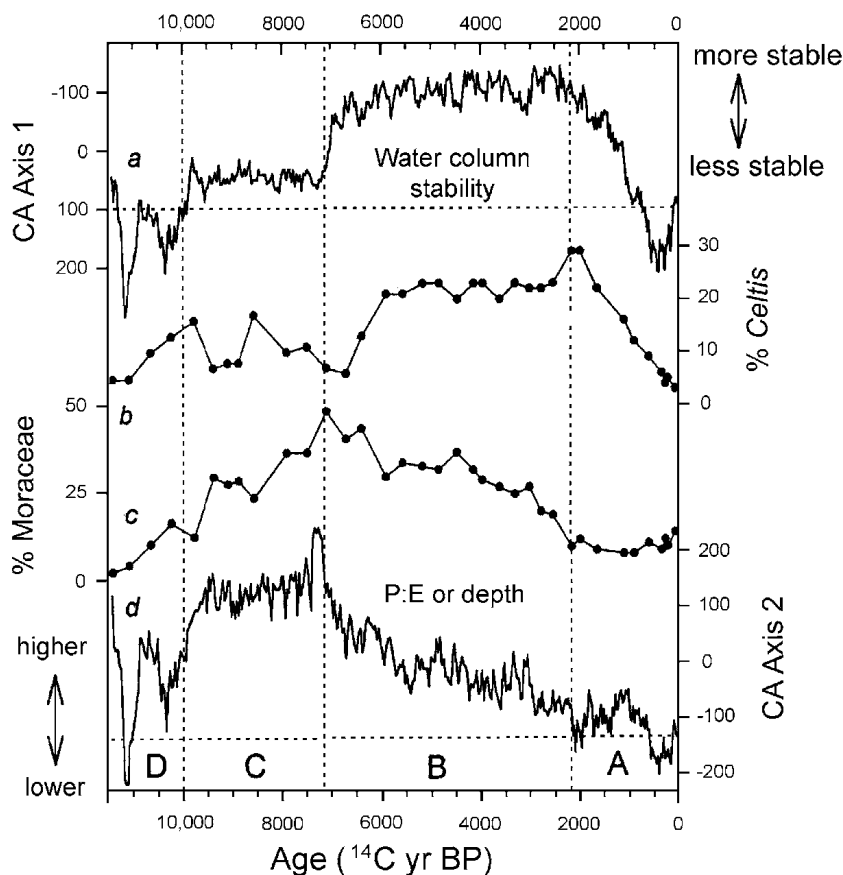


Figure 6. Trends in correspondence analysis (CA) axis-1 and -2 sample scores of fossil diatom assemblages from Lake Victoria's Damba Channel (East Africa) over the past 11,000 years, in relation to changes in the regional abundance of *Celtis* (reflecting seasonally dry forest) and *Moraceae* (reflecting moist forest) as reconstructed at a nearby location in Lake Victoria from fossil pollen. (From Stager et al. 1997, with permission.)

Aulacoseira species, that prefer well-mixed deep water, coincident with high abundances of pollen from humid forest trees (e.g., *Moraceae*); (3) a period of increased seasonality beginning ~7900 cal year BP characterized by high abundances of taxa that thrive under enhanced thermal stratification, including *A. nyassensis* and *Nitzschia* taxa, coincident with evidence of seasonally dry forests (e.g., *Celtis*); and (4) a late-Holocene period (from ~2300 cal year BP) of increasing aridity characterized by a return to higher abundances of *Fragilaria* taxa, benthic diatoms, and grasses and phytoliths (Stager et al. 1997). Virtually identical interpretations have been presented for two other cores from Lake Victoria, one from the center of the lake (Stager and Johnson 2000) and one from a shallow peripheral basin (Stager et al. 2003).

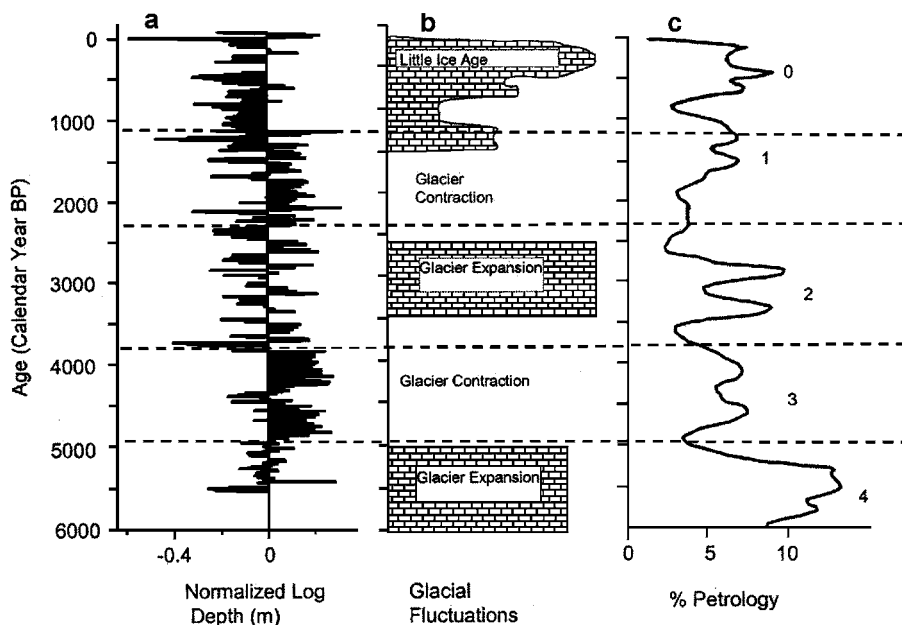


Figure 7. Relationship between (a) diatom-inferred changes in lake depth at Big Lake (British Columbia, Canada) over the past 5500 years and (b) a summary of world-wide glacial fluctuations (Denton and Karlen 1973), and (c) a composite record of ice-rafted-debris (IRD) in the North Atlantic Ocean (Bond et al. 2001). (Modified from Cumming et al. 2002.)

In a study of multi-decadal to millennium-scale climate dynamics in British Columbia (Canada) since the renewal of glacial activity ~5500 years ago, Cumming et al. (2002) recorded major shifts in diatom assemblages and diatom-inferred depth and salinity, corresponding well with millennial-scale variations in the expansion/recession of continental glaciers in the region, as well as with ice-rafting events in the North Atlantic Ocean (Figure 7). This result provides supporting evidence for the sensitivity of such lake systems to broad-scale climatic forcing. However, it has been suggested that reconstructions of lake depth from biological assemblages based on regional calibration-sets, as was done in this study (Figure 7), may need to be interpreted with caution because the specific morphometric features of the study lake may not be adequately represented by a regional reference data-set. Birks (1998) suggested that calibration models for lake depth may be best developed on the basis of surface-sediment samples from different depth transects within the lake under investigation. Laird et al. (2011) provide a summary of how quantitative techniques and selection of sensitive near-shore coring locations can be exploited to produce high-resolution paleoclimatic reconstructions. This approach can yield valuable insights, but has an increased risk of non-analogue situations, in which the dominant species in certain sections of the core profile are not represented in the local surface-sediments today. Consequently, in many instances the reconstruction of a limnological

cally important variable, such as lake depth, can benefit from modern calibration-sets that include both surface-sediment samples from within the lake under study (i.e., a transect across depth) as well as in many lakes across the modern landscape. In some cases, quantitative reconstructions of lake-level change using biotic indicators can be constrained by geophysical or geomorphic data that provide clear physical evidence of lake stage at given points in time. This approach has been used in studies of Quaternary lake-level variation in Lake Malawi in Africa (Stone et al. 2011), where a multi-proxy reconstruction of lake level was compared with seismic data; and in a comparison of diatom-inferred conductivity as a proxy for precipitation minus evapotranspiration in West Greenland with dated Holocene paleoshorelines (Aebly and Fritz 2009).

Finally, several studies from Europe have compared quantitative reconstructions of temperature with other regional reconstructions of temperature change. Korhola et al. (2002) used both a Bayesian multinomial model and a weighted-averaging partial least squares model (see Juggins and Birks 2012: ch. 14) to reconstruct temperature based on chironomid assemblages over the Holocene. The results generally agreed with inferences from the Greenland ice-cores and marine sediments, as well as with previous reconstructions from diatoms and pollen (Korhola et al. 2002). Ampel et al. (2010) used a diatom calibration-function at a site in eastern France to quantify the magnitude of summer temperature change associated with millennial events during the late Pleistocene and compared it with other proxy data from the same site, other regional records, and the patterns of variation manifested in the Greenland ice core.

Quantitative Validation of Biological Proxies Using Independent Evidence of Climatic Change

A number of studies have attempted a quantitative assessment of how much of the variation in biological climate-proxy assemblages can be attributed to climatic forcing, using ordination and partial ordination techniques including VPA. For example, in an 1100-year lake record from northern Sweden, Anderson et al. (1996) (see also Lotter and Anderson 2012: ch. 18) found a weak relationship between changes in diatom species assemblages and tree-ring inferred estimates of summer temperature. However, this relationship could only explain 5.2% of the variation in the diatom assemblages, and only after the temperature data were lagged by 20 years. Interestingly, a stronger relationship (~10% of the observed variation) was found between species richness and temperature. Other investigators have used VPA to compare the relative importance of climate and other factors contributing to changes in biological assemblages. For example, Birks and Lotter (1994) and Lotter et al. (1995) attempted to disentangle the impacts of volcanic tephra and climatic change on terrestrial and aquatic ecosystems (see Lotter and Anderson 2012: ch. 18). Similarly, Barker et al. (2000) used VPA to investigate the relative importance of climate (represented by the ratio between tree

and grass pollen), catchment disturbance (represented by magnetic properties of the sediments), and tephra deposition on a 4100-year diatom record from Lake Massoko (southern Tanzania). The effects of time-dependent ecological and environmental processes were removed by using sample age as a covariable in partial constrained ordination (see Legendre and Birks 2012: ch. 8). Anderson et al. (2008) used independent climatic data (e.g., Greenland ice-core data) to assess the degree to which climate versus in-lake processes explained the community structure of chironomids and other proxies. In this study, catchment changes or biotic relationships explained more variation than Holocene climate, with the exception of the early lake development. VPA also has been used to demonstrate that changes in land-use have been more important than climate in driving changes in the diatom flora of Seebergsee (Switzerland) over the last 2600 years (Hausmann et al. 2002). A recurring theme in many of these studies is that, although climatic forcing has accounted for a significant fraction of the reconstructed biological variation, the amount of variation explained by climate alone, over the time scales examined, has been relatively small.

Other Numerical Techniques Used in Lake-Based Studies of Climatic Change

As is clear from the material discussed above, calibration functions, ordination, and regression techniques are the methods most commonly used to track paleoclimatic signals in biological and other proxies extracted from lake sediments. Calibration functions are continually being tested and refined (e.g., Köster et al. 2004; Eggermont et al. 2006; Battarbee et al. 2008; Birks et al. 2010), and new numerical approaches continue to be developed (e.g., Racca et al. 2003; Hübener et al. 2008). Many examples of these techniques are presented above, and/or are covered in detail in Parts II–IV of this book [H.J.B. Birks, et al., eds., *Tracking Environmental Change Using Lake Sediments* (2012)]. Methods based on aquatic algae have also been summarized in Smol and Cumming (2000), as well as in more detailed accounts of paleoclimatic techniques for semi-arid regions (Bradbury 1999; Fritz 2008; Fritz et al. 2010) and arctic and alpine regions (Smol and Douglas 2007; Douglas and Smol 2010; Lotter et al. 2010). Additionally, there have been substantial developments in the application of chironomids and cladocerans as quantitative indicators of past climatic conditions (e.g., Lotter et al. 1997; Larocque et al. 2001; Korhola et al. 2002; Palmer et al. 2002; Heiri et al. 2004; von Gunten et al. 2008; Eggermont et al. 2008; Kröpelin et al. 2008). For example, Palmer et al. (2002) provided a midge-based consensus reconstruction of Holocene mean July air temperatures for southern British Columbia (Canada) based on sediment cores from four lake sites.

Although the number of lake-based quantitative paleoenvironmental reconstructions has increased rapidly in the past decade, for some time relatively little attention was given to a thorough evaluation and validation of these reconstructions (Birks 1998). This has now improved with the availability of a number of simple approaches to assess the basic reliability of environmental reconstructions (Telford and Birks 2011). For example, Laird et al. (1998a) assessed the reliability

of the Moon Lake salinity inferences over the past 2300 years (Laird et al. 1996a) (Figure 8) by (1) calculating how well a “fossil” sample is represented by modern assemblages (Figure 8b), and (2) assessing the overall “goodness-of fit” of the environmental reconstruction (Figure 8c). The lower the dissimilarity coefficient or the less often a sample is in the extreme of the distribution of the “goodness-of-fit,” the more confidence one can place in a reconstructed value, because the “fossil” assemblages are well represented in the modern data-set (Birks et al. 1990). For their paleosalinity reconstructions based on African chironomid assemblages, Verschuren et al. (2004) and Eggermont et al. (2006) additionally assessed to what extent numerical differences between calibration functions affected reconstructed salinity trends through time. Initially this was deemed necessary because, lacking a traditional calibration data-set of faunal composition based on surface-sediment assemblages, Verschuren et al. (2000b) had performed a hybrid procedure in which a weighted-averaging (WA) inference model calibrated with presence/absence distributional records from the literature was applied to abundance-weighted fossil data. This helped ensure that changes in the relative abundance between taxa, not just their new appearance or complete disappearance, would generate a proxy climatic signal. Verschuren et al. (2004) justified this hybrid procedure by proposing that calibration based on presence/absence data is not dissimilar to an abundance-weighted calibration with down-weighting of rare taxa. Using (semi-) independent paleohydrological reconstructions based on sediment stratigraphy and fossil diatom assemblages (Verschuren et al. 2000b) as a reference framework, coupled with a consideration of modern-day benthic community dynamics in shallow closed-basin African lakes, Eggermont et al. (2006) documented significant variation among calibration functions in reconstructed salinity trends, mainly reflecting their different sensitivity to the presence or relative abundance of certain key taxa. Specifically, WAPLS and maximum likelihood (ML) techniques statistically “camouflage” the step change in chironomid faunal composition near the freshwater-saline boundary, resulting in less robust reconstructions. These authors concluded that selection of the most appropriate calibration function for environmental reconstruction should not solely optimize the statistical performance of the resulting inference model, but carefully consider whether it produces ecologically meaningful reconstruction results with high signal content (see Juggins and Birks 2012: ch. 14).

Confidence in paleoclimatic inferences will also further increase as broad-scale patterns are replicated in space and time. Examples of coherence are starting to emerge at a number of sites, over different temporal and spatial scales, for example, the studies by Sorvari et al. (2002) and Palmer et al. (2002) discussed above. Similarly, several studies (Fritz et al. 2000; Yu et al. 2002; Laird et al. 2003; Schmieder et al. 2011) have presented strong evidence of synchronous changes at various sites in the Great Plains of North America over the last 1500–2000 years.

A number of studies of climatic change have begun to address ecologically interesting questions that attempt to assess changes in stability and diversity (e.g., Anderson et al. 1996; Laird et al. 1998a, 1998b; Wolfe 2003; Stone and Fritz 2006; Hobbs et al. 2010). For example, Laird et al. (1996a, 1998a) found a large switch

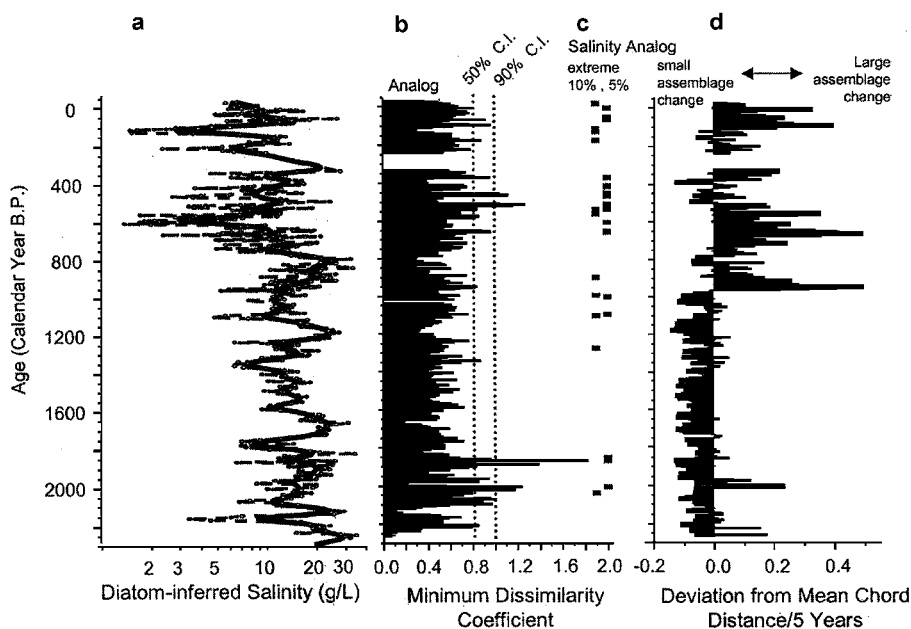


Figure 8. (a) Diatom-inferred salinity changes at Moon Lake (North Dakota, USA) over the last 2200 years. (b) Analogue analysis and (c) “goodness-of-fit” analyses based on comparisons between dissimilarities between core and modern diatom assemblages, and diagnostics from a constrained ordination, respectively (see text for details). (d) The results of a rate-of-change analysis used to assess changes in community stability. (Modified from Laird et al. 1998a.)

in inferred climatic conditions in the record from Moon Lake (North Dakota, USA) indicated by a distinct change in inferred salinity before and after AD 1200 (Figure 8a). The differences in the environmental stability of Moon Lake before and after ~AD 1200 were assessed by estimating the rate-of-change in the diatom assemblages, based on a dissimilarity coefficient between adjacent samples over a fixed time interval (see Birks 2012: ch. 11). The results of this analysis suggested that the diatom assemblages in Moon Lake were significantly more stable prior to AD 1200 (during a period of inferred prolonged aridity) than for the last ~800 years, which were relatively wet (Figure 8d). This approach has also been employed to assess changes in limnological stability between the early- and late-Holocene (Laird et al. 1998b; Clark et al. 2002), and through periods of Holocene cooling and warming (Anderson et al. 1996; Palmer et al. 2002; Wolfe 2003). Heegaard et al. (2006) used cumulative rate-of-change and cumulative relative rate-of-change to assess the detection of aquatic ecotones along an altitudinal gradient in the Swiss Alps for cladocera, chironomids, and diatoms. Assessing changes in biological richness and diversity has become a topic of renewed interest in paleolimnological studies. For example, Sorvari et al. (2002) noticed a decline in richness (estimated as Hill’s (1973) N_2 , a measure of richness of common

species) coincident with the recent inferred warming of lakes in Finnish Lapland. A significant negative correlation between diatom richness and temperature was also found in northern Sweden (Anderson et al. 1996). Conversely, Wolfe (2003) showed that richness increased following climatic deterioration from the climatic optimum, which started ~2000 years BP.

In the complex system of the Mackenzie River and Slave River delta systems, species richness and “indicator” taxa were used to distinguish between three hydrologically distinct lake types (Hay et al. 2000; Sokal et al. 2008). Ordination methods were first used to assess the distribution of diatom assemblages in the three lake categories. Sokal et al. (2008) then used analysis of similarities (ANOSIM: Clarke and Warwick 2001) to test whether the diatom assemblages differed significantly among the three lake categories in the Slave River Delta. Finally, similarity percentage tests (SIMPER: Clarke and Gorley 2006) were performed to identify specific diatom taxa that accounted for these differences and canonical variates analysis was used to assess whether “indicator” taxa significantly discriminate the hydrological lake categories (Sokal et al. 2008). These studies indicate that numerical methods can be used to assess the hydrological and climatic variability within complex delta systems.

Finally, it is becoming increasingly evident that the temporal structure of many paleolimnological records is composed of periodic components. Correct identification of these periodicities and how they vary over time is becoming increasingly important in paleolimnological studies. Aspects of this critical topic are covered in Dutilleul et al. (2012: ch. 16).

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