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Julie A. Wolin

Cleveland State University, j.wolin@csuohio.edu

Jeffrey R. Stone

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Diatoms as indicators of water-level change in freshwater lakes

JULIE A. WOLIN AND JEFFERY R. STONE

9.1 Introduction

Water-level changes result from a variety of geological, biological, and/or climatic processes. Many of these changes occur over long periods; others may be rapid or result from catastrophic events. In aquatic environments, diatoms are highly sensitive indicator organisms and their microfossils, deposited in lake sediments, can be used to infer environmental changes (Smol, 2008). Unambiguous diatom signals can be reconstructed from lakes isolated from marine or brackish waters (e.g. Fritz *et al.*, this volume; Horton & Sawai, this volume). However, in freshwater systems lake-level changes are often recorded as increases in planktonic (free-floating) diatoms – although as discussed below, interpretation of this signal should be supported by additional evidence.

In the Laurentian Great Lakes region of North America (e.g. Finkelstein & Davis, 2006; Wolfe *et al.*, 2000; Wolin, 1996) and the North Sea and Baltic regions of Europe (e.g. Digerfeldt, 1998), freshwater lake levels are commonly affected by geological processes of isostatic rebound, subsidence, and outlet incision following glaciation, and lake isolation by coastal-sediment transport (e.g. Karrow & Calkin, 1985; Larsen & Schaetzl, 2001; Lewis *et al.*, 2008).

Biological processes, such as vegetation succession, can alter drainage patterns and groundwater flow, which in turn affect water levels. As vegetation develops following glaciation, surface runoff patterns change and this can moderate water levels on a seasonal or short-term basis. Natural deposition processes of internal (autochthonous) plant and animal remains, and mineral and organic inputs from the catchment (allochthonous) result in a shallower lake over time (Wetzel, 2001). These processes are accelerated by human activities such as forest clearance, farming, and nutrient inputs (e.g. Coops *et al.*, 2003; Gaillard *et al.*, 1991; Wolin & Stoermer 2005), while dams and channelization by humans or other animals can result in rapid water-level changes.

Hydrology, however, is the most important factor controlling water level. Lake levels are a balance of moisture gains and losses. Inputs include: stream inflow, watershed runoff, groundwater inflow, and lake surface precipitation. Losses occur through stream outflow, lake surface evaporation, groundwater outflow, and, in some cases, deep seepage. Most of these hydrologic responses are associated with climatic or ecological change (e.g. Dearing, 1997).

The ability to determine past water-level changes in freshwater is particularly important for reconstructing past climate variation and developing predictive models for future climate change. Lake levels usually rise during wet periods and fall during dry phases. The magnitude of the corresponding sedimentary signal is dependent on lake type and its sensitivity to climate (some classic reviews include Richardson, 1969 and Street-Perrott & Harrison, 1985). Shallow, closed-basin lakes usually record the strongest signals, while deep open-drainage and small surface-area lakes have the weakest. Unfortunately, from a paleo-reconstruction point-of-view, freshwater (open-drainage) lakes are predominant in many regions of the world and diatom-inferred reconstructions for these lakes are more problematic. Yu & Harrison (1995) and Tarasov *et al.* (1994) compiled two of the first extensive lake-level climate-record data bases for European and northern Eurasian lakes, respectively. Many of the freshwater lake studies found in these data bases use qualitative changes in diatom communities to indicate high or low lake levels.

Several modern diatom and environmental factor data bases, useful in climate-response lake-level reconstruction, have been compiled and are available electronically through the European Diatom Database (EDDI) (Juggins, 2001) and the Diatom Paleolimnology Data Cooperative, the Academy of Natural Sciences, Philadelphia; the National Lakes Assessment diatom data base, US Environmental Protection Agency (USEPA), should be available by 2010. In many cases, human activities can alter or

obscure climatic signals present in the record (e.g. Battarbee, 2000; Heinsalu *et al.*, 2008). This is particularly true in areas where human activity has existed for centuries (Voigt *et al.*, 2008). As the following examples will indicate, with proper consideration of limitations, it is possible to reconstruct water-level changes in freshwater systems. Given the number of freshwater lakes in regions where the only hydrologic signals will be found in such sedimentary archives, it is important to utilize these records to determine the effects of past climate change, geological events, or human manipulations.

9.2 Types of diatom indicators

Water-level fluctuations result in corresponding changes in available habitat, light, chemical conditions, stratification, and mixing regimes that indirectly affect freshwater diatom communities. When lake levels are low, usually more habitat is available for taxa living attached to substrates (benthos) or aquatic vegetation (epiphytes) because a greater area of the lake bottom is exposed to sunlight. Exceptions occur in steep-sided lakes or in shallow lakes where conditions may lead to greater turbidity or productivity-driven light limitation (e.g. Jeppesen *et al.*, 2000; Vadeboncoeur *et al.*, 2008), hence, it is necessary to use multiple lines of evidence to support any diatom-inferred water-level reconstructions and exclude factors that may result in comparable signals (Digerfeldt, 1986; Smol & Cumming, 2000). Such supporting data include: sediment stratigraphy, fine-grained particle analysis, stable-isotope analysis, chemical content, charcoal, chironomids, macrofossils, pollen, and ostracodes. Wind exposure can affect thermal structure, and, in shallow lakes, this can result in a total loss of stratification (e.g. Bennion *et al.*, this volume). As nutrient and chemical concentrations increase, corresponding changes in pH occur (Fritz *et al.*, this volume).

9.2.1 Growth habit

Numerous paleolimnological studies have used the planktic-to-benthic (P:B) ratio to qualitatively infer water-level changes (e.g. Björck *et al.*, 2000 in Denmark; Bergner & Trauth, 2004; Ekblom & Stabell, 2008 in Africa; Finkelstein *et al.*, 2005 in Canada; Tarasov *et al.*, 2000; Xue *et al.*, 2003 in Asia; Tapia *et al.*, 2003 in South America). Planktonic diatoms often dominate open-water environments, while benthic diatoms, epiphytes, and tychoplankton (accidental plankton) typically dominate littoral habitats. Shallow-water conditions expand benthic habitat and macrophyte growth producing a greater percentage of benthic and epiphytic forms preserved in lake sediments.

Conversely, during deeper lake phases, benthic substrates are often reduced, producing a greater percentage of plankton preserved in the sediment. The difficulty in using growth-habit ratio to reconstruct past environments is that the same signals may be caused by other factors.

The ratio of lake size to lake depth can affect benthic productivity, and, by extension, the size of the benthic diatom community. Vadeboncoeur *et al.* (2008) modeled benthic algal productivity across lake-size gradients using published lake to depth ratios and primary production estimates. They found that the contribution of benthic periphyton to whole-lake productivity was highest in high-latitude and oligotrophic shallow lakes (mean depth <5 m), and that such productivity declined as nutrients increased. In moderate-size oligotrophic lake systems (mean depth = 5–100 m), benthic productivity contributed a substantially higher portion to whole-lake productivity, but decreased in importance with increasing nutrients. In agricultural regions, benthic productivity in eutrophic shallow lakes approaches zero as planktonic productivity increases and light limitation occurs.

In a shallow Estonian lake, Heinsalu *et al.* (2008) compared the sedimentary diatom record in a well-dated core to historic water-level fluctuations. They found close correlation of diatom growth-habit ratios with pre-eutrophication water levels, while yearly post-eutrophication water levels were only weakly or negatively correlated to percent planktonic diatoms (Figure 9.1). However, a strong correlation was found between post-eutrophication planktonic biomass and high spring water levels as short, mild winters facilitated earlier and prolonged planktonic diatom productivity.

Lake levels in early post-glacial lake sediments can be underestimated due to the abundance of benthic diatoms characteristic of nutrient-poor lakes and prolonged ice cover (Brugam *et al.*, 1998; Lotter *et al.*, this volume). In alpine and high Arctic lakes, changes in growth habit ratio and increases in *Fragilariaceae* often are indicative of ice-cover duration (Smol, 1988; Lotter & Bigler, 2000; Lotter *et al.*, this volume; Douglas and Smol, this volume). An investigation into abiotic influences on the distribution of *Fragilaria* and *Staurosira* species in oligotrophic and ultra-oligotrophic Austrian alpine lakes by Schmidt *et al.* (2004) found evidence of species size-variation with depth, in addition to depth correlation with benthic and planktonic taxa. Planktonic *Fragilaria gracilis* Østrup had longer valves in deeper lakes, a potential competitive response to increase buoyancy. Further study on the correlation between species size-variation and depth may prove useful for water-level reconstruction.

Figure 9.1 Relationship between measured water level (WL: seven-year moving average) in Lake Vörtsjärv and the percentage of planktonic forms among diatoms in the sediment-core layers over the years 1873–2002. Reprinted with kind permission from Springer Science+Business Media: *Hydrobiology*, Water level changes in a large shallow lake as reflected by the plankton: periphyton-ratio of sedimentary diatoms. Vol. 599, 2008, page 28, Heinsalu, A., Luup, H., Alliksaar, T., Nõges, P. & Nõges, T., Figure 5a. © Springer Science+Business Media B. V. 2007.

9.2.2 Diversity

Several investigators have noted an increase in diversity with increases in benthic diatom populations (e.g. Bruggam *et al.*, 1998; Moos *et al.*, 2005). Although highly dependent upon lake morphometry, as lake levels decline, planktonic species typically are replaced by a more diverse benthic community. Wolin (1996) reported increases in benthic/epiphytic diatoms in Lower Herring Lake, Michigan, as lake levels fell; however this increase did not persist during low-water periods, but was repeated as water levels rose again. Two studies on contemporary lake-level change give insight into mechanisms behind such diversity changes.

Turner *et al.* (2005) investigated the effect of lake drawdown on algal communities, and reported macrophyte diversity and cover decline with the loss of emergent vegetation and increased percentage of barren substrate as littoral area declined. An initial decrease in diatom diversity occurred following drawdown. Little change was observed in the plankton, but benthic algae declined due to disruption of habitat and loss of colonizable area. Although epiphytes were not considered separately, they could also provide an additional lake-level signal.

In Laguna de La Caldera, an oligotrophic mountain lake in the Spanish Sierra Nevada, Sánchez-Castillo *et al.* (2008) documented modern lake-level, nutrient, and diatom-community changes following a severe 10-year drought (1985–1995). In 1996, a dramatic rise in lake level (from 1.5 m to 15 m) resulted in increased bare substrate and a pulse of nutrients as

mineralization of organic matter occurred. This resulted in a drop in diatom diversity due to an initial dominance (93.3%) by a pioneering benthic species. In the following two years, benthic diversity increased as communities developed and algal nutrient utilization increased.

9.2.3 Physical and chemical environment

Other diatom signals can be present as a result of environmental conditions caused by changes in water levels. These signals often reflect physical changes related to stability of the metalimnion, susceptibility to turbulence, nutrient or thermal conditions, or changes in pH (e.g. Bradbury *et al.*, 2002). In deep-water cores from large lakes, where littoral influence is minimal, water-level fluctuations can be signalled by changes in the abundance of dominant planktonic taxa as they respond to such physical or chemical variables (e.g. Rioual *et al.*, 2007). Most studies use these signals in conjunction with some form of littoral/planktonic shifts in reconstructing lake-level change.

9.2.4 Turbulence

Diatoms associated with turbulence regimes have proved useful in lake-level reconstructions, particularly in freshwater African lakes (e.g. Stager *et al.*, 1997; Verschuren *et al.*, 2000; Bergner & Trauth, 2004; Nguetsop *et al.*, 2004; Stager *et al.*, 2005). *Aulacoseira* species are heavily silicified diatoms with high sinking rates. Their ecology requires turbulence to remain in the photic zone (e.g. Bradbury *et al.*, 2002) and they are often found in shallow eutrophic lakes in Europe (Rioual *et al.*, 2007). Increased turbulence and corresponding nutrient increases during low-water stages in a lake can favor this genus over other planktonic species.

The 15,000 year record of varved lake sediments from Elk Lake, Minnesota, is dominated by planktonic diatoms (Bradbury *et al.*, 2002). Within this community, increases in the percentage of *Aulacoseira* indicate low-water conditions during a dry prairie period between 8500 and 4000 years ago. A

combination of low-water conditions and high wind exposure provide the turbulent, high-nutrient conditions favourable to this taxon.

While turbulence is beneficial to heavy diatoms with high nutrient requirements, certain diatom species benefit from stable stratification during high-water periods in clear lakes (e.g. *Cyclotella michiganiana* Skvortzow, *Fragilaria crotonensis* Kitton). Diatoms living in the deep chlorophyll maximum (DCM) are adapted to low light and capture nutrients diffusing from the hypolimnion (Bradbury *et al.*, 2002; Fahnenstiel & Scavia, 1987). Wolin (1996) used increases in taxa associated with the DCM to infer high water levels in Lower Herring Lake, Michigan.

9.2.5 Nutrient environment

Nutrient signals in diatom assemblages are commonly used to indicate human impacts within a lake basin (*see* Hall & Smol, this volume). However, nutrient concentration also increases during low-water levels (Moos *et al.*, 2009). If one can separate anthropogenic signals, these same indicators can be useful for climatic signals. In a small eutrophic lake in Northern Ireland, diatom-inferred total phosphorus increases resulted from climatic rather than anthropogenic forcings (Rippey *et al.*, 1997). A dry period in the 1970s resulted in reduced flushing and increased nutrients due to sediment phosphorus release. In a Michigan lake, Wolin & Stoermer (2005) found a nutrient-response-related lake-level signal in *Cyclotella stelligera* (Cleve *et* Grunow) Van Heurck during a record low-water phase in the 1930s. While in Lake 239, Experimental Lakes Area increased percent abundances in the dominant planktonic *C. stelligera* was associated with higher lake levels (Laird & Cumming 2008; 2009), this may be associated with the DCM and more stable stratification. *Aulacoseira subarctica* (O. Müll.) Haworth and *F. crotonensis* were found indicative of increased nutrient conditions in Lake 239 during large-magnitude lake-level drawdown in the mid Holocene (Moos *et al.*, 2009). Verschuren *et al.* (2000) also found *Aulacoseira* responses to lake-level induced changes in nutrient and light levels in Lake Naivasha, Kenya. During deep-lake/lower-nutrient conditions *Aulacoseira ambigua* (Grunow) Simonsen was dominant while *Aulacoseira granulata* (Ehrenb.) Simonsen dominated during shallow-lake/higher-nutrient and lower-light stages.

In shallow lakes, response to water-level disturbance is often non-linear (Coops *et al.*, 2003) and can result in clear water and turbid lake phases, independent of nutrient enrichment and top-down effects. An overall decline in diatom productivity can occur during low-water phases, particularly in shallow lakes

due to light limitation in benthic communities and nutrient limitation in plankton. Nöges *et al.* (2003) found that light limitation in the plankton community affected the abundance of diatom phytoplankton during high water levels, but that light and nutrient limitations during low water resulted in a community shift from diatoms to cyanobacteria.

9.2.6 pH

Climate changes, or more precisely wetter/drier shifts, are usually inferred indirectly in paleolimnological studies from evidence for water-level changes. Complex hydrologic interactions can result in pH shifts depending on the prevailing source. In Batchawana Lake, Ontario, early work by Delorme *et al.* (1986) connected moisture changes (i.e. lake level) determined by tree pollen data with prehistoric diatom-inferred pH changes (*see* Battarbee *et al.*, this volume). Increases in humification and lower diatom-inferred pH prior to anthropogenic-induced causes were attributed to decreases in moisture, while high water levels resulted in increased circumneutral and alkaliphilous taxa (higher pH). Krabbenhoft & Webster (1995) provide mechanistic explanations for climate influence on pH. They found that during drought conditions, reduced groundwater inflow containing high base-cation concentrations (Ca^{2+} , Mg^{2+}) likely resulted in the acidification of Nevins Lake, Michigan. Increased percentages of acidophilic taxa can also indicate marginal wetland expansion during low-lake phases (e.g. Bunting *et al.*, 1997; Shkarpa, 2006).

In African lakes, diatom-inferred pH signals usually result in the opposite effect. Cation concentrations increase with drier climate, raising pH (e.g. Bergner & Trauth, 2004; Fritz *et al.*, this volume). In the rainforest region of Cameroon, West Africa, Nguéstop *et al.* (2004) found a more complex interaction in Lake Ossa where the pH of prevailing hydrological sources determined the dominant diatom community. During the rainy season, hydrology is dominated by low-pH precipitation (~5 to 6.8) and acidiphilic (low-pH) diatom taxa prevail. During the dry season, alkalinity and pH increase in the deepest regions of the lake with increased evaporation, but low-pH groundwater and wetland discharge maintain low-pH conditions (<7) in littoral regions. Quantitative lake-level reconstructions were based on growth-habit ratios and diatom-inferred pH.

9.3 Quantitative reconstructions

Diatom/depth distribution studies, such as Round's (1961) pioneering work in the English Lake District, remain uncommon.

Figure 9.2 Relative abundance (%) of diatom life forms from surficial sediment samples collected along depth gradients in (a) Lake Ontario, and (b) East Lake (Yang & Duthie 1995).

The development of quantitative models for freshwater diatom-inferred lake-level change has increased since the publication of Wolin & Duthie (1999). New modeling techniques provide greater insight for interpreting changes in P:B diatom signals (Stone & Fritz, 2004) and researchers have increasingly focused on quantitative methods to successfully reconstruct lake-level changes (e.g. Laird & Cumming, 2008, Moser *et al.*, 2000; Nguetop *et al.*, 2004; Rioual *et al.*, 2007).

9.3.1 Regression

Early development of quantitative diatom-inferred depth models relied on regression to determine correlations between diatoms and depth. In most cases, taxa were subjectively assigned growth-habit categories based on the literature. In the North American Great Lakes, researchers (e.g. Stevenson & Stoermer, 1981; Kingston *et al.*, 1983) quantified benthic diatom distributions along depth transects in Lake Michigan. Yang & Duthie (1995) explored the distribution of euplanktonic, tycho planktonic, epiphytic, and benthic life forms in transects along a 240 m depth gradient in western Lake Ontario, and an 8 m depth gradient in East Lake, an isolated embayment (Figure 9.2). Multiple regression was used to explore the relationship between measured water depth of surface samples and sample life-form composition. Strong relationships were found in both

lakes, though the stronger relationship in Lake Ontario was probably due to its greater depth, distance from the shoreline of the deeper samples, and a larger number of samples. The main problem with this approach was the subjectivity involved in the assignment of diatom taxa to life-form categories. Category assignments for each taxon were based on literature references and not all references agreed on life-form designations. Barker *et al.* (1994) developed an early quantitative model in Lake Sidi Ali, Morocco, from depth-transect surface samples using pre-assigned habitat types: planktonic, tycho planktonic, and littoral. They found a logarithmic relationship between depth (D) and the planktonic/littoral ratio (P/L); however, the literature-based growth-habit classification proved problematic in certain taxa (i.e. *Fragilaria*).

9.3.2 Ordination

Several researchers have continued the initial work of Lotter (1988) and Barker *et al.* (1994) using ordination methods (see Birks, this volume) to analyze contemporary diatom communities along surface-sediment depth transects, and identify depth-specific assemblages (e.g. Rautio *et al.*, 2000). These assemblages have then been correlated to subfossil assemblages in cores and used to infer water depth (Lotter, 1988). In Lake Ossa, Cameroon, Nguetop *et al.* (2004) reconstructed high and low lake levels using correspondence analysis (CA) of 74 modern diatom samples from local lakes to determine depth-defined assemblages.

Figure 9.3 Diatom-inferred depth for each of the five gravity cores taken from depths ranging between 7 and 30 m. Vertical lines indicate present-day depth at the respective coring sites. Gray bars indicate drought intervals. Solid circles indicate ^{210}Pb chronology, solid squares indicate ^{14}C dating. Zones are based on a constrained cluster analysis of diatom assemblage data. (Reprinted from *Journal of Paleolimnology*, Vol. 42, 2009, Laird, K. R. & Cumming, B. F., Diatom-inferred lake level from near-shore cores in a drainage lake from the Experimental Lakes Area, northwestern Ontario, Canada., Fig. 5, page 72, © 2008 with permission from Elsevier.)

9.3.3 Weighted-averaging analysis

The optimum abundance of a diatom along a depth or other environmental gradient such as temperature, pH, or nutrient status can be determined by weighted-averaging (WA) analysis (Birks, this volume). Yang & Duthie (1995) were the first to use WA analysis to determine optimum water depths for freshwater diatom species and develop training sets for lake-level reconstruction. Duthie *et al.* (1996) then applied this training set to reconstruct lake-level fluctuations in Hamilton Harbor, Lake Ontario. Yang & Duthie (1995) cautioned, however, that WA can underestimate high levels and overestimate low levels. This trend, reported by other researchers (e.g. Brugam *et al.*, 1998), is attributed to functional interactions among different environmental variables not accounted for by simple inferences (Birks, this volume).

Two primary approaches have been used in developing training sets for freshwater lake-level reconstruction. One is to construct training sets from multiple depths across a small number of regionally close lakes (e.g. Brugam *et al.*, 1998) or from larger sets covering a greater lake size and geographic expanse (e.g.

Moser *et al.*, 2000). The other is to construct lake-specific training sets (e.g. Barker *et al.*, 1994; Moos *et al.*, 2005; Laird & Cumming, 2008, 2009).

9.3.4 Photic zone and diatom habitat availability

Multiple authors sampling surface sediments along depth transects from the near shore to deep environs have observed a rapid transition zone where benthic diatoms dominate, and above which planktonic diatom deposition increases (see Figure 9.3) (e.g. Brugam *et al.*, 1998; Rautio *et al.*, 2000; Moos *et al.*, 2005; Punning & Puusepp, 2007; Laird & Cumming, 2008, 2009). Moos *et al.* (2005) found this corresponded to the region of 1% incident-light penetration and proposed this near-shore location should be the most sensitive for constructing lake-level inferences. Subsequent studies indicate that nearshore cores can provide such sensitive records (Laird & Cumming, 2008; Laird & Cumming, 2009). Several authors have emphasized the necessity of understanding light regime and habitat availability when using benthic and planktonic ratios as proxies for lake-level change. Early work by Earle *et al.* (1988), investigating patterns in sedimentary diatoms of three morphometrically different Canadian lakes, concluded that spatial heterogeneity in sample composition was a function of both water depth and basin morphometry (Figure 9.3).

The shape of a lake basin can have a profound influence on the habitat area available for diatom growth. Stone & Fritz (2004) explored this relationship by developing a three-dimensional modeling technique that calculated incremental changes in physical parameters of a lake (e.g. volume, planar

Figure 9.4 Modeling of available diatom habitat areas; modified from Stone & Fritz (2004). (a) A bathymetric map of Foy Lake, Montana (contour interval = 20 feet/6.1 m); the star indicates where core was taken. (b) Modeled changes in ratio of available diatom habitat area with depth at Foy Lake; the arrow indicates a benthic “notch”, marking a rapid transition between available planktonic and benthic diatom habitat areas. (c) Percent abundance of benthic diatoms from sediment archives of Foy Lake; the arrows indicate spikes in the percentage of benthic diatoms related to specific lake elevations based on modeled changes in available diatom habitat areas.

surface area, lake bottom surface area) based on bathymetric and topographic maps of the basin and surrounding catchment (Figure 9.4a). Once these parameters were established for a given depth interval, the diatom habitat area available for planktonic and benthic diatom growth were calculated by making a few assumptions. The total planar surface area (water–air interface) greater than a depth of 1.5 m was used to estimate the available planktonic habitat area. Because benthic diatom habitat requires sunlight and a substrate, the total area available for benthic diatom production was estimated by calculating the surface area of the basin (sediment–water interface) exposed to sunlight, under different values of light penetration. Then, for all discrete potential lake elevations, available

planktonic to benthic diatom habitat area ratios were estimated (Figure 9.4b).

Modeled diatom habitat area ratios are probably not directly comparable to ratios of planktonic and benthic diatoms from sedimentary archives; however, they can provide context for changes observed in P:B in the sedimentary record. In lake systems with complex bathymetry, as in Foy Lake (Stone & Fritz, 2004), P:B from sedimentary archives probably was a better indicator of mean lake depth than maximum lake depth. At some lake-surface elevations, a small change in lake level has the potential to produce a dramatic shift in relative ratio of available planktonic and benthic diatom habitat area. Rapid transitions appear as spikes or notches in the curve of modeled habitat availability with depth (Figure 9.4b) and represent a sharp break in basin slope, or a decoupling of mean depth from maximum depth. These transitions have the potential to produce “counter-intuitive” responses in diatom P:B in fossil sediments. By creating a sudden increase or decrease in the available habitat area for benthic diatom growth, rising lake levels could potentially increase the available benthic habitat area and lower the P:B. Conversely, a small drop in lake level has the potential to substantially decrease the available benthic habitat area, producing an increase in P:B, potentially

confounding the standard interpretation of P:B in lake-level reconstructions.

Interestingly, in systems where rapid transitions occur, they can also provide a useful indicator of past lake level. Because spikes or notches in the modeled habitat area profile are tied to specific depths, when lake-level changes pass through these depths, a substantial change in P:B is likely to be observed in the sediment archives (Figure 9.4c). Well-constrained reconstruction of paleoclimate from fossil diatom assemblages in any lake system should incorporate an explicit consideration of lake-basin shape and how available planktonic and benthic habitat areas change with lake level; this is particularly true for lakes with complex bathymetry.

9.4 Applications of diatom-inferred depth changes in lakes

Ideally, the most sensitive signals of shoreline and water-level change will be found in marginal lake sediments that provide a sharp transition between planktonic and benthic assemblages (e.g. Battarbee, 2000; Digerfeldt, 1998). A multicore approach sampled along a depth gradient (e.g. Digerfeldt, 1998) should provide a stronger P:B response signal than that found in a single deepwater core. Models constructed from multiple lakes are not always as sensitive due to interactions between diatoms, habitat, and light availability and lake-specific training sets can produce a stronger, more applicable predictive model in many cases, from which robust diatom-inferred reconstructions can be made (Laird & Cumming 2008, 2009). Unfortunately, appropriate marginal lake sediments are not always present in lakes, nor is it always feasible to take multiple transects when constructing multilake training sets. Significant diatom–depth relationships with high predictive ability have been developed from multilake training sets based on single deepwater cores (Brugam *et al.*, 1998; Moser *et al.*, 2000; Rioual *et al.*, 2007), but again, these must be interpreted in relationship to the additional factors that influence P:B ratios.

9.4.1 Lake-specific quantitative modeling

Laird & Cumming (2008) used multiple lines of evidence (fossil diatoms, scaled chrysophyte:diatom valve ratio and percent organic matter) to reconstruct past lake levels in Lake 239, Experimental Lakes Area (ELA), Ontario, Canada. Lake 239 was selected due to its predicted sensitivity to lake-level change based on size, depth, and catchment to lake area ratios (Dearing, 1997). Diatom species data from surface-sample depth transects (Moos *et al.*, 2005) and additional samples were used to develop a quantitative depth model. This model was based

on the modern analogue technique (MAT) (Birks, this volume; Juggins, 2007) because the relationship between diatoms and depth was not linear. Although the model was developed from samples at depths ~ 2 to 32 m, it performed best when estimating depths less than ~ 10 –12 m, due to the predominance of *C. stelligera* in the deeper samples. Diatom-inferred depths identified two periods of climate-driven low lake-level declines of 1–3 m during the late Holocene and ≥ 8 m during the arid mid Holocene. An extended period of high lake levels in the late Holocene was not adequately quantified with single-core analysis, however Laird & Cumming (2009) were later able to quantify the high lake-level stands using multiple-core analysis.

9.4.2 Multi-lake quantitative modeling

Rioual *et al.* (2007) provide an excellent example of freshwater diatom–inferred depth in their high-resolution quantitative climate reconstruction from fossil Eemian lake deposits in the French Massif Central (Figure 9.5). Using the extensive EDDI (Juggins, 2001), they established transfer functions for six environmental variables, including maximum depth, based on modern data from 351 European lakes. Water levels were reconstructed using the locally weighted-averaging technique (Juggins, 2001) which generates a “local” training set for each sample based on the 30 closest analogs in the data base. Diatom-inferred chemical variables (i.e. nutrients, silica, conductivity, pH) were compared with diatom-inferred maximum depth, autecology of major diatom taxa, and pollen data to identify three main climate phases during the Eemian interglacial; an early climatic optimum (~ 8000 years), a cooler wetter period (~ 7000 years) and a final warming (~ 2000 years). Rioual *et al.* (2007) clearly demonstrate that detailed information on long-term climate can be obtained through the application of freshwater diatom-inferred depth reconstructions in conjunction with other environmental variables.

9.5 Summary

The ability to determine water-level changes in freshwater systems is an important tool for use in reconstructing past climate and predicting future climate change, and in geologic and environmental studies. Although complex interactions affect diatom signals in freshwater lakes, multiple responses can be utilized to quantitatively reconstruct water levels from freshwater diatom assemblages. Growth-habit changes based on depth distributions (i.e. benthic *vs.* planktonic) produce the most reliable evidence of water-level change. Autecological diatom response signals to changes in the physical–chemical

Figure 9.5 Diatom-based reconstructions for the whole sequence. The error bars correspond to specific errors of prediction calibrated under bootstrap cross-validation (Birks *et al.*, 1990). (Reprinted from *Quaternary Science Reviews*, Vol. 26, 2007, Rioual, P., Andrieu-Ponel, V., de Beaulieu, J.-L., Reille, M., Svobodova, H. & Battarbee, R. W., Diatom responses to limnological and climatic changes at Ribains maar (French Massif Central) during the Eemian and early Würm. Fig. 8, page 1568. © 2007 with permission from Elsevier.)

environment can also be used. The development of quantitative diatom-inferred depth models to reconstruct water level in freshwater systems has greatly improved our understanding of past climatic and environmental change. However, it must be emphasized that depth reconstructions from freshwater diatom data should be implemented with caution. Many of the authors cited have stressed the importance of understanding the system under investigation and use of independent corroborating evidence before valid reconstructions can be made. The diatom signals observed are open to alternative interpretations. This difficulty is partly responsible for the few quantitative reconstructions found in freshwater systems. Increased efforts with more nearshore and multiple-core analysis are needed to strengthen the interpretation of the diatom data, and more diatom–depth calibration studies are needed, as well as investigations of diatom nutrient, light, and temperature interactions in relation to depth. We still lack large regional data bases for many freshwater lake regions and these should include lake depth. Diatom-inferred water-level reconstructions from multiple lakes can then be combined into regional climate reconstructions (Digerfeldt, 1998) and regional data assembled into wider-ranging continental reconstructions (e.g. Harrison *et al.*, 1996).

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