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Three-dimensional modeling of lacustrine diatom habitat areas: Improving paleolimnological interpretation of planktic : benthic ratios

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Abstract

Three-dimensional modeling of lake morphometry enables the calculation of lake volume, planar surface area, and basin surface area, which are critical components of a conceptual model of how planktic and benthic habitat areas change with changing lake level. We have applied three-dimensional modeling to Foy Lake, Montana, and compared model results of changing ratios of planktic and benthic habitat areas at all possible lake levels to sediment cores recovered from the lake. The model allows us to produce semiquantitative depth reconstructions and greatly improves lake-level reconstruction of this morphometrically complex basin. The conceptual model also was modified to examine the influence of resuspension versus gravity redistribution of diatomaceous material on the sedimentary record. Comparison of the model results with both long and short sedimentary records from Foy Lake, Montana, suggests that planktic : benthic ratios may be a better predictor of mean lake depth than maximum lake depth. The model developed here is simple enough to be easily implemented, has few requirements, can be adapted to suit any lake basin, and can be augmented to examine a variety of different lake processes that affect habitat availability.

The hydrologic response of lakes to climate change varies dependent upon the hydrologic, geomorphic, and climatologic setting of a given lake basin (Almendinger 1990). Regional changes in effective moisture (precipitation minus evapotranspiration) can increase or decrease lake level, altering lake chemistry and the lake surface area to volume ratio (Allen and Anderson 1993; Mason et al. 1994; Wolin and Duthie 1999). Evidence of long-term hydroclimatic variation is apparent in sedimentary records, although the interpretation of past climate from sedimentary signals is often complicated by internal and external factors (Fritz 1996; Dearing 1997; Wolin and Duthie 1999).

Lake-level variations cause an immediate change in environment for lake organisms, particularly benthic (attached) organisms with a limited capacity to adjust to lake-level variations (Hoagland and Peterson 1990). Fossil diatoms have been used frequently to reconstruct past lake-level change because of the sensitivity of diatoms to lake conditions, their widespread distribution, and the common preservation of diatoms in sedimentary records. Many lake-level reconstructions based on fossil diatoms have used the ratio of planktic (free floating) to benthic frustules in lake sediment. Such reconstructions are most robust when there is supporting evidence for lake-level change, such as sediment stratigraphy, isotope or other geochemical analysis, or coincident changes in other fossil remains (Fritz 1996; Wolin and Duthie 1999).

The underlying premise of the planktic to benthic ratio is that benthic diatoms are most common in shallower water where light penetration reaches the sediment–water interface (Fig. 1). Thus, benthic diatoms are deposited primarily in sediments nearer to shore, while planktic organisms contribute cells to the sediment surface below all open-water areas (Wolin and Duthie 1999). However, sediment and associated organisms produced in littoral habitats typically are not retained in these environments because sediments are redistributed by turbulence and slope (gravity) to ''focus'' dense materials to the deepest parts of the lake (Davis 1968; Hilton 1985; Blais and Kalff 1995). Subsequent mixing of sediments from both littoral and pelagic environments produces a gradient from sediments dominated by benthic organisms to planktic-dominated sediments as lake depth increases, in lakes with sufficient depth and nutrients to sustain a robust planktic community (Meriläinen 1971; Anderson 1989).

Particularly in closed-basin lakes without a surface outflow, water levels are rarely static from year to year, and variations in lake level can change the proximity of littoral habitats to the deepest parts of a lake. Thus, as a lake shallows, benthic habitats may increasingly encroach into regions that were previously dominated by sedimentation of planktic diatoms, thereby changing the ratio of planktic to benthic diatoms in the sediments. Effectively, decreasing lake-level shortens the transport distance from littoral habitats to the deepest regions of the lake, coupled with a reduction in area suitably deep for planktic diatoms. The combined effect may result in a decrease in the planktic to benthic (P : B) ratio of diatom frustules in deep-water lake sediments (Wolin and Duthie 1999). The converse effect generally results as lake levels increase.

Acknowledgments

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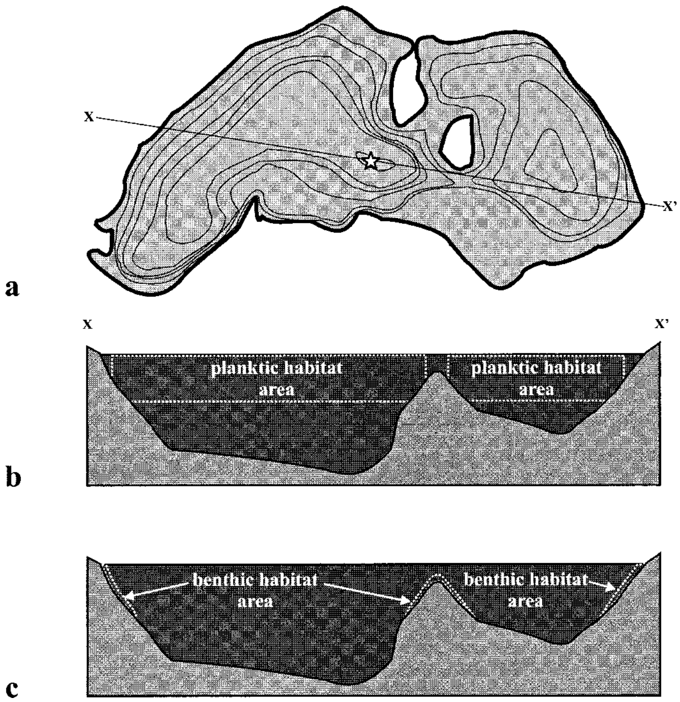

Fig. 1. Conceptual view of planktic and benthic habitat areas of Foy Lake, Montana. (a) A bathymetric map of Foy Lake; the star indicates the deepest point, coincident with the location of sediment core recovery; x–x' is a cross-section used to create the profiles in the figure. (b, c) Transects in profile of the conceptual planktic and benthic areas (respectively) of abundant diatom production.

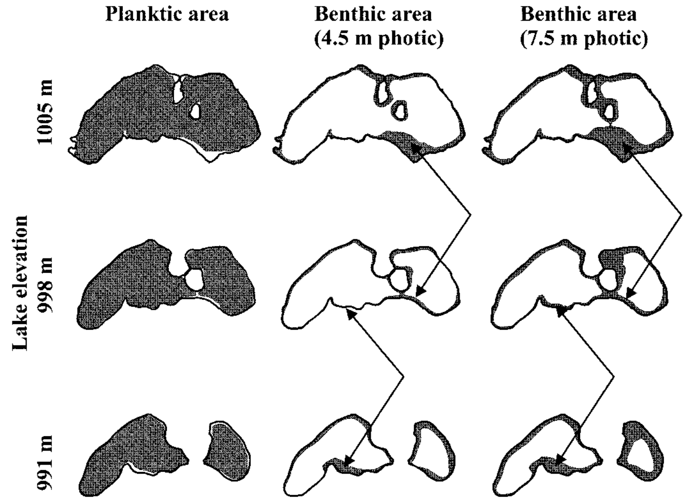

Fig. 2. Models of Foy Lake in map view showing the planar surface area of planktic and benthic diatom habitat areas at three different lake-level elevations. Gray areas indicate the extent of the habitat available at each lake elevation for both planktic and benthic diatoms under different photic penetration regimes. Arrows indicate regions of the lake margin where benthic diatom habitat area is expanded or contracted greatly under different lake-level elevations. Note that benthic habitat areas can increase or decrease throughout the lake with decreasing lake-level elevations.

In lakes with relatively simple bathymetry, it often is assumed that this straightforward model relating P : B ratios and lake level is robust and can allow researchers to reconstruct past changes in lake depth from changes in diatom abundance in sediment cores. Conceptually, the P : B technique is simplistic and is often applied without examining the lake basin morphometry or the nature of available habitat for benthic diatoms within a lake. Strict application of the P : B ratio technique to lake sediment cores provides little quantitative context for specific lake-level changes, unless it is coupled with statistical analyses of diatom abundance along depth transects in the modern lake system (Brugam et al. 1998).

Other factors not related to lake depth also may play a role in the relationship between planktic and benthic diatom growth and, hence, affect P : B ratios without an accompanying change in the lake level (Dearing 1997). Benthic diatom habitats in lakes include aquatic macrophytes, which can be affected by changes in the penetration of photosynthetically active radiation (PAR), ultraviolet (UV) radiation, and nutrient supply independent of changes in lake depth. Water clarity, which affects the habitat available for growth of both planktic and benthic diatoms, also may be affected by both internal and external factors that may not be directly related to changes in lake depth, such as food web interactions, changes in nutrient supply, variations in turbulence, and changes in the dissolved oxygen concentration (Dearing 1997; Wolin and Duthie 1999).

In lake basins with more complex bathymetry, changes in P : B ratios may be less routinely diagnostic because littoral habitat areas can change nonlinearly with lake depth. In lakes with a complex morphometry, the habitat area available for benthic production may *increase* or *decrease* with increasing lake levels (Fig. 2). This nonlinearity can be expressed as a decoupling between maximum and mean depths of a lake, such that an increase in lake level for a lake mantled by a wide low-angle slope will produce a decrease in the mean depth (net surface area increases more rapidly than net volume) concomitant with an increase in the maximum depth. The fact that benthic habitat areas may expand while lake levels increase suggests that P : B ratios may be a better predictor of *mean lake depth* than *maximum lake depth.* The latter is the way this technique is commonly applied.

Here, we demonstrate how lake-level variation can produce nonlinear changes in habitat availability, and we argue that this complex response must be considered explicitly in interpretations of paleolimnological data. We have generated a three-dimensional model of a complex lake basin (Foy Lake, Montana) from a bathymetric and topographic map of the lake and lake catchment. The model allows us to calculate changes in physical parameters of the lake (e.g., volume, surface area, basin surface area) at all possible lake levels. Modeling these parameters allows for the calculation of potential changes in planktic and benthic habitat areas that are directly related to changes in lake depth, based on conceptual limits to diatom growth in both habitats. From model output, we isolate depths at which lake-level change produces the most dramatic shifts in available diatom habitats. These results are then compared with P : B diatom ratios recovered from a short-core from Foy Lake that spans the last century and historical records of changing climate in the region near the lake in order to test the efficacy of model output in elucidating the lake-level response to climate change.

The modeling technique we employed includes two different modes of sediment focusing: gravity-type (slope driven) focusing and resuspension-type focusing. The model of gravity-driven sediment focusing presents a case for local redistribution of sediment, while the resuspension model presents a case for redistribution of sediment from throughout the lake basin. In this study, we also attempt to determine which type of sediment redistribution may be the dominant mode in Foy Lake, based upon the nature of changes observed in the P : B diatom ratios.

Methods

A bathymetric contour map of Foy Lake, Montana (48°17′N, 114°36′W) was imported into Surfer 7.0 (Golden Software, 1999) to produce three-dimensional graphical images and to calculate volume, lake-basin (sediment–water) surface areas, and planar (water–air) surface areas. The digitized contour map data were then gridded (equidistant X and Y grid spacing of approximately 4.5 m), using a triangulation with linear interpolation method; Z data components were gridded with ~0.3-m contour intervals throughout the full depth of the lake (approximately 42 m). Mean lake depth was calculated by dividing the lake volume at a given depth by its surface area for that depth. Volumes for each contour interval were calculated using Surfer 7.0, which averages the values from three estimation techniques (trapezoidal rule, Simpson's rule, and Simpson's 3/8th rule), with an average relative error of approximately 0.02% between the three techniques. Values for planar surface area and bottom surface area for each contour interval also were calculated within Surfer 7.0, using the equation for calculating the area of a polygon with n vertices (where x and y are coordinates in Cartesian space):

$$1/2 \sum_{i=1}^{n} (x_i y_{i+1} - x_{i+1} y_i)$$

Available planktic habitat area—Commonly, planktic diatom communities do not develop fully in water shallower than approximately 1.8 m (Bradbury and Winter 1976; Haworth 1979). Hence, our model uses a minimum depth of 1.8 m for planktic diatom habitat area. To estimate the available planktic habitat area, the total planar surface area of contours where the lake is deeper than 1.8 m was calculated. In the model, the lake level was artificially lowered by one vertical grid step (~0.3 m), and an available planktic habitat area was calculated for the new lake-surface elevation. This process was repeated for each vertical grid step lower than modern lake level (roughly coincident with the maximum possible depth of the lake) to the base of the lake basin. Because phytoplankton are capable of effectively absorbing and deflecting light, self-shading (Garcia-Pichel 1994) probably limits the vertical extent of available planktic diatom habitat in such a fashion that using a planar area to estimate the total available planktic habitat area throughout the photic zone at each grid step is not unreasonable.

Available benthic habitat area—Benthic diatom habitat areas are delimited by the maximum penetration of light into the water column and the presence of a substrate to which the algae can attach; thus, any reasonable estimation of benthic diatom habitat areas requires the calculation of both a surface area and a depth at which benthic diatom production is possible (photic penetration depth). In our model, a simple minimum estimate of the total basin surface area of the lake was calculated for each vertical grid step based upon the bathymetric contour map. Depths of photic penetration sufficient for photosynthesis were generated for the model from winter (through ice) and summer Secchi-disc depth measurements at the lake. Sampling of benthic diatoms during summer months demonstrated that abundant benthic diatom productivity extended to depths of approximately 9 m. In the model, four maximum photic penetration depths were used to calculate the available benthic diatom habitat area, ranging from 3 to 9 m. Based on measured values of light penetration, this range is representative of the typical seasonal range at Foy Lake for photic penetration capable of supporting abundant benthic diatoms.

To calculate available benthic diatom habitat area, the total basin surface area (water–sediment interface only) was calculated from the modern lake surface down to the maximum depth estimated for sufficient photic penetration. After the total surface area was calculated for the modern lake level, lake level was lowered one vertical grid step, and benthic habitat area was recalculated for the new lake-surface elevation. In this fashion, separate benthic diatom habitat areas were calculated for each of the four photic penetration depths at each vertical grid step from the modern lake surface to the base level of the lake.

Sediment coring and diatom analyses—To compare predicted model results with actual P : B diatom ratios from Foy Lake, a frozen sediment core of the uppermost sediments, as well as a piston core spanning the entire lake history, were recovered in February 2000 from the deepest region. Regularly varved lake sediments throughout the first half-meter allowed for sampling of the freeze core at annual intervals. The annual nature of sediment varves was independently verified using lead-210 analysis (Appleby and Oldfield 1978). The piston core was dated using a combination of varve analysis and ^{14}C dating and subsequently sampled at 5- to 7-yr intervals. Diatoms were extracted and mounted in Naphrax for light-microscope analyses using standard preparation techniques (Battarbee 1986). A minimum of 300 diatoms was identified and counted at each level.

Model modifications—The result of the simple model is a ratio of available planktic and benthic habitat areas for every potential water level in a lake basin. In small well-mixed lakes, where sediments are regularly resuspended by wave action, currents, or seasonal overturn, the calculation of available habitat areas probably does a reasonable job of predicting the relationship between the diatom assemblage recovered and the mean lake depth from a sediment core (Lehman 1975; Davis and Ford 1982; Hilton 1985). At Foy Lake, however, the basin morphology is such that after the lake level lowers several meters, the lake divides into two

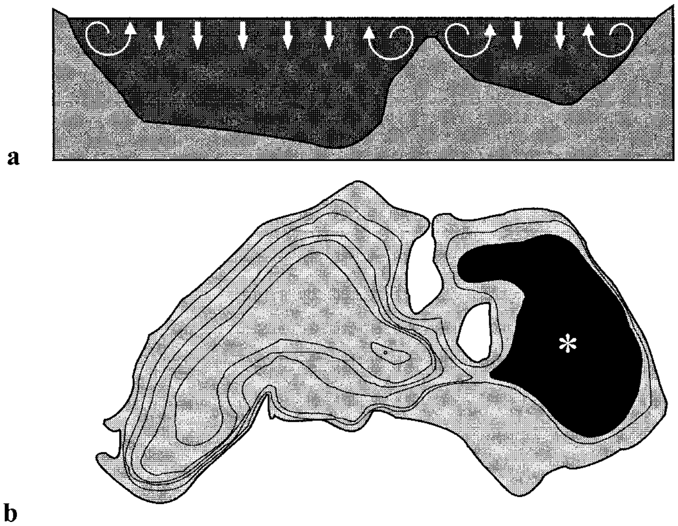

Fig. 3. The model for resuspension sediment focusing used in Foy Lake. (a) Conceptual model of resuspension and redistribution of sedimentary diatoms; downward directed arrows indicate gravity settling, reflexed arrows indicate resuspension of material in shallow water. (b) A map view of Foy Lake. The darkened region, marked with an asterisk, becomes isolated from the main basin when lake levels are lowered and was ignored in this model because it cannot contribute sediment to the deeper basin.

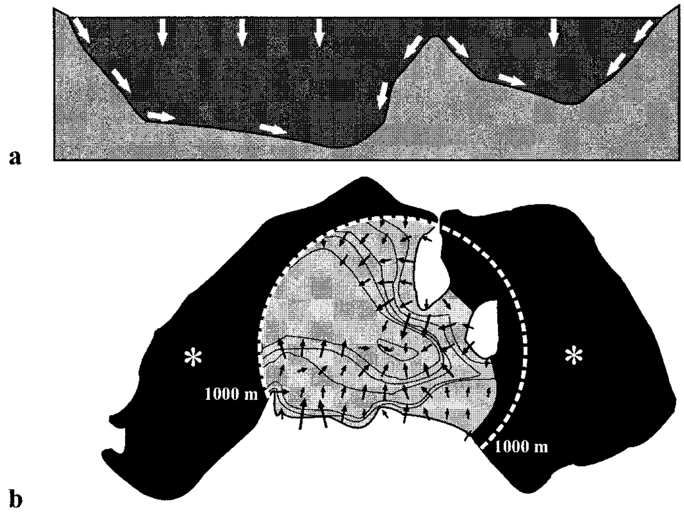

Fig. 4. The model for gravity-driven sediment focusing used in Foy Lake. (a) Conceptual model of downslope sedimentary diatom frustule movement. Arrows along the sediment–water interface indicate the downslope direction of particle movement from gravity; arrows located in open water indicate gravity settling. (b) A map view of Foy Lake. Vector arrows indicate the direction and steepness of slope of the lake basin. Darkened regions of the lake, marked with an asterisk, are farther than 1,000 m from the core location and were not integrated into this model. Any areas within 1,000 m of the core location, where vector arrows indicate that downslope movement of particles would result in flow away from the deep lake basin, have been included into the darkened, unmodeled regions.

isolated basins. Under these circumstances, the model structure needed to be modified so that below the basin isolation point, resuspension between the basins was no longer possible (Fig. 3). In this fashion, diatom sediment could not be carried over unreasonable geographical barriers from one basin to the other, but material could easily be exchanged when the lake basins remained joined. This refinement of the model most reasonably estimates resuspension-type sediment focusing, where water energy redistributes previously deposited sediments uniformly over the lake basin during periods of turbulence (Blais and Kalff 1995).

A second refinement of the model was generated to account for gravity-driven sediment focusing. In this scenario, sediment is not redistributed throughout the entire lake basin but moves downslope through sliding and slumping. Regions of the lake where the slope is between 4% and 14% would be zones of transportation, where gradually material is carried to deeper parts of the lake (Fig. 4). Regions where the slope is 4% or less are zones of sediment accumulation (Håkanson 1977; Hilton 1985). In this fashion, the sediment in the deepest portion of the lake represents the sediment that readily can be carried downslope to the deep basin. Large flat regions likely act as localized traps for sediment (Anderson et al. 1994; Blais and Kalff 1995). This approach may be more appropriate for larger lakes, where breakdown of the thermocline probably occurs more slowly and where complete mixing probably is uncommon and would not produce enough energy to resuspend sedimentary particles in deeper regions of the lake (Hilton 1985; Anderson 1989).

To more reasonably simulate gravity-driven sediment focusing processes, we segmented our three-dimensional lake model into a circular zone extending from the coring site with a radius of 1,000 m (Fig. 4); beyond the limit of these zones, changes in the diatom habitat areas no longer contributed to model predictions. In this manner, we were capable of limiting the extent of our model to a small (localized) region of the lake from which diatoms would likely be contributed. Regions of the lake where the basin slope could only direct sediment into the smaller of the two basins (which was not cored) were ignored by the model.

Results

Resuspension-type sediment focusing model—When the surface of Foy Lake is lowered 3 m below modern lake levels, the resuspension-type model predicts that available P : B diatom habitat area will decrease throughout the range of photic penetration depths modeled, producing a general increase in the relative proportion of benthic diatoms in the sediment (Fig. 5a). Under modeled conditions of shallow photic penetration (3 to 4.5 m), the predicted ratio of available P : B habitat area declines most sharply because benthic diatom habitat areas are expanded dramatically to ~3.5× greater than at modern lake levels. Two characteristics of the basin morphology (Fig. 3) produce this effect: (1) a large broad platform along the margin of the lake that maximizes the benthic diatom habitat area exposed to shallow photic penetration and (2) a pronounced reduction in the total available planktic habitat area (deep water) that occurs just as the two basins begin to isolate. The combined effect on the model output is a sudden decrease in the P : B diatom ratio, which

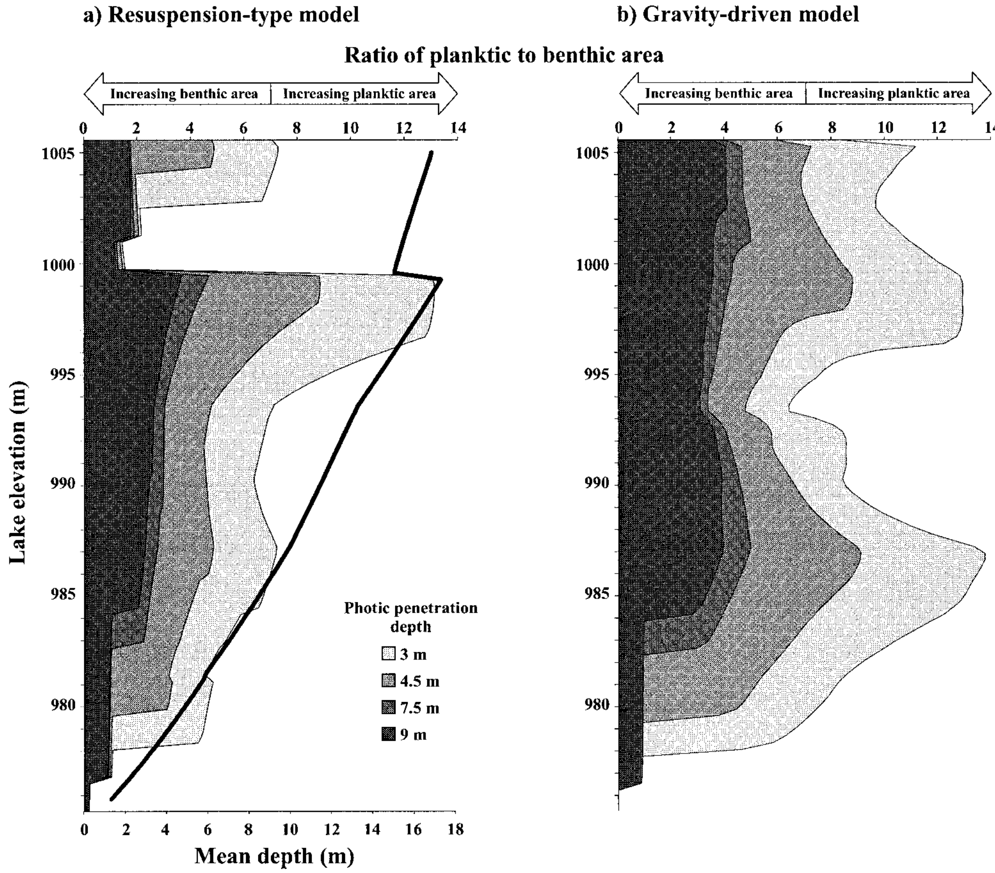

Fig. 5. Output from sediment focusing models of Foy Lake. (a) Output from resuspension-type sediment focusing model compared with mean lake depth (solid line). Sharp transitions in the ratio of planktic to benthic diatom habitat area exist under different photic penetration depths and lake levels. (b) Output from the gravity-driven sediment focusing model. Transitions in the ratio of planktic to benthic diatom habitat area differ from the resuspension-type model but still show distinct changes under different photic penetration depths and lake levels.

should be reflected in the sediment record as a spike (Fig. 5a) in the relative proportion of benthic diatoms.

A second inflection in the ratio of available P : B diatom habitat area in Foy Lake occurs as lake levels are lowered to 6 m below the modern lake level. At lake levels below 6 m, the broad shelf (which produced the spike in available benthic diatom habitat area with a 3-m lake lowering) becomes subaerially exposed (Fig. 3). Thus, the available benthic habitat area is suddenly limited to steeply sloping regions mantling the larger lake basin, effectively increasing the mean depth. The likely effect in the sedimentary record (Fig. 5a) of this sharp reduction in available benthic diatom habitat area would be a dramatic increase in the ratio of planktic diatom frustules in the sediment record (the model predicts a relative increase in available planktic habitat area of roughly 6.5× at lake levels 3 to 6 m below modern lake elevations).

The resuspension-type model predicts that the relative benthic diatom content will increase with decreasing lake levels once the two basins are separated, down to the broad flat base underlying most of the lake. The results from this model are particularly noteworthy because the model predicts that similar P : B ratios may be produced at two very different depths within the lake (compare elevations 1,005–1,003 m to elevations 990–985 m).

Gravity-type sediment focusing model—Planktic : benthic habitat ratios predicted by the gravity-driven sediment focusing model (Fig. 5b) show only a modest (~1.2×) increase in the available benthic diatom habitat for lake levels lowered 1.5 to 4.5 m below the modern lake surface. The predicted pattern is similar to the resuspension-type model in that the change is greatest for photic penetration depths of 3 to 4.5 m. Because this model limits transport distances that can contribute diatoms, expanding benthic habitat within the entire lake generally produces a less dramatic change than that in the resuspension model. The increase in relative benthic habitat with a 1–4.5 m lake-level lowering can be attributed to the relative proximity of the broad platform to the deepest region of the lake.

When the lake level is lowered by 4.5 m or more, the gravity-type model produces a decrease in the relative proportion of benthic habitat. As was the case in the resuspension model, this response (~1.3× reduction in relative available benthic habitat) can be attributed to the subaerial

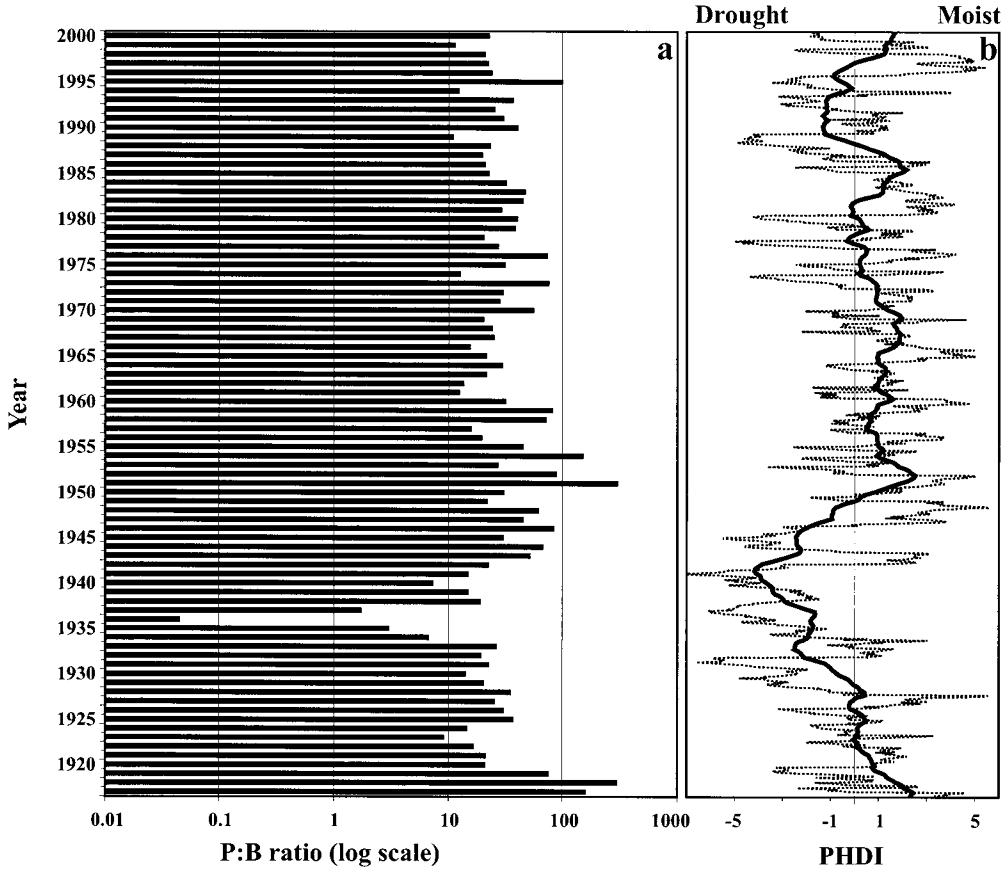

Fig. 6. (a) Annual record of the 20th-century planktic to benthic diatom ratio of Foy Lake, Montana. Note the pronounced increase in benthic species during the 1930s. (b) The monthly regional moisture record (dotted) as measured by the Palmer hydrologic drought index (PHDI). A 5-yr running average of the PHDI is plotted (bold) to show long-term trends.

exposure of the broad platform and steep slopes that limit benthic habitat to a narrow mantle at this lake level.

When lake levels are lowered to 9 m below the modern lake-surface elevation, a more pronounced spike in the relative benthic habitat occurs (Fig. 5b). Here, the transition is very sharp, and benthic habitat areas nearly double in relative proportion to planktic habitats from both higher and lower modeled lake levels. In this case, the relative expansion of benthic habitat area results from exposure of a submersed platform to photic penetration (Fig. 4). The combination of sediment relative to the core site from this submersed platform is increased greatly in the gravity-driven model relative to the resuspension model. Substantial planktic expansion again occurs when lake levels are lowered by at least 17 m. Although muted, the effects of these changes in habitat area also are visible at coincident lake levels in the output from the resuspension-type model (Fig. 5a).

Planktic : benthic diatom ratios from Foy Lake—The annually laminated sediment freeze core taken from the deepest region of Foy Lake, Montana, indicates that fossil assemblages throughout most of the 20th century were dominated by a single planktic diatom species. During the 85-yr record (Fig. 6), only 16 years produced a P : B diatom ratio of less than 15 : 1, and only 6 years had P : B diatom ratios less than 10 : 1. Nearly every sample with an enhanced benthic signal (P : B diatom ratio less than 10 : 1) is coincident with historical records of persistent drought in the region during the Dust Bowl period (1930–1940s), whereas not all dry periods have an elevated benthic input.

Discussion

Modeling available habitat areas can provide insight into the nature of planktic : benthic diatom ratios recovered from lake sediments. The maximum depth of modern Foy Lake is approximately 42 m, and the dominance of planktic diatom frustules in the fossil record of the past 85 yr clearly reflects the vast area available for planktic diatom production within this deep lake. A brief, but very sharp transition from planktic dominance to benthic dominance is evident in the sediments and is coincident with severe persistent regional drought during the 1930s to 1940s (Fig. 6). Distinct annually varved sediments sampled throughout this period preclude the notion that a single postdepositional disturbance may be responsible for the dramatic threshold-like change in the fossil diatom assemblage. A traditional planktic : benthic model would infer a lake-level decrease proportional to the increase in benthic diatom abundance; however, this model is problematic because the sharp transition observed in the sediment record conflicts with the gradual lake-level lowering that occurred over 10–15 yr of changing regional climate. Over roughly 5 yr, the relative abundance of the planktic community in the sedimentary record is reduced from 95% to less than 5%, and recovery is equally rapid. Application of our model demonstrates that this dramatic response is a predictable product of the lake's morphometry because a lake-level lowering of 2 to 6 m dramatically expands the available benthic diatom habitat.

Perhaps one of the most interesting features from the period of the 1930s through the 1940s is the peak in relative abundance of benthic diatoms in the sediment record that occurs well before the peak drought period of the Dust Bowl era (Fig. 6). Because our varve chronology is well constrained, the timing of these events emphasizes the utility of our model to aid in the reconstruction of past lake-level changes. A long-term decline in lake level that eventually lowers the lake more than 6 m quickly produces a dramatic increase in the *mean lake depth* (Fig. 5), despite the fact that maximum lake depth is actually lower. These results are consistent with our resuspension-type model, which demonstrates that the relative abundance of planktic diatoms is likely to *dramatically increase* once the two lake basins have become isolated (Fig. 5a). We believe this adequately explains the sudden increase in the relative abundance of planktic diatoms in the late 1930s and early 1940s, which contrasts strongly with the persistence of severe regional drought. Anecdotal information from long-time local residents suggests that during the latter period of the Dust Bowl drought, lake levels were, indeed, low enough to isolate the two basins.

The threshold-like transition observed in the 20-century sediment record is not unique in Foy Lake. A series of repeating threshold-like responses, identical in character—although greater in magnitude and duration—are also observed in older sediments from Foy Lake, Montana (Fig. 7). The periodic nature of benthic spikes indicates that the sedimentary record likely is recording a threshold response related to the interaction of hydroclimate and lake morphology.

Application of our model results to the late-Holocene sediments from Foy Lake gives us particular insight into the transitions observed prior to 1100 A.D., when the lake shows a marked and sustained increase in the relative abundance of planktic diatoms compared with the modern lake. Using the traditional approach to P : B ratios, this period would represent increased lake levels during the Medieval Period, an interval that was drier than modern climates based on paleoclimatic studies in nearby areas. However, with a modest rise above modern lake levels, Foy Lake will reach the outlet sill and overflow; thus it is unlikely that Foy Lake was significantly deeper than today. Our model suggests that the only feasible way to produce a sustained period of relative planktic abundance greater than modern is to *decrease the lake level* below the isolation threshold (Fig. 5a), where the mean lake depth is actually greater than the modern mean lake depth. Although counterintuitive, this explanation fits our sedimentological data and modeling results most aptly *and* coincides with the general perception of a drier regional hydroclimate during this period.

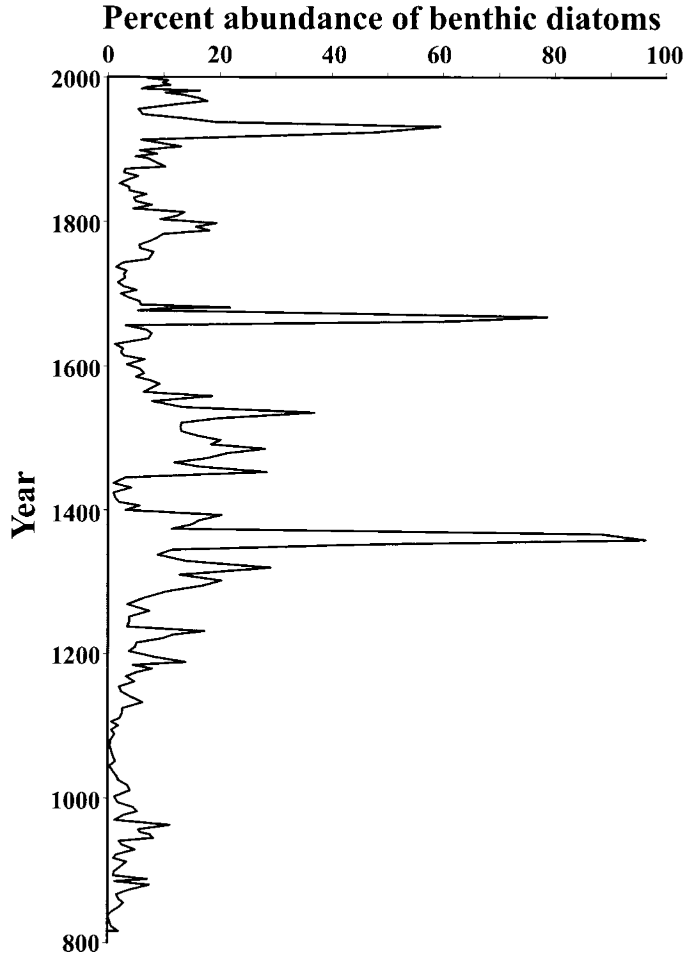

Fig. 7. Stratigraphy of benthic diatom abundance variation from Foy Lake, Montana, showing distinct threshold-like responses throughout the late Holocene. Note the enhanced dominance of planktic diatoms during the Medieval Period prior to 1100 A.D., which likely results from lake-level lowering of greater than 6 m below modern lake level (*see text*).

The measured planktic : benthic diatom ratios observed in the sediment record exceed the values predicted by our model. However, the model is designed to improve interpretation of planktic : benthic ratios in sediment cores by examining how diatom *habitat areas* change with changing lake levels. It is not meant to predict actual ratios within fossil assemblages, which are produced by a complex array of processes and responses. Thus, the model does not calculate the relative seasonal productivity of diatoms from either habitat, which is ultimately what determines the final assemblage found in lake sediments.

The diatom habitat areas that are modeled are minimum estimates of *available habitat* at each lake level. Strict application of these estimates ignores microtopographic features of lake basins and bottom substrates (e.g., stones, macrophytes), both of which may cause the model to underestimate the total benthic diatom habitat area. Likewise, the planktic diatom community of a lake is not restricted to the planar surface of the lake but exists throughout the limit of photic penetration. Seasonal differences in photic penetration resulting from turbidity or shading by nondiatom phytoplankton affect total planktic habitat area. Conversely, not all available habitat area is actually occupied or at least occupied throughout a full open-water season, particularly in lakes that are low in nutrients (Anderson 1989).

There is no a priori reason to assume that changing P : B ratios are related solely to changes in lake level because certainly other factors also influence benthic and planktic production (Wolin and Duthie 1999). Indeed, preliminary statistical analyses of climatological data from a weather station near Foy Lake suggest that years where the P : B diatom ratios are most dramatically reduced are times of persistent drought coupled with extreme ice cover and winter snowfall, all of which hinder overall planktic diatom production (Stone unpubl. data). Robust interpretation of P : B ratios requires not only assessment of morphometric constraints, as demonstrated here, but also the analysis of other proxies in the sediment record that are sensitive to changes in lake levels and hydroclimate (Dearing 1997; Digerfeldt 1998).

The two approaches used to approximate different types of sediment focusing each can produce both abrupt and gradual transitions in P : B diatom ratios with changing lake levels; however, the magnitude of change is smaller in the gravity-driven model. The pattern of abrupt changes in P : B diatom habitat ratios resulting from the resuspension-type sediment focusing model more closely resembles the high-resolution threshold-like changes in the sediment record at Foy Lake, suggesting that resuspension may play a larger role in the short-term dynamics of sediment focusing. However, long-term changes in diatom habitat area probably are affected by a combination of both processes.

Both model approaches show the potential for complex changes in P : B habitat areas as lake levels are lowered, particularly where photic penetration is relatively limited. This response should be expected with the resuspension-type model because it accentuates the complex morphology and bathymetry of a lake basin by incorporating whole-lake morphometry. In contrast, the gravity-type sediment focusing model limits the basin complexity, producing more gradual changes. Within the range of the gravity-type sediment focusing model (1,000-m radius from the deepest region of the lake), the lake basin at Foy Lake is not particularly complex. The broad expansive margins of the lake are limited, and the bathymetry of this region of the lake has few major submersed low-angle slopes, other than the principal lake base. Nonetheless, the model shows that lake-level lowering can either increase or decrease the P : B ratio, dependent on the magnitude of lake-level lowering. In the case of Foy Lake, a 3–6-m decrease in lake level increases benthic habitat area, whereas continued lowering to greater than 6 m may actually decrease the benthic habitat availability. Thus, counterintuitive responses are likely at very low-lake levels. Exceptionally complex lake bathymetry is not required to produce potential nonlinear responses, as demonstrated by the gravity-driven model developed here for Foy Lake. As a result, well-constrained reconstruction of paleoclimate from fossil diatom assemblages in any lake system should incorporate an explicit consideration of lake morphometry and how available planktic : benthic habitat areas change with lake level.

The conceptual foundation of our model can be easily adapted to any lake basin and requires only topographic and bathymetric maps of the basin and readily available software. In basins with complex morphometry, the calculated values of P : B habitat area ratios produced by the model may not have a unique solution (two very different lake-level elevations may have the same P : B habitat area ratio), and therefore this technique cannot be reliably calibrated to produce quantitative values for past lake levels. Moreover, given the potential to vastly underestimate true planktic and benthic habitat areas, semiquantitative estimates of the direction and magnitude of past lake levels may be the best that can be achieved with this technique. But, despite these limitations, the technique greatly improved the interpretation of planktic : bethic ratio from the Foy Lake record by producing a semiquantitative estimate of lake depth and identifying specific lake zones where reconstruction of past climate from P : B ratios may be nonlinear or counterintuitive.

The application of three-dimensional modeling to both modern and past lake systems could be improved greatly by studying lake-specific seasonal nutrient availability and seasonal changes in light penetration and density of diatom growth in each habitat area. Long-term monitoring of these lake processes could provide a means to produce a more accurate estimate of the effects of microtopographic and mesotopographic features on lake-basin surface areas, as well as a mechanism to adapt the model to seasonal changes in diatom production. Although long-term records of past lake levels are exceedingly uncommon, the results of this conceptual model could also be compared to the record from specific lakes with long records of lake level change to attempt to test or calibrate the accuracy of its predictive capabilities.

In summary, modeling of diatom habitat areas significantly improved the interpretation of planktic to benthic diatom ratios recovered from a sediment core from Foy Lake. The model allowed for the calculation of physical parameters of the lake, such as volume and surface area, which were used to create a conceptual model of the effect of changing lake level on diatom habitat areas. Application of this conceptual model to Foy Lake enabled a semiquantitative prediction of changes in the relative proportion of planktic and benthic diatom habitat areas with changing lake levels. Modification of the model created a tool for examining the nature of sediment focusing in the lake based on both local and basinwide calculations of diatom habitat areas. Comparison of the model results with both long and short sedimentary records from Foy Lake, Montana, suggest that planktic : benthic ratios may be a better predictor of mean lake depth than maximum lake depth. At a minimum, the model provides a means for recognizing potentially ambiguous signals of lake-level change in the sedimentary record that may hinder paleoclimatic interpretation. Such an approach can be applied easily to other organisms that are influenced by lake level, such as ostracodes or chironomids, or to address other questions related to lake-level impacts on littoral habitats. The modeling technique is simple enough to be easily implemented and reliably duplicated and relies only on the availability of an adequate bathymetric map and software for calculating lake surface areas and volumes. The model is adaptable enough to allow for modeling of more sophisticated sediment focusing processes and can be designed to fit complex lake basins.

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