Sediment records of phosphorus-driven shifts to phytoplankton dominance in shallow Florida lakes

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Abstract

Primary producer community structure (PPCS) in shallow lakes is influenced by phosphorus (P) load and water column P concentration. Theoretically PPCS may shift between phytoplankton and macrophyte states with intermediate P loading, but phytoplankton dominate when P loading exceeds a critical threshold. We analyzed sediment cores from five shallow, eutrophic lakes (size range: 0.6 to 125 km^2) that are phytoplankton dominated to determine whether the development of the current state was associated stratigraphically with an increase in sediment total P (TP) and a shift in PPCS. We used sponge biogenic silica (BSi$_{Sponges}$) concentrations and total carbon to total nitrogen ratios (TC:TN) as proxies for macrophyte abundance and sediment organic matter source, respectively. Three stratigraphic groups of sediments were identified with k-means cluster analysis. These samples were grouped by increasing TP concentrations and decreasing age and identified as macrophyte, transitional and phytoplankton sediments. Results show that as P loading increased in the late 19th and early 20th centuries, the lakes produced sediments with an increasing contribution from phytoplankton. Four of our lakes may represent a subset of shallow lakes because of their large size (30 to 125 km^2) and relatively rapid historic P enrichment. In these Florida lakes, PPCS shifted to phytoplankton dominance with no paleolimnological record of lake-wide alternating stable states or of lake-wide phytoplankton dominance before anthropogenic P enrichment.

Introduction

Recent models of nutrient enrichment in shallow lakes show that macrophytes typically dominate when P loading is low and that phytoplankton dominate when P loading increases above a critical threshold (Scheffer et al. 1993; Moss et al. 1996). With intermediate P loading, these models indicate that the primary producer community structure (PPCS) in shallow lakes is not stable and may alternate between phytoplankton and macrophyte dominance (Scheffer et al. 1993; Moss et al. 1996). We analyzed sediment cores from five shallow eutrophic lakes, to determine whether a historic change in PPCS could be inferred from the sediment record and whether, if present, it was associated stratigraphically with an increase in sediment total P (TP). Our data show that these systems became phytoplankton dominated after TP increased in the late 19th and early 20th centuries relative to earlier, baseline nutrient conditions. Results were compared to available limnological and paleolimnogical data (Schelske and Brezonik 1992; Schelske et al. 1999, 2000) from one study site, Lake Apopka. We hypothesize that both the rapidity and magnitude with which P loading increased and the large size of four of these lakes precluded a period of alternating macrophyte and phytoplankton states. We conclude that, following P enrichment, the PPCS in

our lakes did not alternate, but went through a transition period with increasing algal production, before reaching phytoplankton dominance.

Sediment records from cores collected in five shallow Florida lakes were used to infer historic shifts in PPCS. Submersed macrophyte dominance was inferred from concentrations of sponge biogenic silica ($BSi_{Sponges}$) and the total carbon (TC) to total nitrogen (TN) ratios of sediment organic matter. Submersed aquatic vegetation is the predominant substrate for freshwater sponges (Pennak 1953) in lakes such as these that lack other solid substrates. Because of high structural C content, TC to TN mass ratio (TC:TN) for submersed macrophytes is greater than that for phytoplankton. As the relative contribution of macrophyte-derived organic matter decreases, the sediment TC:TN decreases. Total C to TN mass ratios, therefore, were used to identify changes in the relative contribution of macrophytes and phytoplankton to sediment organic matter (Muller and Mathesius 1999; Schelske et al. 1999). Sediment TC:TN ratios are a temporal integration of the TC:TN of organic matter sources and, additionally, reflect diagenetic effects associated with sediment burial. TP concentration was used to infer historic changes in P loading (Engstrom and Wright Jr 1984; Schelske et al. 1986).

Site description

The study lakes are as much as 260 km apart (Figure 1) and are therefore subjected to different rainfall patterns and different disturbance histories related to hurricanes and tornadoes. Basin morphometry and geographic orientation to prevailing winds differ among the study lakes. The lakes span a size range of 0.6 to 125 km^2 (Table 1), but all are shallow (mean depth < 4 m) and currently dominated by phytoplankton, rather than submersed macrophytes. Surface sediments are unconsolidated (fraction dry weight $< 5\%$) and composed mainly (i.e. $> 50\%$) of organic matter (Brenner et al. 1999; Brenner and Whitmore 1998; Schelske 1997; Whitmore and Brenner 1997), except Lake Jesup sediments, that are ~30% organic matter (Cable et al. 1997). The timing and intensity of anthropogenic disturbance varied among lakes (Cable et al. 1997; Schelske 1997; Whitmore and Brenner 1997; Brenner and Whitmore 1998; Brenner et al. 1999). Anthropogenic disturbance occurred early (before 1850) in north Florida around Newnans Lake and Orange Lake, but their watersheds were never com-
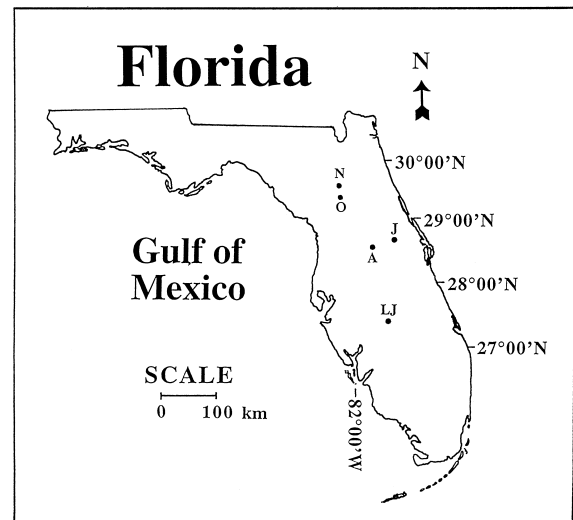

Figure 1. Map of Florida showing the location of Newnans Lake (N), Orange Lake (O), Lake Jesup (J), Lake Apopka (A) and Little Lake Jackson (LJ).

pletely developed. Farther south, anthropogenic disturbance began later, but the basins were ultimately impacted more intensely by agricultural or urban activities.

The study lakes also have diverse hydrologic characteristics. Spring-fed Lake Apopka provides the headwater for the Ocklawaha River system and a weir controls lake outflow. In Newnans Lake and Orange Lake, surface waters are the primary hydrologic inputs and weirs regulate stage. Lake Jesup is hydrologically connected to the St. Johns River and its morphometry has been modified to allow for navigation. Little Lake Jackson has been augmented with alkaline ground waters.

Methods

Sediment/water interface cores (Fisher et al. 1992) were collected from these five lakes in 1995, 1996 and 1997. The 12 cores used in our investigation represent a subset of profiles collected for more extensive studies (Cable et al. 1997; Schelske 1997; Whitmore and Brenner 1997; Brenner and Whitmore 1998; Brenner et al. 1999). We specifically chose cores from depositional areas and not from erosional environments or locations with thin sediment accumulations relative to the rest of the lake. Cores were extruded vertically and sectioned in the field at 2 to 5 cm intervals. Sections were frozen, freeze-dried, and

Table 1. Limnological characteristics for the five study lakes. Total phosphorus (TP) and chlorophyll *a* (Chl-*a*) are recent averages for the water column

Lake	Surface area	Mean depth	TP	Chl-*a*	Location	
	(km^2)	(m)	($mg \cdot L^{-1}$)	($mg \cdot L^{-1}$)	latitude (N)	longitude (W)
Lake Apopka	125	<2	0.200	0.100	28° 39′	81° 39′
Lake Jesup	40.5	<2	0.187	0.118	28° 43′	81° 13′
Little Lake Jackson	0.6	<4	0.050	0.039	27° 28′	81° 28′
Newnans Lake	30.1	<3	0.114	0.251	29° 39′	82° 13′
Orange Lake	51.4	<2	0.034	0.026	29° 27′	82° 10′

ground to particle size less than ~100 μm in the laboratory.

Dried, ground sediment samples were utilized for chemical analyses. Biogenic silica (BSi) was determined with time-course leaching and $BSi_{Sponges}$ was determined as the difference between BSi_{Total} and $BSi_{Diatoms}$ (Conley and Schelske 1993). Non-apatite inorganic P (NAIP) was determined by autoanalyzer after equilibration in 0.1 M NaOH (Williams et al. 1980). Total P was determined by autoanalyzer after persulfate digestion of dried sediment samples (Schelske et al. 1986). Total C and TN were measured with a Carlo Erba NA1500 CNS elemental analyzer equipped with an autosampler (Verardo et al. 1990).

Data from the five study lakes were analyzed with a multivariate statistical computer software package (JMP Statistical Software, SAS 1998). A preliminary screening identified 26 peat sediment samples as outliers. These outliers were eliminated from the data set because of high and variable TC:TN (range: 17–63). These sediments, if present, were the oldest, i.e., found at the bottom of cores. Principal component analysis identified $BSi_{Sponges}$, TC:TN, and TP as variables that explained the majority of the variation in the data set which also included other paleolimnological proxies. K-means cluster analysis was used to objectively group samples into three sediment types. We used $BSi_{Sponges}$, TC:TN, and TP data as input variables. Because TP and $BSi_{Sponges}$ concentrations vary by more than an order of magnitude across our study lakes, we normalized these data for each core relative to the respective core maximum. The results are based on a three-dimensional cluster analysis, but the clusters are evident in the two-dimensional plots in Figure 2.

Although 10 cores were dated previously using ^{210}Pb, pre-disturbance sediments were too old (> ~150 yr) to be ^{210}Pb dated. Instead, we simply determined if excess ^{210}Pb was present in individual sediment samples. Ages of samples with excess ^{210}Pb activity were < ~150 yr old and those samples with no measurable excess ^{210}Pb activity were > ~150 yr old.

Results and discussion

K-means cluster analysis generally grouped sediments in each core by stratigraphic age. The oldest group had the lowest normalized TP concentrations (mean = 0.31 ± 0.13), the greatest TC:TN (mean = 13.7 ± 0.7), and the greatest normalized $BSi_{Sponges}$ concentrations (mean = 0.74 ± 0.20). The next oldest group had intermediate normalized TP concentrations (mean = 0.48 ± 0.17) and intermediate TC:TN (mean = 11.8 ± 0.7), but their mean normalized $BSi_{Sponges}$ concentration (0.74 ± 0.14) was equal to the mean normalized $BSi_{Sponges}$ concentration (0.74 ± 0.20) for the group of oldest sediments The group of most recent sediments had the greatest normalized TP concentrations (mean = 0.79 ± 0.18), the lowest TC:TN (mean = 10.6 ± 0.8), and the lowest normalized $BSi_{Sponges}$ concentrations (mean = 0.40 ± 0.15). Based on normalized $BSi_{Sponges}$ and TC:TN, these results show that samples from the oldest group are macrophyte sediments and samples from the most recent group are phytoplankton sediments. Sediments with intermediate ages and intermediate normalized TP and TC:TN are termed transitional sediments. Stratigraphic distributions of the three sediment types are shown in Figures 3–5.

Our results show that TP increased upcore and that before anthropogenic disturbance, the lakes produced sediments with lower TP concentrations and a greater contribution from macrophytes (Figures 3–5). Sediments deposited most recently in all five lakes have greater contributions from phytoplankton and greater TP concentrations than do older sediments. Transitional sediments with intermediate TP concentrations and TC:TN apparently represent a gradual shift in
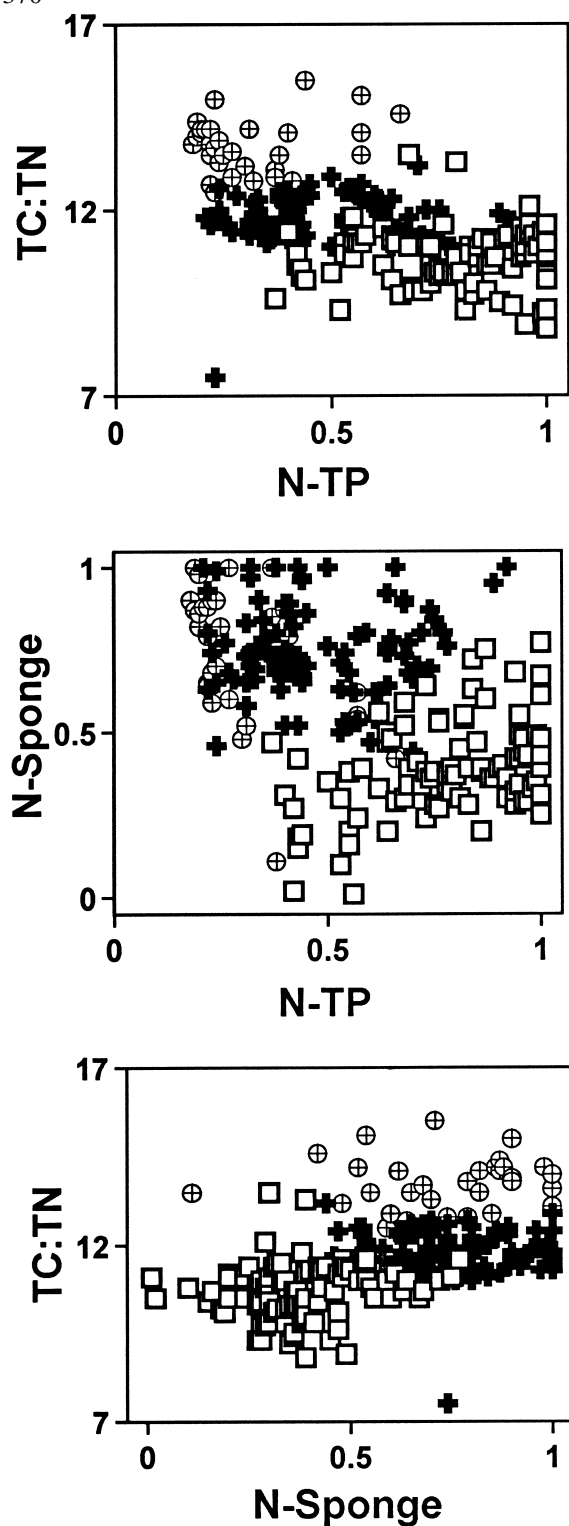
Figure 2. Two-dimensional plots of input variables used in three-dimensional cluster analysis. Normalized total phosphorus (N-TP), normalized sponge biogenic silica (N-Sponge) and the total carbon to total nitrogen ratio (TC:TN) were the input variables. Sediments were classified as phytoplankton (open squares), transitional (dark crosses) or macrophyte (circles with crosses).

PPCS with an increasing contribution of phytoplankton-derived organic matter. $BSi_{Sponges}$ concentrations in transitional and macrophyte sediments are the same, demonstrating that transitional sediments are not a simple mixture of macrophyte and phytoplankton sediments. If transitional sediments were a simple mixture of the two sediment types, the proportions of TC:TN and $BSi_{Sponges}$ from phytoplankton and macrophyte sediments should be equal.

Means for sediment variables in phytoplankton, transitional, and macrophyte deposits were compared among samples from Lake Apopka, Lake Jesup and Little Lake Jackson, the lakes with multiple cores (Table 2). These comparisons show variation from the mean value for each proxy obtained from k-means cluster analysis. This variation illustrates the risks in using single core analysis for paleolimnological inferences. In addition, data for NAIP like TP, show an increasing trend upcore. These results provide an independent proxy from which increased TP loading can be inferred. $BSi_{Diatoms}$ is generally lowest in macrophyte sediments, but $BSi_{Diatoms}$ in transitional sediments was greater than or equal to $BSi_{Diatoms}$ in phytoplankton sediments for 6 of the 12 cores. Dry bulk density, as expected, decreased upcore. In general, the dry bulk density of phytoplankton sediments is < 0.06 g·cm^{-3} except for two cores from Lake Jesup (0.08 g·cm^{-3} and 0.122 g·cm^{-3}). The samples classified as outliers (peat or peat and carbonate) were found in Lake Jesup and Little Lake Jackson.

Our paleo-reconstruction for Lake Apopka (Figure 3) compares favorably with independent analyses of P loading (Battoe et al. 1999), historic shifts in PPCS (Schelske et al. 2000) and changes in diatom community structure (Donar 1999; Schelske et al. 1999). According to anecdotal accounts, the PPCS in Lake Apopka changed from macrophyte-dominated to phytoplankton-dominated during the 1940s (Schelske and Brezonik 1992). This shift in PPCS was identified in the paleolimnological record with TC:TN and diatom microfossils and attributed to a 7-fold increase in TP loading that coincided with the development of ~80 km^2 of riparian farms (Battoe et al. 1999; Schelske et al. 1999, 2000). Data from an 8,000 yr sediment record show that recent sediments sampled by our short cores represent the period of greatest change in diatom abundance and species composition (Donar 1999).

In previous studies, only phytoplankton- and macrophyte-derived sediments were differentiated using TP concentration and TC:TN (Schelske 1997; Schelske et al. 1999). Differentiation of these two sediment
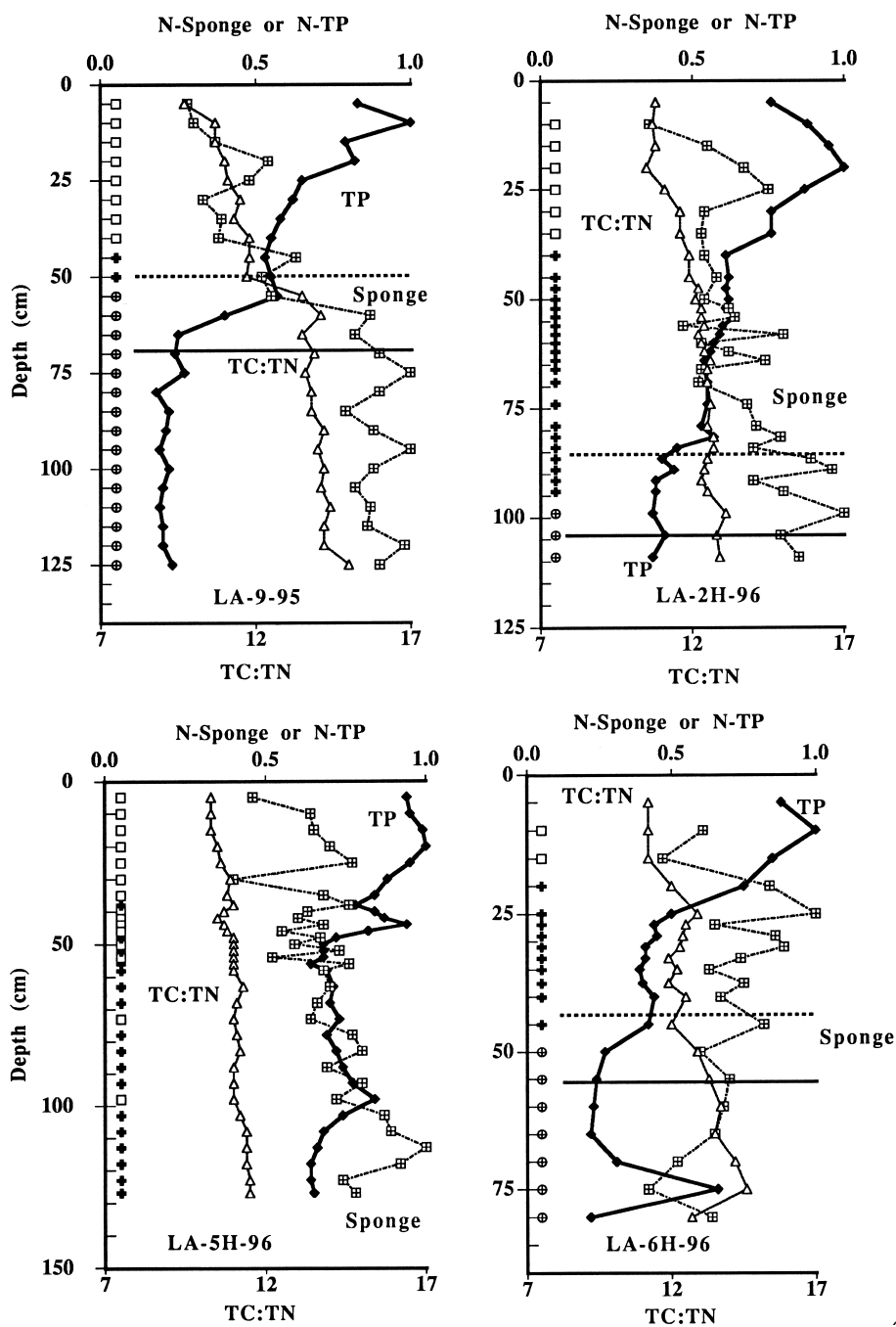
Figure 3. Sediment total carbon to total nitrogen (TC:TN) mass ratios, and normalized sponge biogenic silica (N-Sponge) and normalized total phosphorus (N-TP) concentrations versus depth for four Lake Apopka cores. Macrophyte (open circle with cross), transitional (black cross), or phytoplankton (open square) sediment classifications are presented on the depth axis. Horizontal lines within the graphs represent the maximum depth of samples with excess ^{210}Pb activity (age < ~150 yr). Broken horizontal lines within the graphs identify the ~1945 time horizon.

types was successful in cores with a large relative change in TP concentration and TC:TN, but was problematic in some cores that demonstrate small

relative changes in TP concentrations and TC:TN. Relative changes for all three sediment variables were greater for LA-9-95 and LA-6H-96 than the other two
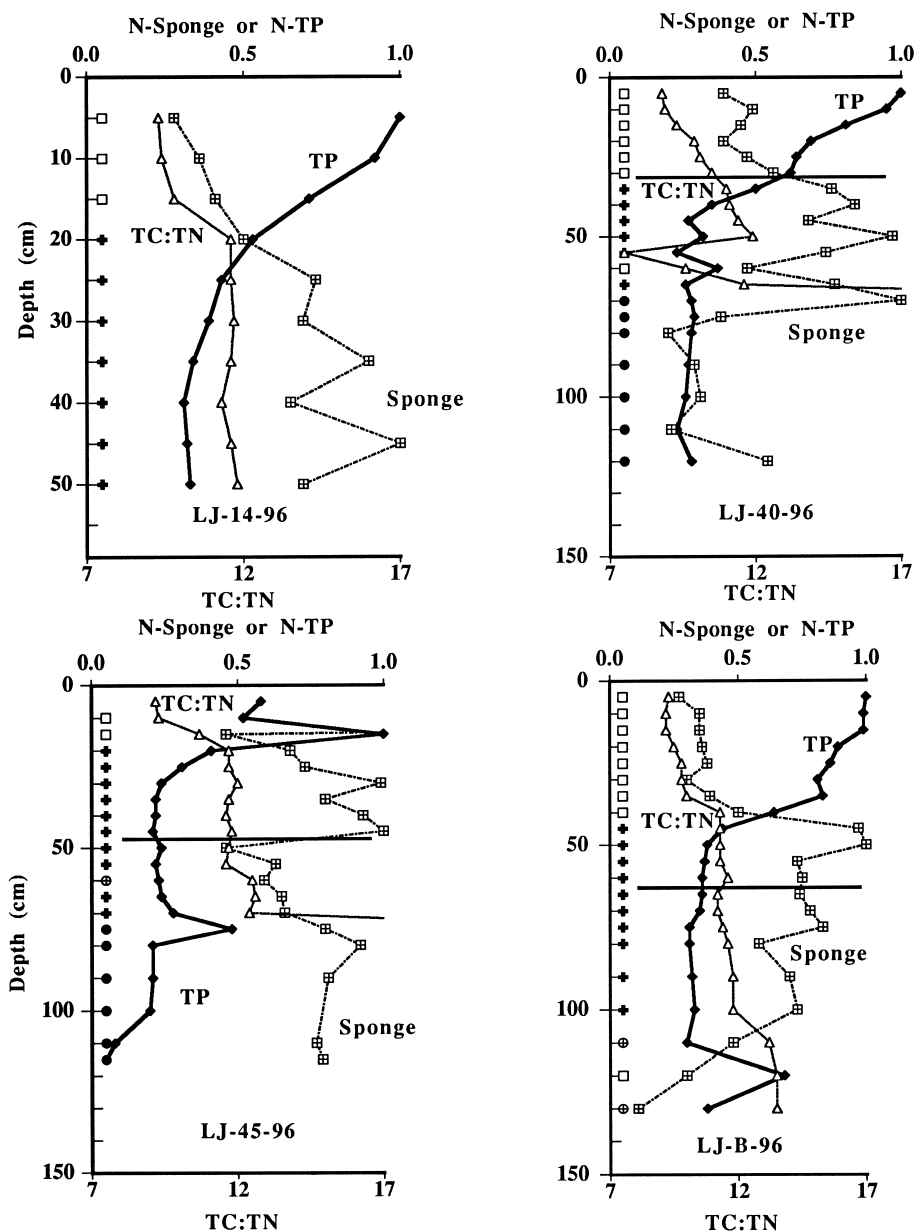
Figure 4. Sediment total carbon to total nitrogen (TC:TN) mass ratios, and normalized sponge biogenic silica (N-Sponge) and normalized total phosphorus (N-TP) concentrations versus depth for four Lake Jesup cores. Macrophyte (open circle with cross), transitional (black cross), or phytoplankton (open square) sediment classifications are presented on the depth axis. Horizontal lines within the graphs represent the maximum depth of samples with excess ^{210}Pb activity (age < ~150 yr). Peat sediment samples (black circle) are outliers, as explained in the text.

cores (Figure 3). In these cores, phytoplankton and macrophyte sediments were readily distinguishable (Schelske 1997). By contrast, LA-2H-96 shows a long record of transitional sediments underlying 35 cm of phytoplankton sediments, whereas LA-5H-96,

which presumably failed to penetrate deep enough to sample macrophyte sediments, shows only phytoplankton and transitional deposits (Figure 3, Table 2).

The deepest sediments from core LA-2H-96, identified here as transitional, were initially termed phyto-
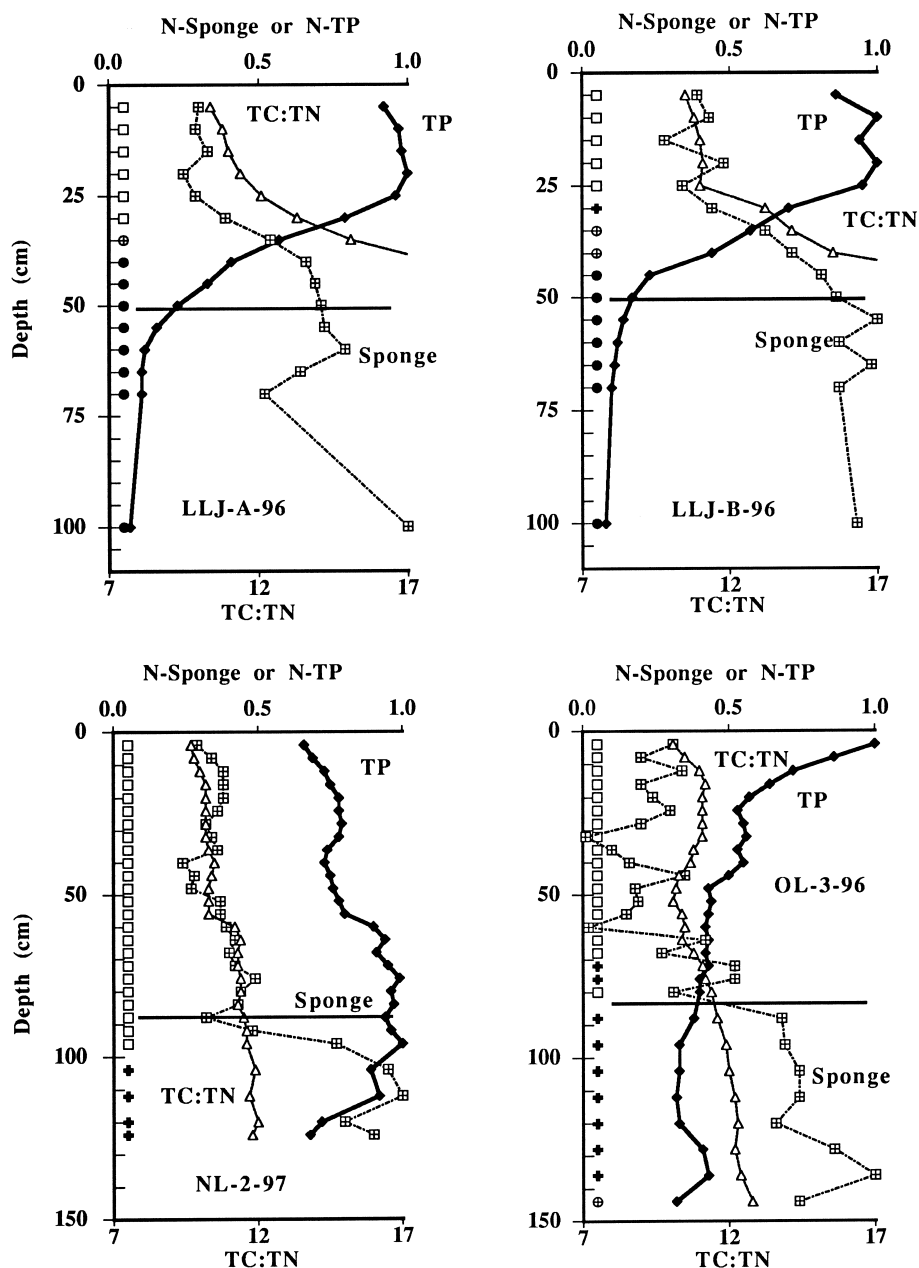
Figure 5. Sediment total carbon to total nitrogen (TC:TN) mass ratios, and normalized sponge biogenic silica (N-Sponge) and normalized total phosphorus (N-TP) concentrations versus depth for two Little Lake Jackson cores, one Orange Lake core and one Newnans Lake core. Macrophyte (open circle with cross), transitional (black cross), or phytoplankton (open square) sediment classifications are presented on the depth axis. Horizontal lines within the graphs represent the maximum depth of samples with excess ^{210}Pb activity (age < ~150 yr). Peat sediment samples (black circle) are outliers, as explained in the text.

plankton sediments based on diatom abundance and species composition (Schelske 1997; Schelske et al. 1999). In samples collected from LA-2H-96 at 69, 82, and 89 cm, the dominant diatoms were *Aulacoseira*

italica, Staurosira construens, and *Pseudostaurosira brevistriata.* In other cores (Schelske 1997; Schelske et al. 1999), *A. italica,* a meroplanktonic diatom, represented 80% of the microfossil assemblage in

Table 2. Total carbon to total nitrogen ratio (TC:TN), sponge biogenic silica ($BSi_{Sponges}$), normalized $BSi_{Sponges}$ (N-Sponge), total phosphorus (TP), normalized TP (N-TP), diatom biogenic silica ($BSi_{Diatoms}$), non-apatite inorganic phosphorus (NAIP) and dry bulk density (rho) in phytoplankton (P), transitional (T), and macrophyte (M) sediments. Data are means with standard deviation listed in parentheses. Peat samples (Peat) and peat samples with carbonates (Peat & CO_3) are listed accordingly. The number of samples is given in parentheses after sediment types. See text for additional explanation

Core	Sediment type (n)	TC:TN	$BSi_{Sponges}$ (mg·g^{-1})	N-Sponge	TP (mg·g^{-1})	N-TP	$BSi_{Diatoms}$ (mg·g^{-1})	NAIP (mg·g^{-1})	Rho (g·cm^{-3})
LA-2H-96	P (6)	11.0 (0.4)	10 (2)	0.57 (0.1)	1.53 (0.2)	0.85 (0.1)	37 (2)	0.63 (0.1)	0.030 (0.012)
	T (20)	12.4 (0.2)	12 (2)	0.67 (0.1)	0.97 (0.2)	0.54 (0.1)	45 (11)	0.37 (0.0)	0.052 (0.011)
	M (3)	12.9 (0.2)	16 (2)	0.88 (0.1)	0.69 (0.0)	0.38 (0.0)	26 (1)	0.30 (0.0)	0.067 (0.002)
LA-5H-96	P (15)	10.7 (0.3)	9 (2)	0.53 (0.1)	1.27 (0.2)	0.71 (0.1)	45 (5)	0.53 (0.1)	0.032 (0.013)
	T (17)	11.1 (0.2)	12 (2)	0.66 (0.1)	1.02 (0.1)	0.57 (0.0)	47 (5)	0.44 (0.0)	0.051 (0.006)
LA-6H-96	P (2)	11.2 (0.0)	10 (2)	0.54 (0.1)	1.33 (0.1)	0.91 (0.1)	34 (2)	0.47 (0.0)	0.023 (0.011)
	T (10)	12.2 (0.3)	14 (2)	0.78 (0.1)	0.67 (0.2)	0.46 (0.1)	34 (3)	0.23 (0.0)	0.063 (0.011)
	M (7)	13.5 (0.7)	11 (2)	0.60 (0.1)	0.45 (0.2)	0.31 (0.2)	12 (6)	0.19 (0.1)	0.088 (0.020)
LA-9-95	P (8)	11.0 (0.6)	7 (2)	0.38 (0.1)	1.34 (0.3)	0.73 (0.2)	32 (2)	0.40 (0.1)	0.034 (0.011)
	T (2)	11.7 (0.1)	10 (1)	0.58 (0.1)	0.99 (0.0)	0.54 (0.0)	34 (1)	0.29 (0.0)	0.051 (0.001)
	M (15)	14.0 (0.4)	15 (2)	0.87 (0.1)	0.46 (0.2)	0.25 (0.1)	7 (4)	0.15 (0.0)	0.083 (0.007)
LJ-14-96	P (3)	9.5 (0.3)	27 (5)	0.35 (0.1)	1.30 (0.2)	0.88 (0.2)	45 (9)	0.31 (0.1)	0.057 (0.019)
	T (7)	11.6 (0.2)	58 (13)	0.74 (0.2)	0.56 (0.1)	0.38 (0.1)	47 (11)	0.11 (0.0)	0.124 (0.014)
LJ-40-96	P (7)	9.6 (0.6)	36 (5)	0.46 (0.1)	1.05 (0.3)	0.73 (0.2)	27 (6)	0.24 (0.1)	0.122 (0.136)
	T (6)	10.8 (1.6)	62 (8)	0.79 (0.1)	0.47 (0.1)	0.32 (0.1)	18 (5)	0.11 (0.0)	0.212 (0.079)
	Peat & CO_3 (7)	34.0 (8.7)	33 (22)	0.42 (0.3)	0.39 (0.0)	0.27 (0.0)	6 (7)	0.11 (0.0)	0.435 (0.087)
LJ-45-96	P (2)	9.7 (0.9)	43 (1)	0.45 (0.0)	1.53 (0.6)	0.70 (0.3)	39 (1)	0.35 (0.0)	0.081 (0.037)
	T (9)	11.8 (0.3)	72 (17)	0.76 (0.2)	0.57 (0.1)	0.26 (0.1)	57 (19)	0.16 (0.1)	0.177 (0.023)
	M (2)	12.6 (0.1)	58 (4)	0.62 (0.0)	0.52 (0.0)	0.24 (0.0)	34 (2)	0.14 (0.0)	0.179 (0.010)
	Peat & CO_3 (4)	37.8 (16.8)	78 (6)	0.83 (0.1)	0.50 (0.3)	0.23 (0.2)	41 (4)	0.12 (0.0)	0.427 (0.188)
LJ-B-96	P (9)	10.2 (1.4)	37 (7)	0.36 (0.1)	1.16 (0.2)	0.86 (0.1)	35 (12)	0.37 (0.1)	0.060 (0.029)
	T (10)	11.4 (0.3)	82 (13)	0.78 (0.1)	0.48 (0.1)	0.35 (0.0)	11 (12)	0.16 (0.0)	0.116 (0.033)
	M (2)	13.3 (0.2)	31 (27)	0.30 (0.3)	0.46 (0.1)	0.34 (0.1)	6 (3)	0.16 (0.1)	0.190 (0.134)
LLJ-A-96	P (6)	11.5 (1.1)	68 (11)	0.31 (0.1)	3.80 (0.3)	0.94 (0.1)	80 (17)	1.67 (0.2)	0.058 (0.021)
	M (1)	15.1 (–)	120 (–)	0.54 (–)	2.32 (–)	0.57 (–)	146 (–)	1.19 (–)	0.115 (–)
	Peat (8)	21.7 (3.0)	159 (31)	0.72 (0.1)	0.78 (0.5)	0.19 (0.1)	153 (44)	0.41 (0.3)	0.228 (0.036)
LLJ-B-96	P (5)	10.9 (0.2)	73 (15)	0.38 (0.1)	4.27 (0.3)	0.95 (0.1)	76 (7)	1.78 (0.2)	0.058 (0.016)
	T (1)	13.2 (–)	84 (–)	0.44 (–)	3.17 (–)	0.70 (–)	104 (–)	1.50 (–)	0.132 (–)
	M (2)	14.8 (1.0)	128 (12)	0.67 (0.1)	2.26 (0.4)	0.50 (0.1)	153 (15)	1.02 (0.1)	0.155 (0.025)
	Peat (7)	21.7 (1.1)	173 (14)	0.90 (0.1)	0.61 (0.2)	0.14 (0.1)	195 (50)	0.32 (0.1)	0.258 (0.019)
LN-2-97	P (24)	10.7 (0.6)	78 (21)	0.38 (0.1)	3.04 (0.4)	0.84 (0.1)	138 (20)	1.36 (0.4)	0.049 (0.018)
	T (4)	11.8 (0.1)	185 (17)	0.91 (0.0)	2.92 (0.4)	0.80 (0.1)	22 (5)	1.41 (0.3)	0.113 (0.018)
OL-3-96	P (18)	10.7 (0.4)	10 (6)	0.22 (0.1)	0.82 (0.1)	0.55 (0.2)	80 (12)	0.19 (0.1)	0.040 (0.014)
	T (9)	11.9 (0.5)	27 (9)	0.72 (0.2)	0.55 (0.1)	0.37 (0.0)	68 (9)	0.12 (0.0)	0.123 (0.064)
	M (1)	12.8 (–)	44 (–)	0.74 (–)	0.48 (–)	0.32 (–)	58 (–)	0.10 (–)	– (–)

recent phytoplankton sediments and benthic diatoms, *S. construens* and *P. brevistriata*, were most abundant in the older phytoplankton sediments. $BSi_{Diatoms}$ concentrations were at least 2- to 4-fold greater in transitional or phytoplankton sediments compared to macrophyte sediments (Table 2). Thus, transitional sediments were formed during and soon after a dramatic increase in the contribution of phytoplankton to sediment organic matter. We hypothesize that these transitional sediments were formed after the 1940s as the lake shifted from macrophyte to phytoplankton dominance. Spatial differences in the sediment records

from Lake Apopka might be expected, particularly if the shift in PPCS occurred slowly (Lowe et al. 1999), in contrast to anecdotal accounts that suggest macrophytes were uprooted by a hurricane in 1947 and replaced by phytoplankton within a few weeks (Schelske and Brezonik 1992; Schelske et al. 2000). Historic meteorological data show that the 1947 hurricane did not pass within 160 km of the lake, but other hurricanes passed much closer to the lake in 1928, 1944 and 1945 without triggering a shift to phytoplankton dominance (Lowe et al. 1999). Thus, transitional sediments may provide a record of spatial

differences in PPCS during the gradual shift to phytoplankton dominance in this large lake.

Our results indicate that areal $BSi_{Sponges}$ production, accumulation, or both increase in transitional systems despite an inferred decrease in the contribution of macrophytes to sediment organic matter. One possible explanation for this apparent discrepancy is that during the decline of macrophytes, an increasing fraction of the standing crop of $BSi_{Sponges}$ on plants was deposited in the sediments relative to a macrophyte-dominated state. Another possible explanation is that sponge production increases in response to increased phytoplankton production as macrophytes become less abundant and the system switches to phytoplankton dominance. Both of these processes may occur simultaneously to produce transitional sediments with higher $BSi_{Sponges}$ concentrations than inferred from intermediate TC:TN ratios.

We determined the relative increase in sediment TP concentration associated with the development of phytoplankton dominance by comparing phytoplankton sediments to macrophyte sediments. Six cores from three of our lakes contained a complete record of the PPCS shift from macrophyte to phytoplankton dominance. In Lake Apopka (LA-9, LA-2H and LA-6H), Little Lake Jackson (LLJ-A, LLJ-B) and Orange Lake (OL-3), TP was 1.7- to 4.4-fold greater in phytoplankton sediments compared to macrophyte sediments (Table 2). For the complete 12 core data set, we calculated a ~2.6-fold increase in mean normalized TP concentration of phytoplankton sediments (mean = 0.79 ± 0.18, Figure 6) compared to macrophyte sediments (mean = 0.31 ± 0.13, Figure 6). When using these analytical results to infer changes in P loading, one must consider that the shift in PPCS may be accompanied by changes in sediment accumulation rates and P retention coefficients. Because sedimentation rates increased in all study lakes (Brenner et al. 1999; Brenner and Whitmore 1998; Cable et al. 1997; Schelske 1997; Whitmore and Brenner 1997), the ~3-fold increase in TP concentrations underestimates the relative change in TP loading. If development of phytoplankton dominance increases the P retention coefficient of the sediments (Schelske 1997; Schelske et al. 2000; Kenney et al. 2001), then the ~3-fold increase in TP concentrations overestimates the relative change in TP loading.

Mass balance studies show nutrient loading from anthropogenic sources contributed ~85% of the P to Lake Apopka from 1987 to 1994 (Battoe et al. 1999). This independent estimate of the increase in P loading
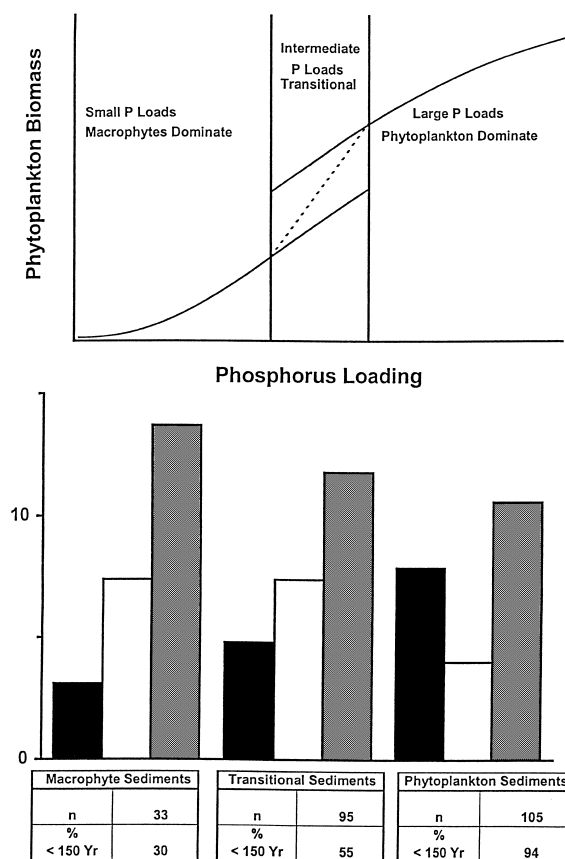

Figure 6. In the upper panel, a conceptual model modified from Scheffer et al. (1993) presents the relationship between phosphorus loading and phytoplankton biomass in shallow lakes. This shows three possible states: macrophyte-dominated, transitional, or phytoplankton-dominated. In the lower panel the three possible states are linked to three sediment types determined in shallow Florida lakes. Cluster means for normalized total phosphorus concentrations (N-TP, black bar), normalized sponge biogenic silica concentrations (N-Sponge, white bar), and the mass ratios of total carbon to total nitrogen (TC:TN, gray bar) are presented in the bar graph. N-Sponge and N-TP are graphed at 10 times the actual values. Descriptive data for each sediment type include the number of samples (n) and the percentage of aged samples with excess ^{210}Pb activity (age < ~150 yr).

to Lake Apopka (~7-fold) is more than double our estimate (~2.7-fold) based on changes in TP concentrations between macrophyte and phytoplankton sediments (LA-9, LA-2H and LA-6H; Table 2). The increase in P loading to this historically P-limited system produced an increase in sedimentation because the highly organic sediments are largely derived from phytoplankton production. Cores dated by ^{210}Pb indicate that sedimentation rates increased at least ~3-fold

after P enrichment to Lake Apopka (Schelske 1997). Thus, our estimated increase in P loading based on TP concentrations and sedimentation rates (~8.1-fold) exceeds the independent estimate (~7-fold), but does not consider the expected increase in the P-retention coefficient associated with the development of phytoplankton dominance in a highly enriched environment (Schelske 1997; Schelske et al. 2000; Kenney et al. 2001). During the recent period of maximum loading, P-retention in the sediments accounts for at least 65% of the external P load to Lake Apopka (Schelske et al. 2000; Battoe et al. 1999).

The TP stratigraphy of Newnans Lake differed from other study lakes because TP concentrations decreased in the surface sediments (Figure 5). The rate of TP accumulation, however, increased 4- or 5-fold over the past ~125 yr because the mass sedimentation rate increased dramatically (Brenner and Whitmore 1998). Water column data show a high ratio (> 2) of chl-a to TP (Table 1). We speculate that nutrient-efficient biomass production by the diazotrophic cyanobacterium, *Cylindrospermopsis raciborskii* (Chapman and Schelske 1997), was a major source of organic matter that diluted sediment TP concentrations during a period of increasing trophic state.

We demonstrated that cluster analysis using appropriate paleolimnological variables may identify changes in sediment organic matter source and detect historic changes in PPCS (Figure 6). In general our results agree with the shallow lakes model of Scheffer et al. (1993) and Moss et al. (1996), but in our lakes intermediate TP concentrations are associated with transitional sediments. These transitional sediments have a distinct BSi$_{Sponges}$ signature that cannot be explained by a simple mixture of phytoplankton and macrophyte sediments. We infer that in these shallow lakes, three PPCS can be ordered along a gradient of increasing sediment TP concentration: predominantly macrophyte, transitional (macrophyte with an increasing proportion of phytoplankton), and predominantly phytoplankton (Figure 6). With the exception of Little Lake Jackson, the smallest study lake (0.6 km^2), the lakes were too large (> 30 km^2) to reasonably expect short-term alternations or shifts in the PPCS. We hypothesize that these large systems had transitional periods characterized by a diverse and variable PPCS at sites throughout the lake. Because of its relatively small size (Table 1), Little Lake Jackson may shift to phytoplankton dominance more rapidly than the other study lakes and thus had the fewest (1 of 30) transitional sediment samples (Figures 2–4). In the other four lakes, the percentage of samples classified as transitional sediments ranged from 14% to 47%. Cores from Lake Apopka, the largest lake (125 km^2), had variable thickness of phytoplankton and transitional sediments (Figure 3), suggesting spatial variability in the gradual shift to phytoplankton dominance.

Conclusions

Sediment records of TP, BSi$_{Sponges}$, and TC:TN from these five shallow Florida lakes show increasing contributions from phytoplankton to sediment organic matter as a result of anthropogenic P enrichment. With paleolimnological techniques and k-means cluster analysis, we inferred the relative magnitude of historic P enrichment and associated change in the PPCS. Inferences of historic P loading based on sediment TP concentrations in our lakes are conservative, because sedimentation rates have increased during the past century in all of the study lakes (Cable et al. 1997; Schelske 1997; Whitmore and Brenner 1997; Brenner and Whitmore 1998; Brenner et al. 1999). Our approach may be improved by combining cross-lake cluster analysis of sediment characteristics with site-specific sediment dating models. It will be necessary to quantify changes in sediment accumulation rates to refine estimates of the increased P loading associated with the shift from macrophyte dominance to phytoplankton dominance. Because of their large size and relatively rapid historic P enrichment, four of our study lakes apparently represent a subset of shallow lakes as described by current models (Scheffer et al. 1993; Moss et al. 1996). In these Florida lakes, PPCS shifted to phytoplankton dominance with no record of lake-wide alternating stable states or of lake-wide phytoplankton dominance before anthropogenic disturbance.

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