

## The use of sedimentary algal pigments to infer historic algal communities in Lake Apopka, Florida

Matthew N. Waters<sup>1,2,\*</sup>, Claire L. Schelske<sup>1,3</sup>, William F. Kenney<sup>1,3</sup> and Andrew D. Chapman<sup>1,4</sup>

<sup>1</sup>Department of Fisheries and Aquatic Sciences, University of Florida, USA; <sup>2</sup>Department of Environmental Sciences and Engineering, University of North Carolina, Chapel Hill, NC 27599, USA; <sup>3</sup>Department of Geological Sciences, Land Use and Environmental Change Institute, University of Florida, Box 112120, Gainesville, FL 32611, USA; <sup>4</sup>GreenWater Labs/BCI Engineers & Scientists, Inc., 205 Zeagler Dr., Suite 302, Palatka, FL 32177, USA; \*Author for correspondence (e-mail: mnwaters@email.unc.edu)

Received 24 January 2004; accepted in revised form 3 July 2004

**Key words:** Biogenic silica, Cyanobacteria, Diatoms, Eutrophication, Phosphorus, Polyphosphate

### Abstract

The primary producer community of Lake Apopka, a large (125 km<sup>2</sup>), shallow (mean depth, 1.7 m), polymictic Florida lake, shifted from macrophyte dominance to phytoplankton dominance in the 1940s. Today, frequent wind resuspension of highly organic, unconsolidated sediments supports a meroplanktonic community that is predominantly diatoms, but during calm periods the algal community is dominated by planktonic cyanobacteria. Sedimentary algal pigments (chlorophyll derivatives and carotenoids) and chemical proxies for nutrient enrichment (polyphosphate, total phosphorus and biogenic silica) in three sediment cores were used to investigate historic changes in primary producers. Sediments were separated into three stratigraphic zones using multivariate statistical techniques. Stratigraphic zonation was established in each core although sediment deposition at one site was insufficient to adequately resolve temporal changes. These results show the importance of selecting suitable sites for paleolimnological studies. The oldest zone represents macrophyte-derived sediments, and the two overlying zones represent phytoplankton-derived sediments deposited since the 1940s. Algal pigments in the most recent sediment zone show little degradation, which might be due to the presence of viable meroplankton in the sediment. After the initial primary producer shift from macrophytes to phytoplankton, the lake experienced a short period of cyanobacterial dominance followed by a period of benthic diatom abundance before being replaced by the present algal community consisting of cyanobacteria and meroplanktonic diatoms. Chlorophyll derivatives and carotenoids were highly correlated with total phosphorus. Historic trends inferred from the data include algal and cyanobacterial productivity that increased with increased phosphorus loading. The study demonstrates that valid paleolimnological proxies for historic eutrophication are available in loosely consolidated sediments of shallow, subtropical lakes.

### Introduction

Sedimentary algal pigments provide information about historic algal communities (Leavitt and

Hodgson 2001). Pigments have been used successfully to infer changes in trophic state, cyanobacterial abundance, hypolimnetic oxygen concentrations and lake primary productivity

(Engstrom et al. 1985). Although pigments have proven to be an important paleolimnological tool, interpretation of raw data is often complicated by post-depositional environmental factors (Leavitt and Hodgson 2001). Sedimentary pigments include chlorophyll derivatives (CD), a proxy for algal chlorophyll, and total carotenoids (TC), a proxy for algal biomass. The CD/TC ratio has been used to evaluate aerobic degradation (Rybak 1988) and relative changes in cyanobacterial abundance in the algal community (Wetzel 1970). Specific cyanobacterial carotenoids such as oscillaxanthin (OSC) and myxoxanthophyll (MYX) can be used to infer changes in cyanobacterial populations. OSC occurs in the genera *Oscillatoria* and *Arthrospira* (Feuillade et al. 1995) and has been used to infer eutrophication associated with blooms of *Oscillatoria* spp. (Griffiths and Edmondson 1975). *Oscillatoria* species are among the first cyanobacteria to occur in newly eutrophic lakes (Swain 1985). MYX is a mixture of MYX and aphanizophyll and is widespread among cyanobacteria. MYX and OSC can provide sediment records of water-column cyanobacterial shifts (Engstrom et al. 1985; Sabater and Haworth 1995).

Sedimentary pigments have been used primarily to infer lake eutrophication histories and algal community shifts in deep, northern temperate lakes (Engstrom et al. 1985; Lami et al. 1994; Feuillade et al. 1995). Very little research has utilized this paleolimnological technique to investigate the eutrophication of shallow, subtropical lakes characteristic of Florida. The primary producer community in this lake shifted from macrophytes to phytoplankton in the 1940s (Schelske and Brezonik 1992). The shift in primary producer community structure has been investigated in several paleolimnological studies. Physical characteristics, total carbon/total nitrogen (TC/TN) ratio of organic matter (Schelske et al. 1999), diatom and sponge spicule biogenic silica (BSi) concentrations (Schelske 1997; Kenney et al. 2002), polyphosphate (PolyP) (Kenney et al. 2001), and total phosphorus (TP) accumulation (Schelske 1997) changed with the shift in the primary producer community from macrophytes to phytoplankton. Three microfossil diatom assemblages have been identified in sediments deposited in Lake Apopka during the 20th century (Schelske et al. 1999), but little is known about changes in

cyanobacteria. In this study, we used sedimentary pigments and chemical proxies to investigate algal community changes and eutrophication of Lake Apopka.

It is generally agreed that the primary producer community in Lake Apopka shifted rapidly from macrophyte dominance to phytoplankton dominance in the late 1940s (Schelske and Brezonik 1992). Different viewpoints, however, have been advanced about causal factors responsible for the shift and its timing and about development of hypereutrophy (Schelske et al. 2000). One disagreement is whether a hurricane in 1947 uprooted dominant submersed macrophytes that were then replaced by phytoplankton within a few days or weeks (Bachmann et al. 1999, 2001). Analysis of hurricane tracks does not support this contention (Lowe et al. 1999). This contention is also challenged by questions about why a specific hurricane and not earlier ones caused the 1947 shift in primary producers (Lowe et al. 1999). A second disagreement concerns the role of sediments and sediment resuspension. It has been proposed that internal nutrient loading from sediment liquefaction and resuspension is the major source of phosphorus loading to the lake and that external nutrient sources are relatively unimportant (Bachmann et al. 1999). Given this scenario, restoration of the lake would be highly problematic, a conclusion that has been challenged (Lowe et al. 2001; Schelske and Kenney 2001). In addition, a phosphorus budget for the lake in the 1990s shows that 85% of the external phosphorus loading was drainage from agricultural sources (muck farms) that were not present until the 1940s (Lowe et al. 1999). In addition, a large increase in TP loading has been inferred from paleolimnological studies (Kenney et al. 2001, 2002). A third disagreement is whether resuspended sediments provide a source of organic matter for 'internal heterotrophy' (Bachmann et al. 2000). Given high levels of autotrophic phytoplankton primary production, diurnal oxygen changes are not adequate to support the proposed importance of heterotrophic metabolism (Schelske et al. 2003). Finally, a new analysis provides a scenario in which the abrupt shift in primary producer structure is related to hydrologic and landuse changes in floodplain wetlands (Schelske et al. accepted). Drainage of the wetlands for agricultural production increased phosphorus loading and established phosphorus

concentrations at discharge points in the lake that exceeded the maximum threshold for macrophyte dominance in the 1940s (Scheffer et al. 1993).

Objectives for this paleolimnological study of Lake Apopka were to (1) identify stratigraphic sediment zones using multivariate statistical techniques and (2) investigate the relationship between historic P loading and changes in the algal community inferred from sedimentary algal pigments and nutrients. We studied three sediment cores and identified three stratigraphic zones in each core. Differences in stratigraphic depths among cores show the importance of utilizing multiple cores in paleolimnological studies. We found that algal and cyanobacterial productivity increased with increased phosphorus loading, that algal pigments in recent sediment had undergone little degradation possibly because viable meroplankton were present and that pigments and nutrients were valid proxies for nutrient enrichment in this shallow, subtropical lake provided suitable coring sites were selected.

## Methods

Lake Apopka is a large (125 km<sup>2</sup>), shallow (1.7-m mean depth), polymictic lake in north central Florida. The lake's large area and shallow depth are characteristics that favor frequent wind resuspension of bottom sediments and meroplanktonic diatoms (Carrick et al. 1993). Meroplanktonic diatoms resuspended from an aphotic benthic environment are most abundant during turbulent periods, whereas the algal community during calm periods is dominated by cyanobacteria (Carrick et al. 1993; Carrick and Schelske 1997). A seasonal cycle in chlorophyll *a* and primary production is not apparent because temporal dynamics of algal communities are influenced by meteorological factors that affect resuspension of sediments and meroplankton (Schelske et al. 1995; Schelske et al. 2003). Due to high historic P loading, Lake Apopka has become hypereutrophic (Schelske et al. 2000) with long-term means (1987–1997) for total phosphorus (TP) and total nitrogen (TN) of 204 µg P/L and 5.14 mg N/L, respectively (Battoe et al. 1999). Long-term means for phytoplankton biomass (chlorophyll *a*, 92 µg/l) and Secchi disc transparency (23 cm) reflect this high degree of nutrient enrichment (Battoe et al. 1999). Phyto-

plankton have become secondarily nitrogen limited (Aldridge et al. 1993) and store surplus P as polyphosphate because of excessive P loading (Newman et al. 1994; Kenney et al. 2001).

Three sediment cores were collected from Lake Apopka in the spring of 1999 using a piston corer (Fisher et al. 1992). Stations LA-2H, LA-9, and LA-25 were chosen to provide spatial coverage in the lake basin (Figure 1) and a range in sedimentation rates among stations (Schelske 1997). Cores were sectioned in the field at 4-cm intervals and returned to the laboratory in Gainesville, Florida. Each section was subsampled for pigment (chlorophyll *a*, pheophytin, CD, TC, MYX, and OSC) and polyphosphate (PolyP) analysis and a subsample of the remaining wet sediment was frozen and then freeze-dried. Loss on ignition (LOI), total phosphorus (TP) and diatom biogenic silica (DSi) were determined on freeze-dried sediment samples.

Loss on ignition was determined by burning dry, pre-weighed sediment in crucibles at 550 °C in a SYBRON/Thermolyne muffle furnace for 2 h and reweighing (Hakanson and Jansson 1983).

Total phosphorus was measured as orthophosphate after persulfate digestion following Standard Methods (Schelske et al. 1986; APHA 1989). Polyphosphate was determined by adding a known volume of deionized water to weighed, wet sediment and sequentially measuring water soluble P (H<sub>2</sub>O-P) after shaking the samples in a shaker bath for 20 h and then again after autoclaving (Kenney et al. 2001). Polyphosphate equals the P concentration after autoclaving minus H<sub>2</sub>O-P. Biogenic silica was extracted following Conley and Schelske (1993). Phosphorus and silica were measured using a segmented flow autoanalyzer and an electronic data acquisition system.

Pigments were measured using the methods in Swain (1985). All extractions were performed in

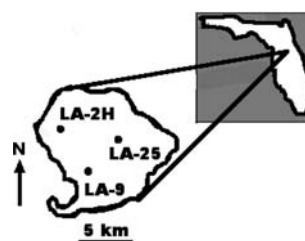


Figure 1. Map of Lake Apopka showing locations of three coring stations.

low light. Pigments were extracted sequentially from approximately 10 g of wet sediment with two 40-ml and one 20-ml aliquots of 90% acetone (100-ml final volume). Each aliquot was added to the wet sediment in a 125-ml polypropylene bottle and shaken in a shaker bath for 15 min at room temperature. The acetone extract was separated from the sediment by centrifugation for 20 min and collected with a pipette. Pigments extracted in acetone were measured using a Hitachi U-2000 spectrophotometer and Beckman 5 cm quartz cells except 1 cm quartz cells were used for OSC and MYX.

Methods for CD, TC, %NC, OSC and MYX followed those described by Swain (1985). Chlorophyll *a* and pheophytin were also determined using absorbance at 665 nm before and after acidification to 0.003 M with HCl (APHA 1989). Pigments were normalized to organic matter so data are not skewed by variable mineral deposition (Swain 1985).

Sediments from Lake Apopka were not dated because land-use and hydrologic changes in the lake basin created conditions that violate assumptions of  $^{210}\text{Pb}$ -dating models (Schelske et al. accepted). Specifically, levees constructed along the north shore in the 1940s allowed the drainage of approximately 40% of the original wetland/lacustrine system. This drainage of wetlands reduced the lake surface area. In addition, the Apopka-Beauclair Canal completed in the late 1890s lowered lake stage approximately 1.0 m and established a permanent outflow.

Sedimentary signals for the 1947 shift from macrophyte dominance to phytoplankton dominance are well established. Dry weight fraction, TC/TN ratio, and TP concentration provide proxies for the shift (Schelske 1997; Schelske et al. 1999). The resulting discontinuities in the sediment record are time dependent and are used to establish a 1947 horizon that can be correlated among cores in the lake basin. Sediment dry mass deposited above this horizon can be used to model sedimentation rates if it is assumed to represent sedimentation since 1947.

Variables for the *k*-means cluster analysis were determined using principal component analysis. The variables, TP-PolyP, PolyP, CD, and DSi accounted for >97% of the variance in the first two principal components as determined by a principal component analysis on the data from all

three cores using the JMP Version 3.2.2, Statistical package (SAS 1995).

Core data were grouped using *k*-means cluster analysis from the JMP Version 3.2.2, Statistical package (SAS 1995). This cluster analysis uses a specified number of cluster seed points and repetitively groups data to minimize standard deviations of means for each group. Three clusters were selected because three sediment zones (macrophyte-derived sediments and two microfossil diatom communities in phytoplankton-derived sediments) were identified previously (Schelske et al. 1999).

Rejuvenation experiments were used to determine whether viable algae were present in Lake Apopka sediments and if so whether the species composition changed with sediment type. Sediments from 12, 16, 32, 68, and 120 cm in LA-2H-99 and 12, 16, 24, 48, and 76 cm in LA-25-99 were used in the experiment. Sample depths were chosen to represent all sediment types identified with *k*-means cluster analysis.

To obtain water for the rejuvenation experiment, Lake Apopka water was filtered through 5-, 1-, and 0.2- $\mu\text{m}$  filters to remove particulate matter including phytoplankton. The 5- $\mu\text{m}$  filter was a TELEDYNE WATER PIK Instapure IR-20 in an AMETEK filter, and the 1- and 0.2- $\mu\text{m}$  filters were Gelman Sciences Polycaps. A Gelman Sciences pressure vessel provided a pressure <80 kPa to minimize lysing. Major nutrient concentrations in the filtered water were 0.008 mg TP/L, 4.47 mg TN/L, and 2.95 mg  $\text{SiO}_2$ /L. No attempt was made to measure soluble nutrients other than silica that were added to the water with the sediment.

For the experiments, filtered water (400 ml) and wet sediment (1–5 g), equivalent to approximately 1 g dry weight, were added to 500-ml Erlenmeyer flasks. The flasks were incubated in a Percival E-30B incubator at 26 °C with a 14/10-h light/dark cycle for 4 weeks. To obtain growth responses, *in vivo* fluorescence (IVF) with pheophytin correction was measured daily on subsamples using a Turner Designs TD-700 fluorometer and normalized to dry weight of added sediment. Flasks were mixed each day prior to subsampling. Subsamples also were collected weekly and preserved in Lugols solution for direct counts of algae. No growth response was obtained from incubation of filtered water alone.

## Results

### Stratigraphic clusters

Three zones (C1, C2 and C3) with stratigraphic continuity were identified from cores LA-9-99, LA-2H-99, and LA-25-99 using cluster analysis based on TP-PolyP, PolyP, CD and DSi. Zones C1 and C2 are phytoplankton-derived sediments deposited over macrophyte-derived sediments in zone C3. Phytoplankton-derived sediments in LA-9-99, LA-2H-99 and LA-25-99 extended to 76, 92, and 16 cm, respectively, and represent the sediment deposited since the primary producer community shift in 1947. Phytoplankton-derived sediments in LA-25-99 found only to a depth of 16 cm minimize the temporal resolution of algal community shifts since 1947. Results from this core, therefore, will be used to verify stratigraphic patterns and will not be utilized extensively for inferences about historical changes. Differences among the cores point to the importance of using lake-basin surveys to identify suitable coring sites (Whitmore et al. 1996; Schelske 1997).

Relative differences in TP-PolyP, PolyP and CD increased from C3 to C1 (Figure 2). Polyphosphate concentrations in C1 were eight times greater than C2 showing that PolyP was deposited primarily in the most recent zone. Diatom silica

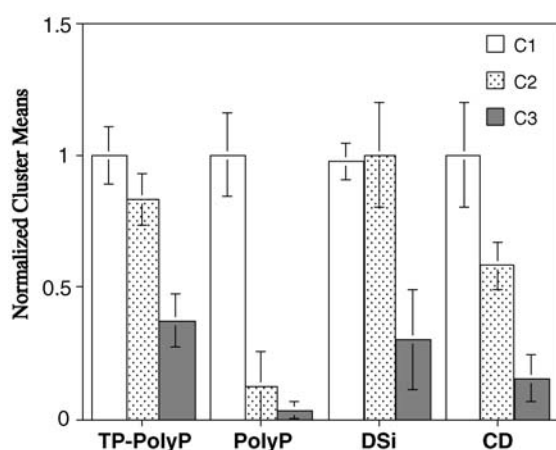


Figure 2. Relative differences between clusters for the four variables used in cluster analysis of sediment samples from Lake Apopka. Cluster means were normalized to the maximum cluster mean for each variable. Error bars represent one standard deviation above and below the mean.

concentrations were not statistically different in C1 and C2 but were smaller in C3.

Relative differences in TC, OSC, MYX, CD/TC and TP increased from C3 to C1 (Figure 3). Mean %NC in C2 and C3 was not statistically different and was three times greater in C1 relative to C2 and C3. The CD/TC ratio was similar in C1 and C2 but smaller in C3 much like the pattern for DSi (Figure 2). Although OSC and MYX increased from C3 to C1, the standard deviations in C1 were extremely high relative to the other variables in all zones.

### Core descriptions and physical characteristics

All three cores were composed of dark organic sediment with little visible stratigraphy other than two shell layers in LA-9-99 at 76 and 156 cm.

Dry/wet ratios were  $< 0.05$  in the flocculent, phytoplankton-derived sediments and ranged to as large as 0.12 in the macrophyte-derived sediments at LA-9-99 and LA-25-99 (Figure 4). Macrophyte-derived sediments at LA-2H-99 were less consolidated than at the other stations with a wet/dry ratio of approximately 0.06. Macrophyte fibers occurred in samples below 68, 96, and 16 cm in cores LA-9-99, LA-2H-99 and LA-25-99, respectively.

Loss on ignition increased upcore in the phytoplankton-derived sediments from 58 to 72% in

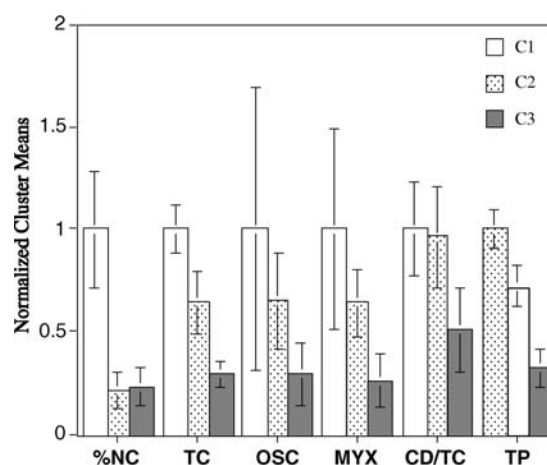


Figure 3. Relative differences between clusters for the six variables not used in the cluster analysis of sediment samples from Lake Apopka. Cluster means were normalized to the maximum cluster mean for each variable. Error bars represent one standard deviation above and below the mean.

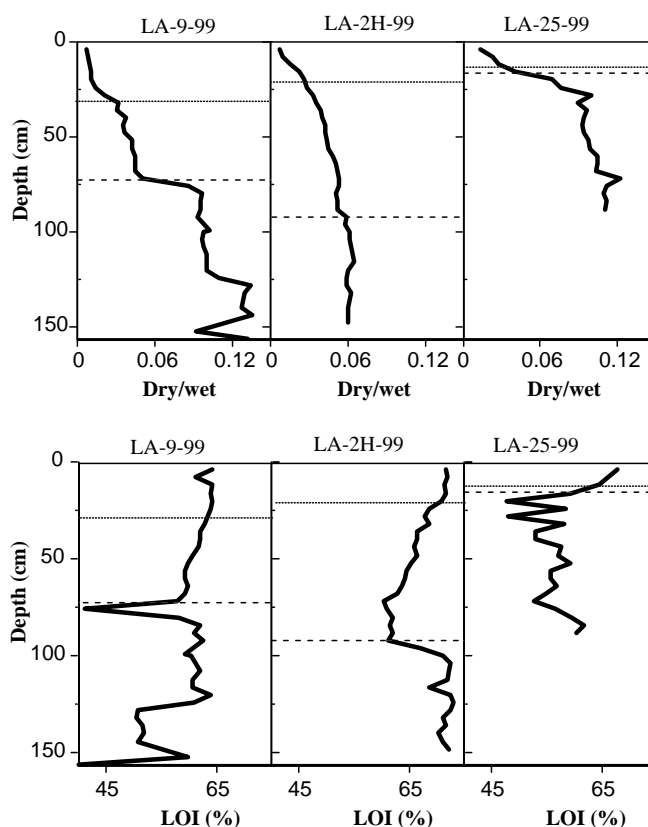


Figure 4. Zonation of dry/wet ratio (top) and loss on ignition (bottom) vs. depth in sediment cores LA-9-99, LA-2H-99 and LA-25-99 from Lake Apopka. Boundaries for three sediment zones identified by *k*-means cluster analysis are shown. The dotted line represents the boundary between zones C1 and C2, and the dashed line represents the boundary between zones C2 and C3. Zones C1 and C2 represent phytoplankton-derived sediments and zone 3 represents macrophyte-derived sediments.

LA-9-99 and LA-2H-99 (Figure 4). Mean LOI in these sediments was 64.1% (SD = 3.8). Loss on ignition in the two shell layers at 76 and 156 cm in LA-9-99 was 41 and 38%, respectively.

#### Chemical proxies

Polyphosphate was near the limit of detection in C3 and increased from this baseline in all three cores to approximately 0.2 mg/g in C1 (Figure 5). Polyphosphate increases began at the bottom of C2 for LA-9-99 and two samples below the C1 and C2 boundary for LA-2H-99. High values characterized C1 for all cores.

Total phosphorus increased from baseline conditions in C3 of all three cores and then increased generally in C2 for both LA-9-99 and LA-2H-99 (Figure 5). Maximum values for all three cores were found in C1.

The depth distribution of DSi varied among the three cores (Figure 5). In LA-9-99 and LA-2H-99, DSi is largest at depth in C2 with a decrease in the upper part of C2. Diatom silica then increases below the C1 and C2 boundary to a larger concentration in C1.

#### Pigment proxies

Percent native chlorophyll was larger in C1 than in C2 and C3 in all cores (Figure 6). Percent native chlorophyll was similar in C2 and C3 for all cores with a mean of 18.5% (SD = 7). In LA-2H-99 %NC increased upcore in C1, but in C1 of LA-9-99 %NC was similar throughout the cluster. Maximum percentages were 103, 137, and 85% in C1 of cores LA-9-99, LA-2H-99, and LA-25-99, respectively. Percentages greater than 100 can be explained through a sensitivity analysis of the

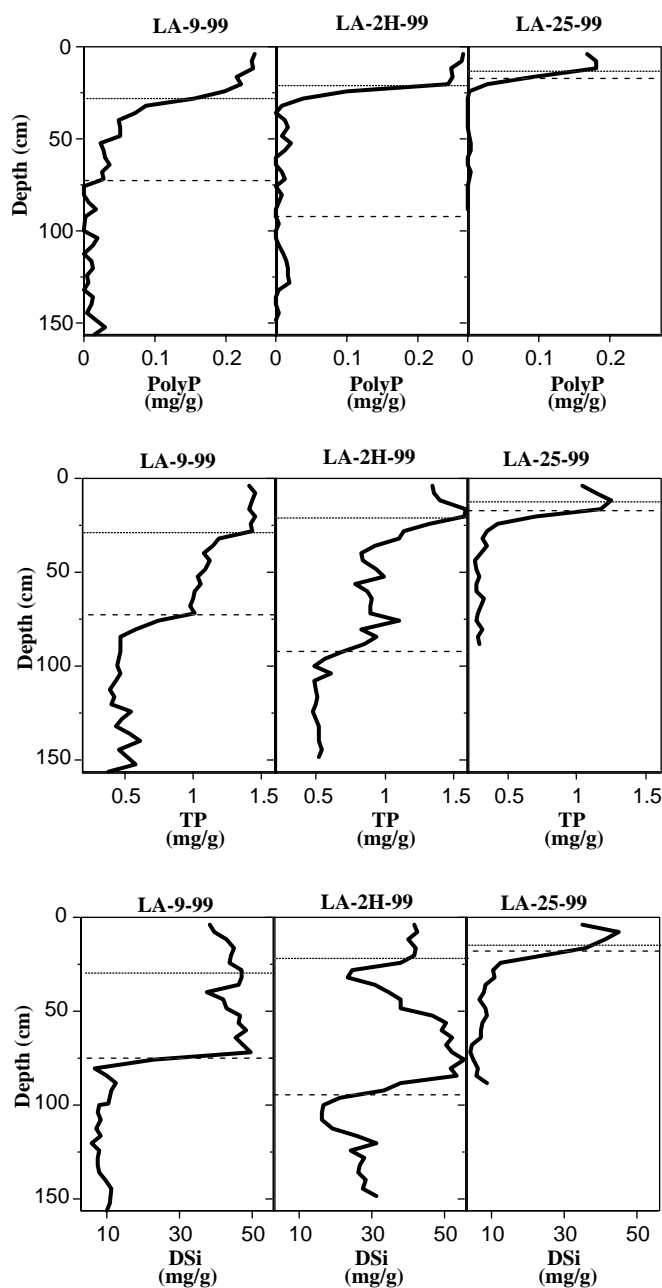


Figure 5. Zonation of polyphosphate (PolyP) (top), total phosphorus (TP) (middle) and diatom silica (DSi) (bottom) vs. depth in sediment cores LA-9-99, LA-2H-99 and LA-25-99 from Lake Apopka. See Figure 4 for additional explanation.

665A measurement. Altering the 665A-absorbance reading by 0.002 and 0.004 (approximately 2.9 and 7.1%, respectively) reduces the 103 and 137% below 100%, respectively.

CD and TC levels increased upcore in all cores from baseline conditions near the top of C3 (Fig-

ure 6). Both pigments varied in C2 with an overall increase up core. CD and TC increased from the top two samples of C2 throughout C1 in LA-9-99 and LA-2H-99. Chlorophyll derivatives and TC correlated with an  $r^2$  of 0.82. The CD/TC ratio was lowest in C3 in all three cores (Figure 7). In

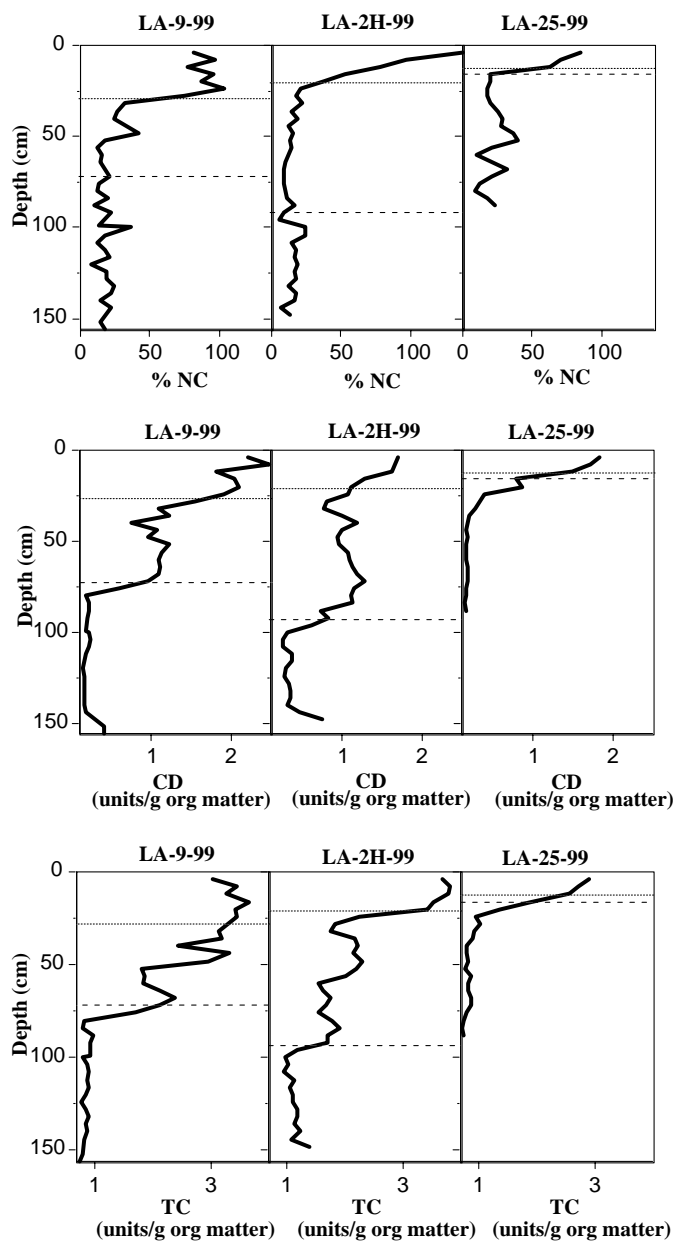


Figure 6. Zonation of percent native chlorophyll (%NC) (top), chlorophyll derivatives (CD) (middle) and total carotenoids (TC) (bottom) vs. depth in sediment cores LA-9-99, LA-2H-99 and LA-25-99 from Lake Apopka. See Figure 4 for additional explanation.

C2 the CD/TC ratio varied with a maximum in the lower half of the zone in both LA-9-99 and LA-2H-99. A maximum was also found in C1 of LA-9-99, but not in LA-2H-99.

Levels of OSC varied throughout all clusters, but generally increased from C3 to C1 (Figure 7). Cluster 1 of LA-9-99 was a region of high values

for OSC with maximum values that were two times greater than the maximum values in the other two cores.

Like OSC, MYX levels varied throughout all clusters but increased from C3 to C1 LA-9-99 and LA-2H-99 (Figure 7). Peaks in MYX occurred in C2 and C1 of LA-9-99. In LA-2H-99, MYX con-

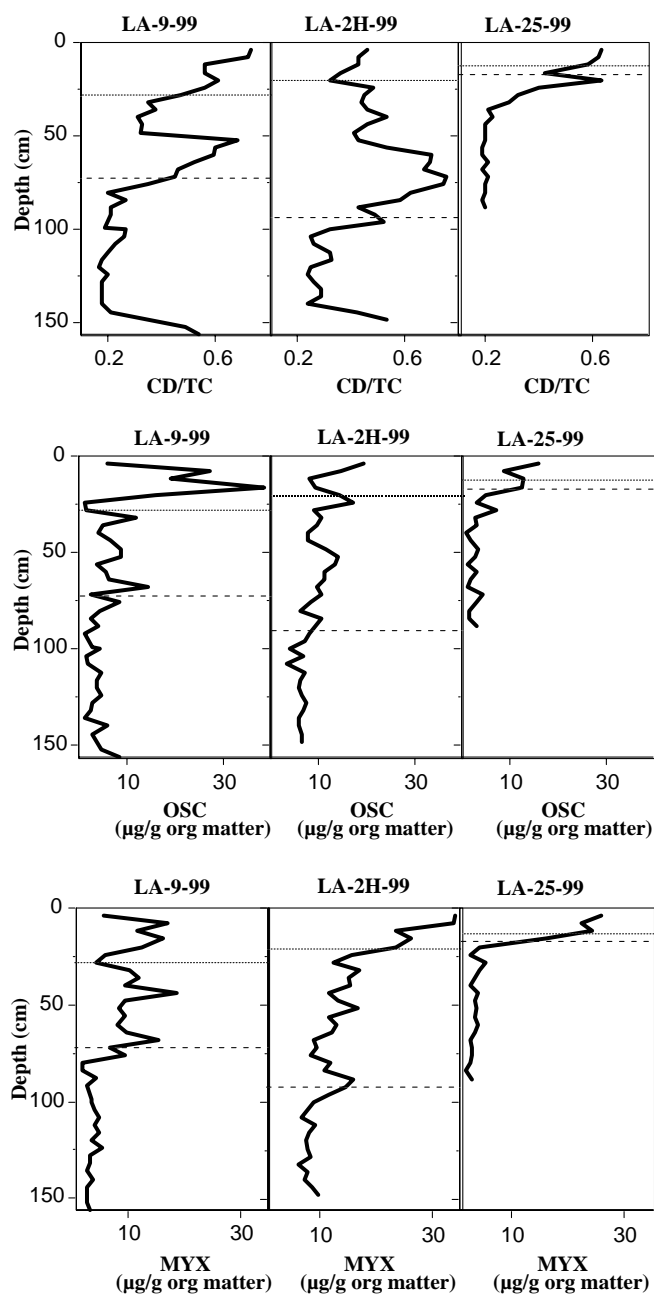


Figure 7. Zonation of CD/TC (top), OSC (middle) and MYX (bottom) vs. depth in sediment cores LA-9-99, LA-2H-99 and LA-25-99 from Lake Apopka. See Figure 4 for additional explanation.

centrations in C1 were greater than those in LA-9-99 with the highest concentration in the top two samples.

Several variables were statistically correlated with PolyP and TP indicating a strong relationship

between sedimentary algal pigments and P loading. Polyphosphate strongly correlated with %NC ( $r^2 = 0.79$ ). Total phosphorus showed a strong correlation with CD ( $r^2 = 0.82$ ) and TC ( $r^2 = 0.88$ ) (Figure 8).

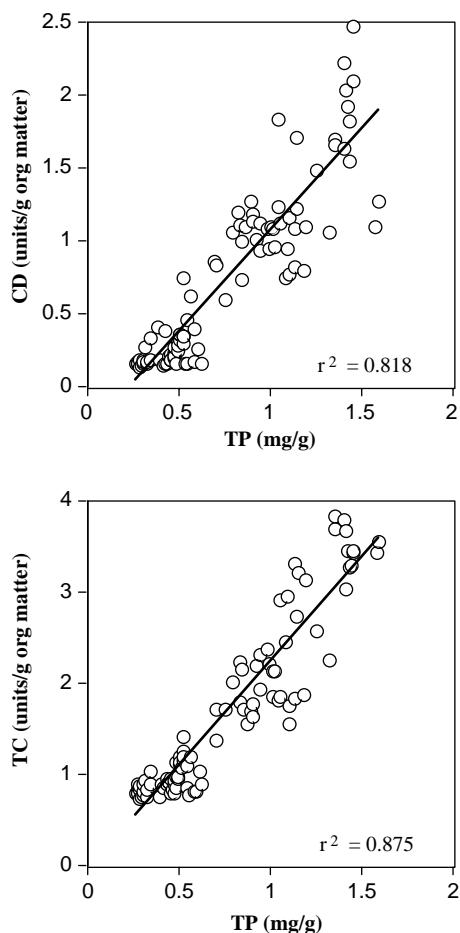


Figure 8. Linear regression of CD vs. total phosphorus (TP) and total carotenoids (TC) vs. TP in Lake Apopka sediments. Combined data from cores LA-9-99, LA-2H-99 and LA-25-99.

#### Rejuvenation study

The time course of algal response in the rejuvenation experiments varied from measurable responses within 7 days for some samples to minimal or no response in 28 days for other samples (Figure 9). Lag times for responses in both cores increased with sample depth and by stratigraphic zone. Algal communities from C1 (12 and 16 cm for LA-2H-99, 12 cm for LA-25-99) responded within the first week of incubation for both cores. Algal communities from C2 (32 and 68 cm for LA-2H-99, 16 cm for LA-25-99) responded during the first 3 weeks of incubation. Algal communities from C3 for LA-2H-99 (120 cm) also responded in 3 weeks, whereas those

from C3 for LA-25-99 (24, 48 and 76 cm) showed only a relatively small response after 4 weeks.

To identify algal populations associated with IVF growth responses, cell counts were determined from preserved subsamples for the maximum response periods (Table 1). The major dominant species varied among periods. The cyanobacterium *Pseudanabaena* spp. and diatoms *Navicula/Fragilaria* spp. dominated C3 for both cores. The cyanobacterium *Planktolyngbya* spp. also occurred in C3. In C2, *Navicula/Fragilaria* spp. and *Planktolyngbya* were the dominant species with *Pseudanabaena* spp. and the meroplanktonic diatom, *Aulacoseira* spp. occurring as well. *Planktolyngbya* spp. and *Aulacoseira* spp. were the dominant taxa in C1 for both cores.

#### Discussion

##### Stratigraphic zonation of sediments

Three stratigraphic zones in sediment cores from Lake Apopka, one zone of macrophyte-derived sediments (C3) and two zones of phytoplankton-derived sediments (C1 and C2), were identified with cluster analysis using TP-PolyP, PolyP, DSi, and CD as variables. Three sediment types were also described using diatom microfossil community structure (Schelske et al. 1999) and TP, sponge biogenic silica and TC/TN ratios. Kenney et al. (2002) also found three sediment types in Lake Apopka in a cross-lake study of Florida lakes. All the proxies from our study demonstrated stratigraphic shifts at one or both of the cluster breaks with TP, CD and TC best describing the three sediment zones (Figures 5 and 6).

Results from the cluster analysis also demonstrate the effects of varying sedimentation rates on the sediment record. Phytoplankton-derived sediments were found only to a depth of 16 cm in LA-25-99. This short record of sediments deposited since 1947 limits the possibility of resolving temporal events. The thickness of the C1 zone is greater in LA-9-99 than in LA-2H-99, but the thickness of C2 sediments is greater in LA-2H-99. The varying thickness for each sediment zone suggest that sedimentation processes such as deposition rate and resuspension are site-specific and may have changed between the periods represented by C2 and C1. Sedimentation patterns

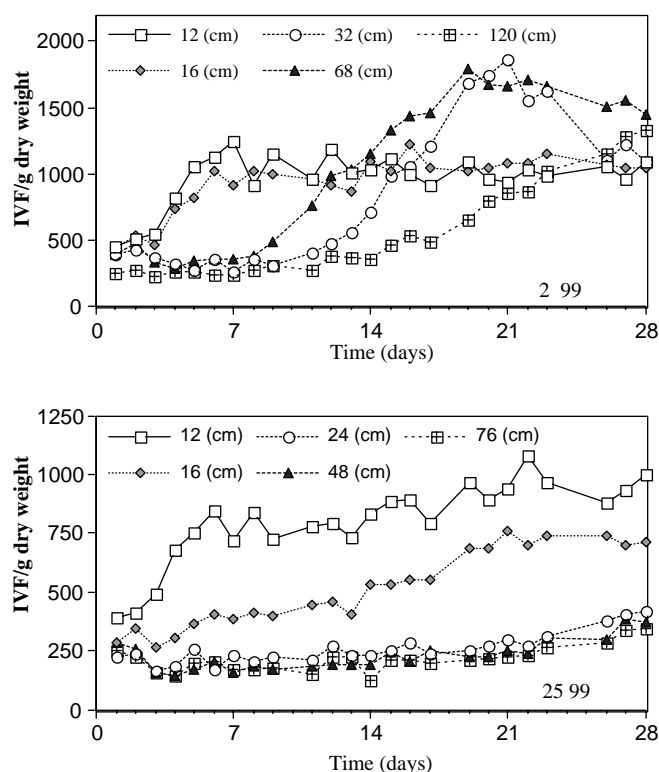


Figure 9. Results of bioassays of sediment samples from Lake Apopka sediment cores LA-2H-99 and LA-25-99. *In vivo* fluorescence (IVF)/g dry weight vs. time for samples from selected depths.

vary over the lake basin such that 46 coring stations could be separated into erosional, transitional and depositional sites (Schelske 1997). This variability in sedimentation rate of phytoplankton-derived sediments between cores points to the potential utility for multiple cores in paleolimnological investigations.

Approximate ages were determined for the C1 zone in LA-9-99 and LA-2H-99 using models based on cumulative dry mass that assumed C1 and C2 sediments were deposited from 1947 to 1999. A fourfold annual sedimentation rate increase (Schelske 1997) and a constant sedimentation rate were used in the model. The range in the age of C1, the most recent zone of phytoplankton-derived sediments, was 2–4 years for LA-9-99 and 3–6 years for LA-2H-99.

#### *The role of phosphorus enrichment*

Effects of increasing P loading on primary producer community structure have been documented

in Lake Apopka as well as other shallow lakes (Scheffer et al. 1993; Schelske et al. 2000). Increased P loading from a citrus processing plant and sewage from the town of Winter Garden began in the 1920s. Development of muck farm agriculture in the 1940s greatly increased loading (Battoe et al. 1999; Schelske et al. 2000). The primary producer community in the lake shifted from macrophyte dominance to phytoplankton dominance in the 1940s and since then has remained phytoplankton dominated (Schelske et al. 2000). Changes in the diatom microfossil record and increased PolyP sedimentation were related to increased sedimentary TP concentration to infer that P loading drove the primary producer community shift (Schelske et al. 1999; Kenney et al. 2001). Correlations between TP and CD and TP and TC for our paleolimnological study provide additional evidence of the influence of P loading on increased algal abundance and production. Several lines of evidence show that increased P loading drove changes in the primary producer community in Lake Apopka.

Table 1. Major dominant algal species identified from rejuvenation experiments on Lake Apopka sediments.

Core	Depth (cm)	Cluster	Species	
LA-2H-99	12	C1	<i>Planktolyngbya contorta</i>	Cyanophyte
			<i>Aulacoseira</i> spp.	Bacillariophyte
			<i>Aphanocapsa</i> spp.	Cyanophyte
			<i>Scenedesmus</i> spp.	Chlorophyte
	16	C1	<i>Pediastrum</i> spp.	Chlorophyte
			<i>Planktolyngbya contorta</i>	Cyanophyte
			<i>Aulacoseira</i> spp.	Bacillariophyte
			<i>Planktolyngbya limetica</i>	Cyanophyte
	32	C2	<i>Pediastrum</i> spp.	Chlorophyte
			<i>Aphanocapsa</i> spp.	Cyanophyte
			<i>Navicula</i> / <i>Fragilaria</i> spp.	Bacillariophyte
			<i>Planktolyngbya contorta</i>	Cyanophyte
	68	C2	<i>Pseudanabaena moniliformis</i>	Cyanophyte
			<i>Aphanocapsa</i> spp.	Cyanophyte
			<i>Merismopedia punctata</i> .	Cyanophyte
			<i>Aphanocapsa cf. delicatissima</i>	Cyanophyte
	120	C3	<i>Navicula</i> / <i>Fragilaria</i> spp.	Bacillariophyte
			<i>Planktolyngbya undulata</i>	Cyanophyte
<i>Pseudanabaena moniliformis</i>			Cyanophyte	
<i>Planktolyngbya tallingii</i>			Cyanophyte	
LA-25-99	12	C1	<i>Navicula</i> / <i>Fragilaria</i> spp.	Bacillariophyte
			<i>Pseudanabaena</i> spp.	Cyanophyte
			<i>Aphanocapsa</i> spp.	Cyanophyte
			<i>Botryococcus</i> sp.	Chrysophyte
	16	C2	<i>Planktolyngbya tallingii</i>	Cyanophyte
			<i>Planktolyngbya contorta</i>	Cyanophyte
			<i>Aulacoseira</i> spp.	Bacillariophyte
			<i>Starastrum</i> sp.	Chlorophyte
	24	C3	<i>Aphanocapsa</i> spp.	Cyanophyte
			<i>Pseudanabaena</i> spp.	Cyanophyte
			<i>Planktolyngbya circumcreta</i>	Cyanophyte
			<i>Navicula</i> / <i>Fragilaria</i> spp.	Bacillariophyte
	48	C3	<i>Planktolyngbya tallingii</i>	Cyanophyte
			<i>Pseudanabaena</i> spp.	Cyanophyte
			<i>Pseudanabaena</i> / <i>Limnothrix</i>	Cyanophyte
			<i>Navicula</i> / <i>Fragilaria</i> spp.	Bacillariophyte
	76	C3	<i>Planktolyngbya contorta</i>	Cyanophyte
			<i>Pseudanabaena</i> spp.	Cyanophyte
<i>Planktolyngbya tallingii</i>			Cyanophyte	
<i>Pseudanabaena moniliformis</i>			Cyanophyte	
			<i>Pseudanabaena</i> / <i>Limnothrix</i> spp.	Cyanophyte
			<i>Planktolyngbya tallingii</i>	Cyanophyte
			<i>Pseudanabaena</i> sp.	Cyanophyte
			<i>Navicula</i> / <i>Fragilaria</i> spp.	Bacillariophyte

Samples were taken to represent the first period of maximum response. Subsamples from C1 were taken after week one of the study, C2 were taken after week three, and C3 were taken after week four. Subsample times were determined from Figure 9.

Three historic periods of increased P loading were inferred from cluster analysis of paleolimnological data. It is inferred from the TP record

that P loading was low throughout most of C3, the period of macrophyte dominance. Increased anthropogenic P loading from Winter Garden

sewage and citrus fruit processing in the 1920s is reflected by increased TP in the top samples of C3 in both LA-9-99 and LA-2H-99 (Figure 5). The increase in CD and TC in the same two samples as those for TP is an indication that the phytoplankton community responded to P loading (Figure 6). Diatom and cladoceran microfossils also increased in the most recently deposited macrophyte-derived sediments (Schelske et al. 1999; Shumate et al. 2002). Battoe et al. (1999) and Schelske et al. (2000) proposed that increased P loading prior to 1947 resulted in increased epiphytic and phytoplankton production and shading of the macrophyte community. Increases in TP, CD and TC at the top of C3 support the hypothesis that the primary producer shift began before 1947 and was driven by increased P loading.

In C2, TP concentrations are greater than in C3, and PolyP concentrations increased from baseline conditions. The PolyP increase in LA-9-99 and LA-2H-99 (Figure 5) supports the hypothesis of increasing P loading during the period represented by C2. Lowe et al. (1999) estimated that TP loading increased approximately sevenfold compared to pristine levels when the lake was macrophyte dominated. Polyphosphate is surplus available P stored by algae as intercellular PolyP bodies (Fitzgerald and Nelson 1966; Sakamoto and Inoue 1996). The increase of PolyP is an indication of excessive P loading and that some factor other than P was limiting algal growth (Kenney et al. 2001).

Maximum TP and PolyP concentrations in the sediment record characterize the period represented by C1. This is the period when P loading from muck farm agriculture reached the highest levels. Maximum PolyP concentrations (Figure 5) indicate that the algal community stored surplus P during this period (Kenney et al. 2001) and reflects experimental evidence that algal growth is nitrogen-limited (Aldridge et al. 1993). Maximum PolyP storage and nitrogen limitation of phytoplankton assemblages are ecological consequences of high P loading to Lake Apopka during C1.

Results of rejuvenation experiments can be related to historic changes in microfossil diatoms. Schelske et al. (1999) show that *Aulacoseira italica* represents approximately 80% of the microfossil diatoms in zone C1. This is the only common genus noted in rejuvenation experiments with sediments from zone C1 in cores LA-2H-99 and

LA-25-99 (Table 1). It was also found commonly in the 16-cm sample (zone C2) in LA-25-99, a sample that was near the boundary between the two zones. *A. italica* is meroplanktonic in Lake Apopka (Carrick et al. 1993). In the remaining samples from zones C2 and C3, *Navicula/Fragilaria* spp. were the dominant diatoms that were regenerated. Three species that were formerly in the genus *Fragilaria*, *Pseudostaurosira brevistriata* (Grun. in Van Heurck) Williams & Round, *Staurosirella pinnata* Ehrenb. and *Staurosira construens* (Ehrenb.) Williams & Round, may be lumped under *Fragilaria* in Table 1 (Schelske et al. 1999). These genera are epiphytic or benthic forms that were dominant when water transparency was high and were then replaced by *A. italica* as the lake became more eutrophic.

#### *Sedimentary pigment preservation*

Lack of knowledge about pigment degradation in sediments may confound using pigments as a proxy for historic algal communities (Swain 1985; Leavitt 1993). Hypolimnetic oxygen concentration, water-column turbulence, light penetration, bulk sediment accumulation rate and water temperature can be substantially different among lakes and influence pigment degradation (Leavitt 1993; Leavitt and Findlay 1994). Moreover, benthic algae are preserved in the sediment to a greater degree than planktonic algae that degrade during sinking (Steenbergen et al. 1994). Cyanobacterial pigments correlated positively with benthic algal production and inversely with lake productivity (Dickman and Han 1995). Increased pigment preservation has been attributed to rapid sinking of the diatom, *Aulacoseira* spp. (Feuillade et al. 1995). Percent native chlorophyll can be used to interpret whether shifts in the pigment concentrations are due to changes in preservation or pigment deposition. Zone C1 in Lake Apopka has high %NC, ranging from 38 to over 100%. High average %NC (82.5, SD = 23.1) and relatively low levels of pheophytin (Figure 10) in this region are indicators of lack of diagenesis in the sediment profile. Below this zone, pigments in C2 and C3 have been degraded as indicated by higher levels of pheophytin and lower %NC. In C2 and C3, the average %NC (18.5, SD = 7.4) is relatively constant and comparable to values in the

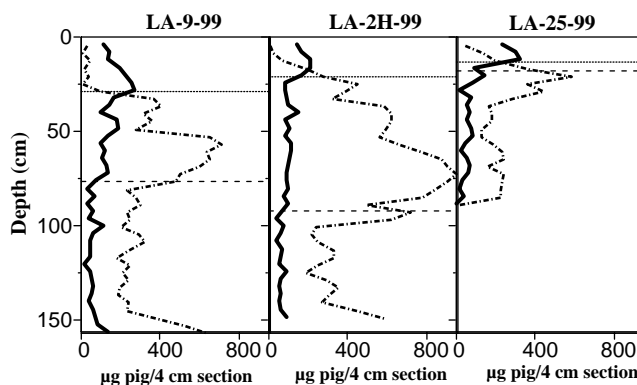


Figure 10. Zonation of chlorophyll *a* (solid line) and pheophytin (dashed line) vs. depth in sediment cores LA-9-99, LA-2H-99 and LA-25-99 from Lake Apopka. See Figure 4 for additional explanation.

literature (Swain 1985; Steenbergen et al. 1994; Feuillade et al. 1995).

Although previous pigment studies have shown non-degraded chlorophyll in surface sediment, the sediment record in Lake Apopka contains an extensive zone of low degradation (C1) that ranges from 12 to 28 cm and averages 20 cm deep in the three cores. This zone is reproducible across cores even at LA-25-99, a station with only 16 cm of C1 and C2 sediment. Swain (1985) stated that 'noisy data sets' could occur because recently deposited sediments contained variable but high percentages of NC. Leavitt (1993) describes a 'zone of degradation' in the top 1–3 cm of sediment where pigment content rapidly declines as a result of diagenesis. Shifts in %NC in the sediment record have been attributed to environmental changes in the lake basin (Leavitt 1993). In C1 of Lake Apopka high %NC occurs in recently deposited sediments with estimated ages ranging from 2 to 6 years for LA-9-99 and LA-2H-99. Because of their flocculent nature (dry/wet < 5%, Figure 4), the amount of mass may be comparable to the surficial sediments of the lakes studied by Swain (1985) and Leavitt (1993). Low pheophytin concentrations and high %NC in C1 are consistent with historic water-column data on Lake Apopka. Annual water-column pheophytin means for 1977, 1978 and 1990 were 21, 2 and 16  $\mu\text{g/l}$ , respectively, yielding %NC of 61, 96 and 80%, respectively, (Tuschall et al. 1979; Aldridge, unpublished). The %NC average of 82.5% in C1 is comparable to these water-column measurements. These data provide additional evidence that C1 is a zone of limited diagenesis.

High amounts of non-degraded chlorophyll *a* in C1 are supported by studies on the meroplanktonic community in Lake Apopka. Carrick et al. (1993) found chlorophyll levels ranging from 2942 and 4227  $\mu\text{g/l}$  in near-bottom water samples, large enough to double the chlorophyll *a* concentration in the water column during resuspension events. The dominant species in the meroplanktonic community is the diatom, *Aulacoseira italica*, which is also dominant in the diatom microfossil record from a 1995 LA-9 core (Schelske et al. 1999). *Aulacoseira* spp. was identified in the rejuvenation experiment for LA-2H-99 and LA-25-99. This genus remains viable in lake sediment for periods of years to decades (Lund 1954; Sicko-Goad et al. 1989). Carrick et al. (1993) proposed that other algal species in the meroplanktonic community also remain viable for extended periods. High %NC and low degradation would be expected if viable algae were present in the sediment. In Lake Apopka, high %NC is associated with flocculent sediments with estimated ages less than 6 years.

Limited pigment degradation in C1 confounds relative comparisons between sedimentary pigments in C1 with those in C2 and C3. Maximum levels of CD and TC in C1, therefore, cannot be inferred as representing the highest concentrations of algae in the lake's history, but they do confirm the existence of substantial algal communities. The lack of degradation in C1 demonstrates one limitation of using algal pigments to infer quantitative algal community histories from sediment cores. Additional research is needed to determine factors involved in establishing these zones with limited

pigment degradation and to establish protocols for comparing data when these conditions are found.

#### *Inferred algal communities or community changes*

The sedimentary record in LA-9-99 and LA-2H-99 showed that pigments could be used to infer algal community structure changes in three zones identified from cluster analysis (Figures 11 and 12). Previous work had identified three zones using the TC/TN ratio and diatom microfossils (Schelske et al. 1999), PolyP accumulation (Kenney et al. 2001) and chemical proxies (Kenney et al. 2002). Two groups of phytoplankton-derived sediments were identified in these studies. It was inferred that the differences resulted from increased phosphorus loading, primarily from muck farm agriculture. Our results show that the older phytoplankton-derived sediments (zone 2) represent three different algal communities (C2a, C2b, and C2c). The most recent zone (C1) represents the period when P loading from muck farm agriculture increased to levels approximately sevenfold greater than that for pre-disturbance period. These phytoplankton-derived sediments overlay macrophyte-derived sediments (zone C3) that were deposited before 1947.

The oldest zone (C3) represents the period of macrophyte dominance and low algal abundance. CD and TC levels are lowest in this period indicating that algal abundance and cyanobacteria were relatively small compared to C2 (Figures 11 and 12). Low cyanobacterial levels at this time can also be inferred from minimum concentrations of

OSC and MYX pigments (Figure 7). A previous paleolimnological study (Schelske et al. 1999) also showed low diatom microfossil abundance at this time. The occurrence of periphytic diatoms and sponge spicules that colonize macrophytes indicate that macrophytes were present (Kenny et al. 2002). The presence of the meroplanktonic diatom *Aulacoseira italica* and other planktonic diatoms provides evidence for areas of open-water habitat during the period of macrophyte dominance (Schelske et al. 2000)

Low CD/TC values suggest that cyanobacteria were present during the macrophyte period (Figures 11 and 12). Although the CD sediment record shows that the algal community was relatively small during this period (Figure 10), the low CD/TC values indicate that cyanobacteria were present. Algal counts from C3 show that cyanobacteria (*Pseudanabaena* spp., *Planktolyngbya* spp.) were present, but *Navicula* and *Fragilaria* spp., two benthic diatom species, were the major dominant algae rejuvenated (Table 1). The low cyanobacteria levels present during the macrophyte period probably also included epiphytic cyanobacterial forms including taxa in the Oscillatoriales, such as *Planktolyngbya*, *Phormidium*, *Leibleinia* and others. Therefore, it is inferred that the macrophyte-dominated period of Lake Apopka supported a relatively small algal community that included planktonic cyanobacteria and planktonic, epiphytic and benthic diatoms.

From the CD record (Figures 11 and 12), it is inferred that algal abundance began to increase during the period represented by the top samples in C3. Cyanobacterial pigments (TC and MYX)

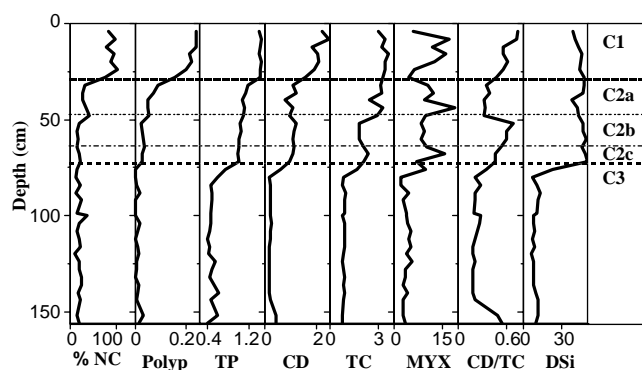


Figure 11. Zonation of selected sediment proxies vs. depth for LA-9-99 Lake Apopka sediment core. For proxy units see Figures 5–7. See Figure 4 and text for additional explanation of sediment zones.

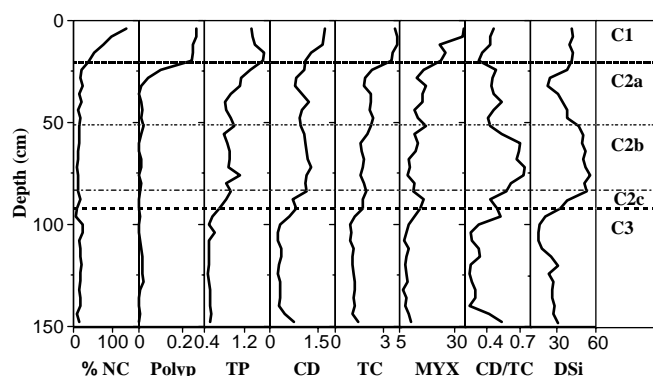


Figure 12. Zonation of selected sediment proxies vs. depth for LA-2H-99 Lake Apopka sediment core. For proxy units see Figures 5–7. See Figure 4 and text for additional explanation of sediment zones.

and the DSi record suggest that the increase included cyanobacteria and diatoms, respectively. Battoe et al. (1999) and Schelske et al. (2000) proposed that epiphytic and phytoplankton production increased prior to 1947 and that their shading contributed to the replacement of macrophytes by phytoplankton. The CD, TC, MYX and DSi sediment records indicate an increase in algal production before the primary producer community shifted from macrophytes to algae.

The period of phytoplankton dominance represented by C2 was separated into three subzones (C2c, C2b, C2a) using sedimentary algal pigments. A brief period of increased cyanobacterial abundance directly after the primary producer shift for C2c is inferred from peaks in MYX and TC pigments (Figures 11 and 12). This pulse may reflect the ability of cyanobacteria to exploit increased available nutrients in the water column (Reynolds 1984). Large stores of nutrients sequestered in macrophytes (Canfield et al. 1983) may have been released by macrophyte decay during the switch from macrophyte dominance to phytoplankton dominance. During this period, the north-shore wetlands became a significant nutrient source as the result of agricultural development. Therefore, an increased supply of nutrients may have been produced either by macrophyte decay or from increased external loading of nutrients or both.

Several proxies provide evidence that C2b is a period of increased benthic diatom abundance. Maximum DSi levels, an inference for diatom abundance, occurred in C2b for both cores (Figures 11 and 12). Diatom abundance from a core

taken in 1995 at station LA-9 supports this inference by showing that a period of maximum abundance occurred after the shift to phytoplankton dominance (Schelske et al. 1999). Diatom counts from Schelske et al. (1999) and algal counts from the rejuvenation experiment show that diatoms from this period are epiphytic and meroplanktonic diatoms (Table 1). Schelske et al. (1999) hypothesized that a benthic community existed because the photic zone extended to the bottom of the shallow lake at this time. The high CD/TC ratio shows that the algal community was influenced less by cyanobacteria than at other periods in the lake's history. The reason for reduced cyanobacteria (C2c) and a larger contribution from diatoms (C2b) is unclear since such a change normally means a decrease in available nutrients in the water column (Reynolds 1980). The change may show that internal supplies of nutrients stored in macrophytes became less important and that external loading from muck farm agriculture was increasing.

Cluster 2a is inferred to be a period of increased productivity caused by an increase in cyanobacterial abundance. The dramatic decline in the CD/TC ratio indicates that the algal community shifted to an increased abundance of cyanobacteria, a shift which began in C2b (Figures 11 and 12). Cluster 2a possibly marks the period where phytoplankton including cyanobacteria shaded the benthic diatom community, establishing the cyanobacterial community that persisted to the top of the core. A corresponding decrease in DSi concentrations provides evidence that the abundance of diatoms decreased, a trend that is

confirmed by changes in abundance of diatom microfossils (Schelske et al. 1999).

Multiple proxies in C1 reflect the current meroplanktonic/cyanobacterial algal structure of Lake Apopka (Carrick et al. 1993; Carrick and Schelske 1997). TC, MYX and OSC pigment concentrations in C1 reflect a productive cyanobacterial community during this period. Water-column samples collected since 1966 show that the phytoplankton community is dominated by cyanobacteria (Brezonik et al. 1977; Tuschall et al. 1979; Carrick and Schelske 1997; St. Johns River Water Management District, unpublished). Intermediate DSi concentrations in C1 for both cores indicate a smaller diatom community during this period (Figures 11 and 12). This diatom community is inferred to represent the meroplanktonic diatom community dominated by *Aulacoseira italica*. All three subsamples from C1 used in the rejuvenation experiment included *Aulacoseira* spp. as the most dominant species (Table 1). In addition, Schelske et al. (1999) found that benthic diatoms in a 1995 LA-9 core increased after the primary producer shift but decreased when the epiphytic taxa were replaced mainly by *Aulacoseira italica*. An increase in the CD/TC ratio in C1 indicates a relative decrease in cyanobacterial abundance. The relative decrease in cyanobacterial abundance may indicate the known development of the meroplanktonic diatom community (Schelske et al. 1999). Meroplankton settle to the sediments in calm periods and do not compete with the planktonic cyanobacteria in the water column. This separation of niches likely allowed for the development of the present, stable cyanobacterial and meroplanktonic communities.

Pigment and chemical analyses of three sediment cores from Lake Apopka were used to investigate proxies for nutrient enrichment in this hypereutrophic lake with loosely consolidated sediments. Three stratigraphic zones were identified with multivariate statistical analyses. Differences in stratigraphic depths among cores show the importance of utilizing multiple cores in paleolimnological studies. We found that algal and cyanobacterial productivity increased with increased phosphorus loading, that algal pigments in recent sediment had undergone little degradation possibly because viable meroplankton were present and that pigments and nutrients were valid proxies for nutrient enrichment in this shallow,

subtropical lake provided suitable coring sites were selected.

### Acknowledgments

We acknowledge Andrea Lami and Melanie Riedinger-Whitmore for their careful review of the manuscript. We acknowledge St. Johns River Water Management District for historic Lake Apopka data. We would also like to acknowledge Donny Smoak, Ed Philips, Ramesh Reddy, Mark Brenner, Tom Whitmore, Rick Aldridge, Martha Love, and Byron Shumate for their aid in this research. Funding was provided by the Carl S. Swisher Endowment, University of Florida Foundation, Inc.

### References

- Aldridge F.J., Schelske C.L. and Carrick H.J. 1993. Nutrient limitation in a hypereutrophic Florida lake. *Arch. Hydrobiol.* 127: 21–37.
- APHA 1989. *Standard Methods for the Examination of Water and Wastewater*, 17th ed. American Public Health Association, Washington, DC, 1081 pp.
- Bachmann R.W., Hoyer M.V. and Canfield D.E. Jr. 1999. The restoration of Lake Apopka in relation to alternative stable states. *Hydrobiologia* 394: 219–232.
- Bachmann R.W., Hoyer M.V. and Canfield D.E. Jr. 2000. Internal heterotrophy following the switch from macrophytes to algae in Lake Apopka, Florida. *Hydrobiologia* 418: 217–227.
- Bachmann R.W., Hoyer M.V. and Canfield D.E. Jr. 2001. Evaluation of recent limnological changes at Lake Apopka. *Hydrobiologia* 448: 19–26.
- Battoe L.E., Coveney M.F., Lowe E.F. and Stites D.L. 1999. The role of phosphorus reduction and export in the restoration of Lake Apopka, Florida. In: Reddy K.R., O'Connor G.A. and Schelske C.L. (eds), *Phosphorus Biogeochemistry in Subtropical Ecosystems*. Lewis Publishers, Boca Raton, pp. 511–526.
- Brezonik P.L., Pollman C.D., Crisman T.L., Allinson J.N. and Fox J.L. 1977. Limnological studies on Lake Apopka and the Oklawaha chan of lakes 1. Water quality in 1977. Report to Florida Department of Environmental Regulation, Tallahassee. Report No. ENV-07-78-01, Department of Environmental Engineering Sciences, University of Florida, 109 pp.
- Canfield D.E., Langeland K.A., Maceina M.J., Haller W.T., Shireman J.V. and Jones J.R. 1983. Trophic state classification of lakes with aquatic macrophytes. *Can. J. Fish. Aquat. Sci* 40(10): 1713–1718.
- Carrick H.J., Aldridge F.J. and Schelske C.L. 1993. Wind influences phytoplankton biomass and composition in a shallow, productive lake. *Limnol. Oceanogr.* 38: 1179–1192.

- Carrick H.L. and Schelske C.L. 1997. Have we overlooked the importance of small phytoplankton in productive waters? *Limnol. Oceanogr.* 42: 1613–1621.
- Conley D.J. and Schelske C.L. 1993. Potential role of sponge spicules in influencing the silicon biogeochemistry of Florida lakes. *Can. J. Fish. Aquat. Sci.* 50: 296–302.
- Dickman M. and Han X. 1995. Paleopigment evidence of competition between phytoplankton and a cyanobacterial algal mat in a meromictic lake near Toronto, Ontario Canada. *Hydrobiologia* 306: 131–146.
- Engstrom D.R., Swain E.B. and Kingston J.C. 1985. A paleolimnological record of human disturbance from Harvey's Lake, Vermont: geochemistry, pigments and diatoms. *Freshwater Biol.* 15: 261–288.
- Feuillade M., Dominik J., Druart J. and Loizeau J. 1995. Trophic status evolution of Lake Nantua as revealed by biological records in sediment. *Arch. Hydrobiol.* 132: 337–362.
- Fisher M.M., Brenner M. and Reddy K.R. 1992. A simple, inexpensive, piston corer for collecting undisturbed sediment/water interface profiles. *J. Paleolimnol.* 7: 157–161.
- Fitzgerald G. and Nelson T.C. 1966. Extractive and enzymatic analysis for limiting or surplus phosphorus in algae. *J. Phycol.* 2: 32–37.
- Griffiths M. and Edmondson W.T. 1975. Burial of oscillaxanthin in the sediment of Lake Washington. *Limnol. Oceanogr.* 20: 945–952.
- Hakanson L. and Jansson M. 1983. *Principles of Lake Sedimentology*. Springer-Verlag, New York 316 pp.
- JMP 1995. Version 3. SAS Institute Inc., Cary, NC, 593 pp.
- Kenney W.F., Schelske C.L. and Chapman A.D. 2001. Changes in polyphosphate sedimentation: a response to excessive phosphorus enrichment in a hypereutrophic lake. *Can. J. Fish. Aquat. Sci.* 58: 879–887.
- Kenney W.F., Waters M.N., Schelske C.L. and Brenner M. 2002. Sediment records of phosphorus-driven shifts to phytoplankton dominance in shallow Florida lakes. *J. Paleolimnol.* 27: 367–377.
- Lami A., Niessen F., Guilizzoni P., Masaferrò J. and Belis C.A. 1994. Palaeolimnological studies of the eutrophication of volcanic Lake Albano (Central Italy). *J. Paleolimnol.* 10: 181–197.
- Leavitt P.R. 1993. A review of factors that regulate carotenoid and chlorophyll deposition and fossil pigment abundance. *J. Paleolimnol.* 9: 109–127.
- Leavitt P.R. and Findlay D.L. 1994. Comparison of fossil pigments with 20 years of phytoplankton data from eutrophic lake 227, Experimental Lakes Area, Ontario. *Can. J. Fish. Aquat. Sci.* 51: 2286–2299.
- Leavitt P.R. and Hodgson D.A. 2001. Sedimentary pigments. In: Smol J.P., Birks H.J.B. and Last W.M. (eds), *Tracking Environmental Changes in Lake Sediments: Volume 3: Terrestrial, Algal, and Siliceous Indicators*. Kluwer Academic Publishers, Dordrecht pp. 281–293.
- Lowe E.F., Battoe L.E., Coveney M.F. and Stites D.L. 1999. Setting water quality goals for restoration of Lake Apopka: inferring past conditions. *Lake Reserv. Manage.* 15: 103–120.
- Lowe E.F., Battoe L.E., Coveney M.F., Schelske C.L., Havens K.E., Marzolf E.R. and Reddy K.R. 2001. The restoration of Lake Apopka in relation to alternative stable states: an alternative view to that of Bachmann et al. (1999). *Hydrobiologia* 448: 11–18.
- Lund J.W.G. 1954. The seasonal cycle of the plankton diatom, *Melosira italica* Kutz. *subarctica* O. Mull. *J. Ecol.* 42: 151–179.
- Newman S., Aldridge F.J., Philips E.J. and Reddy K.R. 1994. Assessment of phosphorus availability for natural phytoplankton populations from a hypertrophic lake. *Arch. Hydrobiol.* 130: 409–427.
- Reynolds C.S. 1980. Phytoplankton assemblages and their periodicity in stratifying lake systems. *Hol. Ecol.* 3: 141–159.
- Reynolds C.S. 1984. *The Ecology of Freshwater Phytoplankton*. Cambridge, 384 pp.
- Rybak M. 1988. The effect of agriculture on the primary production in Lake Beskie (Poland) as recorded in the stratigraphy of fossil pigments. *Hydrobiologia* 157: 21–26.
- Sabater S. and Haworth E.Y. 1995. An assessment of recent trophic changes in Windermere South Basin (England) based on diatom remains and fossil pigments. *J. Paleolimnol.* 14: 151–163.
- Sakamoto M. and Inoue T. 1996. Typhoon-induced temporal change in plankton phosphorus in Lake Biwa. *Jpn. J. Limnol.* 57: 511–522.
- Scheffer M., Hosper S.H., Meijer M.-L., Moss B. and Jeppesen E. 1993. Alternative equilibria in shallow lakes. *Trends Ecol. Evol.* 8: 275–279.
- Schelske C.L. 1997. *Sediment and Phosphorus Deposition in Lake Apopka: Final Report*. Special Publication SJ97-SP21. St. Johns River Water Management District, Palatka, Florida.
- Schelske C.L. and Brezonik P. 1992. Can Lake Apopka be Restored? *Restoration Case Studies*. National Academy Press, Washington, DC, pp. 393–398.
- Schelske C.L. and Kenney W.F. 2001. Model erroneously predicts failure for restoration of Lake Apopka, a hypereutrophic, subtropical lake. *Hydrobiologia* 448: 1–5.
- Schelske C.L., Aldridge F.J., Carrick H.J. and Coveney M.F. 2003. Phytoplankton community photosynthesis and primary production in a hypereutrophic lake, Lake Apopka, Florida. *Archiv. Hydrobiol.* 157: 145–172.
- Schelske C.L., Carrick H.J. and Aldridge F.J. 1995. Can wind-induced resuspension of meroplankton affect phytoplankton dynamics? *J. N. Am. Benthol. Soc.* 14: 616–630.
- Schelske C.L., Conley D.J., Stoermer E.F., Newberry T.L. and Campbell C.D. 1986. Biogenic silica and phosphorus accumulation in sediments as indices of eutrophication in the Laurentian Great Lakes. *Hydrobiologia* 143: 79–86.
- Schelske C.L., Coveney M.F., Aldridge F.J., Kenney W.F. and Cable J.E. 2000. Wind or nutrients: historic development of hypereutrophy in Lake Apopka, Florida. *Arch. Hydrobiol. Spec. Issues Adv. Limnol.* 55: 543–563.
- Schelske C.L., Donar C.M. and Stoermer E.F. 1999. A test of paleolimnologic proxies for the planktonic/benthic ratio of microfossil diatoms in Lake Apopka. In: Mayama, Idei and Koizumi (eds), *14th International Diatom Symposium*, September 2–8, 1996, Tokyo, Japan. Koeltz Scientific Books, Koenigstein, pp. 367–382.
- Schelske C.L., Lowe E.F., Battoe L.E., Brenner M., Coveney M.F. and Kenney W.F. *Abrupt biological response to hydrologic and land-use changes in Lake Apopka, Florida (USA)*. *Ambio*. (accepted).

- Shumate B.C., Schelske C.L., Crisman T.L. and Kenney W.F. 2002. Response of the cladoceran community to trophic state change in Lake Apopka, Florida. *J. Paleolimnol.* 27: 71–77.
- Sicko-Goad L., Stoermer E.F. and Kociolek J.P. 1989. Diatom resting cell rejuvenation and formation: time-course, species records and distribution. *J. Plankton Res.* 11: 375–389.
- Steenbergen C.L.M., Korthals H.J. and Dobrynin E.G. 1994. Algal and bacterial pigments in non-laminated lacustrine sediment: Studies of their sedimentation, degradation and stratigraphy. *FEMS Microbiol. Ecol.* 13: 335–352.
- Swain E.B. 1985. Measurement and interpretation of sedimentary pigments. *Freshwater Biol.* 15: 53–75.
- Tuschall J.R., Crisman T.L., Brezonik P.L. and Allinson J.N. 1979. Limnological studies on Lake Apopka and the Oklawaha chain of Lakes 2. Water Quality in 1978. Report to Florida Department of Environmental Regulation, Tallahassee. Report No. ENV-07-79-02, Department of Environmental Engineering Sciences, University of Florida. 114 pp.
- Wetzel R.G. 1970. Recent and postglacial production rates of a marl lake. *Limnol. Oceanogr.* 15: 491–503.
- Whitmore T.J., Brenner M. and Schelske C.L. 1996. Highly variable sediment distribution in shallow, wind-stressed lakes: a case for sediment-mapping surveys in paleolimnological studies. *J. Paleolimnol.* 15: 207–221.