

# Temporal trends of trophic state variables in a shallow hypereutrophic subtropical lake, Lake Griffin, Florida, USA

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With 6 figures and 3 tables

**Abstract:** Changes in the concentrations of selected trophic state parameters in Lake Griffin were examined over a 22-year period. Parameters included chlorophyll-*a*, total nitrogen and total phosphorus. Additional information was obtained for phytoplankton composition and nutrient limitation status of phytoplankton growth over a shorter period of time, from 2000 to 2002. The central goal of the study was to examine whether the efforts to manage water quality and habitat in the system by management agencies over the study period yielded observable changes in these trophic state parameters and the relationships between them. The results of the study show a downward trend in phosphorus concentrations over the study period. Variability in meteorological conditions had an apparent effect on short-term responses of trophic state parameters. The results also point toward a role for nitrogen availability in phytoplankton dynamics, and a stronger relationship between total phosphorus concentrations and chlorophyll-*a* toward the latter part of the sampling period, suggesting an increasing potential for phosphorus limitation.

**Key words:** phytoplankton, cyanobacteria, chlorophyll, phosphorus, nitrogen, El Niño, water management.

## Introduction

One of the long-standing generalizations about freshwater ecosystems is the predominance of phosphorus limitation of phytoplankton production (Rast et al. 1989). Cultural eutrophication has increased the rates of phosphorus loading to many lakes around the world, leading to increases in algal productivity and a growing list of systems subject to nitrogen limitation (James et al. 2003, Moss et al. 2005), particularly in the subtropical and tropical environments (Thornton 1987, Philips et al. 1997). Lakes subject to nitrogen limitation can be prone to blooms of nitrogen-fixing cyanobacteria, due to their competitive advantage, focusing attention

on the importance of reducing phosphorus availability in the management of trophic status, including harmful algal blooms (Paerl & Fulton 2006).

Over the past century there have been increasing efforts to reduce phosphorus load and concentration in eutrophic and hypereutrophic lakes, with mixed success (Moss et al. 2005, Jeppesen et al. 2005). One of the great challenges in such efforts has been reversing the effects of long-term loading and accumulation of phosphorus within lakes, resulting in large internal nutrient pools (Sas 1989, Marsden 1989, Welch & Cooke 1995). In such lakes, particularly shallow systems, response to reductions in load can be slow, incremental and confounded by inherent inter annual variability

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in environmental conditions that impact the structure and function of ecosystems, such as meteorological conditions or internal reserves of nutrients (Scheffer et al. 1993, Welch & Cooke 1995, Moss et al. 1996). However, there are examples of positive responses to nutrient load reductions in shallow lakes, such as Lake Balaton in Hungary (Istvanovics & Somlyódy 2001), hypereutrophic lakes in England (Beklioglu et al. 1999), and a shallow subtropical lake in Florida (Covenev et al. 2005).

In this study, we examined the changing condition of Lake Griffin, a hypereutrophic lake in central Florida, which has been the target of various phosphorus and aquatic plant management efforts over the past few decades (Fulton & Smith 2008). Lake Griffin is representative of many shallow hypereutrophic lakes in Florida and provides an opportunity to examine a condition that is widespread and growing in warmer latitudes throughout the world. There are indications that management activities in Lake Griffin have been associated with changes in the relationships between three major trophic state indicators; nitrogen, phosphorus and chlorophyll concentrations. It is also clear that these changes must be viewed within the broader context of trends in meteorological patterns and events, such as El Niño, or prolonged droughts. Several studies have demonstrated that major weather events, like El Niño, as well as longer-term trends, can have important consequences for the structure and function of lakes that may last for months or years (Gerten & Adrian 2000, Straile & Adrian 2000, Philips et al. 2007).

The goal of this study was to examine long-term trends in trophic state parameters, including total nitrogen, total phosphorus and chlorophyll-*a* concentrations, over a 22-year period of management efforts aimed at lowering the trophic status of Lake Griffin. These changes were investigated in relation to the influences of shifts in meteorological regimes between drought and flood conditions.

## Methods

### Study site

Lake Griffin is located in Lake County, central Florida, USA. The lake is a part of the Harris chain of lakes of the southern Ocklawaha River watershed (Fig. 1). It receives inflow from Haines Creek located north of the midpoint of the lake where its northern and southern basins meet. Haines Creek also connects Lake Eustis to Lake Griffin. Water flows north and out of the lake into the Ocklawaha River and eventually into the St. Johns River. Lake Griffin is shallow, with a mean depth of 2.2 m, and

polymictic. The lake has a surface area of 36.2 km<sup>2</sup>. Substrates within the lake range from flocculent organic-rich sediment to sandy bottoms, with the deepest flocculent layer concentrated at the center of the lake.

Three major management activities were carried out during the 22-year study period: a lake drawdown, a lake-wide herbicide treatment, and an integrated effort conducted by St. Johns River Water Management District to reduce external nutrient loads and internal nutrient recycling in the lake (Fulton et al. 2004, Fulton & Smith 2008). The first major management event in Lake Griffin was a lake drawdown from March through September in 1984, which dropped the lake level by almost two meters. In 1987 the lake was treated with a herbicide to reduce the extensive *Hydrilla verticillata* population which developed subsequent to the drawdown. A major component of the third management effort included wetland restoration of former farmlands adjoining the lake, beginning in the 1990s. The first phase of this effort included the integration of a marsh flow-way onto the lake ecosystem to remove nutrients from the lake. The flow-way operated during 1994–1998, and subsequently the area was managed as a wetland and to limit nutrient discharges to Lake Griffin (Fulton et al. 2004, Fulton & Smith 2008). Finally, in 2002 harvesting of gizzard shad was begun to reduce nutrient recycling and remove nutrients in the fish biomass.

Recent studies of Lake Griffin provide general ranges for basic physical-chemical parameters, including temperatures from 12–32 °C, Secchi disk depths from 0.2 to 1.2 m, conductivities from 0.357–0.388 mS cm<sup>-1</sup>, turbidities from 5–28 NTU, and color values from 21 to 52 PCU (Philips & Schelske 2004, Philips et al. 2005).

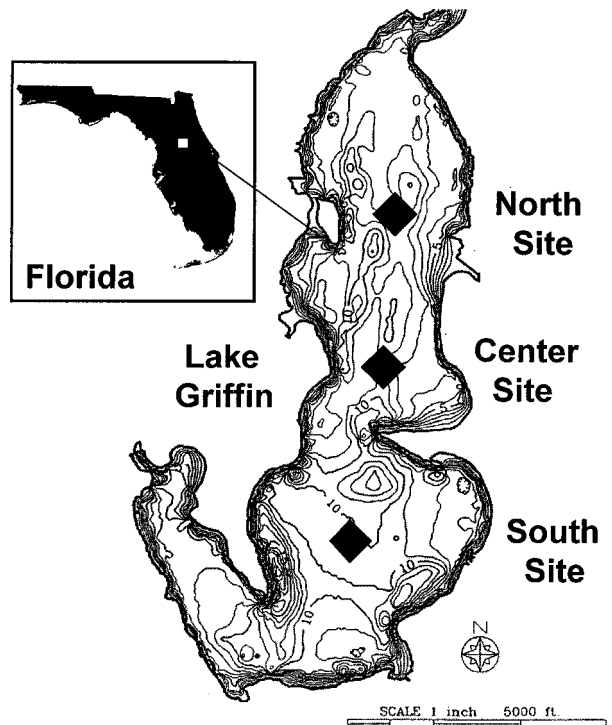


Fig. 1. Sampling site map of Lake Griffin.

## Historical data

A 22-year (1982–2004) historical data set for total phosphorus, total nitrogen and chlorophyll-*a* concentrations was obtained from the St. Johns River Water Management District (SJRWM-D), the Florida Fish and Wildlife Conservation Commission-Eustis (FFWCC), and Florida Department of Environmental Protection (FDEP). The data set is associated with collections from a 'Center Site' in Lake Griffin (Fig. 1). Meteorological information was obtained from the National Oceanographic and Atmospheric Administration web site (<http://www.srh.noaa.gov>).

## Field procedures

Lake water was collected monthly from August 2000 through March 2002, from two sites in the lake, one in the north and one in the south basin (Fig. 1). Previous analyses of variability of water column characteristics in Lake Griffin have shown little significant spatial variability in the open water region of the lake (Phlips & Schelske 2004, Phlips et al. 2005). Water was collected with an integrating tube that collects water evenly through the water column from the surface to 0.1 m from the bottom. Samples for phytoplankton analysis were preserved with Lugol's solution. Eleven of the sampling events carried out from August 2000 to March 2002 were used to study nutrient limitation of phytoplankton growth. Two sites were involved in this study, one in the northern basin (North Site) and one in the southern basin (South Site) of the lake. The nutrient enrichment bioassay was conducted in a laboratory at the University of Florida's Department of Fisheries and Aquatic Sciences.

## Phytoplankton analyses

Phytoplankton composition was determined microscopically using the Utermöhl method (Utermöhl 1958). Phytoplankton cells were identified and counted at 400× and 100× magnification with a Nikon inverted microscope using phase contrast according to methods described by Phlips et al. (1997). Cell biovolumes were estimated by assigning combinations of geometric shapes to fit the characteristics of individual taxa (Smayda 1978). Cell counts were transformed to biovolume.

## Nutrient limitation bioassays

Water collected at a 30-cm depth from the North and South Sites was used to determine the primary limiting nutrient for the growth of natural phytoplankton populations from the lake. The nutrient enrichment bioassay method developed for Lake Okeechobee (Aldridge et al. 1995, Phlips et al. 1997) was used in the study. The assays were conducted under controlled laboratory conditions in 500-ml Erlenmeyer flasks with 400 ml of whole lake water. Treatment groups included control (no nutrient additions), phosphorus spike (final starting concentration of 100 µg l<sup>-1</sup> of P as PO<sub>4</sub>), nitrogen spike (final starting concentration of 1000 µg l<sup>-1</sup> of N as NO<sub>3</sub>) and combined nitrogen and phosphorus spikes. Each treatment was done in triplicate at two sites in the lake, north and south (Fig. 1). Initial and final chlorophyll-*a* was determined for all treatment groups. Chlorophyll-*a* was determined from water samples filtered onto Gelman A/E glass-fiber and extracted with 95 % ethanol (APHA 1989, Sartory & Grobbelaar 1984). Daily change in chlorophyll-*a* was estimated using the *in vivo* fluorescence

(IVF) method for chlorophyll-*a* determination, using a Turner Design Model 10 fluorometer. Treatment flasks were incubated at 25 °C and light flux of 100 µmole photons m<sup>-2</sup> s<sup>-1</sup> of fluorescent light for up to two weeks. Mean values for maximum growth yield in each treatment group were compared using Duncan's Multiple Range test (SAS Institute). Since the two sampling sites used in the bioassay studies always yielded the same results, the limiting nutrient status is only reported once for each experimental date.

## Data analysis

Statistical analyses were performed using SAS Statistics Version 8.1 for Personal Computers. Duncan's Multiple Range tests, linear regression analyses, and Pearson's Correlations were used to analyze the data.

## Results and discussion

The results of this study reveal shifts over the 22-year study period in key trophic state variables and the relationships between them. An examination of temporal changes in trophic state indicators in Lake Griffin provides insights into the existence of trends in the ecology of the system, both as it relates to management activities and changes in climatic conditions. From a broad climatic perspective, it is possible to distinguish five phases in rainfall abundances over the 22-year study period. The rainfall record demonstrates extended periods of substantial above and below average precipitation (Fig. 2). The longest periods of below average rainfall occurred from 1984 to 1990 and 1998 to summer of 2001. By contrast, 1982 and 1983, 1991 to 1997, and late summer of 2001 through the spring of 2004, were generally characterized by above average rainfall. The final few months of the study period in the summer and fall of 2004 were punctuated by series of major tropical storms and hurricanes, making that year

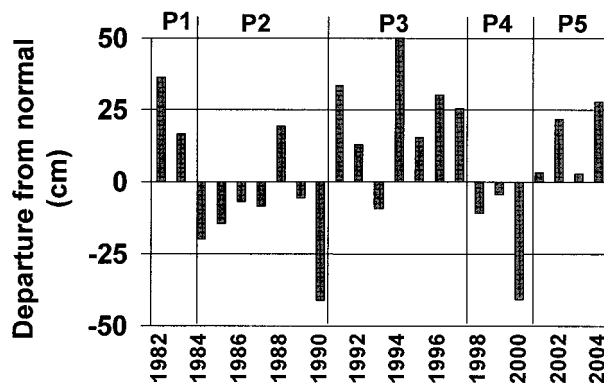


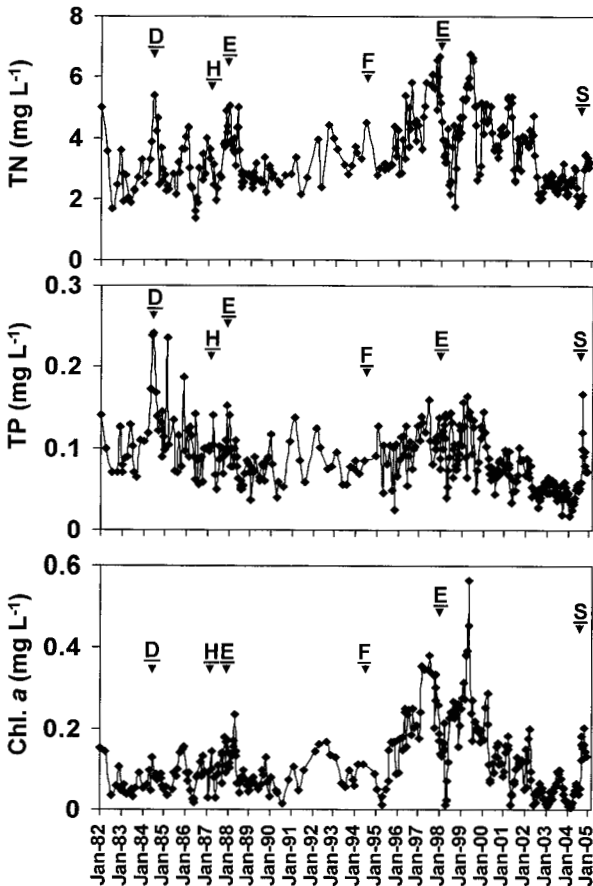
Fig. 2. Annual rainfall totals at the Lisbon meteorological station in the Lake Griffin watershed from 1982 through 2004. Five phases of above or below average rainfall are delineated in the figure as P1 through P5.

an exceptionally active storm season. The latter period was not designated as a major phase due to its short duration, but did have a short-term impact on the lake.

Embedded within five major climatic phases were three major management activities, including the 1984 lake drawdown, the 1987 herbicide treatment and the marsh restorations of adjoining farmlands began in the early 1990's (Fulton et al. 2004, Fulton & Smith 2008). The changes observed in trophic state parameters over the study period are examined from the context of the interaction between these natural and anthropogenic changes in conditions over time.

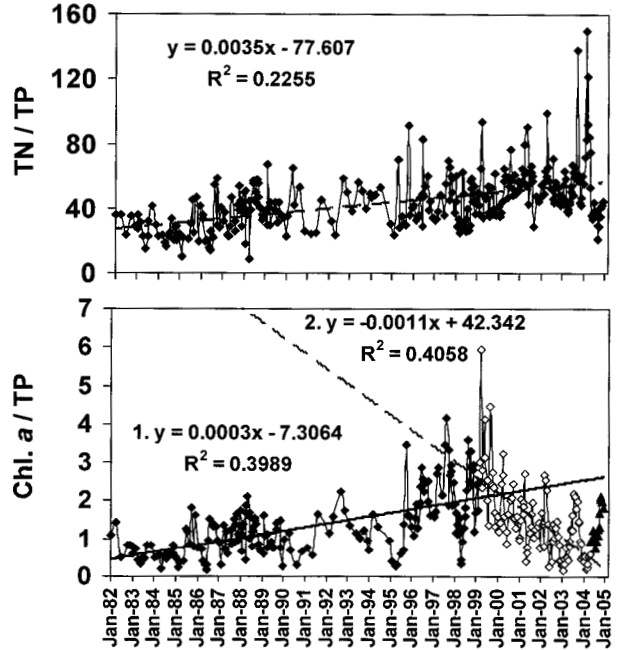
**Climatic phases**

Climatic Phase 1 was a period of above average rainfall leading up to a drawdown of the lake in 1984 (Fig. 2). The period included the El Niño event of 1983, which was associated with the highest annual rainfall total



**Fig. 3.** Total nitrogen (TN), total phosphorus (TP) and chlorophyll-*a* (chl) concentrations in Lake Griffin from 1982–2004. Major climatic and management events are highlighted by letter and arrow designations: D, drawdown; H, herbicide treatment; F, flow-way; E, El Niño; S, major tropical storm season of 2004.

in the region over the past 50 years (National Climate Data Center, <http://www.srh.noaa.gov>). TP and TN concentrations increased during the period (Fig. 3), particularly around the time of the lake drawdown. It is known that drawdowns can result in short-term increases in nutrient concentrations (Mitchell & Baldwin 1998, Wagner 2001). Phase 1 was also a period of relatively low TN/TP ratios (Fig. 4, Table 1), Chl-*a*/TP ratios (Fig. 4, Table 1), and chlorophyll-*a* concentra-



**Fig. 4.** TN/TP and chlorophyll-*a*/TP ratios in Lake Griffin from 1982–2004. Trend lines are provided for each parameter (dashed line), along with linear regression relationships and R<sup>2</sup> value.

**Table 1.** Mean values for total nitrogen (TN), Total phosphorus (TP), chlorophyll-*a* (Chl), TN/TP and Chl/TP during five climatic 'Phases' of the 22-year study period. Standard deviations are shown below the mean in parentheses.

Phase	TN (mg L <sup>-1</sup> )	TP (mg L <sup>-1</sup> )	Chl (mg L <sup>-1</sup> )	TN/TP	Chl/TP
1	2.946 (1.004)	0.115 (0.052)	0.071 (0.037)	27.3 (7.4)	0.65 (0.28)
2	3.085 (0.977)	0.097 (0.046)	0.088 (0.042)	36.0 (12.7)	0.99 (0.45)
3	4.111 (1.077)	0.095 (0.035)	0.174 (0.104)	46.6 (9.0)	1.79 (0.60)
4	4.250 (1.075)	0.095 (0.030)	0.189 (0.098)	47.7 (14.6)	1.99 (0.98)
5	2.840 (0.681)	0.052 (0.017)	0.056 (0.042)	59.6 (21.7)	1.08 (0.72)

tions (Fig. 3, Table 1). The latter characteristics may reflect the influence of high levels of macrophyte cover within the lake prior to the herbicide treatment in 1987. Similar characteristics have been noted for other macrophyte-dominated lakes (Canfield et al. 1983, Moss et al. 1996).

The second climatic phase, a period of generally below average rainfall from 1984 to 1990, following the drawdown of the lake (Fig. 2), was characterized by a general decline in TP concentration, but no consistent trend in TN or chlorophyll-*a* concentrations (Fig. 3). The change in TP concentrations is reflected in the upward trend in the TN/TP and Chl-*a*/TP ratios (Fig. 4, Table 1). Herbicide treatment of the lake in 1987 was followed by a high rainfall El Niño event in fall-spring of 1987/88. After the herbicide treatment, TN, TP and chlorophyll-*a* concentrations increased temporarily (Fig. 3), probably due to a release of nitrogen and phosphorus into the water column from decomposing plant material. The increase in chlorophyll-*a*/TP ratio during Phase 2 may, in part, be related to a shift toward greater domination of the lake by phytoplankton. Spikes in TP following El Niño events were a re-occurring feature over the study period, suggesting a flushing out of phosphorus from Lake Griffin's watersheds under high rainfall conditions.

Climatic Phase 3 was a period from 1991–1997, characterized by well above average annual rainfall totals in six of seven years (Fig. 2). Phase 3 was a dynamic period for all three trophic state parameters. TN and TP concentrations increased over the seven years (Fig. 3). Chlorophyll-*a* levels fluctuated over a wide range (0.025–0.150 mg L<sup>-1</sup>) from 1990 to 1995, before increasing dramatically from 1995 to 1997, reaching concentrations in excess of 0.4 mg L<sup>-1</sup> (Fig. 3). Prior to the surge in chlorophyll-*a* concentration in 1995, a marsh flow-way was connected to Lake Griffin, with the goal of lowering nutrient levels in the lake. However the introduction of the flow-way was during an extended period of above-normal rainfall that resulted in large discharges from the watersheds leading to the lake, including the marsh. The 1997–1998 El Niño resulted in a temporary decrease in TN, TP, and chlorophyll-*a* concentrations, followed by a rapid increase. It may be hypothesized that the elevated nutrient loads from the lakes various watersheds during this period of time provided the ingredients for the observed dramatic increase in phytoplankton biomass from 1995 through 1998, expressed in terms of chlorophyll-*a* concentration. The impact of the combined increase in TN and TP is also reflected in the increasing Chl-*a*/TP ratio (Fig. 4, Table 1).

The fourth climatic phase, from 1998 to the late summer of 2001, was a major drought period for Florida (Fig. 4), and saw a reversal of the trend in Phase 3, with decreasing concentrations of all three trophic state parameters (Fig. 3). TN/TP ratios increased modestly because the decrease in TP concentrations was greater than the decline in TN levels (Figs 3–4, Table 1). Chl-*a*/TP ratios showed a declining trend (Fig. 4), due to the strong decline in chlorophyll-*a* from the very high values observed in 1996 and 1997 (Fig. 3). Nutrient loading to the lake also decreased during this period of time (Fulton et al. 2004, Fulton & Smith 2008).

In the final climatic period, Phase 5, the responses of trophic state parameters to the return of higher rainfall conditions were different than observed in the first two high rainfall phases of the study period. Despite increased rainfall, and putative increases in watershed inflows, concentrations of TN, TP and chlorophyll-*a* all declined from the levels observed during the drought period (Fig. 3). Overall, TP and chlorophyll-*a* levels reached new lows for the study period in Phase 5. The strong decline in TP relative to TN resulted in a continued increase in the TN/TP ratios (Fig. 4). At the same time chlorophyll-*a*/TP ratios continued the decline initiated in Phase 4 (Fig. 4). In consort with lower TN and TP concentrations, estimates of phosphorus and nitrogen load to the lake were also lower than in previous wet periods during the study (Fulton et al. 2004, Fulton and Smith 2008). Gizzard shad harvesting, begun in 2002, may also have contributed to the declining nutrient and chlorophyll-*a* levels during Phase 5.

The final few months of the study period, in the summer of 2004, were highlighted by a series of severe storms and hurricanes. The impacts of these storms can be seen as a pronounced pulse in TP, chlorophyll-*a*, and to a lesser extent TN concentrations (Fig. 3). After the storm season values for these parameters began a downward trend.

### Nutrient status

Over the entire 22-year study period the three trophic state parameters showed somewhat different trends. Outside of the dramatic increase in TN during the flood period of 1995–1997, there was no major net change in mean concentrations (Table 1). Mean chlorophyll-*a* showed a modest decrease from the beginning to the end of the study period (Table 1). However, TP concentrations showed a substantial net reduction from the beginning to the end of the study period (Fig. 3, Table 1), even though there were upward and down-

ward trends in the concentration gradient over the 22-year period (Table 2), which generally followed rainfall patterns until Phase 5. In Phase 5, rainfall amounts were above average (Fig. 2), but TP concentrations declined over time (Table 2). The trend in TP concentration is also reflected in the steady increase in TN/TP (Fig. 4).

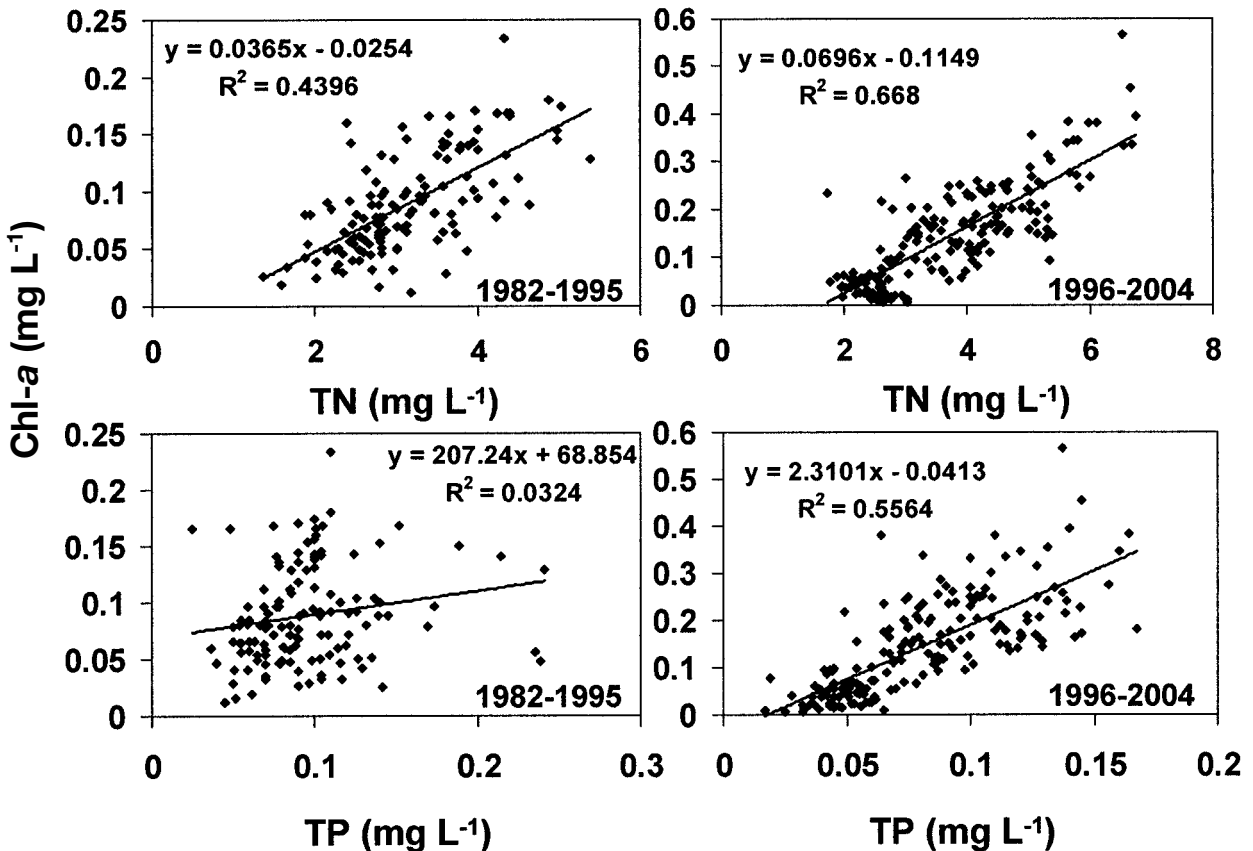
There are indications that a change may have occurred in the nutrient-limiting status of the phytoplankton community over the study period. Over the first thirteen years of the study period, chlorophyll-*a* concentrations were correlated to TN, yielding a posi-

tive regression relationship between the two parameters for the period from 1983 to 1995 (Fig. 5). No relationship between TP and chlorophyll-*a* was evident for the same time period, suggesting that nitrogen availability was a more important limiting factor for phytoplankton growth than phosphorus. Nitrogen limitation in phosphorus-enriched lakes has been observed in other major freshwater ecosystems in Florida, such as Lake Okeechobee (Phlips et al. 1997) and Lake George (Paerl et al. 2002). By contrast, during the next nine years of the study period chlorophyll-*a* concentrations were correlated to both TN and TP concentrations (Fig. 5), indicating that phytoplankton biomass levels were tracking TP concentrations.

The importance of nitrogen availability in Lake Griffin is corroborated by the results of the nutrient limitation bioassays. The results of the nutrient enrichment bioassays indicated that nitrogen was an important limiting nutrient for phytoplankton growth in Lake Griffin during the experimental period (Table 3). On six of eleven bioassay dates, the addition of a nitrogen spike alone resulted in algal standing crop significantly greater than that observed in the control

**Table 2.** Pearson's correlation coefficients for the relationship between time (days of sampling) and total phosphorus concentrations in each climatic phase of the study. All of the relationships were significant at a 'p' level of 0.05 level.

	Coefficient	p-value
Phase 1	0.5446	0.0159
Phase 2	-0.3509	0.0010
Phase 3	0.2830	0.0363
Phase 4	-0.4163	0.0002
Phase 5	-0.6739	<0.0001



**Fig. 5.** Regression relationships between chlorophyll-*a*, and TN and TP for two periods of time, 1982-1995 and 1996-2004.

group (i.e. without addition of nutrients). However, nitrogen was not always the pre-dominant limiting nutrient. Phosphorus was the primary limiting nutrient on two of the bioassay dates. On four of the bioassay dates, additions of both nitrogen and phosphorus were required to obtain a large growth response. The latter results indicate that there was little bioavailable nitrogen or phosphorus in the water column of the lake at the time of collection.

Another indication of the importance of nitrogen limitation in Lake Griffin is the prominence of nitrogen-fixing cyanobacteria. Phytoplankton composition was determined on 16 sampling dates from August 2000 through March 2002. In terms of biovolume, the major phytoplankton group was cyanobacteria (blue-green algae) (Fig. 6). Diatoms were also commonly represented, but they never dominated the community. Minor components of the phytoplankton included

chlorophytes, dinoflagellates, cryptophytes, chrysophytes and euglenoids (Cichra & Phlips, unpubl. data). Among the cyanobacteria, *Cylindrospermopsis* sp. was numerically and biovolumetrically dominant from August 2000 through May 2001 (Fig. 6). Nitrogen limitation and the presence of significant populations of nitrogen-fixing cyanobacteria, such as *Cylindrospermopsis*, is a feature shared by several lakes and rivers in Florida, including Lake Okeechobee (Cichra et al. 1995, Phlips & Ihnat 1995), and the St. Johns River (Phlips et al. 2007). The prevalence of *Cylindrospermopsis* in Lake Griffin during the later phase of the study period may also be indicative of phosphorus limitation potential, since *Cylindrospermopsis* has been shown to be an excellent competitor for phosphorus at low concentrations (Padisak 1997, Phlips et al. 2005).

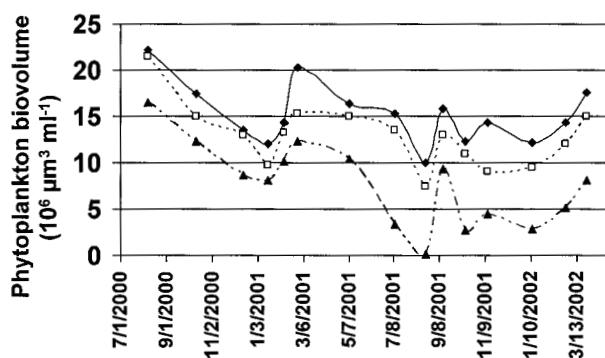
## Conclusions

From a management point of view, the central issue for Lake Griffin, and many shallow eutrophic lakes around the world, is whether recent efforts to manage nutrient loads have yielded demonstrable changes or improvements in trophic state. The changes observed in trophic state parameters in Lake Griffin over the 22-year study period suggest that long-term efforts to manage external nutrient loads to Lake Griffin may have resulted in reductions in the trophic state of the lake, particularly in terms of phosphorus concentrations. A shift in trophic state is supported by the substantial increase in TN/TP ratios over the 22-year study period, largely attributable to a greater overall decline in TP relative to TN concentrations (Table 1). It is possible to hypothesize that the trend of declining TP concentrations was related to declines in load (Fulton & Smith 2008). The increased strength in the regression relationship between chlorophyll-*a* and TP in the last nine years of the study period suggest a greater potential for phosphorus limitation of phytoplankton biomass. The latter hypothesis is further supported by the results of nutrient limitation bioassays, which reveal phosphorus limitation of phytoplankton growth during the periods of exceptionally low chlorophyll-*a*/TP ratios in May 2001 and January 2002.

While the results of this study provide support for the hypothesis that nutrient-load reduction strategies for Lake Griffin have resulted in measurable changes in key trophic state parameters, it is also clear that variability in meteorological conditions (Straile & Adrian 2000, Anneville et al. 2005, Phlips et al. 2007), and changes in the structure of the primary producer com-

**Table 3.** Results of nutrient enrichment bioassays at the North and South stations in Lake Griffin (August 2000 – March 2002). Designations refer to the primary limiting nutrient for phytoplankton growth, in terms of the comparative increase in chlorophyll-*a* levels in the various nutrient addition groups relative to the control.

Date	Primary Limiting Nutrient
August 7, 2000	Nitrogen
January 17, 2001	Nitrogen & Phosphorus
February 28, 2001	Nitrogen & Phosphorus
May 7, 2001	Phosphorus
July 9, 2001	Nitrogen
August 20, 2001	Nitrogen
October 12, 2001	Nitrogen & Phosphorus
November 12, 2001	Nitrogen
January 12, 2002	Phosphorus
February 26, 2002	Nitrogen
March 27, 2002	Nitrogen



**Fig. 6.** Total phytoplankton biovolume (solid line), cyanobacteria biovolume (open square/dashed line), and *Cylindrospermopsis* biovolume (filled triangle/dashed line).



munity resulting from herbicide treatment of the lake (Moss et al. 2005) complicate interpretations of short-term trends and can dampen the immediate effects of management efforts on nutrient levels. The potential importance of the former issue is manifested by the increase in the levels of trophic state parameters associated with prolonged periods of above average rainfall, or storm events, which result in elevated loads of nutrients from a number of tributaries to the lake, as well as surface water runoff (Fulton 1995, Fulton et al. 2004).

In the case of Lake Griffin, the full 22-year study period was needed to arrive at even these preliminary conclusions about trends. The importance of long-term data are well recognized within scientific community, but are only available for a limited number of ecosystems impacted by cultural eutrophication, particularly in subtropical and tropical environments (Jeppesen et al. 2005).

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