Lake level and trophic state variables among a population of shallow Florida lakes and within individual lakes

Mark V. Hoyer, Christine A. Horsburgh, Daniel E. Canfield, Jr., and Roger W. Bachmann

Abstract: Monthly total phosphorus, total nitrogen, and chlorophyll concentrations, Secchi depth, and lake water level data for 84 Florida lakes were used to examine relations between trophic state variables and water level fluctuation. Lake size averaged 566 ha (range 4.0 to 5609 ha), with the period of record for individual lakes averaging 57 months (range 7 to 175 months). Lake level fluctuation for individual lakes averaged 1.3 m (range 0.1 to 3.5 m). The lakes also ranged from oligotrophic to hypereutrophic, with average chlorophyll values for individual lakes ranging from 1 to 97 $\mu g \cdot L^{-1}$. No overall relation between trophic state variables and lake level fluctuation could be found among the population of lakes. However, individual lakes showed direct, inverse, or no significant relations between lake trophic state variables and water level fluctuation, regardless of the magnitude of water level fluctuation. These data suggest that predicting how water level fluctuations will impact trophic state variables among a population of lakes will be difficult, if not impossible, and that any accurate predictions will have to be made after first examining several mechanisms within individual lake systems.

Résumé : Les concentrations mensuelles de phosphore total, d'azote total et de chlorophylle, les profondeurs de Secchi et les données de niveau des eaux dans 84 lacs de Floride nous ont servi à examiner les relations entre les variables du niveau trophique et les fluctuations du niveau d'eau. Les lacs ont en moyenne 566 ha de surface (4,0 ha à 5609 ha); ils ont été suivis individuellement en moyenne pendant 57 mois (7 mois à 175 mois). Les fluctuations des niveaux des lacs individuels sont en moyenne de 1,3 m (0,1 m à 3,5 m). Les lacs varient aussi d'oligotrophes à hypereutrophes et les valeurs moyennes des concentrations de chlorophylle dans les lacs individuels vont de 1 $\mu g \cdot L^{-1}$ à 97 $\mu g \cdot L^{-1}$. Nous ne trouvons pas de relation globale entre les variables de l'état trophique et les fluctuations des niveaux des lacs dans cet ensemble de lacs. Cependant, dans les lacs individuels, il y a des relations positives, négatives et (ou) non significatives entre les variables de l'état trophique et les fluctuations du niveau de l'eau, indépendamment de l'importance de la fluctuation du niveau de l'eau. Ces données laissent croire qu'il est difficile, voire impossible, de prédire comment les fluctuations du niveau de l'eau vont affecter les variables de l'état trophique dans un ensemble de lacs et que toute prédiction précise ne pourra se faire avant d'avoir d'abord examiné plusieurs mécanismes dans des systèmes de lacs individuels.

[Traduit par la Rédaction]

Introduction

Studies examining the ecology of shallow lakes have increased greatly over the last couple of decades, leading to the concept that nutrient-rich shallow lakes can occur in two alternative stable states (Scheffer 1998; Jeppesen et al. 1998). One state is characterized by low transparency and high phytoplankton densities (turbid), and the other by high transparency and abundant submerged vegetation (clear-water state). Many mechanisms working together and independently tend to keep a shallow lake in one state or the other (Scheffer 1998). However, water level fluctuation is thought to be a major factor impacting some of these mechanisms and causing lakes to shift from one state to the other (Scheffer and Jeppesen 1997; Blindlow et al. 1997). For example, the water level of Lake Tamnaren in Sweden was intentionally lowered 1.5 m between 1870 and 1954 to decrease flooding of farmlands (Scheffer 1998). After the water level was decreased, aquatic macrophytes expanded strongly and the lake became famous for its waterfowl. However, in the spring of 1977, the water level rose 0.3 m, leading to dramatic changes in the ecology of the lake. The submersed, floating leafed, and part of the emergent vegetation vanished, after which swans and other aquatic birds dis-

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appeared from the lake. Because water level changes can completely change the biota of lake systems, scientists participating in an international workshop on shallow lakes systems suggested that water level fluctuation could have an overriding effect on the ecology, functioning, and management of shallow lakes (Coops et al. 2003).

One area of limnological research suggests that changes in water level are very important to sediment resuspension and that water level is a major environmental factor influencing water quality. There are many examples of shallow lakes that have high nutrient concentrations and low water clarity resulting from the resuspension of sediments (Kristensen et al. 1992; Havens et al. 1999; Bachmann et al. 1999). In these and other lakes, individual lakes show increases in nutrient concentrations and decreases in water clarity as lake levels decrease (Noges et al. 1998). For example, decreasing water level caused increases in nutrient and chlorophyll concentrations of Lake Newnan, Florida, by increasing sediment resuspension and internal nutrient loading (Nagid et al. 2001). However, decreasing water levels have also caused decreases in chlorophyll concentration and increases in water clarity because of increasing aquatic macrophyte abundance (Blindlow 1992). There are many examples of increases in aquatic macrophyte abundances as a result of decreasing water level in shallow lakes that cause decreases in nutrient and chlorophyll concentrations and increases in water clarity (Blindlow et al. 1993; Faafeng and Mjelde 1997; Scheffer 1998). Alternately, there are examples of increasing water levels causing decreases in aquatic plant abundance resulting in turbid conditions. Lake Okeechobee is a good Florida example of increasing water level allowing turbid pelagic water to move into the nearshore areas on the edge of the western marshes, increasing turbidity and causing declines in macrophytes (Havens et al. 2004). Thus, two major mechanisms (sediment resuspension and aquatic macrophyte abundance) that can impact nutrient and chlorophyll concentrations and water clarity in shallow lakes work in opposite directions with decreasing or increasing water level.

There are many other mechanisms, e.g., nutrient loading (Dillon 1975), color (Brown et al. 2000), retention time (Garcia de Emiliani 1997), biotic interactions (Gasith and Hoyer 1997), and others (Nagid et al. 2001; Havens et al. 2004), that are also related to water level changes in a lake that may impact trophic state characteristics. These mechanisms alone or in combination may overshadow the impacts of sediment resuspension and macrophyte abundances on nutrient concentrations and water clarity. Thus, water level changes in individual lakes should have differing impacts on nutrient and chlorophyll concentrations and water clarity depending on the lake's unique characteristics. However, if changes in water level drive one overriding mechanism in a population of lakes, thereby influencing nutrient and chlorophyll concentrations and water clarity, then most of the lakes should change in the same direction with increases or decreases in water level. This would provide an additional tool for limnologists attempting to understand and manage shallow lakes.

Limnologists have long sought patterns in lake functioning to provide a basis for predictions to manage lakes, but their approaches to prediction and explanation have often differed (Peters 1991). We decided to examine the impact of changes in lake water levels on total phosphorus (TP), total nitrogen (TN), and chlorophyll (Chl) concentrations and Secchi depth among a population of Florida lakes and within individual Florida lakes. This is important because Florida has over 7700 lakes and water level fluctuation is being proposed by management agencies as a key to maintaining water quality. Emphasizing the importance of water level fluctuation seems reasonable because most Florida lakes are shallow, with the majority of them having mean depths less than 5 m (average mean depth for 360 Florida lakes is 2.99 m; Florida LAKEWATCH 2003).

Table 1. Descriptive statistics for physical, chemical, and aquatic plant variables measured in 84 Florida lakes.

Parameter	Mean	Standard deviation	Minimum	Maximum
No. of months	57	29	7	175
[TP] ($\mu g \cdot L^{-1}$)	21	19	3	105
[TN] ($\mu g \cdot L^{-1}$)	735	533	60	3396
[Chl] ($\mu g \cdot L^{-1}$)	13	18	1	97
Secchi depth (m)	2.2	1.5	0.3	7.1
Mean depth (m)	3.1	1.4	1.2	7.8
Surface area (ha)	566	1089	4	5609
Dynamic ratio	1.03	1.03	0.16	5.92
Range in level (m)	1.3	0.6	0.1	3.5
PAC	27	24	0	94

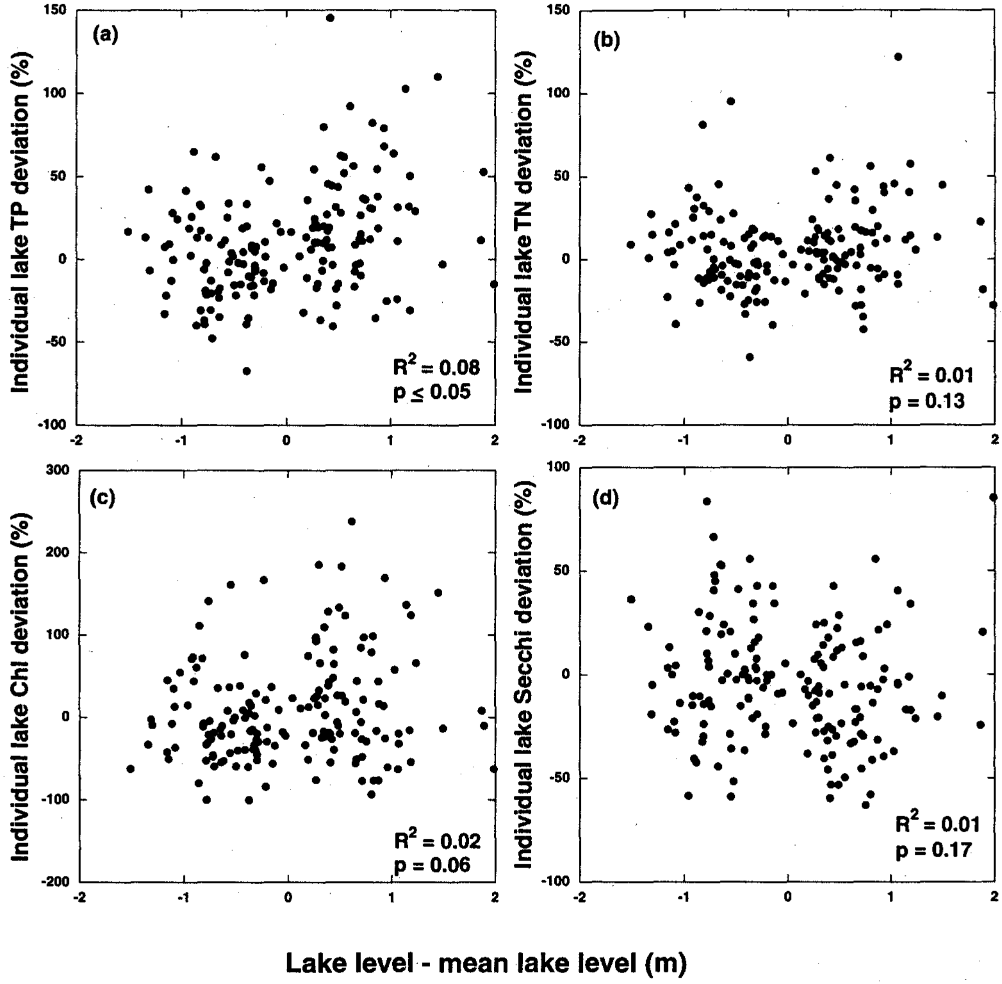
Note: TP, Total phosphorus; TN, total nitrogen; Chl, chlorophyll; PAC, percent area covered with aquatic plants.

Methods

Florida LAKEWATCH is a citizen volunteer monitoring program started in 1986 with the goal of collecting credible data on TP, TN, and Chl concentrations and Secchi depth from a large number of lakes on a monthly basis (Canfield et al. 2002). The citizens are trained by professionals to collect, prepare, and preserve surface water samples, which are then sent to a laboratory and analyzed. In 1991, a comparative study of 125 lakes found that the data collected by volunteers were comparable to those collected by professionals. Mean Secchi depth and TP, TN, and chlorophyll values obtained by the citizens were strongly correlated ($r > 0.99$) to mean values obtained by the professionals. A detailed description of all methods used in the Florida LAKEWATCH program can be found in Canfield et al. (2002).

Total phosphorus concentrations ($\mu g \cdot L^{-1}$) were determined by the procedures of Murphy and Riley (1962) with a persulfate digestion (Menzel and Corwin 1965). Total nitrogen concentrations ($\mu g \cdot L^{-1}$) were determined by oxidizing water samples with persulfate and determining nitrate nitrogen with second derivative spectroscopy (Crumpton et al. 1992; Bachmann and Canfield 1996). Chlorophyll concentrations ($\mu g \cdot L^{-1}$) were determined spectrophotometrically following pigment extraction with 90% ethanol (Sartory and Grobbelaar 1984) and using the tricromatic equation for chlorophyll *a* (Method 10200 H; APHA 1992). Because we did not

Fig. 1. Plots of monthly deviations (%) from long-term means for total phosphorus (TP), total nitrogen (TN), chlorophyll (Chl) and Secchi depth (Secchi) for individual lakes versus the corresponding monthly deviations (as actual metres) from long-term levels. Only data for the lowest and highest monthly water levels during the period of record for each individual lake were used, yielding two data points for each lake.



correct for pheophytins, we consider measurements to be total chlorophyll.

All five Florida Water Management Districts maintain staff gauges on a number of lakes, and monthly water level data are available corresponding to lakes in the Florida LAKEWATCH program. All monthly lake level measurements corresponding to LAKEWATCH water sampling events were obtained and matched with the individual lake's nutrient, chlorophyll, and water clarity data. A total of 84 lakes had matching monthly water quality and lake level data, with a period of record ranging from 7 to 175 monthly measurements (Table 1). The range in water level fluctuation, which is the difference between the highest and lowest lake level throughout the period of record, ranged from 0.1 to 3.5 m. Water levels in these 84 lakes fluctuated according to the balance between rainfall, runoff, and evaporation. Unless large rainfall events occurred, the monthly changes in water level for individual lakes were small compared with the whole period of record. Available water level data were monthly averages; thus it was not possible to match water level reading and water samples to the same day.

Florida LAKEWATCH professionals measured percent area covered with aquatic plants (PAC) of all 84 lakes on one day during the period of record (Florida LAKEWATCH 2003). PAC was determined according to the methods of Maceina and Shireman (1980). Mean depths for the 84 lakes were estimated from the fathometer transects used to estimate PAC. Surface areas for all 84 lakes were obtained from Shafer et al. (1986) or from bathymetric maps constructed by Florida LAKEWATCH (2003; 56 of the 84 lakes). Maps were created using Trimble Global Positioning System (Trimble Unit Pro XRS with a TSC1 data logger) and a Lowrance depth finder (LMS-350A). Map contours were generated using a kriging technique in Surfer software package (Golden Software, Golden, Colorado).

As a measure of potential sediment resuspension caused by wind-driven waves (Bachmann et al. 2000), we calculated the dynamic ratio (square root of lake surface area (km^2) × mean depth (m)) for each of the 84 lakes. The ratio was also calculated for lower lake levels at each contour (contours were recorded in feet (ft)) of the 56 lakes for which bathymetric maps were available to assess how the dynamic

Table 2. Mean least squares regression statistics (range in parentheses) for lakes that showed significant direct (group 1), inverse (group –1), or no (group 0) relations between actual water level and trophic state variables (TP, total phosphorus; TN, total nitrogen; Chl, total chlorophyll; Secchi, Secchi depth) within individual lakes.

		Regression statistics		
Regression group	No. of lakes	Mean intercept	Mean slope	Mean R^2
TP vs. water level				
TP group –1	9	241 (38 to 463)	–10.7 (–20.5 to –2.3)	0.31 (0.07 to 0.72)
TP group 0	44	32 (–370 to 456)	–0.3 (–8.4 to 10.9)	0.03 (0.0 to 0.10)
TP group 1	31	–223 (–936 to –13)	13.6 (1.8 to 57.1)	0.19 (0.04 to 0.68)
TN vs. water level				
TN group –1	12	9007 (1 001 to 33 414)	–316 (–831 to –280	0.20 (0.07 to 0.53)
TN group 0	41	949 (–6 925 to 26 236)	–7.9 (–696 to 307)	0.04 (0.0 to 0.45)
TN group 1	31	–4099 (–28 426 to –57)	263 (31 to 1583)	0.22 (0.06 to 0.84)
Chl vs. water level				
Chl group –1	8	287 (19 to 1424)	–17.6 (–74.9 to –2.6)	0.20 (0.08 to 0.39)
Chl group 0	52	32 (–370 to 1803)	–0.6 (–45.2 to 13.2)	0.03 (0.0 to 0.17)
Chl group 1	24	–303 (–3174 to –8)	15.1 (1.02 to 168.8)	0.16 (0.04 to 0.56)
Secchi vs. water level				
Secchi group –1	24	27.5 (1.5 to 229)	–1.1 (7.1 to 0.1)	0.24 (0.05 to 0.97)
Secchi group 0	48	1.3 (–147 to 29)	–0.1 (–1.5 to 2.8)	0.03 (0.0 to 0.19)
Secchi group 1	12	–9.1 (–35.5 to –1.1)	0.6 (0.1 to 2.3)	0.30 (0.12 to 0.53)

ratio would change with decreasing water level. Dynamic ratio changes with increasing water level could not be examined because contours above the water level were not available.

The potential area of a lake where submersed aquatic vegetation will grow, assuming light is the limiting factor, can be calculated using a relation between the maximum depth of plant colonization and Secchi depth (Canfield et al.1985) and overlaying this depth on a bathymetric map. The potential PAC was also calculated for each contour to see how it would change with decreasing water level. This was done for the 56 lakes, but potential PAC changes with increasing water level could not be examined because contours above the water level at the time the maps were generated were not available.

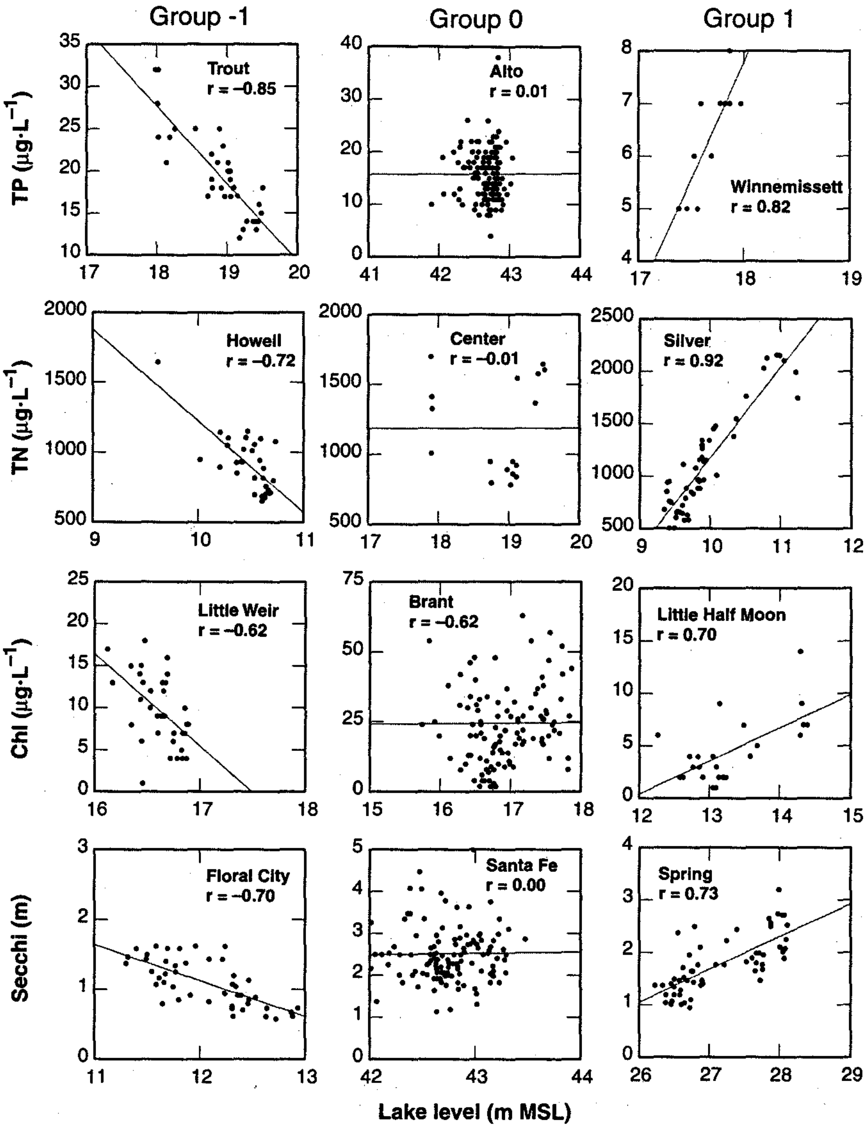
To determine if there is one overriding mechanism impacting the relation between nutrient and chlorophyll concentrations and Secchi depth and water level fluctuations among lakes, we calculated the deviation from the long-term mean for each TP, TN, chlorophyll, and Secchi depth monthly measurement within each individual lake. Each deviation was listed as a percent of the lake's long-term mean. The difference between the actual monthly water level and the long-term average water level was also calculated. Plotting all of these data together to look for trends among lakes would not be proper because each lake has a different period of record and the lakes with the longest record would weight the analysis. Thus, for each lake we selected the matched monthly data with the lowest and highest lake level yielding two data points for each lake and then plotted these deviations for trophic state variables against the corresponding deviations in lake level.

Least squares linear regression was used to determine if each trophic state variable was related to water level fluctuations within each lake, which we considered the experimental unit. These analyses were used to separate lakes into three groups per trophic state variable. Group 1 included lakes that showed significant direct relations, group –1, significant inverse relations, and group 0, no significant relations between individual trophic state variables and corresponding lake level. A two-way analysis of variance with an interaction term (Snedecor and Cochran 1967) was used to determine if trophic state variables (factor 1 values are TP, TN, and chlorophyll concentrations and Secchi depth), group classification (factor 2 values are group –1, group 0, and group 1), and (or) the interaction of these two class variables accounted for significant variance in the range of water level fluctuation for individual lakes, dynamic ratio, and measured PAC. Three separate analyses were done, one for each variable (lake level range, dynamic ratio, and PAC). For each particular factor combination in any one of the analyses, there were 84 replicate observations, each one corresponding to a lake. Dynamic ratio values were transformed to their logarithms (base 10) and PAC values were transformed using an arcsine transformation before statistical analyses to accommodate heterogeneity of variances (Snedecor and Cochran 1967). We used the JMP statistical package (SAS Institute Inc. 2000) for statistical computations and statements of significance are at $p \leq 0.05$.

Results and discussion

The period of record for the 84 individual lakes having both water level and trophic state data ranged from 7 to 175 months, with an average of 57 months (Table 1). The lakes ranged from oligotrophic to hypereutrophic (Forsberg and Ryding 1980), with long-term average chlorophyll concentrations within individual lakes ranging from 1 to 97 $\mu g \cdot L^{-1}$. Overall, chlorophyll concentration averaged 13 $\mu g \cdot L^{-1}$. TP and TN concentrations averaged 21 $\mu g \cdot L^{-1}$ and 735 $\mu g \cdot L^{-1}$, respectively, and individual lake averages ranged from 3 to 105 $\mu g \cdot L^{-1}$ and from 60 to 3400 $\mu g \cdot L^{-1}$, re-

Fig. 2. Plots of total phosphorus (TP), total nitrogen (TN), and chlorophyll (Chl) concentrations and Secchi depth (Secchi) versus corresponding monthly water levels for selected lakes (MSL, mean sea level). Group –1 includes lakes with significant inverse relationships, group 0, no relationships, and group 1, direct relationships between trophic state variables and lake levels.



spectively. Average Secchi depth for individual lakes averaged 2.2 m, with average water clarity readings ranging from 0.3 to 7.0 m.

Overall, the 84 Florida lakes used in this study are shallow, with 90% of the lakes having mean depths < 5 m. The lakes had an average mean depth of 3.1 m, with individual lake mean depths ranging from 1.2 to 7.8 m. The study lakes were also typically small, with 90% of the lakes having surface areas < 2000 ha. The recorded surface areas ranged from 4 to 5600 ha, with an overall average of 566 ha. The average fluctuation in water level during the individual lake's period of record was 1.3 m, with a range of 0.1 to 3.5 m.

If there were one dominant mechanism impacting changes in nutrient and chlorophyll concentrations and Secchi depth with water level changes, then plots of long-term deviations should show significant relations with a positive or negative slope (Fig. 1). Only the deviations for TP concentrations among all lakes were significantly related to water level deviations. However, water level deviation accounting for only 8% of the variance in TP deviations (Fig. 1*a*), and deviations in TN and chlorophyll concentrations and Secchi depth were not significantly related to water level deviations, suggesting that (*i*) more than one mechanism is working within individual lakes among this population of lakes, (*ii*) there are no relations between nutrient and chlorophyll concentrations, Secchi depth, and water level fluctuations among these lakes, or (*iii*) a combination of both.

To examine relations between nutrient and chlorophyll concentrations, Secchi depth, and lake water level within individual lakes, we plotted monthly nutrient and chlorophyll concentrations and Secchi depth measurements against actual monthly water levels (independent variable). For each dependent variable, lakes were found with significant inverse relations, significant direct relations, and no significant relations (Table 2), which may explain why no strong relations

Table 3. Descriptive statistics for groups of lakes that showed significant direct (group 1), inverse (group –1), or no (group 0) relations between actual water level and trophic state variables (TP, total phosphorus; TN, total nitrogen; Chl, total chlorophyll; Secchi, Secchi depth) using least squares regression statistics within individual lakes in each group.

		Range in lake level (m)			Dynamic ratio			PAC		
Regression group	*N*	Mean	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Minimum	Maximum
TP vs. water level										
TP group –1	9	1.29	0.70	1.88	0.70	0.29	1.56	19	0	74
TP group 0	44	1.27	0.10	3.50	0.98	0.19	3.56	28	0	93
TP group 1	31	1.27	0.34	3.04	1.19	0.16	5.92	29	0	94
TN vs. water level										
TN group –1	12	1.13	0.38	1.89	1.11	0.19	5.92	27	0	93
TN group 0	41	1.26	0.10	3.50	0.99	0.24	4.24	26	0	74
TN group 1	31	1.34	0.34	2.45	1.05	0.16	3.73	30	0	94
Chl vs. water level										
Chl group –1	8	1.02	0.57	1.53	1.39	0.30	3.56	26	4	52
Chl group 0	52	1.35	0.10	3.50	0.97	0.19	5.92	27	0	94
Chl group 1	24	1.19	0.34	2.40	1.03	0.16	4.24	28	0	92
Secchi vs. water level										
Secchi group –1	24	1.21	0.40	2.13	0.90	0.16	3.63	24	0	92
Secchi group 0	48	1.28	0.10	3.50	1.20	0.19	5.92	29	0	94
Secchi group 1	12	1.35	0.58	2.02	0.60	0.29	0.84	29	0	74

Note: The mean, minimum, and maximum are listed for range in lakes level (m), dynamic ratio, and percent area covered by aquatic plants (PAC). *N* is the number of lakes in each group. A two-way analysis of variance showed that neither trophic state variable nor group classification nor the interaction of these two class variables accounted for significant variance in the range of water level fluctuation for individual lakes, dynamic ratio, or measured PAC.

Table 4. The 25% quantile, median, 75% quantile, and range of calculated dynamic ratios using three different contours from 56 bathymetric maps.

	Quantiles for dynamic ratio			
	25%	Median	75%	Range
Contour 0.0 m	0.3	0.51	1.01	0.07 to 5.39
Contour 0.91 m	0.29	0.55	0.96	0.07 to 5.63
Contour 1.52 m	0.33	0.6	1.12	0.07 to 7.52
Contours 0.91 and 0.0 m	–0.02	0.02	0.1	–0.37 to 1.20
Contours 1.52 and 0.0 m	–0.01	0.06	0.21	–0.58 to 3.64

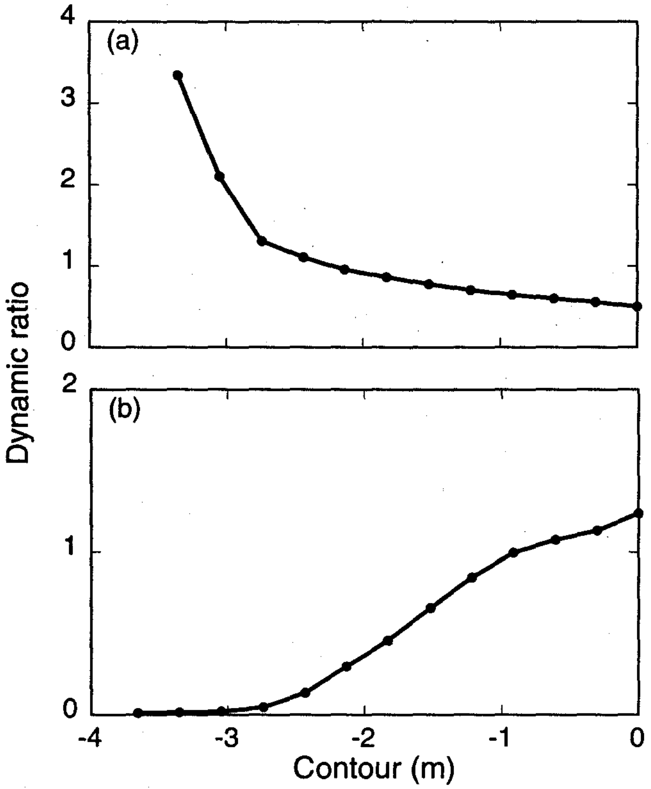
Note: The quantiles and ranges for the difference in dynamic ratios between contours 0.91 m and 1.52 m and 0.0 m are also listed.

were seen when all of the data were standardized and plotted together (Fig. 1). Some of the significant relations were quite strong (Fig. 2), suggesting that in these lakes, water level could be used as a predictor of nutrient and chlorophyll concentrations and Secchi depth. However, approximately half or more of the lakes showed no significant relation between water level and nutrient and (or) chlorophyll concentrations and (or) Secchi depth (Table 2), clearly indicating that statements regarding the positive or negative influence of water level fluctuation on the water quality of shallow lakes must be made cautiously.

There were only seven lakes that followed conventional trophic state theory in which if nutrient concentrations went up or down significantly with lake water level, then chlorophyll concentrations responded accordingly, and Secchi depth responded inversely to chlorophyll. Examining all other combinations of the relations between trophic state variables and lake water level within individual lakes revealed 31 different groups among all lakes. The largest group was 18 lakes that all showed no relations between each nutrient, chlorophyll, Secchi depth, and lake water level. This examination suggests that several mechanisms may be impacting trophic state variables differently as lake levels change within individual lakes.

Lakes with small (0.2–0.5 m) or large (>0.5 m) changes in water level have been shown to exhibit significant changes in trophic state variables due to several mechanisms (Scheffer 1998; Nagid et al. 2001; Havens et al. 2004). To examine if the magnitude of water level change determines a lakes potential for significant relations between water levels and trophic state variables, lakes were grouped as to whether nutrient and chlorophyll concentrations and Secchi depth showed significant inverse relationships (group –1), no significant relationships (group 0), or significant direct relationships (group 1) with water level (Table 3). A two-way analysis of variance using trophic state variables, group, and the interaction between these two class variables as independent variables and the range in lake level over the period of record as a dependent variable showed no significant effects (Table 3). Thus, although small and (or) large changes

Fig. 3. Dynamic ratio calculated for lower lake water levels at individual depth contours from bathymetric maps of (*a*) Lake Tsala Apopka, Citrus County, Florida, and (*b*) Lake Como, Putnam County, Florida, versus the contour depths.



in water level can impact trophic state variables in lakes (Scheffer 1998; Nagid et al. 2001), predicting how trophic state variables change based on the magnitude that lake levels fluctuate among a large population of shallow Florida lakes can not be demonstrated.

Using a sample of Florida lakes, Bachmann et al. (2000) showed that for lakes with a dynamic ratio > 0.8, the entire lake bed was subjected to wave disturbance at least some of the time. Similar ratios have been used as screening tools to determine which lakes might be susceptible to sediment disturbance by wind-driven waves (Hakanson 1982; Osgood 1988). To examine if dynamic ratio is a factor determining a lake's potential for significant relations between water level and trophic state variables, we used the lake groupings (Table 2) where nutrient and chlorophyll concentrations and Secchi depth showed significant inverse relationships (group –1), no significant relationships (group 0), or significant direct relationships (group 1) with water level. A two-way analysis of variance using trophic state variables, group, and the interaction between these two class variables as independent variables and dynamic ratio as the dependent variable showed no significant effects (Table 3). These data suggest that the dynamic ratio is not an overriding mechanism determining relations between nutrients, chlorophyll, and Secchi depth and water level fluctuations. However, the above analysis assumes that the dynamic ratio does not change with water level fluctuation.

Bathymetric maps were available for a subset of 56 of the 84 lakes used in this study. To test whether the dynamic ratio changes as water level decreases, the maps were used to calculate the dynamic ratio at the 0.0, 0.91 (3 ft), and 1.52 m (5 ft) contours. These contours were selected because they cover approximately 80% of the actual measured ranges in lake level fluctuations. The median dynamic ratio of the 56 lakes showed an increasing trend from 0.51 in the 0.0 m contour to 0.60 in the 1.52 m contour (Table 4). Examining the difference between the 0.0 m contour and both other contours, however, showed that the dynamic ratio would both increase and decrease in individual Florida lakes as water level decreased. For example, Lake Lochloosa shows a dramatic increase in the dynamic ratio as water level decreases, whereas Lake Como shows a decrease in the dynamic ratio as water level decreases (Fig. 3). For approximately 25% of the lakes, the dynamic ratio decreased from 0.0 m to either 0.91 m or 1.52 m contours. We were not able to examine potential changes in the dynamic ratio that might occur with increasing water level because contours were not available above the 0.0 m contour on the day of mapping (Florida's lakes are known for significant increases in water level during floods because of the state's low relief). However, data for this population of lakes clearly indicate that water level fluctuations can increase or decrease the potential for lakes to experience sediment resuspension, depending on the lake's individual morphology. Again, this probably helps explain why no relations were seen when all of the data were standardized and plotted (Fig. 1).

Historically, many studies have shown inverse relations between abundance of submersed aquatic vegetation and trophic state variables (Goulder 1969; Canfield et al. 1984; Jeppesen et al. 1990). To examine if aquatic plant abundance as estimated with PAC is a major factor determining a lake's potential for significant relations between water level and trophic state variables, we used lake groupings where nutrient and chlorophyll concentrations and Secchi depth showed significant relationships (group 1 or group –1) or no significant relationships (group 0) with water level (Table 2). A two-way analysis of variance using trophic state variables, group, and the interaction between these two class variables as independent variables and PAC as a dependent variable showed no significant effects (Table 3). These data for our study lakes, therefore, indicate that the PAC is not the overriding mechanism determining relationships between nutrient and chlorophyll concentrations and Secchi depth and water level fluctuations. The above analysis, however, once again assumes that PAC does not change with water level fluctuation.

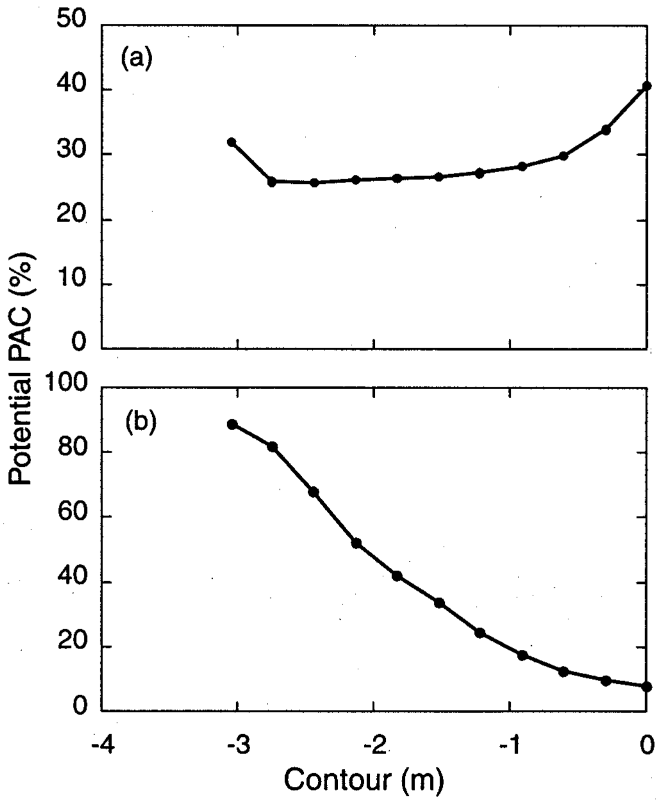
To ascertain if the potential PAC value changes as water level decreases, each lake's average Secchi depth was used with an equation from Canfield et al. (1985) to predict the maximum depth of colonization for submersed aquatic plants. We then used this maximum depth of colonization with the bathymetric maps to calculate potential PAC values at the 0.0, 0.91, and 1.52 m contours (~80% of the actual measured ranges in lakes level). The potential PAC of the 56 Florida lakes showed an increase from a median of 49% in the 0.0 m contour to 56% in the 0.91 m contour and 64% in the 1.52 m contour (Table 5). Examining the range of differ-

Table 5. The 25% quantile, median, 75% quantile, and range of measured percent area covered with aquatic plants (PAC) and potential PAC using three different contours from 56 bathymetric maps.

	Quantiles for PAC			
	25%	Median	75%	Range
Measured PAC	9	17	32	2 to 93
Potential PAC contour 0.0 m	33	49	66	8 to 100
Potential PAC contour 0.91 m	33	56	84	26 to 100
Potential PAC contour 1.52 m	40	64	93	18 to 100
Potential PAC contours 0.91 m and 0.0 m	1	5	11	–12 to 43
Potential PAC contours 1.52 m and 0.0 m	3	10	22	–14 to 74

Note: The potential PAC was estimated by calculating maximum depth of plant colonization (Canfield et al. 1984) using average Secchi depth values for each lake and overlaying it on the bathymetric maps. The quantiles and ranges for the difference in potential PAC between contours 0.91 m and 1.52 m and potential PAC at 0.0 m are also listed.

Fig. 4. Potential percentage area covered with aquatic plants (potential PAC) calculated at individual contours from bathymetric maps of (*a*) Lake Charlotte, Highlands County, Florida, and (*b*) Lake Harris, Lake County, Florida, versus the individual contour. The potential PAC was estimated by calculating maximum depth of plant colonization (Canfield et al. 1985) using average Secchi depth values for each lake and overlaying it on the bathymetric maps.



ences between the potential PAC at the 0.0 m contour and both other contours, however, showed that potential PAC could both increase and decrease in individual lakes as water level decreases. For example, Lake Charlotte shows a decrease in potential PAC as water becomes deeper, but Lake Harris shows an increase (Fig. 4). Therefore, potential PAC in individual lakes can increase or decrease as lake levels change, depending on lake morphology. It is also important to point out that the median for the actual measured PAC is much less than the median potential PAC for contours 0.0, 0.91, and 1.52 m (Table 5), suggesting that factors other than light can impact a entire lake's PAC, as other authors have suggested (Spence 1982; Duarte and Kalff 1986; Bachmann et al. 2002). Thus, water level fluctuations can either increase or decrease plant abundance, and the ultimate effect on lake trophic state variables can be uncertain despite the well-documented inverse relationship between phytoplankton and aquatic macrophytes.

In conclusion, limnologists have long sought general patterns in lake functioning to aid lake management (Dillon and Rigler 1974; Jones and Bachmann 1976; Peters 1991). Water level fluctuations are often assumed to be a general lake functioning pattern that has an overriding effect on the ecology and management of shallow lakes (Coops et al. 2003). We, however, could find no overall relation between trophic state variables and lake level fluctuation among a population of 84 Florida lakes. Based on our available data, individual lakes can show direct, inverse, and (or) no significant relation between lake trophic state variables and water level fluctuations, regardless of the magnitude of water level fluctuation.

Individual lake studies have shown that sediment resuspension and aquatic macrophyte abundance can impact (both independently and in combination) lake trophic state parameters as lake water levels change. However, in Florida lakes, sediment resuspension (estimated with the dynamic ratio) and potential PAC (assuming light is the limiting factor for plant abundance) can increase or decrease as water level increases or decreases, depending on lake morphology. Many other mechanisms related to water level fluctuations also have the potential to override the importance of sediment resuspension and (or) aquatic plant abundance. Thus, although many scientists continue to emphasize the importance of water level fluctuations, we strongly feel the prediction of the effects of water level fluctuations on lake trophic state parameters will remain difficult without examining several mechanisms within an individual system.

There have been and probably will continue to be debates regarding the best approach towards understanding the limnological functioning of lakes (Lehman 1986; Peters 1986). Some of the philosophical arguments are related to defining the parameters of interest (e.g., trophic state variables) and understanding the uncertainties associated with predictions (Canfield and Bachmann 1981; Canfield 1983). Other arguments are directly related to how the arguments are constructed. For example, what is a shallow lake (Padisak and Reynolds 2003)? Padisak and Reynolds (2003), in their overview of the role of depth in ecosystem functioning of inland waters, observed there are absolute and relative measures, as well as pragmatic concerns. Lake managers have to be concerned about pragmatic issues, and it is clear based on our study that managers should no longer categorically state that water level fluctuation would improve water quality as measured by trophic state parameters. Although there are general patterns of limnological functioning for the population of Florida lakes (Brown et al. 2000), water level fluctuation is not a predictor of trophic state variables, and individual lake properties must be considered before predictions are made.

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