



The restoration of Lake Apopka in relation to alternative stable states: an alternative view to that of Bachmann et al. (1999)

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Abstract

Bachmann et al. (1999) postulated that wind energy initiated, and has maintained, high turbidity in hypertrophic (mean chlorophyll *a* = 92 $\mu\text{g l}^{-1}$) Lake Apopka, Florida (mean depth = 1.6 m; area = 12 500 ha). They asserted that the turbid condition was initiated by a hurricane in late 1947 that destroyed submersed plant beds and that high turbidity has since been maintained by wind-driven resuspension of fluid sediments. In their view, there has been sufficient light for re-establishment of submersed plants over about 38% of the lake bottom, but plant growth has been precluded by the fluid character of the sediments. They concluded that the restoration program of the St. Johns River Water Management District, which includes reduction of the phosphorus (P) loading rate, will not restore water clarity or submersed vegetation. An alternative explanation for Lake Apopka's turbid state is that it was initiated, and has been maintained, by excessive P loading that led to algal blooms and elimination of submersed vegetation through light limitation. The transition to the turbid state was contemporaneous with drainage of 7300 ha of the floodplain wetland to create polders for farming, beginning in the early 1940s. Lake P budgets indicate that drainage of the farms caused a seven-fold increase in the P loading rate (0.08 g TP $\text{m}^{-2} \text{yr}^{-1}$ to 0.55 g TP $\text{m}^{-2} \text{yr}^{-1}$). Paleolimnological analysis of lake sediments also indicates an increase in the P loading rate in mid-century, concomitant with the decline in submersed vegetation and the increase in phytoplankton abundance. After the increase in P loading, wind disturbance may have accelerated the transition to the turbid state; but, before the increase in P loading, wind disturbance was insufficient to elicit the turbid state, as evidenced by the stability of the clear-water state in the face of 14 hurricanes and 41 tropical storms from 1881 to 1946. Measurements of photosynthetically active radiation (PAR) indicate that light limitation has inhibited submersed plant growth except on the shallowest 5% of the lake bottom. Further, the correlation between the diffuse attenuation coefficient (K_{PAR}) and chlorophyll *a* (CHLA) indicates that light limitation would be removed over about 82% of the lake bottom with a reduction in CHLA from 92 $\mu\text{g l}^{-1}$ to 25 $\mu\text{g l}^{-1}$. Recently, following a 40% reduction in the P loading rate, the mean total P (TP) concentration, mean CHLA, and total suspended solids fell by about 30% while mean Secchi depth increased by more than 20%. Submersed plant beds appeared in areas devoid of macrophytes for nearly 50 years. These improvements, during a period with no change in mean wind speeds measured at Lake Apopka, provide the strongest evidence that the turbid state has been maintained by excessive P loading and that the current restoration program, which combines P load reduction with planting and removal of planktivorous fish, will be effective.

Introduction

Bachmann et al. (1999) postulated that the turbid condition of Lake Apopka is an alternative stable state initiated, and sustained, by wind energy rather than excessive phosphorus (P) loading. In their view, the turbid state was initiated in the fall of 1947, after a hurricane uprooted plants, and has been maintained since that time by wind-driven resuspension of sediments, which also created a fluid mud layer. They presented analyses that suggest the fluid mud, not high turbidity, has prevented recolonization by macrophytes and the associated return to a clear-water condition. They concluded that “the shallowness of Lake Apopka and not external nutrient loading must be considered the dominant limnological factor in determining its current state”. Consequently, they asserted that the restoration program of the St. Johns River Water Management District, which includes P load reduction, will be ineffective because excessive P loading and algal turbidity do not maintain the present condition. Here, we discuss their position and present evidence to support an alternative view.

A brief discussion of the lake’s history is necessary to frame our discussion. Before mid-century, Lake Apopka was the second largest lake in Florida with a surface area of about 21 000 ha (Lowe et al., 1999). It had clear water, abundant submersed vegetation, and a large (ca. 9000 ha) floodplain marsh (Clugston, 1963; Lowe et al., 1999). In the 1940s, more than 3000 ha of the floodplain marsh were diked, ditched and drained to create polders for farming. Drainage of the floodplain continued in subsequent decades creating more than 7300 ha of farmed polders (Lowe et al., 1999). Since the early 1940s, water has been pumped from the farms into the lake to prevent flooding of the fields. Lake Apopka had clear water and abundant submersed plants through 1946; but by 1950, the submersed plants were nearly absent, the water was turbid and there was a continuous algal bloom (Clugston, 1963). Hypertrophic conditions (e.g. mean chlorophyll *a* was $92 \mu\text{g l}^{-1}$ during 1986–1996) persisted during the remainder of the century.

Initiation of the turbid state

From 1886 through 1946, 14 hurricanes and 41 tropical storms passed within 160 km of Lake Apopka (Lowe et al., 1999). If storms alone could have elicited the turbid state, then one or more of these earlier

storms should have been sufficient; but, the lake retained clear water and macrophyte dominance through 1946 (Clugston, 1963). Aerial photographs indicate Lake Apopka was turbid, due to an extensive algal bloom, in March 1947: six months before the September 1947 hurricane and more than a year after the storms of 1945 (Lowe et al., 1999). Apparently, the turbid state was initiated in a time period uninfluenced by a major storm.

In our view, the turbid state was initiated by creation of farmed polders on the floodplain and the concomitant increase in P loading, not by a hurricane, as suggested by Bachmann et al. (1999). We recognize that the accuracy of estimates of the increase in P loading in the 1940s can be debated, but few would argue that conversion of more than 3000 ha of floodplain wetlands to farmed polders would elicit an insignificant increase in the P loading rate. As the farming area grew to more than 7000 ha, the P loading rate would have grown concomitantly. Using modern data for the total P loading rate and for P loading from natural sources, pumping from the farms into the 12 500 ha remaining lake increased the total P loading rate from approximately $0.08 \text{ g TP m}^{-2} \text{ yr}^{-1}$ to approximately $0.55 \text{ g TP m}^{-2} \text{ yr}^{-1}$, a seven-fold increase (Battoo et al., 1999; Lowe et al., 1999).

Paleolimnological analysis of lake sediments indicates that the P deposition rate increased three to four-fold over the past 50 years and, on average, the sediment concentration of TP increased about four-fold (Schelske, 1997). Lake sediments also indicate a concomitant decrease in macrophyte abundance, as indicated by the species composition and abundance of diatom microfossils and sponge spicules (Schelske, 1997; Schelske et al., 1999, 2000). Finally, the concentration of polyphosphate (hot water extractable P minus water soluble P) increases upcore in the sediments, as does the proportion of TP as polyphosphate, indicating progressively excessive P loading relative to phytoplanktonic requirements (Schelske et al., 2000).

The storm hypothesis of Bachmann et al. (1999) suggests a transition to the turbid state in a matter of weeks. The paleolimnological record also indicates a rapid transition to algal dominance; but over a period of years, not weeks, as implied by the storm hypothesis (Schelske et al., 1999). The written historical record also indicates that transition to the stable turbid state required several to many years (Lowe et al., 1999). Changes in Lake Apopka were noted in the early 1940s, well before the change to algal dominance. Beginning in about 1940, a dense growth of

aquatic weeds appeared (Sheffield & Kuhrt, 1970). This would be an expected response to increased P loading. In Dutch lakes the transition to algal dominance was typically preceded by an increase in abundance of submersed macrophytes (Klinge et al., 1995). We propose that progressive shading by phytoplankton and epiphytes associated with the increasing P load was the ultimate cause of the decline in macrophyte abundance. Observations of submersed macrophytes as late as 1959 (Clugston, 1963) support a gradual decline in macrophyte abundance. Earlier writers also attributed the loss of macrophytes to shading (Clugston, 1963; Sheffield & Kuhrt, 1970).

Bachmann et al. (1999) used the theory of alternative stable states in shallow lakes to support their assertion that Lake Apopka switched states due to the 1947 storm. Their position was that uprooting of macrophytes was the cause of the change to algal dominance. In their view, if the macrophytes had not been removed by the storm no fundamental change in the lake would have occurred – even in the face of the many-fold increase in TP loading.

This reasoning does not adequately consider the history of the lake or the fact that the theory of alternative stable states in shallow lakes retains the primacy of the TP concentration in determining potential states (Scheffer, 1990; Scheffer et al., 1993; Klinge et al., 1995; Moss et al., 1996). In this theory, lakes with sufficiently low or sufficiently high TP concentration have only one stable state. This is aptly demonstrated by the history of Lake Apopka. Before the increase in P loading, numerous forward switches (*sensu* Moss et al., 1997), in the form of intense storms, were insufficient to elicit a change in state to algal dominance. After the increase in P loading, macrophytes could not prevent the development of extensive algal blooms, even in a period without storms, as shown by the extensive algal bloom in the spring of 1947, when macrophytes were still abundant (Clugston, 1963; Lowe et al., 1999). Storms may have accelerated the loss of macrophytes *after* the increase in P loading, but many strong storms apparently failed to reduce macrophyte abundance and failed to elicit the turbid state *before* the increase in P loading.

The point here is that, after several years of high TP loading, no forward switch was required for establishment of a new stable state. During the last part of the 20th century, the mean TP concentration in Lake Apopka was so high ($>200 \mu\text{g l}^{-1}$) that only one stable state has been possible: high turbidity and algal dominance. In Danish lakes, the depth of macrophyte

colonization was reduced to 1–1.5 m at TP levels of 60–150 $\mu\text{g l}^{-1}$ and macrophytes were absent at levels above 250 $\mu\text{g l}^{-1}$ (Jeppesen et al., 1991). Both observation and theory indicate that in large lakes processes leading to high turbidity and algal dominance occur at lower levels of TP than in small lakes (Jeppesen et al., 1991; Klinge et al., 1995). These studies indicate that the upper limit for macrophyte dominance in large (>10 ha), shallow lakes is in the range of 60–150 $\mu\text{g TP l}^{-1}$. Lake Apopka has had mean TP levels well above this range. The theory of alternative stable states and its supporting data indicate that switching between the clear water and turbid states should not be expected at TP levels above 150 $\mu\text{g l}^{-1}$ for a lake as large as Lake Apopka.

Maintenance of the turbid state

Bachmann et al. (1999) hypothesized that the turbid state has been maintained by wind-driven sediment resuspension, not by excessive P loading. They used the correlation between Secchi depth (SD) and the concentration of chlorophyll *a* (CHLA) in Lake Apopka, and in surveys of northern lakes (Jones & Bachmann, 1978) and other Florida lakes (Canfield & Hodgson, 1983), to show that Lake Apopka differs from northern lakes and from other Florida lakes by having a lower SD for a given level of CHLA. They attributed the difference to resuspended, non-living materials. Using a regression for CHLA vs. TP for Florida lakes and the SD–CHLA relationship for Lake Apopka, they calculated that an 80% decrease in TP concentration to 41 $\mu\text{g l}^{-1}$ would reduce CHLA from 92 $\mu\text{g l}^{-1}$ to 31 $\mu\text{g l}^{-1}$, which would increase SD from 0.23 m to 0.34 m. They concluded that this difference “would be visually difficult to notice”.

We agree that a large fraction of Lake Apopka’s turbidity results from non-living particles and we accept the conclusion that a change in SD from 0.23 to 0.34 m would be visually difficult to notice. We wish to point out, however, that a large reduction in algal biomass, as indicated by CHLA, would significantly improve the light climate for submersed plants. Bachmann et al. (1999), using a regression relating the depth of macrophyte colonization to SD (Canfield et al., 1985), predicted that an increase in SD from 0.23 m to 0.34 m would increase the potential maximum depth for growth of submersed plants from 1.39 m to 1.63 m and, consequently, increase the percentage of lake bottom that could support macrophytes

from 39% to 78%. A doubling of the area potentially suitable for macrophyte growth is clearly a significant benefit.

Direct measurements, in Lake Apopka, of photosynthetically-active radiation (PAR) better correspond with the current paucity of submersed vegetation and indicate an even stronger benefit from reduced algal biomass. Schelske et al. (1992) measured PAR and reported a negative correlation between the diffuse attenuation coefficient (K_{PAR}) and CHLA. Using these data, a decrease in CHLA from $92 \mu\text{g l}^{-1}$ to $25 \mu\text{g l}^{-1}$ would be expected to more than double the compensation depth, from 0.84 m to 1.93 m, if it is assumed that the compensation depth is at 1% of surface light (Schelske et al., 2000). This increase in the compensation depth would increase the potential area for colonization by macrophytes over 16-fold, from 5% to 82% of the lake bottom.

Thus, the analysis based on PAR indicates a greater effect from reduction of CHLA than does the analysis of Bachmann et al. (1999) based on SD, but both analyses indicate a substantial benefit from reduced algal biomass. SD is strongly influenced by light scattering and is an unreliable indicator of light penetration if turbidity is variable (Scheffer, 1998) so it is not unexpected that the analysis based on PAR predicts greater benefits than that based on SD.

Both analyses discussed above likely underestimate the improvements that could be expected in water clarity following a reduction in algal biomass. Although a large portion of the light attenuation currently appears to be due to non-living particles, a large fraction of the non-living particles must be recently-produced, algal detritus. Schelske et al. (2000) found that the rate of algal production of organic material exceeded the rate of sedimentation of organic material nearly 10-fold. Thus, algal production alone could account for most of the sedimented and suspended matter. Because production greatly exceeds sedimentation, organic matter must be rapidly decomposed in the water column. Therefore, a large fraction of the non-algal turbidity can be attributed to autochthonous production that is rapidly decomposed and can only be maintained by continued high levels of algal production. The resuspended, surficial sediments are of algal origin (Schelske et al., 2000). As algal production falls with increasing P limitation during restoration, algal and non-algal turbidity also will diminish.

Finally, we note that Lake Apopka does not appear unique with respect to other Florida lakes when the Jones & Bachmann (1978) and Canfield & Hodg-

son (1983) regressions are examined more carefully (Fig. 1). We modified Figure 3 of Bachmann et al. (1999) by showing the data points and the full range of the data set used to develop the regression line for Florida lakes of Canfield & Hodgson (1983). Our modification shows that both regression lines are poor predictors of the relationship between SD and CHLA not only for Lake Apopka, as pointed out by Bachmann et al. (1999), but also for other Florida lakes with CHLA levels greater than about $75 \mu\text{g l}^{-1}$ (Fig. 1). These regression lines simply do not accurately describe the condition of Florida lakes with high CHLA and low SD, like Lake Apopka. The monthly means and the overall mean for Lake Apopka do not appear to be outliers with respect to other hypertrophic Florida lakes.

Inhibition of macrophyte recolonization

For most of the past 50 years, submersed plants have been virtually absent from Lake Apopka. Using the regression model of Canfield et al. (1985), Bachmann et al. (1999) predicted that, at the modern mean SD of 0.23 m, "39% of the lake bottom has sufficient light for plant colonization". They concluded (p. 228) that "these data indicate that some other factor limits plant re-establishment in Lake Apopka". They suggested that this other factor is the fluid sediments and stated that "plant roots would not be able to establish themselves against the forces of wind-driven water movements and plant re-establishment would be precluded".

We agree that the flocculent sediments of Lake Apopka may retard re-establishment of submersed plants but we do not agree that the sediments preclude plant re-establishment. Light measurements in Lake Apopka indicate that, prior to recent improvements in water quality, only 5% of the lake bottom received $\geq 1\%$ of surface illumination as PAR (Schelske et al., 1992; Schelske et al., 2000). Thus, no reference to the flocculent sediments is required to explain the absence of submersed macrophytes over the vast majority of the lake for the past five decades. The relationship between K_{PAR} and CHLA predicts significant improvements in the light climate concomitant with reductions in CHLA (Schelske et al., 1992; Schelske et al., 2000), a prediction in accord with the recent recurrence of submersed plants at many locations where they had been absent for decades. This regrowth of submersed plants occurred during a period of increas-

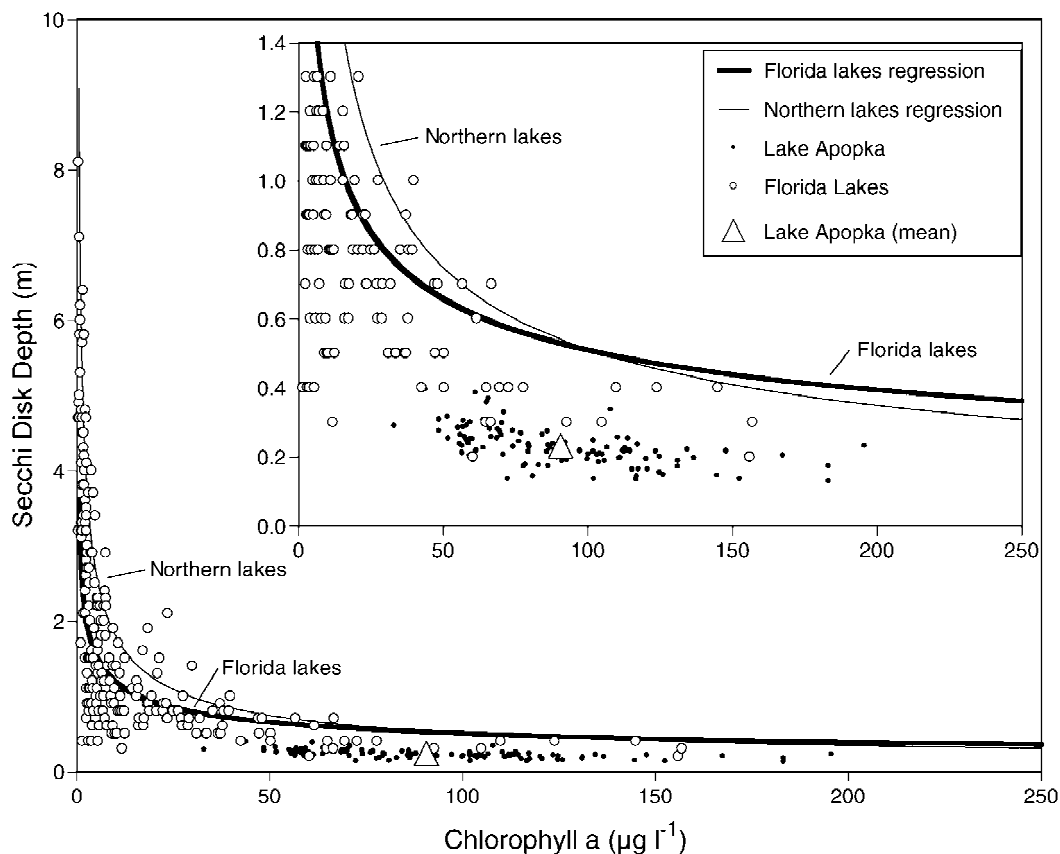


Figure 1. The relationship between SD (m) and concentration of CHLA ($\mu\text{g l}^{-1}$) (cf. Bachmann et al., 1999; Fig. 3). Regression lines are shown for Florida lakes with water colour 34 Pt l^{-1} (Canfield & Hodgson, 1983) and for northern lakes (Jones & Bachmann, 1978). Open circles are data for Florida lakes from Canfield & Hodgson (1983), and solid dots are monthly mean values for Lake Apopka (1988–1998). The triangle is the overall mean for Lake Apopka. Insert shows detail for $\text{SD} < 1.4 \text{ m}$.

ing SD (Battoe et al., 1999), further indicating that light limitation, and not the physical character of the sediments, has prevented colonization by submersed plants for the past 50 years.

The difference between our view and that of Bachmann et al. (1999) with regard to submersed plants may be explained by the choice of models to predict the depth of macrophyte growth. We believe direct measurement of PAR in Lake Apopka provides a more accurate assessment of the light climate than does SD, the light parameter in the Canfield model. Although the Canfield et al. (1985) model may provide reasonable approximations of the expected depth distributions of submersed macrophytes it cannot be considered strong evidence of a light climate sufficient for macrophyte growth. The model is based on a survey of 26 Florida lakes and is termed by the authors a “first approximation of how . . . SD values . . . may affect the extent of macrophyte colonization” (Canfield et al.,

1985; p. 27). Moreover, the correlation is weak ($r = 0.66$) and the 95% confidence limit for the regression is large: 46–236% of the predicted maximum depth of colonization. The authors of the model also stated that it “tends to . . . over estimate colonization depths when Secchi disc depths are low” (Canfield et al., 1985; p. 27). Finally, we note that an among-lakes regression line predicts the central tendency for a population of lakes. About half of all lakes in the population will lie below the line, and thus, theoretically, will not support macrophytes at the depth predicted from a given SD.

Internal P loading

Bachmann et al. (1999) also asserted that internal P loading will make it very difficult to reduce the TP concentration through reduction of external P loading. Internal P loading can delay the achievement of a new

equilibrium TP concentration following reduction of the P load (e.g. Jeppesen et al., 1991). Often, however, there is a significant decline in the TP concentration soon after reduction of the TP load (e.g. Chapra & Canale, 1991) and net P release from the sediments generally will be temporary, even in lakes with large sedimentary P stores (Marsden, 1989; Chapra & Canale, 1991; Cooke et al., 1993; Welch & Cooke, 1995).

Sas (1989) reviewed the responses of 18 lakes to P-load reduction and concluded that the period of net P release from the sediments was transient and was generally 5 years or less, even for shallow lakes. In Lake Apopka, the mean TP concentration fell by about 30% following a reduction in the P loading rate of about 40% (Battoe et al., 1999). Thus, both the general experience with shallow lake restoration and the specific experience at Lake Apopka indicate that substantial reduction of the P load will lead to substantial reduction of the TP concentration within a few years, even though the new equilibrium concentration may not be attained until much later.

The restoration program

The restoration program for Lake Apopka consists of four major steps: (1) reduce external P loading by recreating wetlands on the floodplain farms; (2) remove total suspended solids (TSS) and sestonic phosphorus through wetland filtration of lake water; (3) remove phosphorus and restructure the food web through large-scale removal of gizzard shad (*Dorosoma cepedianum*), and (4) accelerate reestablishment of submersed, floating-leaved and emergent vegetation by planting shallow areas and by increasing the range of fluctuation in lake level (Dean & Lowe, 1998; Battoe et al., 1999). Modest reductions of the P load (ca. 40%) have been achieved and large-scale removal of shad has been underway for several years. Small-scale planting of shallow areas has begun. Wetland filtration and increased lake level fluctuation have not yet been implemented.

Bachmann et al. (1999) discussed only the first two components of this restoration plan and concluded that the restoration program for Lake Apopka will not restore water clarity or submersed macrophytes. Their argument against the effectiveness of the restoration program can be summarized as follows:

- (1) Internal P loading will make it very difficult to reduce the TP concentration through reduction of external P loading.
- (2) If the TP concentration can be reduced, however, and algal density falls, water clarity will not significantly improve.
- (3) Even if water clarity can be improved macrophytes will not recolonize the lake because the fluid sediments will not support macrophyte growth.

We have discussed general and specific evidence that contradicts each of these assertions: evidence that indicates significant benefits will follow reduction of the P loading rate. The other aspects of the restoration program will accelerate and improve the response to P load reduction. Indeed, a strategy of P load reduction combined with in-lake measures such as planktivorous fish removal, lake-level fluctuation, and planting is advocated by shallow lake managers (e.g. Moss et al., 1996).

We wish briefly to mention the comments of Bachmann et al. (1999) regarding the role of the wetland filter in restoration of Lake Apopka. They constructed a mass balance model of sediments in Lake Apopka and used that model to conclude that, in the absence of cultural eutrophication, wetland filtration would elicit "little, if any, improvement in water clarity" for more than 1100 years. This conclusion rests on the assumption that TSS in the water column, and therefore turbidity, will not decline if any fine organic sediments remain in the lake. Implicit in this assumption is that turbidity would remain constant during the removal of more than 7×10^9 kg of sediments, during deepening of the sediment surface by an average of more than 0.75 m, and during the associated decline in areal coverage of fine organic sediments. It is not surprising that these unrealistic assumptions, which provided the only linkage of the mass balance model to the water column, yielded an extraordinary conclusion. Schelske & Kenney (2001) also question the validity of using the time required to remove all the sediments as the basis for predictions regarding turbidity.

The level of TSS in a lake is controlled by a dynamic equilibrium set by outflow, sedimentation, resuspension, gross primary production and community respiration. This dynamic equilibrium cannot be predicted from the size of the sediment pool. The recent sustained decline in TSS in Lake Apopka (Battoe et al., 1999) during a period when there has been no change in wind speeds measured at Lake Apopka (Fig. 2) and no removal of sediments, indicates that

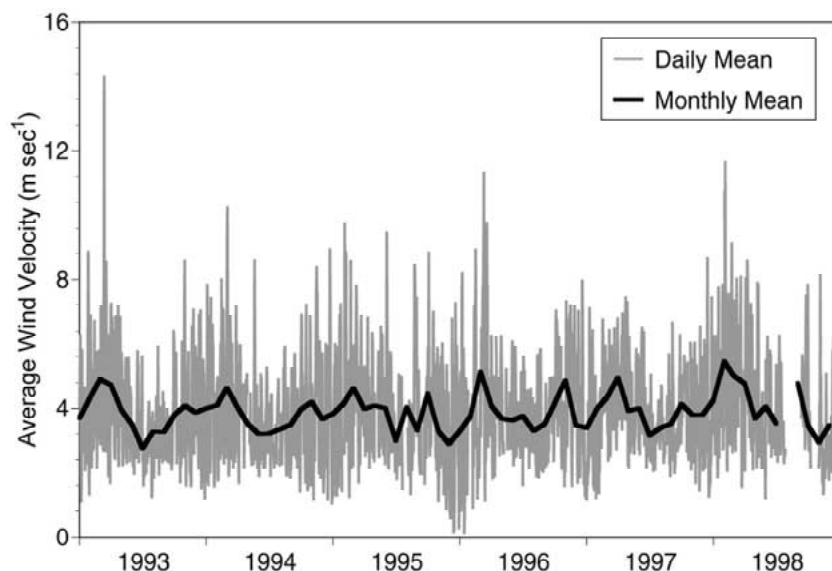


Figure 2. Daily and monthly wind velocities measured at Lake Apopka. The slope of a regression of log-transformed daily wind speed against time is not significantly different from zero ($p = 0.19$). Furthermore, mean log daily wind speeds for the periods before and after August 1, 1995 are not significantly different (t -test; $p = 0.22$). The period after mid-1995 corresponds to a time of significant improvement in water quality in Lake Apopka (Battoe et al., 1999).

the level of TSS is not well-buffered by sediment resuspension. The decline in TSS has been concomitant with, and roughly proportional to, declines in concentrations of TP, total nitrogen (TN) and CHLA, which indicates that these constituents are more influential on TSS than the size of the sediment pool.

The wetland filtration system was not intended to remove all the surface sediments. Its primary role in the restoration program is to accelerate achievement of the new equilibrium TP concentration following P load reduction by removing sestonic TP (Lowe et al., 1992). Wetland filtration is not needed to significantly improve water clarity: reduction of P loading is sufficient. Wetland filtration will, however, significantly affect components of the dynamic equilibrium controlling TSS. It will increase outflow of TSS from the lake and reduce gross primary production by accelerating and enhancing reductions in concentrations of TN and TP. Turbidity will fall during the restoration program due to (1) decreasing algal production (and, consequently, decreasing levels of algae and algal detritus), (2) continued sedimentation of TSS within the lake and removal of TSS by the wetland filter, (3) declining area of resuspendable sediments due to macrophyte colonization, and (4) decreasing volume of readily suspendable material (due to decreased rates of production and removal of easily suspended material by the wetland filter).

Recent improvements in Lake Apopka

Perhaps the greatest obstacle to acceptance of the conclusions of Bachmann et al. (1999) is the recent improvements in Lake Apopka during a period of partial implementation of the restoration program. Bachmann et al. (1999) estimated that 0.34 m would be the SD associated with an 80% reduction in the TP concentration. Recently, however, concomitant with a modest (ca. 30%) decline in the TP concentration, monthly mean SD equaled or exceeded 0.34 m for 5 months in 1998 (as compared to a mean of 0.23 m before the decline in TP concentration) (St. Johns River Water Management District, unpublished data). Reduced P loading and several years of removal of gizzard shad (average = 4.4×10^5 kg yr⁻¹; 1993–1997) have been followed by improvements in all indicators of trophic state (Battoe et al., 1999). These improvements in water quality were highly significant statistically and occurred during a period with normal wind speeds (Fig. 2). The improvements have persisted to date and do not appear to be a fluctuation about the old steady state. Moreover, submersed plant beds have appeared in areas devoid of vegetation for nearly 50 years. Such changes would not be expected if, as Bachmann et al. (1999) have postulated, the TP concentration cannot be reduced due to internal P loading, water clarity cannot be improved due to sediment resuspension,

and submersed plants cannot grow due to the fluid character of the sediments.

Theory cannot carry the weight of observation. When observations are incongruent with theory, the theory should be re-examined and, perhaps, rejected. The final arbiter of divergent theories must be the responses of the subject of those theories. We suggest that the recent improvements in Lake Apopka contradict theoretical arguments that the restoration program will not be effective.

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References

- Bachmann, R. W., M. V. Hoyer & D. E. Canfield, Jr., 1999. The restoration of Lake Apopka in relation to alternative stable states. *Hydrobiologia* 394: 219–232.
- Battoe, L. E., M. F. Coveney, E. F. Lowe & D. L. Stites, 1999. The role of phosphorus reduction and export in the restoration of Lake Apopka, Florida. In Reddy, K. R., G. A. O'Connor & C. L. Schelske (eds), *Phosphorus Biogeochemistry in Subtropical Ecosystems*. Lewis Publishers, New York: 511–526.
- Canfield, D. E. & L. M. Hodgson, 1983. Prediction of Secchi depths in Florida lakes: Impact of algal biomass and organic color. *Hydrobiologia* 99: 51–60.
- Canfield, D. E., K. A. Langeland, S. B. Linda & W. T. Haller, 1985. Relations between water transparency and maximum depth of macrophyte colonization in lakes. *J. Aquat. Plant Manage.* 23: 25–28.
- Cooke, G. E., E. B. Welch, S. A. Peterson & P. R. Newroth, 1993. *Restoration and Management of Lakes and Reservoirs*. 2nd edn. Lewis Publishers, Boca Raton: 548 pp.
- Chapra, S. & R. Canale, 1991. Long-term phenomenological model of phosphorus and oxygen for stratified lakes. *Wat. Res.* 25: 707–715.
- Clugston, J. P., 1963. Lake Apopka, Florida, A changing lake and its vegetation. *Florida Academy of Sciences* 26: 168–174.
- Dean, H. & E. Lowe, 1998. The Restoration Program for Lake Apopka, Florida, Volume 5. Proceedings of Water Environment Federation 71st Annual Conference and Exposition, October 1998, Orlando, FL: 313–316.
- Jeppesen, E., P. Kristensen, J. P. Jensen, M. Sondergaard, E. Mortensen & T. Lauridsen, 1991. Recovery resilience following a reduction in external phosphorus loading of shallow, eutrophic Danish lakes: duration, regulating factors and methods for overcoming resilience. *Mem. Ist. ital. Idrobiol.* 48: 127–148.
- Jones, J. R. & R. W. Bachmann, 1978. Trophic states of Iowa lakes in relation to origin and glacial geology. *Hydrobiologia* 57: 267–273.
- Klinge, M. M., M. Grimm & S. Hosper, 1995. Eutrophication and ecological rehabilitation of Dutch lakes: presentation of a new conceptual framework. *Wat. Sci. Technol.* 31: 201–218.
- Lowe, E. F., L. E. Battoe, D. L. Stites & M. F. Coveney, 1992. Particulate phosphorus removal via wetland filtration: an examination of potential for hypertrophic lake restoration. *Envir. Manage.* 16: 67–74.
- Lowe, E. F., L. E. Battoe, M. F. Coveney & D. L. Stites, 1999. Setting water quality goals for restoration of Lake Apopka: Inferring past conditions. *Lake and Reserv. Manage.* 15: 103–120.
- Marsden, M., 1989. Lake restoration by reducing external phosphorus loading: the influence of sediment phosphorus release. *Freshwat. Biol.* 21: 139–162.
- Moss, B., J. Madgwick & G. Phillips, 1996. *A Guide to the Restoration of Nutrient-enriched Lakes*. Broads Authority, Norwich, U.K.: 180 pp.
- Sas, H., 1989. *Lake Restoration by Reduction of Nutrient Loading: Expectations, Experiences, Extrapolations*. Academia Verlag Richarz, Sankt Augustin: 497 pp.
- Scheffer, M., 1990. Multiplicity of stable states in freshwater systems. *Hydrobiologia* 200/201 (Dev. Hydrobiol. 61): 475–486.
- Scheffer, M., 1998. *Ecology of Shallow Lakes*. Chapman and Hall, New York: 357 pp.
- Scheffer, M. S., S. Hosper, M. L. Meijer, B. Moss & E. Jeppesen, 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, FL.
- Schelske, C. L., F. J. Aldridge & H. J. Carrick, 1992. Phytoplankton–nutrient interaction in Lake Apopka. Special Publication SJ92-SP9, St. Johns River Water Management District, Palatka, FL.
- Schelske, C. L., M. F. Coveney, F. J. Aldridge, W. F. Kenney & J. E. Cable, 2000. Wind or nutrients: historic development of hypereutrophy in Lake Apopka, Florida. *Limnology and Lake Management 2000+*. *Archiv für Hydrobiologie – Special Issues Advances in Limnology* 55: 543–563.
- Schelske, C. L., C. M. Donar & E. F. Stoermer, 1999. A test of paleolimnological proxies for the planktonic/benthic ratio of microfossil diatoms in Lake Apopka. In Mayama, Idei & Koizumi (eds), *14th International Diatom Symposium*, Tokyo, Japan. Koeltz Scientific Books, Koenigstein: 387–407.
- Schelske, C. L. & W. F. Kenney, 2001. Model erroneously predicts failure for restoration of Lake Apopka, a hypereutrophic, subtropical lake. *Hydrobiologia* 448: 1–5.
- Sheffield, C. & W. Kuhrt, 1970. Lake Apopka – its decline and proposed restoration. In Proceedings of Florida's Environmental Engineering Conference on Water Pollution Control. Florida Engineering and Experiment Station, Gainesville, FL: 130–146.
- Welch, E. & G. Cooke, 1995. Internal phosphorus loading in shallow lakes: importance and control. *Lake and Reserv. Manage.* 11: 273–281.