How anthropogenic darkening of Lake Apopka induced benthic light limitation and forced the shift from macrophyte to phytoplankton dominance

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Abstract

　　Controversy exists about the historic shift of primary producer community structure (PPCS) in Lake Apopka, a shallow, 125-km^2 lake in central Florida, U.S.A. The controversial questions are: was a lake-wide shift from macrophyte to phytoplankton dominance triggered by a 1947 hurricane or tornadoes spawned by the hurricane within a few weeks or months, or was the shift forced by progressive cultural eutrophication over several years? In 1947, fringing wetlands (35 km^2) were being diked and drained for agricultural purposes changing their function from nutrient sinks to nutrient point sources to the lake. We examined whether anthropogenic darkening of the water column induced the PPCS shift during a 0.6-m lake-stage rise. Darkening was defined as lake-bottom photosynthetically available radiation (PAR) ≤ 1.0% of incident PAR. We simulated darkening from changes in the light extinction coefficient (K_d) due to water color, chlorophyll *a*, and rising lake stage. Simulations predicted that darkening was restricted to 80% of the lake deeper than 2.16 m, a finding consistent with persistence of shallow-water submersed macrophytes after 1947. Anthropogenic wetland draining increased water color, lake stage, and phytoplankton blooms stimulated by phosphorus enrichment, causing a progressive shift to lake-wide phytoplankton dominance over at least several years. The relationship between the 1947 hurricane and the PPCS shift was not causal, but only a temporal coincidence. Our darkening model can be applied to other systems with known bathymetry to predict submersed aquatic vegetation (SAV) coverage from SAV light requirements and water-column light attenuation.

　　Lake Apopka, a shallow, subtropical lake in central Florida, U.S.A., underwent a shift in primary producer community structure (PPCS) in 1947 (Schelske and Brezonik 1992). Before 1947, Lake Apopka was a clear-water lake with lush growth of submersed aquatic vegetation, including *Potamogeton illinoensis* (pond weed) and *Vallisneria americana* (eel grass, tape grass, or water celery), and a prized largemouth bass fishery (Clugston 1963). According to anecdotal accounts, a 1947 hurricane uprooted the submersed aquatic plants and the first phytoplankton bloom occurred a few weeks later (Schelske et al. 2005). The sport fishery improved after the shift, but declined within a few years after planktivorous gizzard shad began to dominate the fish community. The PPCS shift is not disputed. Controversy, however, does exist over whether a lake-wide shift was forced by stochastic factors within a few weeks or months, or by anthropogenic factors over a longer period.

　　A hurricane as a stochastic trigger for a catastrophic shift has received considerable attention in the literature to support the theory of alternate stable states (Scheffer et al. 2001; Scheffer and van Nes 2007). The September 1947 hurricane, however, was far (> 250 km) from Lake Apopka; in addition, other hurricanes in 1944 and 1945 passed closer to the lake but did not elicit a PPCS shift (Lowe et al. 1999). Tornadoes spawned by the 1947 hurricane reportedly uprooted submersed aquatic vegeta-

tion in a small area of the lake and forced the PPCS shift (Bachmann et al. 2001). If only a small area were affected, this hypothesis fails to account for a lake-wide PPCS shift on a time scale of a few weeks or less. Another stochastic factor was a 0.6-m lake-level rise in 1947 that we hypothesize led to macrophyte shading (Blindow et al. 1993).

　　Cultural eutrophication that began in the 1920s also was advanced as a causal factor for the PPCS shift (Clugston 1963; Schelske and Brezonik 1992; Lowe et al. 2001). Nutrient loading accelerated in 1942 when levee construction began along the north shore so low-marsh wetlands could be drained and utilized for agriculture (Lowe et al. 1999). By March 1947, approximately half these floodplain wetlands had been or were being converted to 'muck' farm agriculture on the highly organic soils (Schelske et al. 2005). At that time, 6 months before the September 1947 hurricane, nutrient enrichment from agricultural drainage had produced an extensive phytoplankton bloom that was identified from aerial photography (Lowe et al. 1999).

　　In addition to being nutrient rich, dissolved organic matter in drainage water was colored. Both colored water and phytoplankton biomass can shade the submersed macrophyte community and its associated periphytic and benthic algae. Progressive shading during cultural eutrophication first affects benthic algae, then inhibits submersed macrophyte recruitment and growth, and finally periphytic growth shades macrophyte leaves as submersed aquatic vegetation (SAV) is replaced by phytoplankton (Phillips et al. 1978; Dobberfuhl 2007). Photosynthetically

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active radiation (PAR) attenuated by epiphytic growth on SAV has been studied in Chesapeake Bay (Kemp et al. 2004).

Light penetration in the water column is important in regulating PPCS in lacustrine systems (Moss et al. 1996; Scheffer 1998). Light inhibition of phytoplankton by water color has been studied previously in other Florida systems (Aldridge et al. 1998; Phlips et al. 2000). Photosynthetic intensity in these polymictic systems is a function of I_m, the daily quantum flux of PAR. In polymictic systems, I_m depends on daily incident PAR, vertical extinction coefficient (K_d), and water-column depth. The main components of K_d, in shallow waters with some turbidity are chlorophyll a (Chl a), water color, and nonalgal suspended solids (Håkanson 2006; Gallegos et al. 2008; V.-Balogh et al. 2009). The maximum depth of macrophyte colonization and abundance can be predicted using K_d (Vant et al. 1986; Dennison 1987; Duarte 1991). Loss of SAV in estuarine systems has been attributed to light attenuation increased by cultural eutrophication (Gallegos 2001; Kemp et al. 2004; Biber et al. 2008). Such studies are used to establish criteria for maintaining or predicting SAV habitat.

We examined precipitation records, historic lake stage in Lake Apopka, and modeled darkening of the lake bottom to evaluate whether stochastic events or anthropogenic factors forced the PPCS shift in 1947. The hypothesis that the 1947 hurricane uprooted submersed macrophytes over the lake basin is not supported. Likewise, it is unlikely that associated tornadoes forced a lake-wide PPCS shift on short time scales. We show here that the 0.6-m rise in lake level was related to neither increased precipitation nor the 1947 hurricane. Instead, hydraulic loading from the north-shore wetlands and muck farms increased lake stage. We also show the temporal relationship between the September 1947 hurricane and the PPCS shift was not causal and conclude the shift resulted from cultural eutrophication and other anthropogenic factors related to north-shore wetland drainage. We hypothesize that the combined effects of colored drainage water, phytoplankton blooms stimulated by nutrients in drainage water, and higher lake stage darkened lake waters. We designed simulations using K_d to test the hypothesis that darkening shaded the macrophyte community and forced a progressive PPCS shift. Simulations predicted benthic light limitation (1.0% of incident PAR) at the high lake stage for depths $\geq$ 2.16 m, accounting for about 80% of the lake surface area. Submersed macrophytes persisted in shallow waters after the shift (Clugston 1963) and may have persisted until 1950.

We conclude that phytoplankton blooms stimulated by phosphorus-enriched drainage water, together with rising lake stage and increased water color, progressively darkened the lake and caused a shift to lake-wide phytoplankton dominance over at least several years.

Methods

Study site—Lake Apopka, located about 25 km northwest of Orlando, is the headwater lake in the Ocklawaha Chain of Lakes and the Ocklawaha River (Fig. 1). At present, it has a mean depth of 1.62 m, surface area of
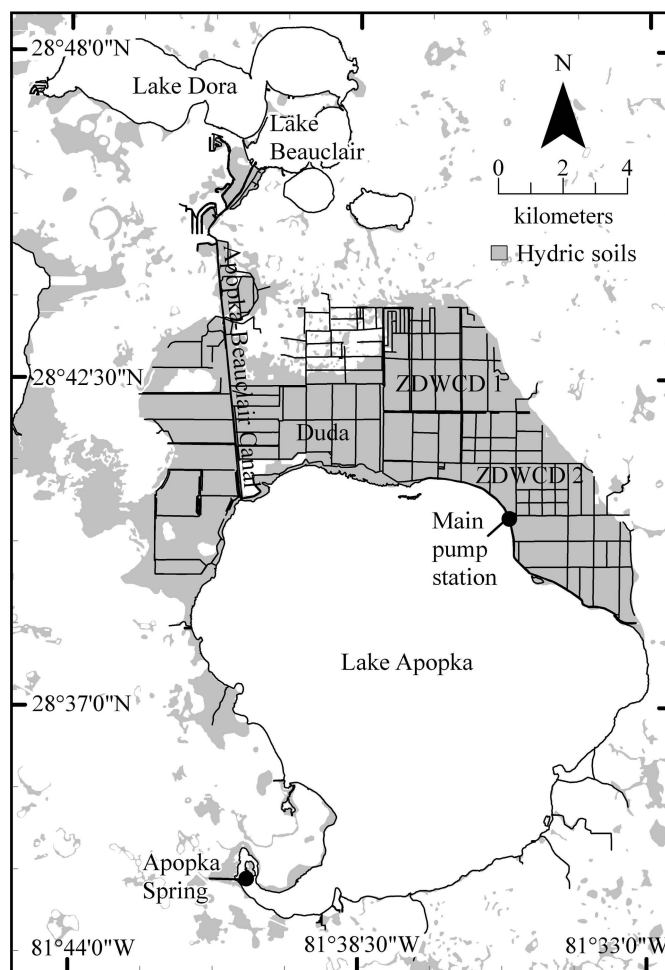

Fig. 1. Map of Lake Apopka showing north-shore hydric soils and outflow via the Apopka–Beauclair Canal to Lake Beauclair and Lake Dora. Hydric soil distribution and drainage network are for the 1980s after the wetlands were diked and drained for agricultural purposes. Zellwood Drainage and Water Control District (ZDWCD) 1 and 2 were under development in 1947 (*see* text).

125 km² and a mean hydraulic residence time of 2–3 yr (Coveney et al. 2005). The drainage area is small, about 480 km² (Lowe et al. 1999). The watershed was disturbed severely in the early 1940s when levees were constructed along the north shore so fringing floodplain wetlands could be drained for agricultural development (Lowe et al. 1999; Schelske et al. 2005). These wetlands occupied 80 km² of the lake's predisturbance area of 205 km². Levee construction changed the wetlands from a nutrient sink to a nutrient source for the lake. Point-source discharge of drainage waters from wetlands and muck farms along the north shore then became the major source of nutrients for the lake (Schelske et al. 2005).

No reliable water-quality data are available before and for several decades after the PPCS shift in 1947. In the formerly clear-water body, much of the lake bottom was visible from the lake surface. Now, highly organic, readily resuspended sediments characterize the benthic environment previously stabilized by submersed macrophytes

(Schelske 2006). By the mid-1980s, water column characteristics had changed dramatically; means for Secchi disc transparency, Chl *a*, and total phosphorus (TP) were 22 cm, 96 μg L^{-1}, and 200 μg TP L^{-1}, respectively (Lowe et al. 1999). Means (1990–1991) for Chl *a*, Secchi disc transparency, and K_d(PAR) were 103 μg L^{-1}, 22.5 cm, and 5.86 m^{-1}, respectively (Schelske et al. 2003). Inorganic nitrogen in this phosphorus-limited lake became a secondary limiting nutrient for phytoplankton growth as a consequence of excessive phosphorus loading (Aldridge et al. 1993).

Hydrology of Lake Apopka and its large size must be considered in proposing mechanisms for the PPCS shift. Major hydrologic inputs after the early 1940s were direct precipitation on the lake, an artesian spring at the south end of the lake, and back-pumping from muck farms along the north shore (Fig. 1). The only surface outlet was the Apopka–Beauclair Canal on the northwest shore that discharged through Lake Beauclair to Lake Dora. Zellwood Drainage and Water Control Districts (ZDWCD) 1 and 2, with a combined surface area of 35 km², discharged drainage water directly to the lake (Shofner 1982). Duda farms discharged to the Apopka–Beauclair Canal. Circulation patterns in the lake can be considered to be random; therefore, response patterns to drainage water inputs along the north shore, such as phytoplankton patches, developed randomly.

Morphometric factors underlie the hypothesis that anthropogenic darkening in Lake Apopka led to the PPCS shift in 1947 when lake stage rose from 20.5 m to 21.1 m above sea level (masl). The lake has a flat bottom. Most of the bottom area lies between the 1.0-m and 2.0-m depth contours when the lake stage is 20.1 masl (Fig. 2) or between the 2.0-m and 3.0-m contours when the stage is 21.1 masl. Percent bottom area changes rapidly with depth (Fig. 3). Depth contours are offset by 0.60 m because lake area was nearly constant for these lake-stages after the north-shore levees were constructed.

Darkening model—We designed a model to simulate darkening from changes in K_d in the lake during the 6-month rise in lake stage. Darkening was defined as bottom illumination $\leq$ 1.0% of incident PAR. This intensity is assumed to be light-limiting for benthic algae (Phillips et al. 1978). It is also suboptimal for submersed macrophytes that reach maximum density where bottom illumination ranges from 1.0% to as much as 20% (Canfield et al. 1985; Kemp et al. 2004; Dobberfuhl 2007).

To assess darkening in Lake Apopka, we modeled light intensity at depth as a function of K_d using Eq. 1

$$Z = (\ln I_O - \ln I_Z)/K_d \qquad (1)$$

where Z is depth (m), I_O is surface light (100%) and I_Z is light (%) at depth Z. The compensation depth for benthic algal photosynthesis is assumed to be 1.0% of incident PAR. Although K_d(PAR) changes with depth due to wavelength selective absorption (Kirk 1994), we use K_d(PAR) as a depth-integrated constant, following the standard field practice of fitting a single extinction coefficient to PAR
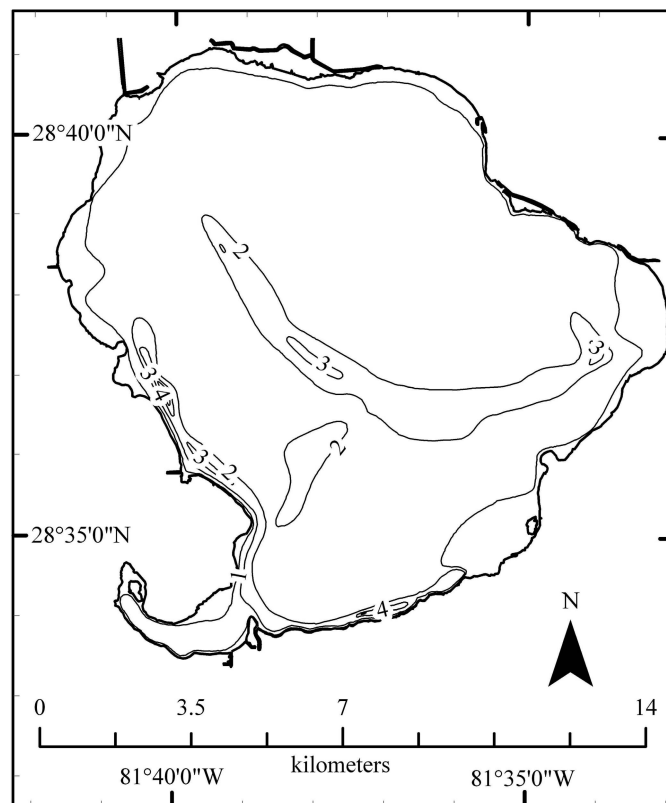

Fig. 2. Bathymetry of Lake Apopka in 1989 with depth contours in meters (Danek and Tomlinson 1989). Depths are referenced to a surface elevation of 20.12 masl National Geodetic vertical datum (NGVD)1929. This elevation was revised to 20.18 masl NGVD1929 by a resurvey of the vertical control (St. Johns River Water Management District).

measurements along the depth gradient. Measurement of total PAR at depth is important because PAR irradiance ultimately controls plant growth.

We assumed that extinction coefficients for water color (K_{col}) and phytoplankton biomass measured as Chl *a* (K_{Chl}) were the main components of K_d(PAR). Light is also attenuated by water, which is negligible in our shallow study system, and by nonalgal suspended solids (primarily tripton). Tripton is an unknown component in drainage water that would have contributed to light extinction. Because macrophytes were abundant before agricultural pumping began, tripton attenuation alone was insufficient to induce benthic light limitation in the lake. Kirk (1994) addresses the complexities of underwater optics. Underwater optics have been investigated in a blackwater river (Phlips et al. 2000) and in other environments (Gallegos 2001; Gallegos et al. 2008). Our general model to determine bottom darkening, which is conservative because tripton is excluded, is then reduced to

$$K_d(\text{PAR}) = (K_{col} + K_{Chl}) \qquad (2)$$

Data for K_d(PAR) and water color were available from three stations in the lower St. Johns River (Table 1). Color ranged from 93 Pt units to 434 Pt units and K_d(PAR)
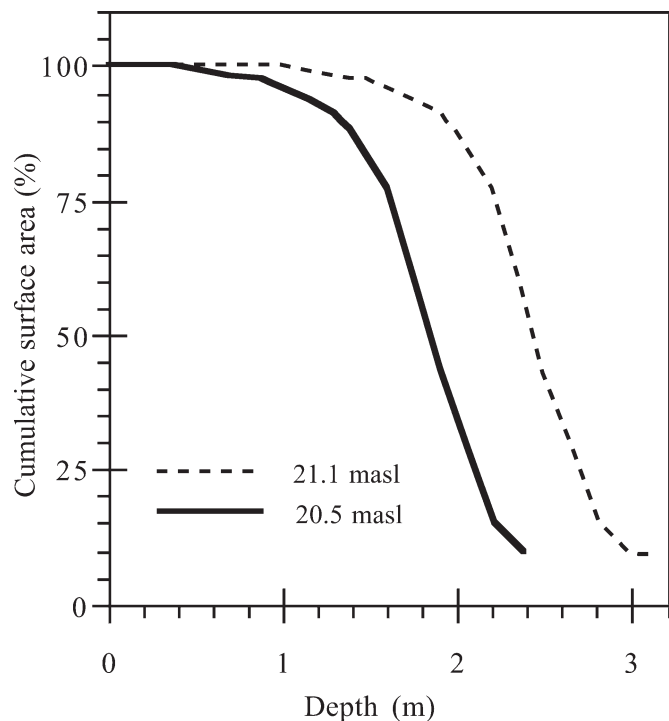
Fig. 3. Change in cumulative surface area (%) vs. lake depth (m) in Lake Apopka. The two curves represent high (21.1 masl) and low (20.5 masl) stages during a 9-month increase in lake stage in 1947. Morphometric data from Danek and Tomlinson (1989).

Table 1. Water color and vertical extinction coefficients (K_{col} and K_d) from selected environments in Florida, U.S.A. Mean ($\bar{x}$), standard deviation (SD) and number of observations (n). Range for color is K_{col} (m^{-1}). Photosynthetically available radiation (PAR) was measured using cosine 2 pi PAR underwater and deck sensors (LICOR model L1192) to determine K_d(PAR; Aldridge et al. [1998]). The regression slope (Eq. 2) was used to predict K_{col}.

	$\bar{x}$	SD	n	Range
Color (Pt units)				
Blue Cypress Lake*	228	126	206	0.68–9.12
Blue Cypress Marsh*	253	119	129	1.14–9.12
Federal Point†	221	89	27	1.23–4.95
Picolata†	213	90	27	1.06–4.32
Mandrin Point†	215	84	27	1.19–4.17
Muck farms*	—	—	—	5.70–9.12
Vertical extinction coefficient, K_d(PAR) (m^{-1})				
Federal Point†	4.69	1.25	25	2.73–7.63
Picolata†	4.08	1.25	25	2.17–7.66
Mandrin Point†	4.00	1.07	25	2.03–5.78
Lake Apopka‡	5.86	2.4	33	3.14–12.8
Lake Washington§	3.86	—	—	—

* St. Johns River Water Management District unpubl.
† Lower St. Johns River, Aldridge et al. (1998).
‡ Lake Apopka, Schelske et al. (2003).
§ F. J. Aldridge and C. L. Schelske unpubl.

ranged from 1.06 m^{-1} to 4.95 m^{-1}. The slope of the linear regression of K_d(PAR) on water color from these data was used to predict K_{col} (Eq. 3).

$$K_{col} = 0.0114 \times [\text{Color}] + 1.726 \left(R^2 = 0.639\right) \quad (3)$$

In our modeling we set the y-intercept, which represents light-absorbing components other than water color, to zero. We assumed that the slope is determined by variation in color only and, therefore, that $K_{col} = 0.0114 \times [\text{Color}]$. Phlips et al. (2000) applied a larger slope (0.014) in studies on the St. Johns River.

No data are available for color in either drainage water from the north-shore wetlands or Lake Apopka in the 1940s. More recent data on water color, however, are available for Blue Cypress Lake and Blue Cypress Marsh Conservation Area, an undisturbed sawgrass marsh in the headwaters of the St. Johns River basin (Table 1). These data show water color in Blue Cypress Lake is related closely to that in the surrounding sawgrass marsh. In these environments, Eq. 3 predicts that K_{col} ranged from 0.68 m^{-1} to 9.12 m^{-1}. Measured K_d(PAR) in Lake Washington, a nearby lake with drainage from surrounding sawgrass marshes, was 3.86 m^{-1}. We attributed this K_d(PAR) to water color because particulate matter was low (2 μg L^{-1} Chl a). High predicted K_{col} in farm discharges to Lake Apopka after the 1980s ranged from 5.70 m^{-1} to 9.12 m^{-1}. For comparison, K_d(PAR) for Lake Apopka in 1990–1991 averaged 5.86 m^{-1} and ranged from 3.07 to 12.8 m^{-1} (Schelske et al. 2003).

Data from Schelske et al. (2003) were used to predict K_{Chl} from the slope of the linear regression of K_d(PAR) on Chl a (Eq. 4).

$$K_{Chl} = 0.0479 \times [\text{Chl } a] + 1.338 \left(R^2 = 0.775, n = 33\right) (4)$$

As with K_{col}, for modeling we set the intercept to zero. The K_{chl} slope has a coefficient at the high range reported in the literature (V.-Balogh et al. 2009). Some of these data, however, are based on Chl a alone. The slope in Eq. 4 would be larger because it includes algal particulate matter. The y-intercept represents the contribution from light-absorbing components other than Chl a and its associated algal particulate matter in Lake Apopka waters in the early 1990s. Suspended particulate matter, primarily high phytoplankton biomass ($\bar{x}$ Chl a = 103 μg L^{-1}), was then the major factor limiting light penetration. Water color was low at that time (Lowe et al. 1999). We therefore assume that $K_{Chl} = 0.0479 \times [\text{Chl } a]$.

We simulated the effect of rising lake stage and drainage water input on darkening in Lake Apopka. This required a hydrologic budget, including the lake-volume increase (ΔV) during the 9-month period with a 0.6-m rise in lake stage (Eq. 5).

$$\Delta V = \text{inputs} - \text{outputs} \quad (5)$$

Inputs are Apopka Spring (S) and farm drainage (F) and the major output is outflow (O) through the Apopka–Beauclair Canal (Eq. 6). We assumed that precipitation on the lake was balanced by evaporation. Equation 7 is rearranged to solve for F_t, an unknown that is constrained later.

$$\Delta V = S + F_t - O_t \tag{6}$$

$$F_t = O_t + \Delta V - S \tag{7}$$

It was assumed that V increased at a constant rate from 231 $\times 10^6$ m^3 at low stage to 303 $\times 10^6$ m^3 at high stage during 38 weeks of rising lake stage. Outflow for each time step was calculated for the new volume using a 3-yr residence time. The mean flow of Apopka Spring is 2.2 m^3 s^{-1} (69.4 $\times 10^6$ m^3 yr^{-1}; Coveney et al. [2005]).

Simulations of darkening in Lake Apopka modeled changes in lake-water K_{Chl} and K_{col} associated with farm drainage water discharged to the lake; K_{Chl} is derived from Chl *a* produced in phytoplankton blooms stimulated by nutrients (Eq. 8) and K_{col} is due to water color (Eq. 9).

$$K_{Col}(t) = [(0.0114 \times [Color] \times F_t) + \\ (1 - f_d) \times K_{col(t-1)} \times V_{t-1}]/V_t \tag{8}$$

$$K_{Chl}(t) = [(0.0479 \times [Chl\ a] \times F_t) + \\ (1 - f_d) \times K_{Chl(t-1)} \times V_{t-1}]/V_t \tag{9}$$

All simulations were run using 19 iterations of 14-d steps (t) to simulate the observed 9-month increase in lake stage. This step interval was selected as a representative time scale for development of phytoplankton blooms. Regression slopes for K_{col} and K_{Chl} are 0.0114 and 0.0479, respectively (Eqs. 3 and 4). Color and Chl *a* are assumed input concentrations. Assumed step-by-step decays (f_d) are 2.0% and 3.0%, respectively, for color and Chl *a*.

Low, intermediate (int), and high values for water color and Chl *a* were used in the simulations. Low, int, and high input coefficients for K_{col} were 2.60 m^{-1}, 3.86 m^{-1}, and 5.70 m^{-1}; these values represent the value calculated for mean water color in Blue Cypress Lake (228 Pt units), measured K_d(PAR) in Lake Washington, and the low range in K_{col} for muck farms, respectively (Table 1). Low, int, and high simulated inputs for Chl *a* were 60 μg L^{-1}, 80 μg L^{-1}, and 100 μg L^{-1}, respectively, with calculated K_{Chl} of 2.87 m^{-1}, 3.83 m^{-1}, and 4.79 m^{-1}, respectively. These values represented TP of 60 μg L^{-1}, 80 μg L^{-1}, and 100 μg L^{-1}, respectively, with the assumption of a 1.0 : 1.0 molar ratio of Chl *a* : TP. Initial conditions in the lake for K_{col} and K_{Chl} were assumed to be 0.285 m^{-1} and 0.479 m^{-1}, respectively. These were calculated from 25 Pt units water color and 10 μg L^{-1} Chl *a*. Temporal variation in K_d was also modeled by adding the effects of K_{col} and K_{Chl} (Eq. 2).

To allow for continuous output from the darkening model, data from Danek and Tomlinson (1989) were used to obtain percent lake area (Y) deeper than depth (X) for the 20.5- and 21.1-masl lake stages. These data were then fitted to a sigmoid function, $Y = K/(1 + aX^b)$. Because 100% of the lake is deeper than 0.0 m, $K = 100$ for both stages. Coefficients *a* and *b* were determined by solving simultaneous equations with different data pairs of Y and

X. Fits were good except for the tail ends of the curves (R^2 = 0.993 for 20.5 masl and R^2 = 0.997 for 21.1 masl.). The sigmoid equations were

$$Y = 100/(1 + 0.0124 \times X^{7.71}) \tag{10}$$

$$Y = 100/(1 + 0.0001225 \times X^{9.87}) \tag{11}$$

Depths (X) for 1.0% incident PAR were calculated from representative data for K_d, K_{col}, and K_{Chl} using Eqs. 10 and 11 and were then used to calculate cumulative bottom darkening (%) and incremental (step) bottom darkening (%).

Results

The hypothesis that PPCS in 1947 shifted in response to high lake stage was tested by examining the historic record (Fig. 4). Lake stage was at a record high in 1947. Lake stage, however, also exceeded 21.0 masl in 1936 and may have been higher in 1926 (Shofner 1982). PPCS was not affected by lake stage in 1926 and 1936.

We then tested the hypothesis that record high stage in Lake Apopka was a stochastic factor that resulted from increased precipitation, the 1947 hurricane, or both. Precipitation records and anomalies in monthly lake stage and precipitation show that this high stage cannot be explained by precipitation (Fig. 5). Precipitation in September 1947, the month of the distant hurricane, did not show a large positive deviation. The 1947 high stage followed a seasonal deviation in precipitation, but unlike the typical pattern the high stage persisted for 8 months. In addition, high monthly precipitation anomalies in 1944 and 1945 did not correspond with high lake stage in Lake Apopka. We then compared relative lake stage in Lake Apopka with that in Lake Dora, a downstream lake, to determine whether lake stage in 1947 was high in both lakes. This comparison shows that relative stages were fairly similar until 1944 and 1945 when, as might be predicted from increased precipitation, stage in Lake Dora peaked at higher levels than Lake Apopka. It is possible, however, that these high stages in Lake Dora resulted from drainage water that was back-pumped from the Duda Farms and discharged directly to the Apopka–Beauclair Canal, bypassing Lake Apopka (Fig. 1). Of greater importance, the lake stage relation between the two lakes was reversed in 1947 with a higher stage in Lake Apopka. Stage in Lake Apopka increased to 21.1 masl in September 1947, about 0.6 m above the seasonal low. The Apopka–Beauclair Canal was frequently clogged with debris before it was dredged and a permanent lock was installed in 1956 (Shofner 1982; Schelske et al. 2005). Presumably, restricted outflow through the canal and possibly back flow from direct discharge to the canal from the Duda muck farms caused the rise in Lake Apopka. We conclude that this prolonged period of high lake stage resulted largely from draining low-lying marshes on the north shore.

To assess the role of lake stage, cumulative and incremental bottom darkening were modeled as a function
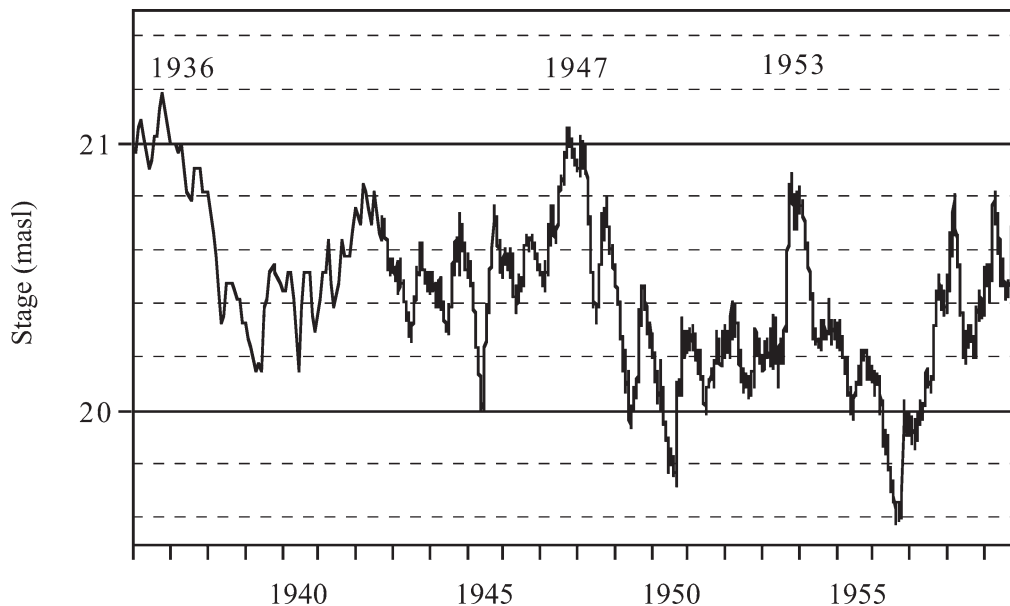
Schelske et al.

Fig. 4. Lake stage (masl) in Lake Apopka (1936–1959).

of K_d for high and low lake stages (Fig. 6). As expected, darkening occurred at a smaller K_d and the incremental rate was greater for 21.1 masl than for the lower lake stage.

Modeled cumulative and incremental bottom darkening at the high lake stage show the magnitude of water color and Chl *a* needed to darken the lake and the largest incremental change for each variable (Fig. 7a,b). Thresholds at which darkening is initiated were $\sim$ 100 Pt units water color, 20 μg L^{-1} Chl *a*, and 1.0 m^{-1} K_d (Fig. 6). Incremental darkening peaked at 160 Pt units water color, 38 μg L^{-1} Chl *a*, and 1.82 m^{-1} K_d. Darkening increased rapidly with a relatively small change in input variables over the flat-bottom portion of the lake. Simulated darkening from $Z_{20\%}$ to $Z_{80\%}$ occurred over small ranges: 141–187 Pt units, 33–44 μg L^{-1} Chl *a*, and 1.70–2.14 m^{-1} K_d.

No simulation (low, int, or high) for water color or Chl *a* alone darkened the bottom. Combined K_{col} and K_{Chl}, however, darkened the bottom in 12 and 16 steps for int and high simulations, respectively (Fig. 8a). For the combined low simulation of K_{col} and K_{Chl}, cumulative darkening occurred on only 52% of the bottom after 19 steps. Incremental darkening tracked lake morphometry (Fig. 8b). Rates of darkening were high where the bottom was relatively flat. For the high simulation, incremental darkening peaked at 16% (step 10) and 68% of cumulative darkening occurred in five steps (steps 8–12).

Positive feedback of nutrients from macrophyte community shading was not simulated; however, its time course can be inferred from the time course of darkening. The transition from 20% to 80% bottom area darkening occurred over 9 and 12 weeks, respectively, for high and int simulations (Fig. 8a,b). This transition darkened 60% of the lake bottom that was presumed to support a large macrophyte standing crop, which could become a source of internal phosphorus loading.

Discussion

We tested the hypothesis that macrophytes are shaded at high lake stages when light extinction increases with water depth and suspended matter (Blindow et al. 1993). This condition favors a change in PPCS and a switch to phytoplankton dominance. Lake stage was at record highs that exceeded 21.0 masl in 1936 and 1947 (Fig. 4). In addition, lake stage may have been even higher in 1926 when rainfall from a hurricane flooded marshlands to a depth 1.8–2.4 m (Shofner 1982). This flooding was so severe that attempts to reclaim north-shore wetlands for agriculture were abandoned until the 1940s when construction of levees and canals to drain the marshes was finally successful. Neither the high lake stage in 1926 nor the one in 1936 forced a shift to phytoplankton dominance. Thus, high lake stage alone in 1947 was insufficient to cause a shift in PPCS at Lake Apopka. High lake stage in 1947, which coincided with the known shift to phytoplankton dominance, was accompanied by increased phosphorus loading from the north-shore wetlands (Lowe et al. 1999; Schelske et al. 2005). After the primary producer shift, lake stage was low beginning in 1949 and remained low until 1953. This 4-yr period of low lake stage did not force the reverse switch in PPCS as might be expected from the theory of alternate stable states (Scheffer et al. 1993).

The theory of alternative stable states predicts that perturbations, such as unusually high or low water levels, can cause a switch to the alternative PPCS (Moss et al. 1996; Scheffer 1998). For Lake Apopka, high water levels in the 1920s and 1930s before the shift and low water levels in the 1950s after the shift failed to change PPCS. Our analysis indicates that high water levels and increased water color could have forced the shift from macrophyte to phytoplankton dominance, but only in combination with
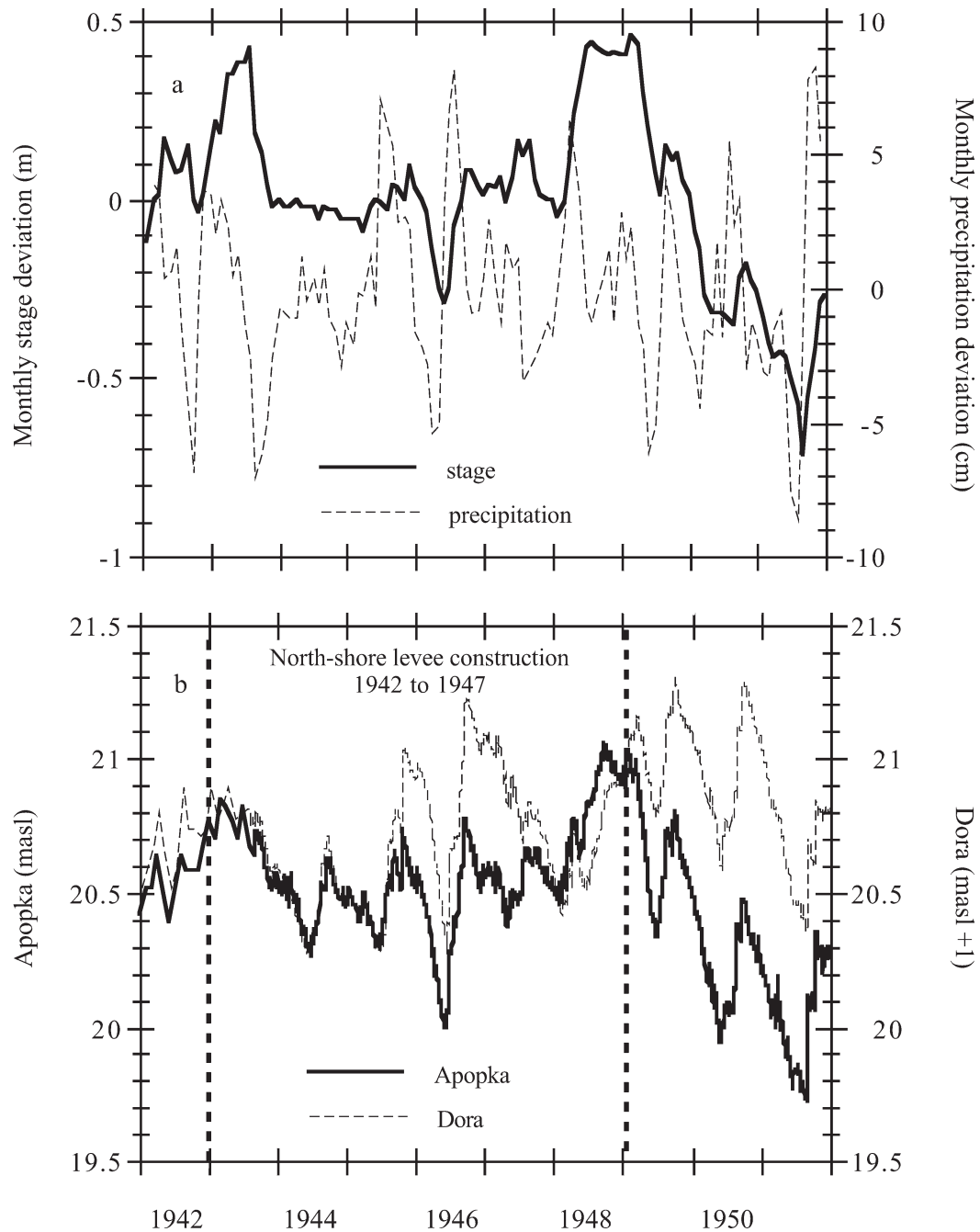
Fig. 5. (a) Monthly deviations of lake stage (masl) in Lake Apopka and precipitation (cm) relative to decadal means from 1941 to 1950. (b) Relative lake stage (masl) in Lake Apopka and Lake Dora (1941–1950). Dashed vertical lines represent period for levee construction along the north shore of Lake Apopka. Note 1.0-m offset in lake stage for Lake Dora.

effects of the preceding increase in phosphorus loading. A perturbation-induced shift to the alternative state is expected by the theory only if phosphorus loading is between rates associated with obligatory clear and turbid states. Our analysis lends support to the concept that nonnutritive perturbations can elicit a transition to phytoplankton dominance if phosphorus loading is sufficient to support the new turbid state.

We have shown that anthropogenic perturbations, secondary to increased phosphorus loading, could have

hastened the shift to phytoplankton dominance in Lake Apopka. By contrast, the literature on the theory of alternate stable states invokes a stochastic perturbation, the 1947 hurricane, as the cause of the PPCS shift from macrophyte to phytoplankton dominance (Scheffer et al. 2001; Scheffer and van Nes 2007). However, from 1886 through 1946, 7 hurricanes and 21 tropical storms passed much closer to the lake, but did not force the PPCS shift (Lowe et al. 1999). We believe the relationship between the 1947 hurricane and the PPCS shift was not causal, but only
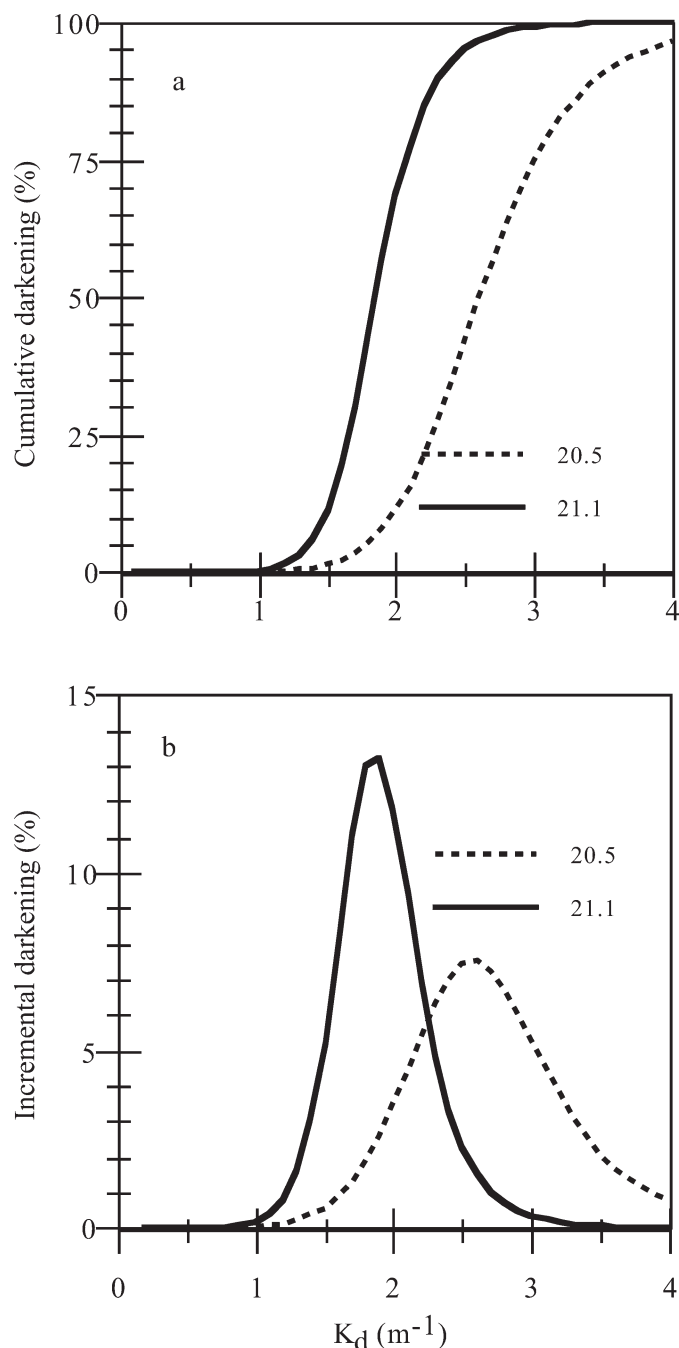
Fig. 6. Model results for (a) cumulative bottom darkening (%), and (b) incremental bottom darkening (%) vs. K_d (m^{-1}) for high (21.1 masl) and low (20.5 masl) lake stages in Lake Apopka.

capacity (Schelske et al. 2005). With an expanding phytoplankton standing crop, plus increasing water color and rising lake stage, the macrophyte community was not competitive. Collapse of the macrophyte community then resulted from progressive shading (Phillips et al. 1978). In addition, positive feedback of nutrients regenerated from senescence and collapse of macrophytes could have accelerated the shift to phytoplankton dominance.

Evidence shows the PPCS shift was not driven by biotic community changes. Major changes in the fish community occurred after 1947 (Clugston 1963; Lowe et al. 1999). Microfossil evidence also indicates zooplankton community structure changed after the shift (Shumate et al. 2002). Schelske et al. (2000) found diatom microfossils changed in a pattern consistent with macrophyte shading driven by progressive nutrient enrichment (Phillips et al. 1978) and inconsistent with the theory of alternate stable states (Scheffer et al. 1993).

We used retrospective modeling to track the time course of anthropogenic darkening, a response to progressive nutrient enrichment driven primarily by drainage water discharged from the north-shore wetlands. This highly colored, nutrient-rich drainage water stimulated phytoplankton growth near point-source discharges. Effects of water color and Chl *a* on light attenuation were simulated using K_{col} and K_{Chl} as extinction coefficients. Darkening, by definition, occurred when 80% of the benthic environment was light-limited ($\leq$ 1.0% incident PAR). This threshold represents an inflection point (2.1 m) on the cumulative area vs. 21.1-masl depth curve where cumulative area increases rapidly over the flat-bottom portion of the lake (Fig. 3). To darken the bottom at 1.0 m, where about 95% of the bottom would be dark, K_d would have to be about twice as large. Neither simulated K_{col} nor K_{Chl} alone produced bottom darkening. However, 80% darkening was simulated with combined int and high K_d (K_{col} + K_{Chl}).

Our simulations demonstrated that light extinction from a combination of increasing water color and Chl *a* could darken roughly 80% of the bottom during a 6-month period of rising lake stage. Darkening would lead to a progressive change in PPCS that was not lake wide because three benthic zones existed in Lake Apopka. In the deepest zone, representing about 20% of the lake (25 km^2), macrophytes were either absent or present in relatively small abundance compared to the remainder of the lake. Clugston (1963) reported that before the shift a 'heavy growth of pondweed *P. illinoensis*' beginning near the shoreline extended only to a depth of 2.4 m. Planktonic diatom microfossils also indicate that areas of open water existed as 'phytoplankton refugia' before the shift to phytoplankton dominance (Schelske et al. 2000). In a mid-depth zone, dominant submersed macrophytes on the flat-bottom area of the lake were eliminated first by progressive darkening. This zone encompassed $\sim$ 60% of the lake. In remaining shallow waters representing $\sim$ 20% of the lake, another sign of increasing fertility before the shift was water hyacinth, *Eichhornia crassipes*. Hyacinth "grew very profusely around the edge of the entire lake" and large floating mats "occasionally shifted around on the lake surface" (Clugston 1963). According to Clugston

a temporal coincidence. External phosphorus loading had increased since the 1920s (Clugston 1963; Schelske and Brezonik 1992) and was accelerated beginning in the early 1940s by nutrient-rich drainage water discharged from the north-shore wetlands that were being reclaimed for agriculture (Lowe et al. 1999). Increased phosphorus loading enriched the lake to levels that first stimulated benthic primary producers in the macrophyte community, but eventually exceeded the community's assimilatory
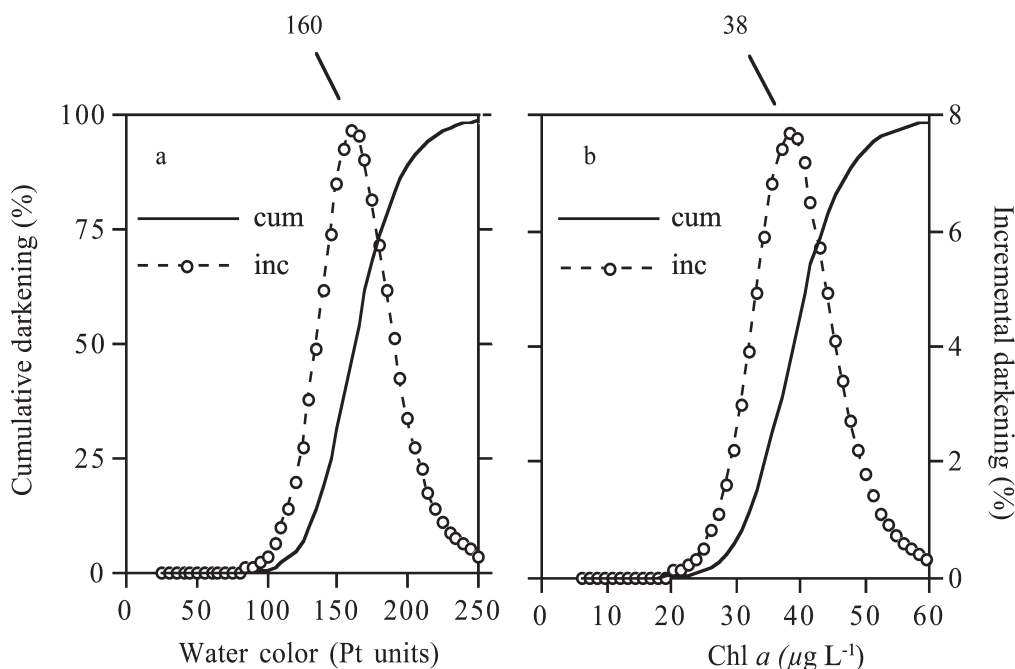
Fig. 7. Modeled cumulative (cum) bottom darkening (%) and incremental (inc) bottom darkening (%) vs. biweekly steps (t) for (a) water color (Pt units) and (b) Chl *a* (μg L^{-1}) for high (21.1 masl) lake stage in Lake Apopka. Data for K_d at 21.1 masl (plotted in Fig. 6b) follow a similar pattern.

(1963), pondweed "began to disappear as the plankton bloom persisted and shaded it out" and could not be found in the lake by 1950. Lake stage decreased markedly to a low of 19.7 masl in 1950 (Fig. 4). Turbidity (including phytoplankton biomass) at this time may have eliminated macrophytes that remained in shallow waters that were being nutrient enriched and reduced in area.

Our model demonstrated that lake darkening could be achieved using combinations of input variables over a 9-month period. Because there is no unique modeling solution, the model assumptions and limitations should be examined in greater detail. Nutrient loading from the muck farms occurred over a time span longer than the 9 months in 1947 that we simulated, probably beginning as early as 1942. Over a longer time span, smaller perturbations would have darkened the lake at a reduced rate compared to our simulations (Fig. 8). The phytoplankton standing crop would have increased at a smaller rate, but it would have been greater in 1947 than the initial condition we simulated. A Chl *a* standing crop of ~ 40 μg L^{-1}, with only a small contribution from water color, could have darkened the lake (Fig. 7).

Two processes we did not model should be considered. Darkening at a slower rate would have induced internal TP loading earlier than simulated, but at a slower rate. Increased periphytic growth that shaded submersed macrophyte leaves (Phillips et al. 1968; Kemp et al. 2004; Dobberfuhl 2007) would have begun early and preceded internal TP loading. In our simple box model we assumed a well-mixed water column with a constant I_m (Phlips et al. 1995). At present, the lake is polymictic, but this type of mixing may not have occurred in areas with submersed

macrophyte beds. Such conditions would favor phytoplankton blooms in waters above the macrophyte beds and nutrient uptake by periphyton on macrophyte leaves. Because macrophytes store photosynthate, there may be a delayed response to seasonal or short-term decreases in I_m or K_d (Dennison 1987). In September 1947, incident PAR and I_m were decreasing seasonally, a condition that would accelerate darkening relative to our implicit assumption of constant incident irradiance.

Two studies of shallow Florida lakes provide data to evaluate potential internal TP loading from the macrophyte community. Canfield et al. (1983) found that TP in the submersed macrophytes of four lakes ranged from equivalents of 42 μg TP L^{-1} to 404 μg TP L^{-1} in the water mass. From several hundred lakes, Bachmann et al. (2002) reported a mean of 130 mg TP m^{-2} (1.41 mg TP g^{-1} dry weight) in submersed macrophytes. Mean macrophyte abundance in Lake Apopka, however, may have been at least two or three times greater than the reported average, which included lakes with no macrophytes. Many of the lakes studied by Bachmann et al. were in this range; some macrophyte dry weights were > 1410 mg TP m^{-2}. Potential internal TP loading also can be compared to simulated TP input from farm discharge. For the 38-week simulation, farm discharge was 86.1 × 10^6 m^3. If TP in the discharge water were 100 μg L^{-1}, then this external TP load was 8.61 × 10^6 g. If TP regenerated from submersed macrophytes were twice the mean (260 mg TP m^{-2}), then potential internal TP loading was 32.5 × 10^6 g, nearly four times larger than the simulated TP input. As darkening progressed, positive feedback from nutrient regeneration alone could have produced a standing crop of phytoplank-
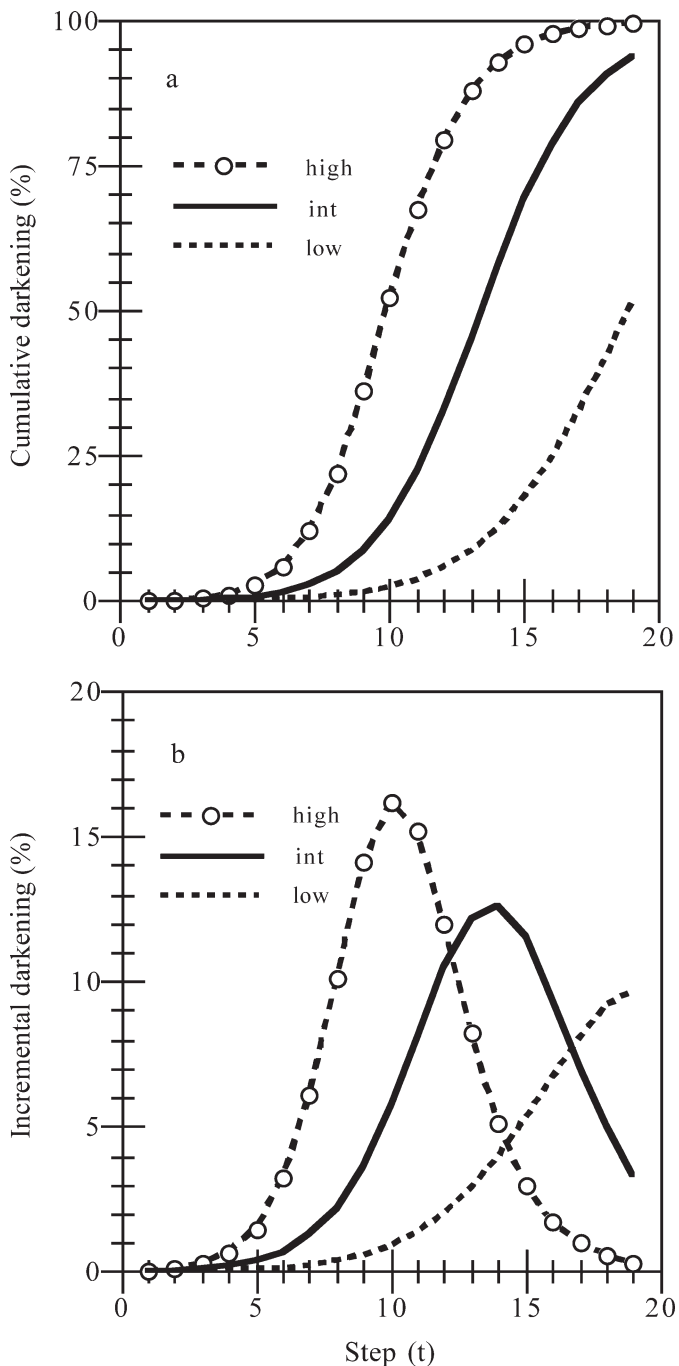
Fig. 8. Modeled (a) cumulative bottom darkening (%), and (b) incremental bottom darkening (%) vs. biweekly steps (t) for high, intermediate (int), and low combined inputs of water color (Pt units) and Chl *a* (μg L^{-1}).

that was optimal for growth of submersed macrophytes and associated microflora (Schelske et al. 2005). Subsequent increases in phosphorus loading were assimilated and stored in the expanding macrophyte community. This is reflected in the large standing crop of macrophytes in Lake Apopka before the PPCS shift (Clugston 1963) and also by increased TP deposition in the sediment record before the shift (Kenney et al. 2002; Schelske et al. 2005).

We evaluated data used in the simulations. Coefficients for K_{col} were calculated from data for an undisturbed sawgrass marsh ecosystem and the muck farms (Table 1). Extinction attributed to Chl *a* is reasonable because we assumed that Chl *a* and TP ranged from 60 μg L^{-1} to 100 μg L^{-1}, data that are consistent with the historical analysis by Lowe et al. (1999). Values selected for K_{col} and K_{Chl} were derived from the literature. Simulated TP loading from farm discharge was at least an order of magnitude less than that after farms were developed for agriculture when mean TP in discharge water was 870 μg L^{-1} (Lowe et al. 1999). Information is available to constrain farm discharge rates in simulations. Simulated hydraulic inputs for farm discharge increased from 4.10 $\times$ 10^6 m^3 step^{-1} to 4.97 $\times$ 10^6 m^3 step^{-1}. The capacity of the largest of five pumps that discharged directly to Lake Apopka from the ZDWCD was 8.0 $\times$ 10^6 m^3 month^{-1} (Central Florida Agricultural Institute 1985). Farm discharge also can be constrained using the area drained. Surface area of ZDWCD 1 and 2 was 35 km^2 (Shofner 1982) or 44% of the original fringing wetlands that were being converted to muck farms. If we assume that drainage from 35 km^2 of low-lying marsh is pumped into the lake, the discharge volume would be 35 $\times$ 10^6 m^3 per meter lowered without correcting for seepage and maintenance back-pumping of precipitation and runoff over the drainage basin. These sources, in addition to water stored in the marsh, were hydrologic inputs to the lake. Drainage water input in the 9-month simulation was 86.1 $\times$ 10^6 m^3, an input equivalent to 1.78 m of water drained from the marsh. Thus, on first analysis, data utilized in the simulations appear to be reasonable and defensible.

Our conclusion that darkening, once initiated on the flat-bottom portion of the lake, encompassed $\sim$ 80% of the lake bottom within a few weeks or months (Fig. 8a), is consistent with what at first might appear to be conflicting literature accounts of the widely reported PPCS shift. Lowe et al. (1999) report evidence for an extensive phytoplankton bloom on 17 March 1947, 6 months before the 1947 hurricane. The water at that time was more turbid than on 01 December 1941 when bottom vegetation was visible from aerial photography. Patches and increasing phytoplankton biomass are anticipated in the early stages of nutrient enrichment from the north-shore wetlands (Schelske et al. 2005). Thus, our assumed initial Chl *a* concentration of 20 μg L^{-1} may have been conservative. Finding submersed macrophytes in shallow waters after the shift (Clugston 1963; Lowe et al. 1999) is consistent with the absence of simulated bottom darkening in shallow waters. Localized uprooted vegetation observed and attributed to tornadoes spawned by a hurricane (Bachmann et al. 2001) also can be reconciled with our conclusion. Observed uprooted vegetation may have been due to a localized dieback during the

ton Chl *a* comparable to or greater than the smallest simulated level (60 μg L^{-1}) given a 1:1 molar ratio for Chl *a*:TP.

The potential for internal TP loading from macrophyte senescence and decay was relatively large because it represents the legacy of historic phosphorus enrichment. Completion of the Apopka–Beauclair Canal in 1893 lowered water level $\sim$ 1.0 m, increasing the benthic area

final stages of darkening or senescent plants transported to a specific location by wind, currents, or both. Submersed macrophytes undoubtedly had been affected by progressive nutrient enrichment from farm discharge before the September 1947 hurricane.

Our research identifies two misconceptions in the literature about PPCS in Lake Apopka. The first is that the submersed macrophyte community dominated the entire lake at the time of the PPCS shift. The second misconception is that the shift from macrophyte to phytoplankton dominance was abrupt and lake-wide after submersed macrophytes were purportedly uprooted by a hurricane. As an alternative to an abrupt shift to phytoplankton dominance driven by stochastic factors, we conclude that the shift to phytoplankton dominance resulted from inputs of highly colored, nutrient-rich drainage water from the north-shore wetlands. This drainage water increased water color and lake stage and stimulated phytoplankton growth near point-source discharges. Simulations using K_d (K_{col} + K_{Chl}) showed that light extinction from a combination of rising lake stage, increasing water color and Chl a could darken roughly 80% of the bottom during a 6-month period of rising lake stage. The time course for progressive darkening probably began early and, consequently, was forced by smaller perturbations than those simulated. Anthropogenic wetland draining increased water color, lake stage, and phytoplankton blooms stimulated by phosphorus enrichment, causing a progressive shift to lake-wide phytoplankton dominance over at least several years. Thus, not only cultural eutrophication, but also nonnutritive factors contributed to anthropogenic darkening and benthic light limitation. Our darkening model can be applied to other systems with known bathymetry to predict SAV coverage from SAV light requirements. Depending on the water body in question, to model light attenuation it may be necessary to include light-extinction coefficients for water, nonalgal particulate matter, and macrophyte epiphytes in addition to those for Chl a and water color.

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