

Abrupt Biological Response to Hydrologic and Land-use Changes in Lake Apopka, Florida, USA

Lake Apopka is a shallow, hypereutrophic lake in north-central Florida that experienced an abrupt shift in primary producer community structure (PPCS) in 1947. The PPCS shift was so abrupt anecdotal accounts report that dominant, submersed aquatic vegetation was uprooted by a hurricane in 1947 and replaced by phytoplankton within weeks. Here we propose two hypotheses to explain the sudden shift to phytoplankton. First, hydrologic modification of the drainage basin in the late 1800s lowered the lake level ca. 1.0 m, allowing the ecosystem to accommodate moderate, anthropogenic nutrient enrichment through enhanced production in the macrophyte community. Second, additional hydrologic changes and large-scale agricultural development of floodplain wetlands began in 1942 and altered the pattern and scale of phosphorus loading to the lake that triggered the rapid shift to phytoplankton dominance in 1947. Historic land-use changes and paleolimnological data on biological responses to nutrient loading support these hypotheses.

INTRODUCTION

According to anecdotal accounts, primary producer community structure (PPCS) in Lake Apopka, Florida (USA), shifted abruptly in 1947 from macrophyte to phytoplankton dominance when a hurricane uprooted submersed macrophytes that were never reestablished. The observed PPCS shift is consistent with the theory of alternate stable states in shallow lakes (1). This theory predicts a macrophyte-dominated stable state at low nutrient concentrations and a phytoplankton-dominated stable state at high levels of nutrient enrichment, with the possibility of either state existing at intermediate nutrient levels. Some lakes at intermediate nutrient levels may shift between the two states (2). Although there is debate on the causal mechanisms and timing

of the PPCS shift in Lake Apopka, there is consensus regarding the change to phytoplankton dominance (see 3–5). Whether increased phosphorus loading or the 1947 hurricane was the driving factor is the subject of debate. The nutrient-loading hypothesis argues for a transition over several years or even decades (3, 6) whereas the hurricane hypothesis presents another mechanism for the shift to phytoplankton dominance (7) and invokes a time scale of days to weeks (8) or longer (9). Light attenuation, self-shading, and internal nutrient feedback coupled with increased phosphorus loading also have been proposed as important mechanisms that played a role in the shift to phytoplankton dominance (3, 10). Here we propose mechanisms to explain both the abrupt PPCS shift in 1947 from an accelerated increase in nutrient loading and the lake's delayed response to earlier increased nutrient loading.

Several paleolimnological investigations document the 1947 PPCS shift in Lake Apopka (3, 11–13). Planktonic diatom and cladoceran microfossils were present in the lake before 1947 (3, 13). We infer from these results that planktonic refugia existed in the lake during the period of macrophyte dominance. Other shallow Florida lakes displayed historic increases in phytoplankton abundance earlier than Lake Apopka, but not a rapid shift in PPCS (14). These changes were driven by progressive increases in anthropogenic phosphorus loading that began in the 1800s. As we demonstrate here, Lake Beauclair, the downstream lake from Lake Apopka, also was affected by increased phosphorus loading in the mid-1800s. Rapid changes in PPCS in other Florida lakes have been induced by biological or chemical control of macrophytes (15, 16).

Previously recognized anthropogenic influences on nutrient loading to Lake Apopka began as early as 1920 when farmers planted citrus groves along the well-drained southern shoreline and the town of Winter Garden constructed a sewerage system and two large septic tanks permitting domestic wastes to enter the lake directly (Table 1). Nutrients from municipal waste and runoff from the citrus groves at first seemed beneficial for the popular sport fishery (7). Watershed disturbance and hydro-

Table 1. Chronology of anthropogenic modifications in the upper Ocklawaha River Basin.

Early 1880s	Early attempts to farm portions of north-shore wetlands led to a plan to drain these wetlands to "reclaim thousands of acres of productive marsh lands" (17).
1880–1890	The Apopka Canal Company attempts unsuccessfully to dredge a canal connecting Lake Apopka and Lake Beauclair (17). The canal's purpose was to drain wetlands that could be used for farmland and open a transportation route to ship vegetables and citrus to Lake Dora, Lake Eustis, and the Ocklawaha River.
1893	Apopka-Beauclair Canal completed. Lake level "lowered nearly 4 feet" (17), from water depths of 2.4–2.7 m to present mean of 1.62 m.
1893	Lateral canals (32 miles, 51 km) were constructed to drain portions of the north-shore wetlands, diverting this drainage to Lake Beauclair so that "sawgrass land was 3 feet above the lake level" and dry enough for cultivation (17).
1915	Farms were abandoned until the 1940s after the failure to successfully cultivate the drained wetlands that were wet periodically and subject to crop loss during spring freezes. Farms were abandoned and Lake Apopka was allowed "to recapture the mucky peat areas once again" (17).
1922–1927	Sewage discharges from Winter Garden to Lake Apopka begin (3).
1924	Wastewater discharges from fruit processing begin (3).
1926	Hurricane in September "placed 6 to 8 feet of water" in the north-shore wetlands (17).
1942	Drainage water discharges from muck farms begin (20).
1942–1947	Expansion of muck farms (20).
1947	First phytoplankton bloom reported in March (6), earlier than September as reported by others (7, 10).
1947	Hurricanes before 1947 did not trigger phytoplankton blooms, particularly three in 1945 and 1946 with tracks close to the lake (6). Paths of September and October hurricanes were at least 160 km south of Lake Apopka (35).
1950	No pond weed is found in the lake (10); common name for <i>Potamogeton illinoensis</i> , probably the dominant macrophyte before 1947 (10).
1956	Permanent water control structure is installed on Apopka-Beauclair Canal (20).
1973–1978	Anecdotal accounts attribute phytoplankton bloom to submersed macrophytes being uprooted by a 1947 hurricane (37, 38).

logic changes before 1900 received little attention. In the early 1940s, a lush growth of submersed macrophytes, including *Vallisneria americana* and *Potamogeton illinoensis*, covered large areas of the lake bottom, provided cover for young fish, sequestered nutrients, and produced exceptionally clear water. The first plankton blooms reported in 1947 represented a dramatic change in water quality. Within a few years, the dense beds of rooted aquatic macrophytes disappeared and were never reestablished (6), probably because of the competitive advantage for planktonic algae in nutrient-rich waters with low water transparency. Within a decade, the highly prized sport-fish community comprising large-mouth bass (*Micropterus salmoides*) and other species was replaced by a fish community dominated by planktivorous gizzard shad (*Dorosoma cepedianum*). Present efforts to restore Lake Apopka are based on reduction of external phosphorus loading and other means of reducing the total phosphorus (TP) concentration in the water column. These include harvesting gizzard shad, constructing an experimental marsh flowway to sequester phosphorus, and experimental planting of aquatic vegetation (3, 16). Important goals of the restoration plan include reestablishing the historic,

native submersed macrophyte community and a viable sport fishery. These goals are based on the reduction of lake-water P concentrations.

Before anthropogenic disturbance in the 19th century, Lake Apopka was a large lake fringed with extensive, shallow saw grass marshes (*Cladium* sp.) along its north shore (Fig. 1). Water flowed out of the pristine lake by sheet flow, and major hydrologic inputs were precipitation on the lake surface and underwater discharge (mean $2.2 \text{ m}^{-3} \text{ sec}^{-1}$) from Apopka Spring located at the south end of the lake. Anthropogenic modification of the Lake Apopka drainage basin began early in the 19th century with construction of canals that were built to drain the fringing, floodplain wetlands and facilitate agriculture (Table 1). These activities provided marginal flood control for agriculture and navigation channels for limited access to nearby lakes and the Ocklawaha River (17). Engineering projects culminated in 1893 when the Apopka-Beauclair Canal was completed, establishing a navigation channel and a permanent outflow to Lake Beauclair (17).

Attempts in the early 19th century to drain the north-shore wetlands and farm the rich muck soils met with limited success

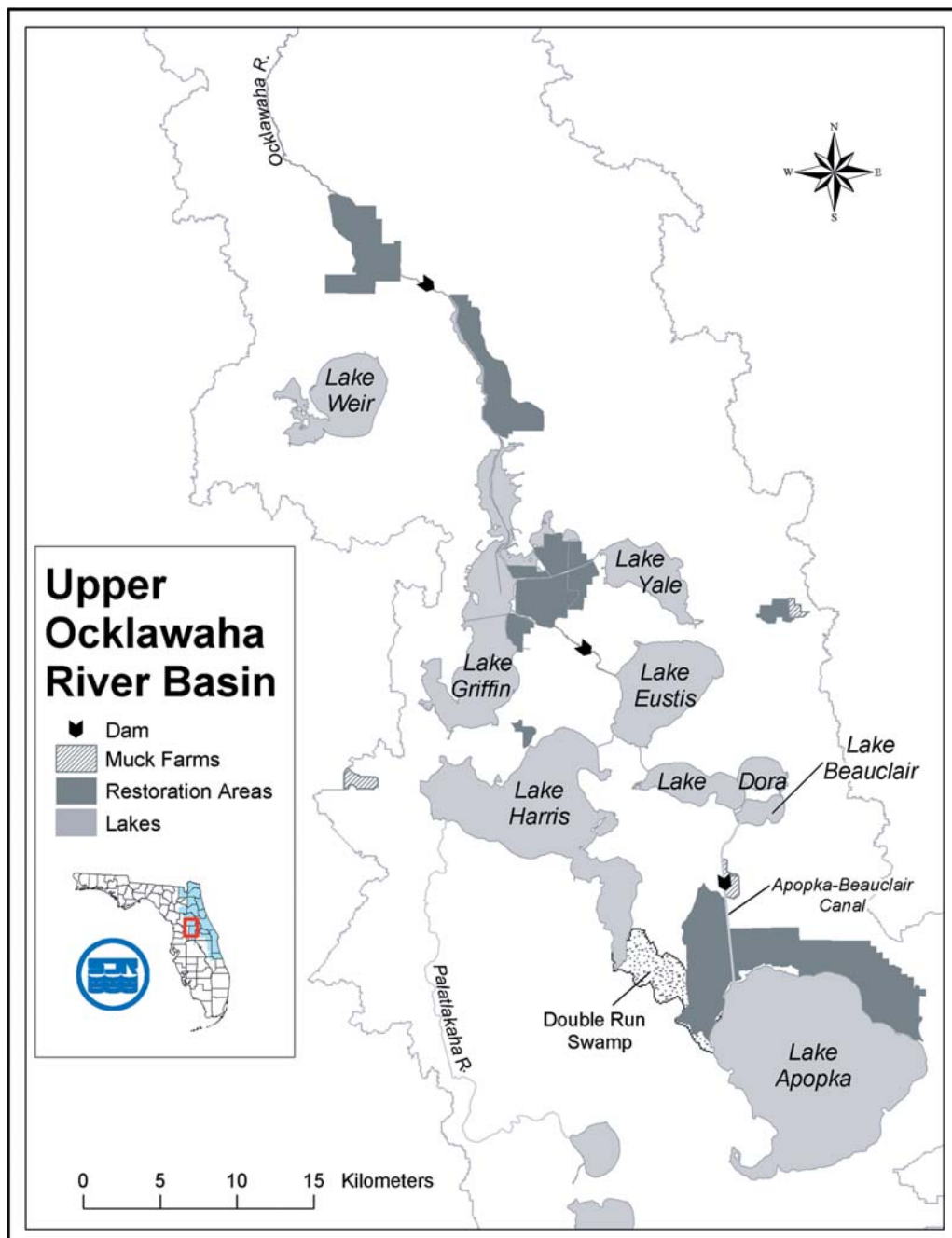


Figure 1. Map of the upper Ocklawaha River basin showing Lake Apopka, Lake Beauclair, and other lakes in the Ocklawaha Chain of Lakes. North-shore wetlands are shown as shaded areas on north shore of Lake Apopka.

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(Table 1). Opening the Apopka-Beauclair Canal in the 1890s allowed the drainage of some marshlands, primarily during periods of low lake stage, and facilitated a limited amount of agricultural development in the north-shore marshes (17). Lateral canals in the former wetlands drained into the Apopka-Beauclair Canal when hydrologic conditions were favorable. This effort, like earlier attempts at agricultural development, was only marginally successful because these low-lying areas were flooded during periods of high lake level. Agricultural development was abandoned in 1915, and in 1926 drained fields were flooded by a hurricane (Table 1). Agricultural use of the north-shore wetlands was limited until the early 1940s when levees were constructed and marshlands were drained permanently so they could be farmed without fear of flooding. Aerial photographs from 1941 through 1985 show progressive, agricultural land-use changes (Fig. 2). By March 1947, more than half of the wetlands east of the Apopka-Beauclair Canal had been or were being drained and converted to muck farms. Thus, extensive land-use changes occurred when the levees were constructed beginning in 1942. The agricultural area increased by 1953 and essentially replaced the

north-shore wetlands by 1985, occupying ca. 40% of the original lacustrine-wetland system (6). "Back pumping" of drainage water to the lake established point sources of phosphorus loading along the north shore. Nutrients in the drained, phosphorus-rich muck soils and crop fertilizers collected in drainage waters provided new sources of phosphorus (18). These sources and double- and triple-cropping of farm produce increased phosphorus loading to the lake nearly sevenfold, from $0.077 \text{ g P m}^{-2} \text{ yr}^{-1}$ in the predisturbance period to $0.504 \text{ g P m}^{-2} \text{ yr}^{-1}$ by the 1990s (6). The source for approximately 85% of the load in the 1990s was drainage from muck farms (6).

In this article, we hypothesize that lowering lake level in the late 1890s increased macrophyte production and initially provided a mechanism for ecosystem accommodation to moderate anthropogenic nutrient enrichment. Perturbation associated with large-scale agricultural development of flood-plain wetlands in the early 1940s, however, altered hydrologic inputs and provided increased point-source phosphorus loading that enriched lake water and rapidly triggered events leading to the first phytoplankton bloom in 1947.

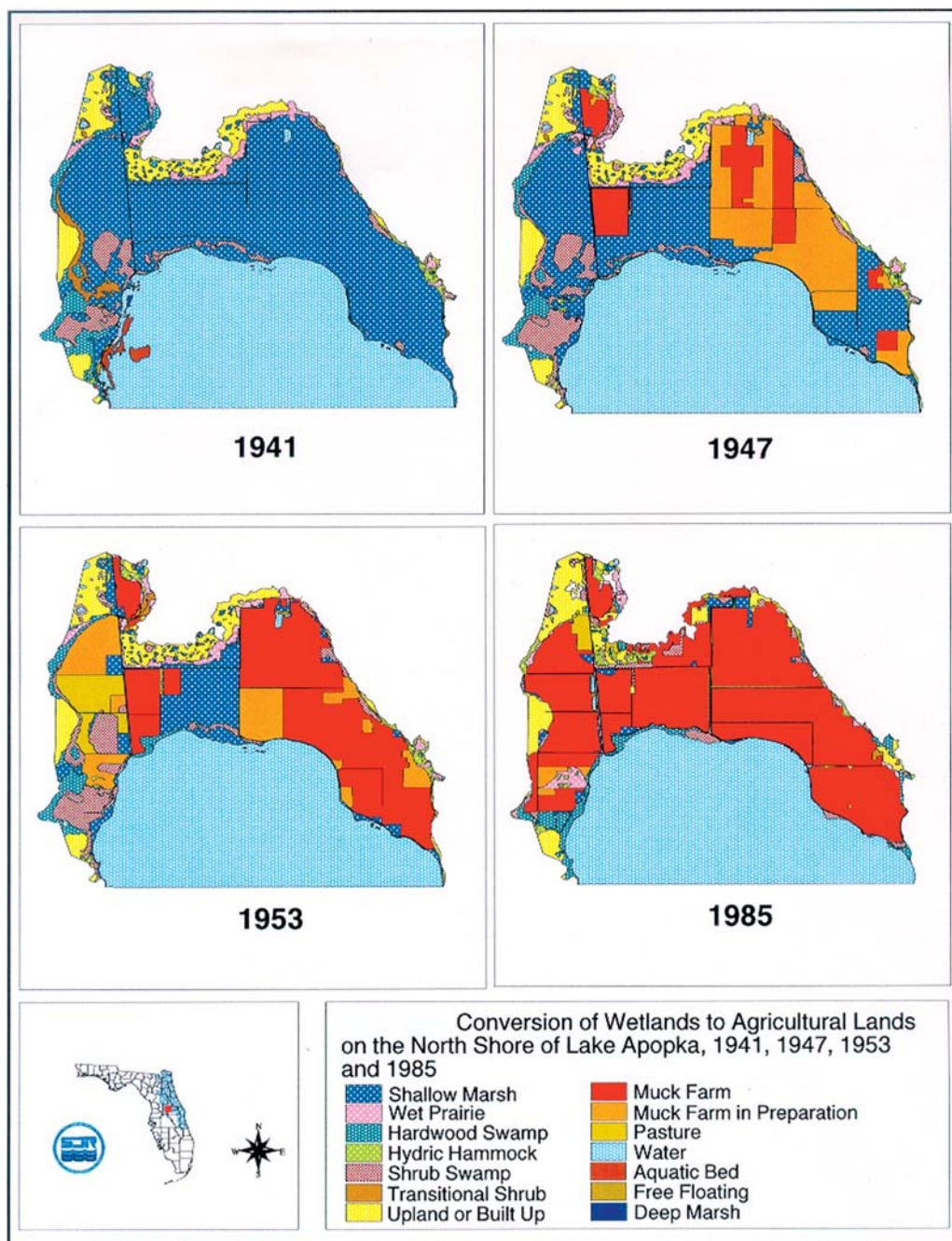


Figure 2. Land-use changes and agricultural development of north-shore wetlands, Lake Apopka. Photo interpretation by St. Johns River Water Management District of aerial photographs (U. S. Department of Agriculture) for 1941, 1947, 1953, and 1985.

MATERIALS AND METHODS

Lake Apopka, located 25 km northwest of Orlando, Florida, is presently a large ($A = 12\,500$ ha), shallow lake (1.62 m mean depth) with a mean hydraulic residence time of 3 years (19). It has a small drainage basin (48 500 ha) relative to its surface area and forms the headwaters of the Harris Chain of Lakes that drain to the Ocklawaha River (Fig. 1). Lake Beauclair, the immediate downstream lake, is much smaller ($A = 4400$ ha) and somewhat deeper (2.05 m mean depth) than Lake Apopka (20). It has a relatively short hydraulic residence time (40–100 days) and small drainage area and responds quickly to nutrients that enter via outflow from Lake Apopka. Sediments from Lake Beauclair, therefore, provide an integrated record of the outflow from Lake Apopka and the north-shore wetlands. Until the mid-1990s, both Lake Apopka and Lake Beauclair were hyper-eutrophic with long-term mean TP concentrations of 203 and $235\ \mu\text{g L}^{-1}$, respectively (16, 20).

Limnological data collected before the 1970s are sparse, so we relied on paleolimnological inferences to assess historic changes in trophic state and water quality (21). Sediment cores ~ 1.5 m long were collected with a piston corer designed to retrieve undisturbed sediment–water interface profiles (22). Cores were sectioned, and samples were stored in plastic containers and kept on ice for transport to the laboratory. Samples were stored frozen until they could be freeze-dried. The bulk density of samples was determined from the amount of dry mass per unit wet volume. Dry samples were ashed at 550°C to determine organic matter (OM) content and nonvolatile solids (NVS), the residual remaining after ashing. Freeze-dried sediments from each section were analyzed for TP and the total carbon (TC) and total nitrogen (TN) content of organic matter (14). The TC/TN ratio of sedimented organic matter for a specific lake varies in response to changing PPCS because submersed, floating-leaved, and emergent macrophytes utilize cellulose for structural support and thus have a larger TC/TN ratio than phytoplankton (11).

The sediment core from Lake Beauclair was dated with ^{210}Pb using the constant rate of supply (CRS) model (23). Total phosphorus accumulation rate (TPAR) and organic matter

accumulation rate (OMAR) for each section were calculated by multiplying the mass sedimentation rate (MSR) obtained from the CRS ^{210}Pb dating model times TP concentration and OM content, respectively. Sediments from Lake Apopka were not dated because anthropogenic modifications in the lake basin created conditions that violate assumptions of the CRS ^{210}Pb -dating model (24). Hydrologic changes, combined with a reduction in lake area and back pumping from agricultural fields, altered the natural supply rate of unsupported ^{210}Pb to the lake sediments. However, the TC/TN weight ratio in Lake Apopka sediments provides an identifiable, time-dependent stratigraphic marker for the 1947 shift to phytoplankton dominance (11). Although the transition probably occurred over several years, we refer to 1947 as the date in which the shift occurred.

We assume that temporal changes in TPAR are proportional to both the water column TP concentration and the phosphorus-loading rate in a specific lake. We also assume that OMAR measures the biological response to production changes in the primary producer community and as such is a proxy for lacustrine primary productivity.

RESULTS

Historic nutrient enrichment inferred from TP profiles in sediment cores from Lake Beauclair and Lake Apopka suggests different patterns of eutrophication in the two water bodies (Fig. 3). Increased TP loading to Lake Beauclair inferred from either TP concentration or accumulation rate (TPAR) began before 1900 (Fig. 3A, D, and E). An obvious discontinuity in TP concentration and particularly TPAR after 1900 probably reflects completion of the Apopka-Beauclair Canal in 1893. Levee construction and wetland draining caused a second discontinuity in TP concentration and TPAR after 1950. By contrast, increased TP loading in Lake Apopka inferred from TP concentrations was stepwise compared with the exponential increase after 1900 in Lake Beauclair (Fig. 3B). Increased loading to Lake Apopka began much later than in Lake Beauclair and is evident in only two samples before the inferred PPCS shift in 1947. Relatively small increases in TP loading are magnified as areal loads in Lake Beauclair because its surface

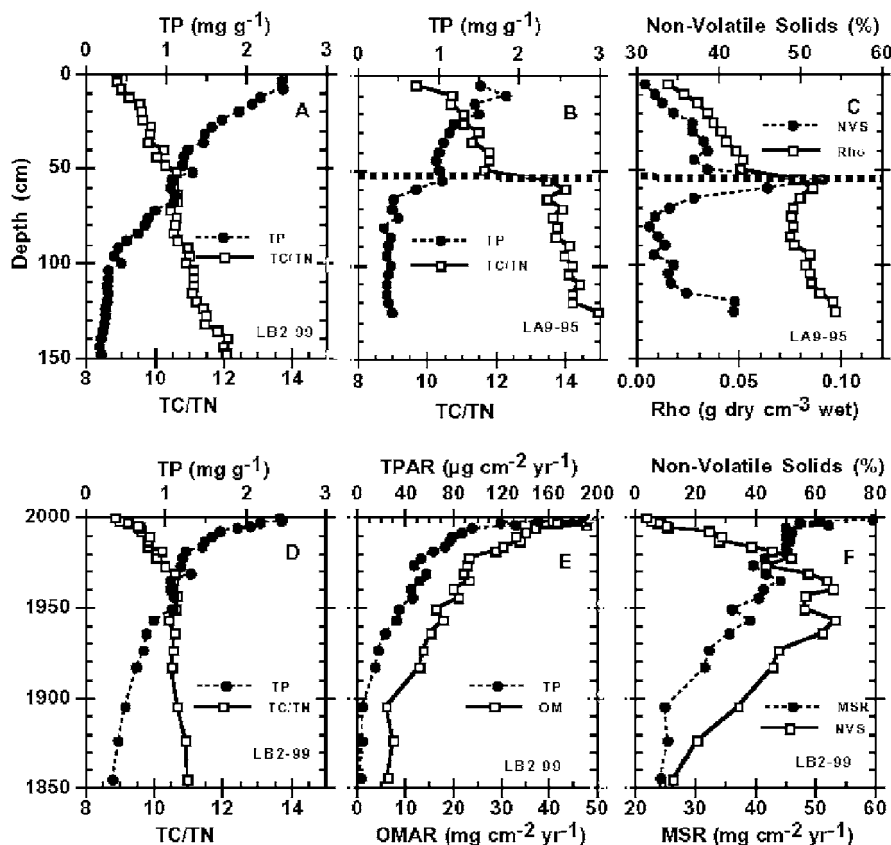


Figure 3. Sediment records from Lake Beauclair (LB2-99) and Lake Apopka (LA9-95). (A) Profiles of TP and TC/TN vs. depth for core LB2-99. (B) Profiles of TP and TC/TN vs. depth for core LA9-95. (C) Profiles of nonvolatile solids (NVS) and bulk density (ρ) vs. depth for core LA9-95. (D) Profiles of TP and TC/TN vs. date for core LB2-99. (E) Profiles of total phosphorus accumulation rate (TPAR) and organic matter accumulation rate (OMAR) vs. date for core LB2-99. (F) Profiles of mass accumulation rate (MSR) and percent nonvolatile solids (NVS) vs. date for core LB2-99. Dotted lines in parts B and C represent the boundary between phytoplankton-derived and macrophyte-derived sediments.

area is small compared with Lake Apopka. Historic increased TP loading in Lake Beauclair is also reflected in higher OMAR, a biological response to nutrient loading (Fig. 3E).

Cores from the two lakes also display different temporal patterns in PPCS inferred from the TC/TN ratio. In Lake Beauclair, the ratio decreased from 12 to 11 before 1850 and remained between 11 and 10.6 until about 1970 (Fig. 3B and D). It then decreased to about 10 from 1970 to 1980. The largest decrease from about 10 to 8.9 occurred after 1980 when increases in TPAR and OMAR were greatest. By comparison, the TC/TN ratio in Lake Apopka decreased sharply from about 13.5 to 11.5 between 55 and 50 cm (Fig. 3B), a change that reflects the 1947 PPCS shift (11). Loose, flocculent, phytoplankton-derived sediments formed after 1947 are readily distinguished by low bulk density ($< 0.05 \text{ g dry cm}^{-3} \text{ wet}^{-1}$) (Fig. 3C). The inferred rapid shift to phytoplankton dominance that is so prominent in the Lake Apopka record apparently did not occur in Lake Beauclair, the downstream lake.

Deposition of sediments in Lake Beauclair increased historically. MSR increased from ca. $25 \text{ mg cm}^{-2} \text{ yr}^{-1}$ before 1900 to $50 \text{ mg cm}^{-2} \text{ yr}^{-1}$ in 1980 (Fig. 3F). After 1980, MSR was relatively constant, but OMAR increased as NVS decreased (Fig. 3E). The sediment profile for Lake Beauclair also displays a large increase in NVS (Fig. 3F). NVS increased from ca. 50% to values $> 60\%$ from 1936 to 1965, during and after the time that levees were constructed to drain the north-shore wetlands. The magnitude of NVS input from construction of levees and associated anthropogenic changes is evident from a second core in Lake Beauclair that was collected nearer the point of discharge from the Apopka-Beauclair Canal. Approximately 1.0 m of sediment with high NVS was deposited at this site (25). During the period of levee construction, the fraction of NVS in sediments also increased in the Lake Apopka core to $> 45\%$ at 55 and 60 cm, the two intervals below the boundary delimiting phytoplankton-derived sediments (Fig. 3C). These data indicate increased influx of inorganic materials to Lake Apopka before the 1947 shift in PPCS.

DISCUSSION

We have inferred historic increases in phosphorus loading from sediment records of two hypereutrophic lakes. In Lake Beauclair, TPAR and OMAR increased exponentially after 1900 (Fig. 3). Both of these proxies also increased in Lake Apopka after the 1947 shift in PPCS (3). Either of these proxies provides evidence for eutrophication of these lakes. However, we prefer the classical definition: that eutrophication is the available nutrient enrichment of receiving waters (26). Conceptually, nutrient enrichment is driven by external loading of the nutrient that limits primary production. The hypereutrophication of Lake Apopka was a process by which phytoplankton production was controlled by phosphorus supply (3, 4, 16). We infer that OMAR in Lake Apopka and Lake Beauclair sediments increased in response to TPAR, an index of phosphorus enrichment. Other workers define eutrophication in terms of rate of organic matter generated by primary producers (27, 28). This definition has been broadened to include external loading of dissolved and particulate inorganic and organic matter that increase the potential for high biological production (29). Such a definition states explicitly that the limiting nutrient and other essential nutrients may be loaded in either inorganic or organic form and that external loading may be a source of organic matter for heterotrophic metabolism. Primary production in Lake Apopka is adequate to account for measured basinwide accumulation of OM in sediments (30). OMAR in Lake Beauclair and Lake Apopka, therefore, is an index of eutrophication because sedimented OM is largely a by-product of phytoplankton production and is therefore autochthonous in origin.

Three historic periods with differing hydrology can be distinguished for the Lake Apopka drainage basin (Fig. 4). During the predisturbance period (Fig. 4A), the natural drainage was sheet flow of water from Lake Apopka through

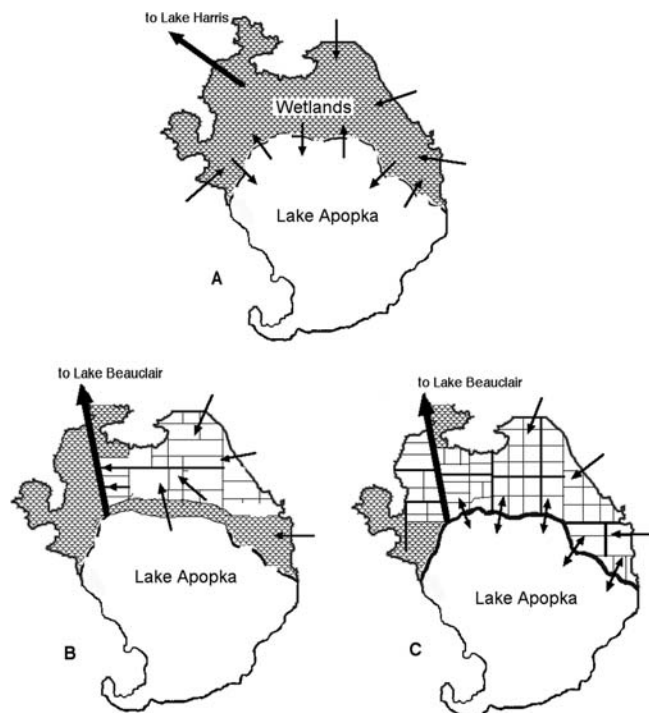


Figure 4. Hydrologic and land-use changes for Lake Apopka and northshore wetlands that form the upper Ocklawaha River drainage basin. Diagrams illustrate changes in the northshore wetlands for three time periods. Arrows and size show direction and relative magnitude of water flow. (A) Predisturbance: water exchange between wetlands and lakes was unrestricted in the early 1800s. Outflow during periods of high lake stage was through Double Run Swamp to Little Lake Harris (17). (B) Outflow diversion: the Apopka-Beauclair Canal, completed in 1893, diverted outflow from Lake Apopka to Lake Beauclair and lowered lake level ca. 1.0 m (17). Northshore wetlands were ditched, drained, and connected to the Apopka-Beauclair Canal with lateral canals. (C) Agricultural development: levee construction in the early 1940s isolated northshore wetlands from the lake. Pump stations along the levees controlled periodic flooding through point-source discharges to the lake and provided irrigation water during dry periods.

fringing wetlands along the north shore, primarily through Double Run Swamp to Little Lake Harris (17). Hydrology was altered in the late 1890s by the construction of the Apopka-Beauclair Canal that lowered the water level ca. 1.0 m and established a permanent outflow to Lake Beauclair (17). The Apopka-Beauclair Canal then became the major hydrologic input to Lake Beauclair (Fig. 4B). Another major hydrologic disturbance was the construction of levees in the 1940s along the north shore so marshlands could be drained permanently and farmed intensively (Fig. 4C). The levees permanently isolated the lake from north-shore marshes and drainage canals in the marshes provided the avenue for water exchange with the lake (17). The constructed network of canals in the reclaimed wetlands discharged to the lake and provided irrigation water during dry periods and water to flood fields for pest control. More important, however, from the perspective of lake function, the canals collected rainfall, runoff, and seepage that was pumped directly into the lake as point-source discharges.

Why was PPCS structure in Lake Apopka so resistant to change before 1947? Low nutrient loading and shallow, clear waters in the relatively undisturbed lake provided an ideal environment for submersed macrophytes and associated microflora. Permanently lowering the lake stage ca. 1.0 m with the completion of the Apopka-Beauclair Canal in 1893 further enhanced the competitive advantage for the submersed macrophyte community. Several biological consequences of lower lake level can be hypothesized. First, increased irradiance on the bottom provided a competitive advantage for the established, submersed macrophyte community in this shallow lake. Second, shallower waters increased the area for optimum macrophyte colonization. Finally, these changes enhanced the capacity of

the submersed macrophyte community to assimilate and sequester nutrients (31). Nutrient storage increased with expansion and increased production of the macrophyte community and its associated microflora, allowing for biological assimilation of the increasing nutrient loads (32, 33). This process maintained clear water with low nutrient concentrations and provided resistance to a nutrient-driven PPCS shift before 1947.

Historical data and paleolimnological evidence support the hypothesis for accommodation of the macrophyte community to increased nutrient loading in Lake Apopka before 1947. Increased nutrient loading to the lake that began in the 1920s from a combination of domestic and agricultural inputs apparently increased the abundance of submersed macrophytes (10). Inferred TP loading to Lake Apopka increased before the 1947 PPCS shift, as indicated by the near doubling of TP concentration between 65 and 50 cm in sediments that are shown to be macrophyte-derived based on their TC/TN ratios (Fig. 3B). Diatom and cladoceran microfossil abundance, proxies for phosphorus enrichment, also increased at 55 cm before the PPCS shift (11, 13). Both planktonic and benthic species of diatom and cladoceran species increased, indicating that planktonic refugia were present in the lake (3). PPCS, however, was affected little by increased TP loading as inferred by concurrent change in the TC/TN ratio (Fig. 3B). This indicates that PPCS in Lake Apopka before the 1947 shift was resistant to increased TP loading. In Lake Beauclair, OMAR, which is driven by increased phosphorus loading, increased approximately fourfold from 1900 to 1980, with only a relatively small change in TC/TN ratio (Fig. 3D and E). We, therefore, infer that until the 1980s, PPCS in Lake Beauclair was affected relatively little by phosphorus enrichment during a long period of increased lacustrine productivity. We conclude that PPCS in Lake Apopka was also resistant to phosphorus enrichment until the switch from macrophyte dominance to phytoplankton dominance in 1947.

Several factors related to changes in land use and hydrology after 1942 interacted to enhance the effect of phosphorus loading from muck farms on PPCS in Lake Apopka (Table 2). First, soils were dehydrated with drainage of the wetlands. This eliminated uptake and storage of nutrients and long-term accretion of organic matter produced by wetland plants. Draining, therefore, caused losses of the highly organic soils by drying, subsidence, oxidation, and wind erosion. Second, phosphorus leached from muck soils was concentrated in water collected in the drainage canals, initially because the muck soils themselves were a rich source of phosphorus and later because these muck soils were amended with commercial fertilizers (18). Third, before levees were constructed, water transport in and out of the wetlands was by sheet flow. With the construction of levees, drainage canals collected and transported water between the former wetlands and the lake (Fig. 4). Fourth, water

transport was altered in that exchange with the lake no longer occurred diffusely along the sheet-flow boundary, but at the point of discharge from drainage canals to the lake. Fifth, nutrient loading was no longer distributed along the entire sheet-flow boundary, but occurred only where drainage canals discharged to the lake. Sixth, high nutrient gradients then occurred where drainage water was discharged to the lake, whereas low nutrient gradients existed before levees were constructed. Thus, phosphorus loading from this developing agricultural enterprise on the north-shore wetlands was concentrated in point discharges from drainage canals located along the shoreline. Finally, the filtering and assimilatory capacity of the north-shore wetlands was lost with levee construction. Draining and farming the north-shore wetlands therefore transformed these areas from nutrient sinks to nutrient sources.

We believe a nutrient-driven hypothesis addresses the following questions: *i*) Why was the PPCS in Lake Apopka no longer resistant to nutrient enrichment in 1947? *ii*) Did accelerated phosphorus loading induce the PPCS shift in Lake Apopka that was observed in 1947? Land-use and hydrologic changes associated with construction of the north-shore levees from 1942 to 1947 increased phosphorus loading from drainage canals that carried phosphorus-enriched water to the lake (Table 2). Phosphorus loads at the points of discharge mixed with lake water and created mixing areas or "critical zones" with increased TP concentrations. In these zones, the TP concentration exceeded the assimilatory capacity of the macrophyte community and reached "the maximum perturbation that can be taken without causing a shift to an alternative stable state" (8). When construction began in 1942 and nutrient loading was initially relatively small, the shift in PPCS was restricted to relatively small mixing areas or critical zones. Continued and increased loading increased the size of these critical zones. As the size of the critical zones increased, internal feedback of phosphorus mobilized from dying and decaying submersed macrophytes provided a significant source of internal phosphorus loading (32), expanding the critical zones until the PPCS in the entire lake was dominated by phytoplankton.

Two factors in addition to increased phosphorus loading probably exacerbated the shift in PPCS, until algae became the dominant primary producers throughout the lake. A large influx of inorganic materials associated with dredging and construction of levees may have decreased light penetration and shaded the macrophyte community, providing a competitive advantage to phytoplankton. Support for this scenario is provided by the increased influx of NVS in both the Lake Apopka and Lake Beauclair cores during the period of levee construction. The second factor is the shallow, uniform bathymetry of Lake Apopka. The lake is relatively flat with 79% of the lake bottom area between the 1.5- and 2.0-m contours and only 2.3% of the bottom shallower than 0.5 m (34). Internal phosphorus loading, therefore, would have a relatively uniform and large effect on water column phosphorus in such a shallow lake. Our hypothesis is that by 1947, increased external phosphorus loading and internal feedback of phosphorus mobilized from dying and decaying macrophytes, possibly coupled with physical factors, produced sufficient nutrient perturbation to induce the well-known, lakewide PPCS shift that was first observed in 1947.

The role of the 1947 hurricane in the PPCS shift is still debated (see 4, 5). This role is questioned (6) from an analysis of reported hurricanes and tropical storms over 50 years before 1947 (35). The macrophyte state was stable through 1946 even though 7 hurricanes and 21 tropical storms passed over or near the lake from 1886 through 1946. These include three hurricanes in 1944 and 1945 that had no reported effect on PPCS in Lake Apopka. By comparison, the track of the 1947 hurricane was too distant to have a direct impact on the lake. In addition, aerial photographs from March 1947 show an extensive algal bloom, 6 months before the 1947 hurricane and more than

Table 2. Anthropogenic alteration of the hydrology of northshore wetlands and effects on nutrient loading to Lake Apopka: comparison of effects with conditions before and after levees were constructed in the early 1940s.

Factor	Before	After
Wetland soils	Long-term accretion and nutrient storage	Loss due to drying, subsidence, oxidation, and wind erosion
Nutrient balance	Sink in wetland vegetation	Source due to decomposition of old, wetland soils
Water advection	Sheet flow through wetlands	Drainage canals discharge to lake
Water exchange	Diffuse along sheet flow boundary	Mixing zone at point of canal discharge
Nutrient loading	Dispersed along sheet flow interface	Concentrated at discharge point
Nutrient gradient	Relatively small	Large, dissipated in mixing zone
Ecosystem function	Filtering and sequestering of nutrients	Point discharge of nutrients to lake

a year after the hurricanes of 1945. We therefore conclude that the 1947 hurricane was not a major factor in the abrupt shift in PPCS.

The hurricane hypothesis, including tornado effects (5), is attractive because abrupt elimination of submersed macrophytes by a stochastic event provides a mechanism to explain the anecdotal accounts of the rapid shift to phytoplankton dominance within weeks. Lake managers, for this reason or others, may accept a stochastic trigger for ecosystem disturbance while overlooking the underlying, causal perturbation (8) and lost ecological functions of nearby transition zones such as wetlands (36). Loss of ecological functions in Lake Apopka occurred when north-shore wetlands were converted to agricultural production, changing the wetlands from nutrient sinks to very significant nutrient sources (Table 2). Previous explanations for the PPCS shift in Lake Apopka relied on the convenience of accepting the hurricane as a stochastic trigger. The origin of the hurricane hypothesis, however, can be traced to unsubstantiated anecdotal accounts in a nonrefereed publication and an agency report (37, 38). It is perhaps significant that no mention is made of the hurricane hypothesis in an earlier comprehensive account of the PPCS shift (10) and that other hypotheses were ignored (7, 10). Thus, nutrient loading as a causal factor in hypereutrophication of Lake Apopka was obscured by the hurricane hypothesis (3). We realize that nutrient loading before the PPCS shift was a significant anthropogenic disturbance that produced ecosystem changes (3, 7, 10). We hypothesize, however, that hydrologic modification of the drainage basin initially provided a mechanism for ecosystem resistance to moderate anthropogenic nutrient enrichment. The perturbation associated with large-scale agricultural development of floodplain wetlands in the early 1940s, however, altered hydrologic inputs and provided increased point-source phosphorus loading and phosphorus enrichment of lake water that triggered the lakewide PPCS shift to a new stable state beginning with the first reported phytoplankton blooms in 1947.

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