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Hurricane effects on a shallow lake ecosystem, Lake Okeechobee, Florida (USA)

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South Florida Water Management District

With 10 figures and 3 tables

Abstract: This unique case study of Lake Okeechobee – a large, shallow and culturally eutrophic lake in south Florida – documents the effects of hurricanes on its water quality, sediment, phytoplankton and submersed aquatic vegetation (SAV). Three hurricanes (Frances and Jeanne in 2004 and Wilma in 2005) that swept directly over the lake led to a number of expected changes throughout the system: 1) high winds produced large seiches, strong waves and currents that redistributed bottom sediments and uprooted SAV and emergent macrophytes; 2) sediment disturbance resulted in increased suspended solids and nutrients in the water column, reduced Secchi transparency and affected SAV recovery, phytoplankton biomass and phytoplankton species dominance; and 3) heavy rainfall increased flows, nutrient loads and lake water levels. Changes in suspended solids, most nutrient concentrations, phytoplankton and SAV persisted for two years after the hurricanes. This persistence was attributed to unconsolidated surface sediment that increased in thickness because of the storms and was more easily resuspended during subsequent wind events. Drought conditions and low lake levels in the second year after the hurricanes led to some recovery of SAV, primarily in the form of the non-vascular musk grass (*Chara* spp.). The absence of high-intensity hurricanes in the near future should aid in SAV recovery and return the nearshore region to a macrophyte-dominated clear-water state. Our results demonstrate the importance of sediment disturbance and water levels in shallow lakes that are vulnerable to extreme weather events.

Key words: Lake Okeechobee, hurricane, water quality, sediments, sediment resuspension, phytoplankton, submersed aquatic vegetation, drought, water levels, alternative stable state.

Introduction

Lake Okeechobee has a long history of anthropogenic effects (Havens et al. 1996a). Encircled by the Herbert Hoover Dike, surface inflow, surface outflow and lake level are managed for the competing needs of water supply, flood control and environmental benefits. For decades, excessive phosphorus (P) loads from the surrounding watershed have lead to increased eutrophication (Havens et al. 1996a), which is expressed as: 1) total P (TP) concentration that has more than doubled in the past 30 years (Havens & James 2005), 2) reduced nitrogen (N) to P ratios (Havens et al. 2003) and 3) increased frequency of algal blooms (Havens et al. 1995, Havens et al. 1996a). In addition, there has been a decline in Secchi transparency (Havens & James 1999) as easily resuspended mud sediments have accumulated in the lake (Brezonik & Engstrom 1998).

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Environmental reconstructions based on multi-proxy sediment records (geochemistry, fossil pigments, stable isotopes and diatoms) extend these trends back to the early 1900s and suggest that the current eutrophic state of the lake is largely a consequence of land-use changes and altered hydrology of the south Florida landscape (Stoermer et al. 1992, Brezonik & Engstrom 1998, Engstrom et al. 2006).

Extreme natural events, such as intense storms, can amplify the effect that environmental stressors like eutrophication have on this ecosystem. Few studies, however, have examined the effects of hurricanes on lakes. Short-term studies have focused on hydrology and hydrodynamics (Chimney 2005), water quality (Havens et al. 2001a, Hoyer et al. 2008, Presley et al. 2006) or submersed aquatic vegetation (SAV) (Havens et al. 2001a). Long-term studies have mainly examined sediment cores (e.g., Schwimmer & Frazier 1994, Liu & Fearn 2000, Donnelly et al. 2001, Liu & Fearn 2002) or change in lake trophic state (e.g., Lake Apopka: Lowe et al. 2001).

From August 2004 to October 2005, Lake Okeechobee was influenced by five hurricanes (Charley, Frances, Ivan and Jeanne in 2004; Wilma in 2005) that produced strong winds and/or torrential rainfall. Hurricane Charley was a compact, intense storm that affected the upper portion of the Lake Okeechobee watershed on August 13, 2004 with 6 to 9 cm of rainfall. After striking the panhandle of Florida on September 16, 2004, the remnants of Hurricane Ivan passed over south Florida on September 20 adding 3 to 5 cm of rainfall to the watershed. The eye walls of Hurricanes Frances on September 5, 2004, Jeanne on September 26, 2004 and Wilma on October 24, 2005 passed directly over the lake and had the greatest environmental effect. These storms delivered between 9 to 16 cm, 8 to 20 cm and 14 to 17 cm of rainfall, respectively, to the lake and watershed. It had been over 50 years since storms of this magnitude had affected the lake.

The South Florida Water Management District (District) has conducted an extensive monitoring program on Lake Okeechobee since the mid-1970s (James et al. 1995a, 1995b). Routine acquisition of physical, chemical and biological data provided us with the unique opportunity to document changes in the lake that resulted from these extreme events. A previous study by Havens et al. (2001a) documented short-term changes to water quality, hydrodynamics and the SAV community in Lake Okeechobee after Hurricane Irene in 1999. The subsequent recovery of SAV and water quality resulted from reduced water levels in the year following the hurricane. In this paper, we use Lake Okeechobee monitoring data to evaluate the longer-term effects (over two years) that the much stronger storms, Hurricanes Frances, Jeanne and Wilma, had on the lake's phytoplankton and SAV communities, hydrology, water quality and sediments.

The objectives of this paper are to document hurricane-related changes to water quality and the phytoplankton and SAV communities in Lake Okeechobee. Because of the unique opportunity of obtaining sediment cores prior to (in 2003) and after (2005) Hurricanes Frances and Jeanne, we also were able to relate differences observed in sediment cores to other changes that took place in the lake. Our results provide information on changes that may be anticipated and managed for in other eutrophic lakes that are vulnerable to extreme weather events.

Methods

Site history and description

Lake Okeechobee is a large (1730 km^2), shallow (average depth 2.7 m) eutrophic lake located in south Florida (Fig. 1A). It is a highly managed system that provides irrigation water for regional agriculture, flood control for the surrounding watershed, water supply for several local municipalities and ground water recharge for urban areas to the south and east. The lake also is a recreational and ecotourism destination and supports a multi-million-dollar sport fishery.

The lake can be divided into three regions: 1) littoral, 2) nearshore and 3) offshore (Fig. 1B). The shallow (water depth approximately 1 m depth) littoral region comprises 24 % of the total surface area (350 km^2), contains a diverse plant community with 61 plant species (Richardson & Harris 1995) and is a spawning and nursery area for many fish species. The nearshore region comprises approximately 15 % of total lake surface area, resides on a shelf with slightly deeper water (1–2 m) that can support an extensive SAV community and wave-tolerant emergent plants. The offshore region comprises the remaining 61 % of the lake area. It is the deepest portion of the lake (2.5–5 m), turbid, light limited, nutrient rich (TP > 100 $\mu g\ l^{-1}$) and devoid of rooted plants or attached algae (Havens 1995). A large portion of this offshore region (an area encompassing 666 km^2 and approximately 37 % of the lake bottom) is underlain by flocculent mud sediments (Fisher et al. 2001). Due to the lake's exceptionally long fetch (up to 56 km) and shallow depth, even moderate breezes (< 5 m sec^{-1}) can produce waves of sufficient energy to resuspend sediments causing the turbid conditions often prevalent in this region (Jin & Ji 2004).

Field and laboratory procedures

The District operates four automated meteorological stations on Lake Okeechobee (Fig. 1A) that measure wind speed and direction, and lake stage (i.e., water surface elevation relative to the National Geodetic Vertical Datum [NGVD] of 1929). Observations are averaged every 15 minutes and recorded to a CR10 datalogger (Campbell Scientific Inc., Logan, UT). Weather

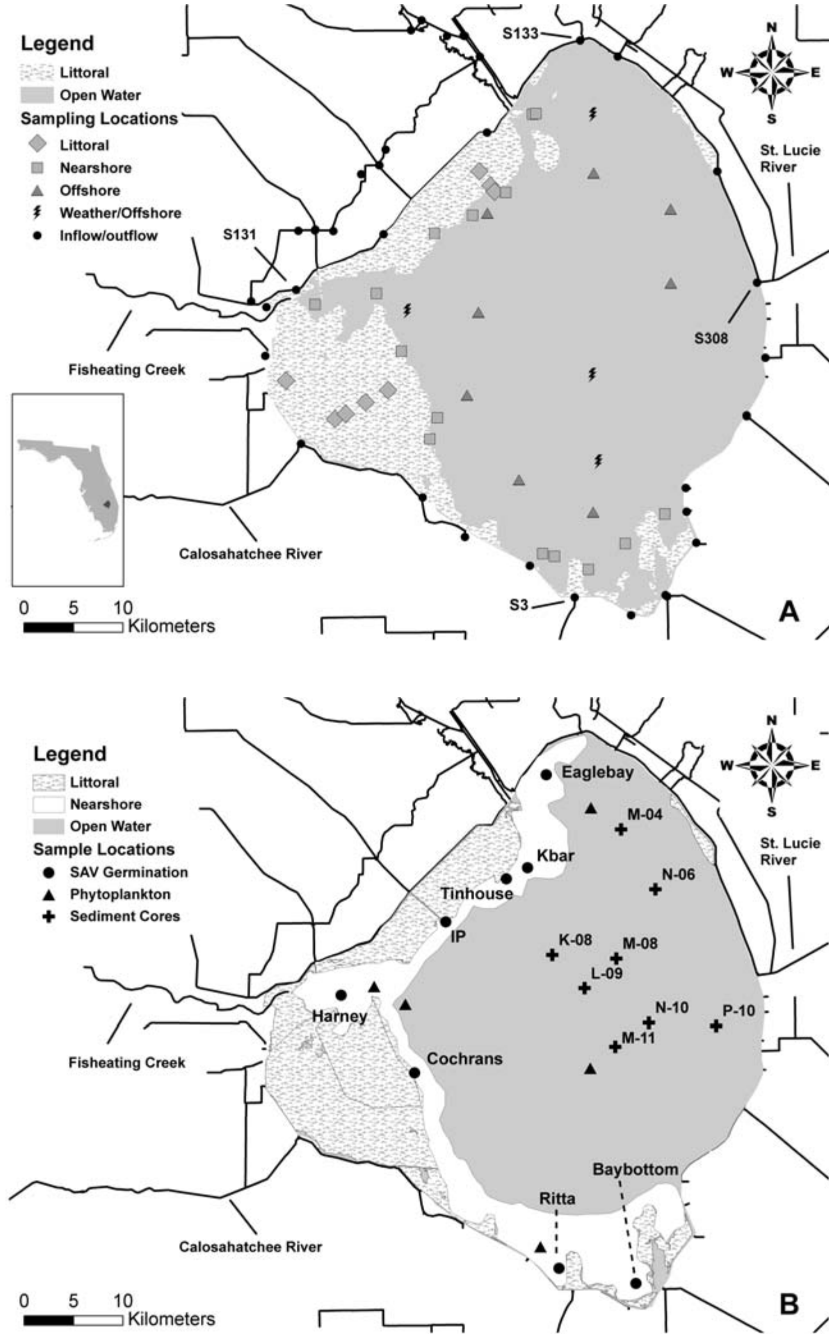

Fig. 1. Maps of Lake Okeechobee showing the location of **(A)** weather stations, tributaries and sample sites for flow, load and in-lake water quality; and **(B)** littoral, nearshore and offshore regions and sampling sites for submersed aquatic vegetation (SAV) germination, phytoplankton and sediment cores. Lake regions are based on dominant primary producers (Havens 2003).

data were used by the Lake Okeechobee Environment Model (LOEM: Jin & Ji 2004, Jin et al. 2007) to estimate sediment resuspension, current velocity, and flow patterns during and immediately after the hurricanes.

Rainfall was estimated from weather stations located in and near the lake. Rainfall water quality collected weekly in wet bucket Aerochem Metrics® collectors located at two lake structures (S131 and S308, Fig. 1A) was averaged for the period of January 2000 to November 2003 (monitoring was discontinued thereafter). These average values were multiplied by estimated rainfall volume over the lake to obtain rainfall nutrient loads. All other hydrological, meteorological and water quality data used in our analyses were collected from September 1, 2002 to October 31, 2007.

Lake stage is monitored at the four weather stations in the lake and at 11 flow structures at the lake's perimeter. Because the north-south lake axis experienced the greatest surface seiche during each hurricane, we calculated seiche height as the difference in stage data between structures S133 on the north side of lake and S3 on the south side of lake (Fig. 1A).

The volume and water quality of surface inflow to the lake is monitored at 34 flow structures and one free-flowing tributary, Fisheating Creek (Fig. 1A). Most of the water discharged from the lake goes to the Caloosahatchee and St. Lucie Rivers; five other locations discharge smaller volumes of water to the south. Monthly estimates of nutrient loads for Lake Okeechobee were developed as described by James et al. (1995a) for the period September 2003 to October 2007.

In-lake water quality is monitored on a monthly basis at 34 sampling locations (Fig. 1A). The monitoring program has been described elsewhere (James et al. 1995b). Secchi transparency and concentrations of chlorophyll-*a*, N and P species are measured at each site using standard methods (U. S. Environmental Protection Agency [USEPA] 1983, APHA 1998). All water quality samples are analyzed by laboratories certified by the National Environmental Laboratory Accreditation Program and followed District QA/QC procedures (South Florida Water Management District [SFWMD] 1999).

Sediment cores were collected from the offshore region of Lake Okeechobee (Fig. 1B) prior to the 2004 hurricane season. Cores were first collected in 1988 to reconstruct changes in historical P loading (Brezonik & Engstrom 1998) and again in 2003 (Schottler & Engstrom 2006). Profiles of these sediment cores were dated with ^{210}Pb analysis. Another set of cores was taken from the same locations in April 2005 to assess the amount of change that had occurred in the sediment profile after Hurricanes Frances and Jeanne. Sediments were collected by piston corer, sectioned at 0.5–2 cm intervals in the field and analyzed for water content; two of these cores (stations L9 and M8) also were analyzed for ^{210}Pb as described in Schottler & Engstrom (2006).

Phytoplankton biovolume and densities have been monitored in Lake Okeechobee at five locations since 1994 (Fig. 1B). Samples used in this study were collected on a quarterly basis from October 2003 to October 2006 (the latest analyzed). Sample collection and analysis are described in Havens et al. (2003).

Annual surveys of the aerial coverage and species composition of the SAV community have been conducted on Lake Okeechobee in the months of August to September since 2001. Field procedures are documented in Havens et al. (2002). Briefly, the lake is partitioned into 1 km^2 grids and SAV at the center point of each grid (determined by GIS) is sampled using a rake system that scraped one m^2 of sediment bed and a visual estimate of the abundance of the major species is determined. Assuming the point sample represented conditions throughout the entire grid, the number of vegetated grids is summed to determine the areal extent of SAV for each year. Because vascular and non-vascular SAV species overlapped within the grids, the percent coverage of each plant type is determined semi-quantitatively. The percent coverage of vascular species is the total coverage of vascular species divided by the sum of the total coverage of vascular species and the total coverage of non-vascular species. The percent coverage of non-vascular species is simply 100 percent minus the percent coverage of vascular species.

To determine the viability of SAV propagules in Lake Okeechobee after Hurricane Wilma, we conducted a germination experiment. Sediment cores were collected in August 2006 from eight locations (Fig. 1B). Sites were selected that historically had high SAV density and species diversity. Ten 7.7 cm diameter × 10 cm deep cores were collected at each site (a total of 80 cores) using a PVC corer. The cores were kept in PVC tubes, covered with plastic wrap and secured in an upright position. The cores were transported back to the laboratory and transferred in their PVC sleeves to individual 2.4 l opaque buckets containing enough deionized water to cover the entire core. The buckets were covered with clear plastic wrap to prevent evaporation and positioned randomly in a Revco environmental chamber (Thermo Electron Corporation, Asheville, NC). The chamber was maintained between 25–30 °C and illuminated at 240 µMole photons m^{-2} s^{-1} on a 13/11 hr day-night cycle. An initial inspection of the cores found no plants. The abundance and diversity of SAV species that germinated in each core was observed every seven days for 12 weeks.

Data analysis

Environmental data were separated into approximately 12-month periods: the 2003 (September 1, 2002 to August 31, 2003) and 2004 (September 1, 2003 to August 31, 2004) years represent pre-hurricane periods. The 2005 year (October 1, 2004 to September 30, 2005) represents the post-Frances and Jeanne period. The 2006 year (November 1, 2005 to October 31, 2006) represents the post-Wilma period and the 2007 year (November 1, 2006 to October 31, 2007) represents a period of extended drought and lake-level decline (see below). Water quality data for the post-hurricane and drought periods were compared to the pre-hurricane periods for each region of the lake using a mixed model analysis of variance (ANOVA) based on least square means comparisons and an anisotropic exponential covariance structure to account for correlation of replicate measures over time (Littell et al. 1996, James & Havens 2005). Unless otherwise specified, a probability value of 0.01 or less was considered significant. Where appropriate, data were normalized using transformations recommended by SAS/LAB software (SAS version 8.2, SAS Institute Inc., Cary, NC). All other statistics were performed using SAS version 9.1.

Results

Sediment resuspension and disturbance

The most direct hurricane effects on Lake Okeechobee were related to wind speed and duration (Table 1). High winds caused a large surface seiche to develop along the lake's north-south axis during each storm (Fig. 2). The greatest difference between maximum wind set-up and set-down, i.e., the total deviation in lake stage, was 4.9 m at the north site during Hurricane Jeanne. High winds also created strong currents and large waves (Table 1). While Hurricane Frances was the weakest of these three hurricanes, it persisted for the longest time over the lake because it moved very slowly across south Florida. Wind speeds exceeding 29 km hr^{-1}, the critical speed at which the LOEM predicts sediment resuspension occurs throughout the offshore region, lasted for 4.7 days, resulting in the highest bottom shear stress (16 N m^{-2}) of the three storms. In contrast, the other two storms were much stronger – based on wind speed – but had less impact on sediment resuspension because their persistence was shorter (2.5 and 1.5 days for Hurricanes Jeanne and Wilma, respectively). The LOEM estimated a net sediment flux to the water column during Hurricane

Table 1. Hurricane wind statistics and Lake Okeechobee Environment Model simulation results for all hurricanes passing over Lake Okeechobee from 2004 to 2005.

Hurricane	Date and time of peak storm intensity	Maximum hourly and 15-minute wind speed (km h^{-1})	Storm persistence (days wind >29 km h^{-1})	Maximum bottom current velocity (m s^{-1})	Maximum bottom shear stress (N m^{-2})	Estimated net sediment resuspension (millions of t)	Significant wave height (cm above average water depth)
Frances	9/5/2004 0200	106 (108)	4.7	0.18	16.0	2.1	115
Jeanne	9/26/2004 1300	113 (119)	2.5	0.11	13.2	0.7	114
Wilma	10/24/2005 1100	126 (146)	1.5	0.12	13.4	1.4	117

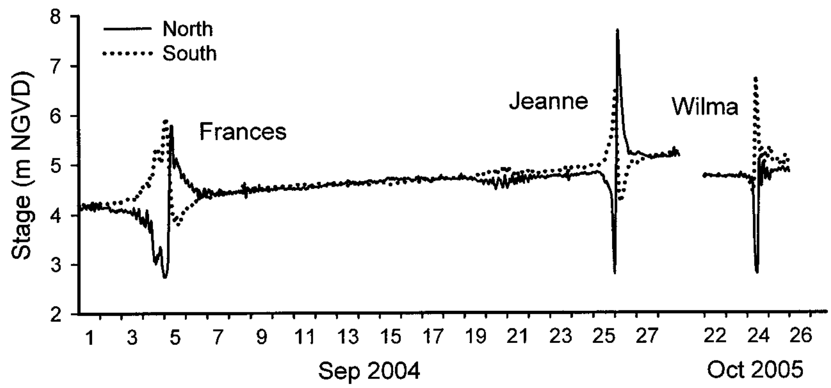

Fig. 2. Change in lake stage at a north (S-133) and south (S-3) shoreline location on Lake Okeechobee during Hurricanes Frances, Jeanne and Wilma.

Frances of 2.1 × 10^6 t of solids; the net sediment flux was substantially lower during the other storms.

Based on the dry bulk density of sediment cores obtained in 2005 (0.05–0.10 g cm^{-3}), the net sediment load predicted by the LOEM (2.1 × 10^6 t) and the assumption that all suspended sediment came from the central mud zone of the lake, sediment entrained into the water column by Hurricane Frances represented the complete resuspension of 3 to 6 cm of the sediment column from this zone. Because the estimated resuspension of solids is a net load, it is likely that the sediments were disturbed to an even greater depth (see below).

Comparisons of ^{210}Pb profiles of sediment cores collected in 1998 and 2003 with cores taken in April 2005, indicate that the sediments were disturbed to a depth greater than 6 cm (Fig. 3A, B). The sharp exponential decline in ^{210}Pb content with depth in pre-hurricane sediments is consistent with a conformable and unmixed sedimentary record and contrasts with the more uniform distribution of ^{210}Pb down to a depth from 9 to 12 cm in post-hurricane cores. These results

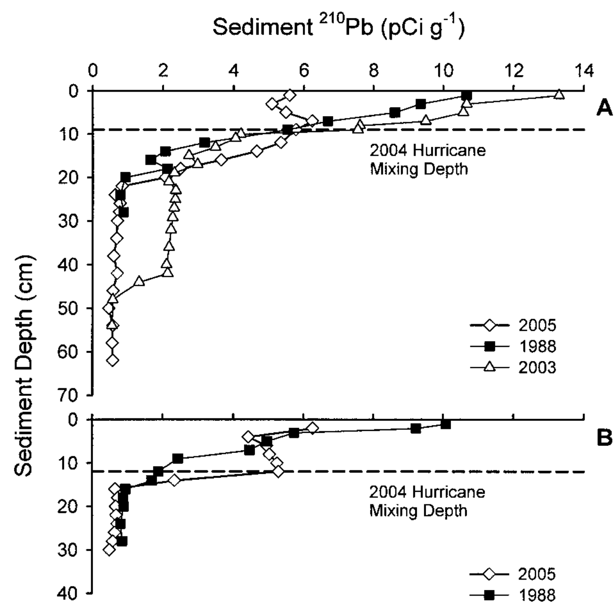

Fig. 3. Comparisons of ^{210}Pb vertical profiles in sediment cores collected from Lake Okeechobee at sample locations (**A**) L9 and (**B**) M8 (see Fig. 1B) in 1988 (Brezonik & Engstrom 1998), 2003 (Schottler & Engstrom 2006) and 2005 (current study).

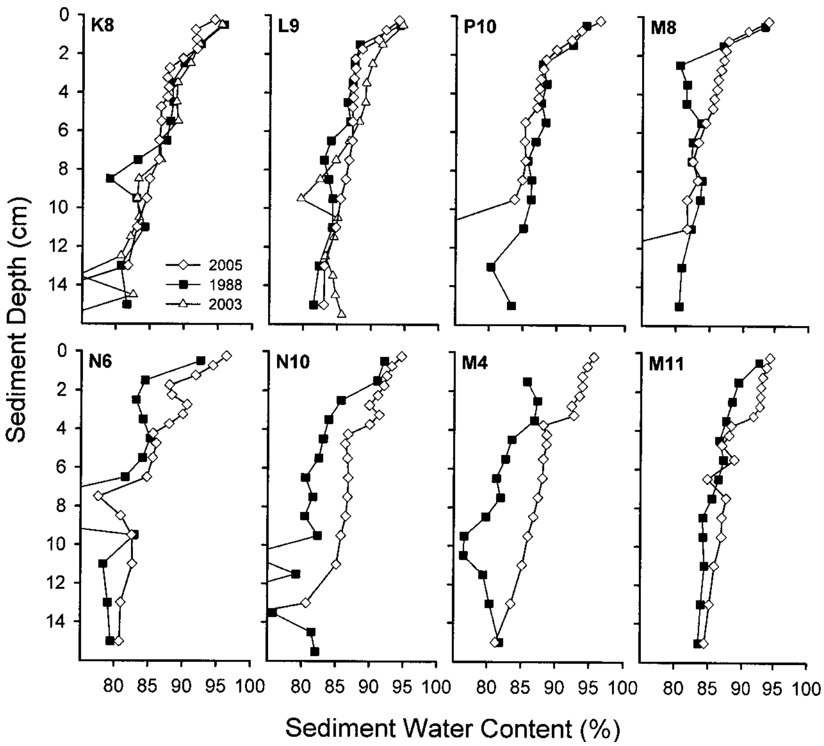

Fig. 4. Percent water content in sediment cores collected from Lake Okeechobee at eight locations (see Fig. 1B) in 1988 (Brezonik & Engstrom 1998), 2003 (Schottler & Engstrom 2006) and 2005 (current study).

indicate that the upper mixed zone was not present prior to 2004 and implies that considerable mixing occurred after the 2003 samples were collected. The older profiles (1988 and 2003) show a nearly exponential decline in ^{210}Pb with depth, which is strong evidence that mixing on par with the 2004 storms had not occurred in the past 50 or more years (Pollman & Engstrom, unpubl. data).

In addition to mixing, the sediments were less cohesive after the hurricanes than before. A comparison of sediment profiles for eight offshore cores showed higher water content in the upper sediment column in 2005 than in 1988 at five sites and similar profiles in the other three locations (Fig. 4). For three of those sites showing elevated water content in 2005 (N6, M8 and M11), the divergence from the 1988 profiles was greatest between approximately 2 and 5 cm depth, with values for both years converging at sediment depths above and below this stratum. At the other two sites (N10 and M4), the 2005 cores showed elevated water content to a depth of 15 cm, implying even deeper sediment mixing.

After the 2004 hurricanes, total suspended solids (TSS) in the water column increased and did not return to pre-hurricane levels (Figs 5A and 6A). The TSS peaks in December 2004, February 2005, and January and February 2006 in the offshore region were the largest monthly average concentrations on record and could be related to cold fronts that moved through south Florida. These weather systems typically are associated with high constant unidirectional winds that produce strong currents, large waves and increased bottom shear stress in the lake (Jin et al. 2002, Jin & Ji 2004), which results in increased TSS in the water column.

Secchi transparency also declined dramatically throughout the lake, although the littoral region had the highest and most variable changes after 2004 (Figs 5B and 6B). Secchi transparency in the offshore region was the least changed because of its very low values prior to the hurricanes. Nearshore Secchi transparency declined by more than half in the 12 months after the 2004 hurricanes, but increased thereafter. In 2007, only five samples were taken from the littoral region stations due to low water levels resulting from the drought and no nutrient, sediment or Secchi transparency data are reported. A significant inverse logarithmic relationship between TSS and Secchi transparency was observed for data pooled over all years in the littoral region ($r^2 = 0.65$, Fig. 5C).

The relationship between antecedent wind conditions and TSS in the offshore region changed following the hurricanes (Fig. 5D). For both pre- and post-hurricane periods, the strongest relationship was between TSS and wind speed averaged over the two days prior to sample collection. The slope of the post-hurricane

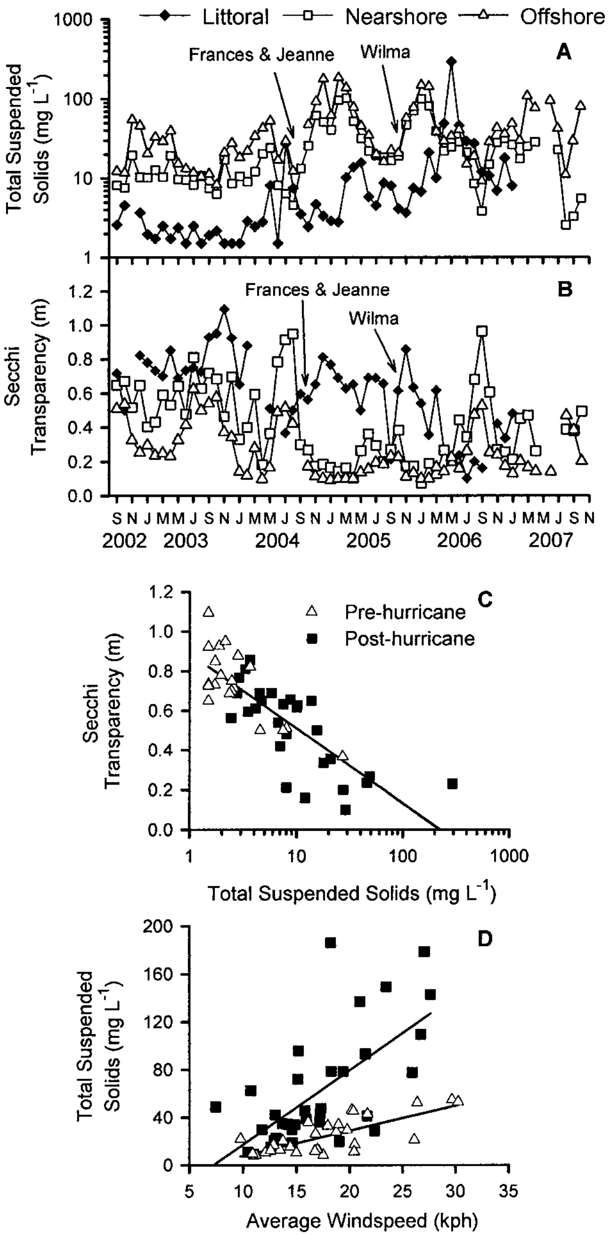

Fig. 5. Monthly average **(A)** total suspended solids (TSS) concentration and **(B)** Secchi transparency in the three regions of Lake Okeechobee from September 2002 to September 2007; **(C)** relationship of monthly average Secchi transparency in the littoral region with pre- and post-hurricane TSS concentrations; and **(D)** relationship of average offshore TSS concentration with average wind speed for the previous two days. Labeled arrows indicate approximate dates of hurricanes.

wind speed-TSS regression (6.23 mg TSS [km h^{-1}]$^{-1}$) was significantly higher ($p < 0.05$) than the pre-hurricane slope (2.10 mg TSS [km h^{-1}]$^{-1}$), based on an Analysis of Covariance, suggesting that the sediments were more easily resuspended after the hurricanes.

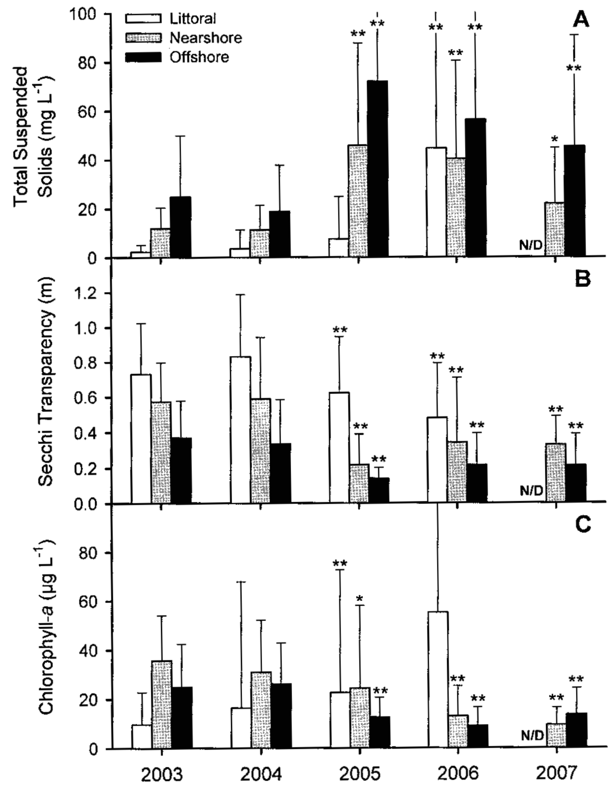

Fig. 6. Yearly mean values, standard deviations and pre-post hurricane mean comparisons in the three regions of Lake Okeechobee for **(A)** total suspended solids, **(B)** Secchi transparency and **(C)** chlorophyll-*a* from September 2003 to October 2007. Least square mean comparison key ($p < 0.01$) : * – significantly different from 2003 or 2004; ** – significantly different from 2003 and 2004; N/D – not determined.

The significantly higher TSS concentration and lower Secchi transparency in the offshore region continued throughout all post-hurricane years (Figs 6A and B). Increased TSS most likely resulted in the redistribution of sediment throughout the lake, as indicated by the significant increase of TSS in the littoral region in 2006. In the post-Wilma year (2006), all regions of the lake had higher TSS levels. Only in the drought year (2007) was there an indication of reduced TSS in these regions. Preliminary results of a post-storm study to determine the distribution of mud sediments throughout Lake Okeechobee indicate some accumulation of this material in the littoral and nearshore regions (BEM & University of Florida 2007).

Flows and loads

Rainfall, primarily from Hurricanes Frances and Jeanne, led to greatly increased surface water inflow and corresponding P and N loads (Figs 7A, B and C).

Table 2. Nutrient load calculations for Lake Okeechobee during the 2004 three month hurricane period and the following 18 month draw down period.

Date	Calculation	millions of m^3	TP (t)	SRP (t)	TN (t)	DIN (t)	TSS (t)
August 1 2004 to October 30, 2004	Surface Inflow/Load	3,010	794	618	5,363	843	42,978
	Surface Outflow/Load	1,110	167	55	2,043	554	36,018
	Rainfall	915	9	7	493	326	0
	Resuspension[a]	N/A	2,100	420	19,110	1,848	2,100,000
November 1, 2004 to April 30, 2006	Surface Inflow /Load	5,716	871	583	7,951	1,096	36,928
	Surface Outflow/Load	6,222	1,131	344	11,547	2,565	237,379
	Rainfall/Atmospheric Deposition[b]	2,560	52	40	1,845	751	0

[a] estimated from the Lake Okeechobee Environment Model for Hurricane Frances and Fisher et al. (2001).
[b] Nutrient atmospheric deposition estimated from James et al. (2005).

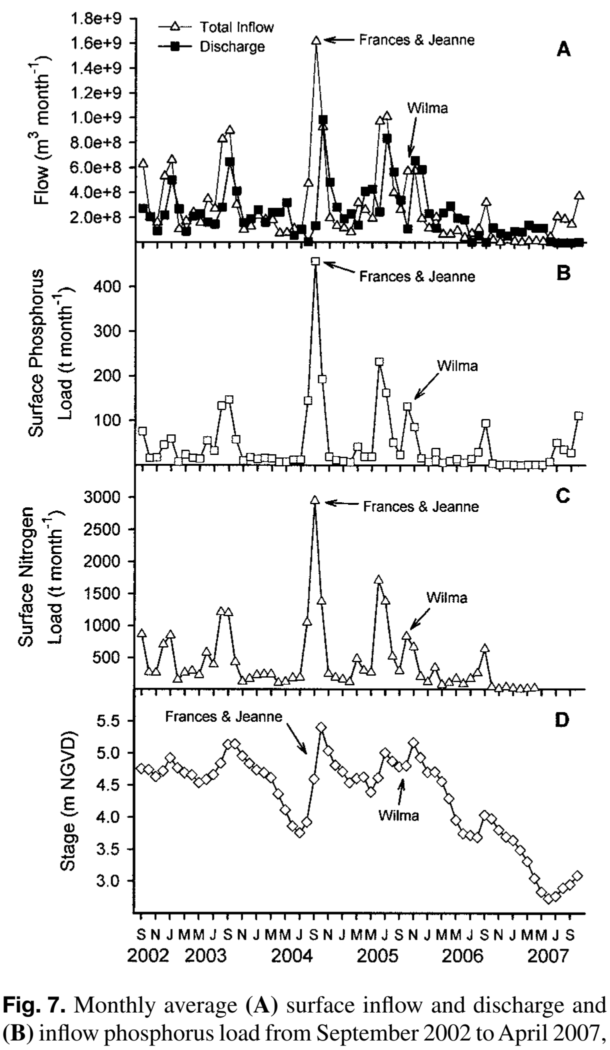

Fig. 7. Monthly average **(A)** surface inflow and discharge and **(B)** inflow phosphorus load from September 2002 to April 2007, and **(C)** inflow nitrogen load and **(D)** lake stage from September 2002 to October 2007 in Lake Okeechobee. Labeled arrows indicate approximate dates of hurricanes.

While some of the monthly differences in inflows and loads reflect normal weather changes from wet (June to November) to dry (December to May) seasons in south Florida, the 2004 hurricanes generated much more load and flow than normal (Table 2). Phosphorus loads from surface water inflows from August to October 2004 were equivalent to average annual P loads in years without hurricanes (Havens & James 2005). Nitrogen loads for the same three-month period were high as well. Rainfall directly on the lake was estimated at 53 cm for these three months, or 915 million m^3. Based on averaged rainfall nutrient concentrations (Table 3), rainfall contributed less than 10 % of the total load of all nutrients with the exception of dissolved inorganic N (DIN), which accounted for 38 % of the load (Table 2).

Table 3. Wet rainfall nutrient chemistry from January 2001 to November 2003 collected weekly at stations S131 and S308.

	DIN	TN	SRP	TP
Mean ($\mu g\ l^{-1}$)	356	539	7	10
Standard deviation ($\mu g\ l^{-1}$)	276	348	6	8
N	108	112	114	83

Using the net resuspension of sediments estimated for Hurricane Frances from the LOEM and the nutrient content of mud sediments in the offshore region of the lake (Fisher et al. 2001), sediment nutrient loads were calculated (Table 2). These estimated internal loads exceeded external loads, with the exception of soluble reactive phosphorus (SRP).

High surface water inflows, which exceeded 1.6 billion m^3 for the month of September 2004, greatly exceeded the District's capability to discharge water from the lake, which peaked at nearly 1.0 billion m^3 in October 2004 (Fig. 7A). The difference between inflow and discharge resulted in a rapid increase of lake stage from 3.9 m NGVD in August 2004 to 5.4 m NGVD by October 2004 (Fig. 7D). Water releases continued through April 2006 when lake stage declined to 4.13 m

NGVD, more than a full meter below the highest stage following the 2004 hurricanes.

During the drawdown period from November 2004 to April 2006, discharges from the lake were greater than inflow and loads to the lake for all nutrients except SRP (Table 2). Over this longer period, atmospheric deposition (which included estimates of dry and wet loads) was based on estimates of James et al. (2005). Net sediment resuspension could not be calculated for this period of time.

Releases of lake water to the Caloosahatchee River, coupled with drier than normal conditions in 2006, resulted in lake stage reaching 3.7 m NGVD by summer 2006 (Fig. 7D), which was within the range of optimum water level for SAV growth (Havens et al. 2005). Subsequent drought conditions in late 2006 and early 2007 led to a further decline in lake stage to 2.7 m by July 2007.

Water-column nutrients

In addition to the TSS increase during Hurricanes Frances and Jeanne (Fig. 6A), SRP and TP concentrations in the nearshore and offshore regions (Figs 8A, B) also increased substantially. SRP concentrations in the nearshore and offshore regions following Hurricanes Frances and Jeanne were two to four times greater than pre-hurricane concentrations. In the littoral region, post-hurricane SRP levels were six to 13 times greater than pre-hurricane values. All comparisons of pre-post hurricane concentration differences were significantly different.

Similar to changes in SRP, DIN concentrations after the 2004 hurricanes (Fig. 8C) exceeded pre-hurricane concentrations by three to four times in the offshore region, and six to eight times in the nearshore region. Dissolved inorganic N like SRP began to decline after 2005. As of 2007, the offshore concentration was not significantly different from the pre-hurricane years.

In the littoral region, the DIN concentration tripled in the year after Hurricanes Frances and Jeanne (2005) compared to pre-hurricane levels and was six times greater after Hurricane Wilma (Fig. 8C). Increased littoral DIN concentrations paralleled the increased concentrations in other lake regions but were not as large, probably because the continued presence of emergent and submersed vegetation, shallow water depth and good light conditions resulted in uptake of these nutrients by plants.

Total N (TN) in the littoral region was never significantly different from levels in the pre-hurricane years (Fig. 8D). The nearshore and offshore concentrations

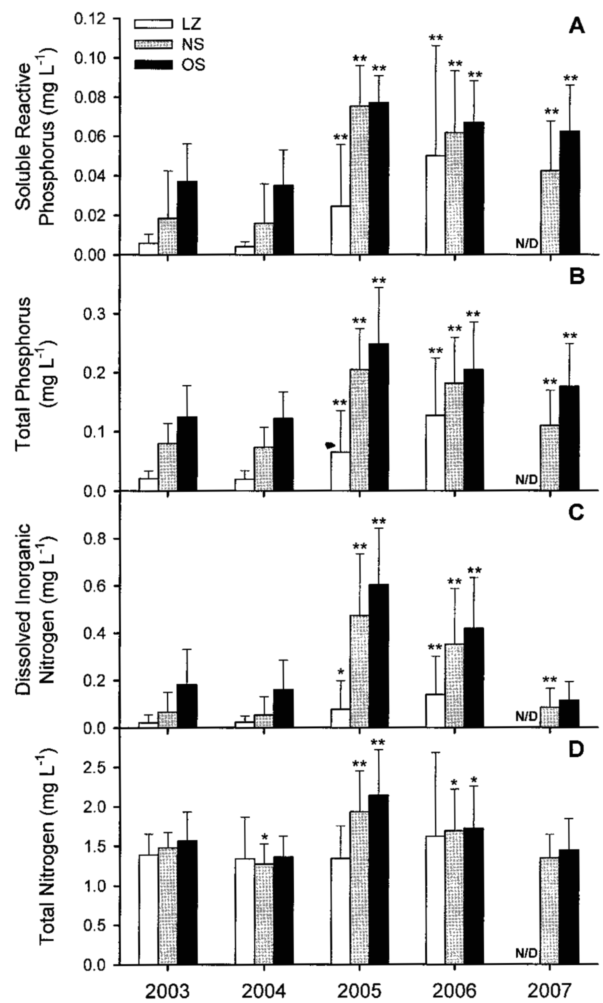

Fig. 8. Yearly mean concentrations, standard deviations and pre-post hurricane mean comparisons in the three regions of Lake Okeechobee for **(A)** soluble reactive phosphorus, **(B)** total phosphorus, **(C)** dissolved inorganic nitrogen and **(D)** total nitrogen from September 2002 to September 2007. Least square mean comparison key ($p < 0.01$): * – significantly different from 2003 or 2004; ** – significantly different from 2003 and 2004; N/D – not determined.

in 2005 were significantly higher than levels in both pre-hurricane years, but in 2006, these regions were only significantly different from one pre-hurricane year (2004). In 2007, neither the nearshore region nor the offshore region was statistically different from pre-hurricane years.

Submersed aquatic vegetation

The large surface seiches coupled with high wave action during Hurricanes Frances and Jeanne uprooted large quantities of aquatic plants along the western and southern portions of the littoral and nearshore regions

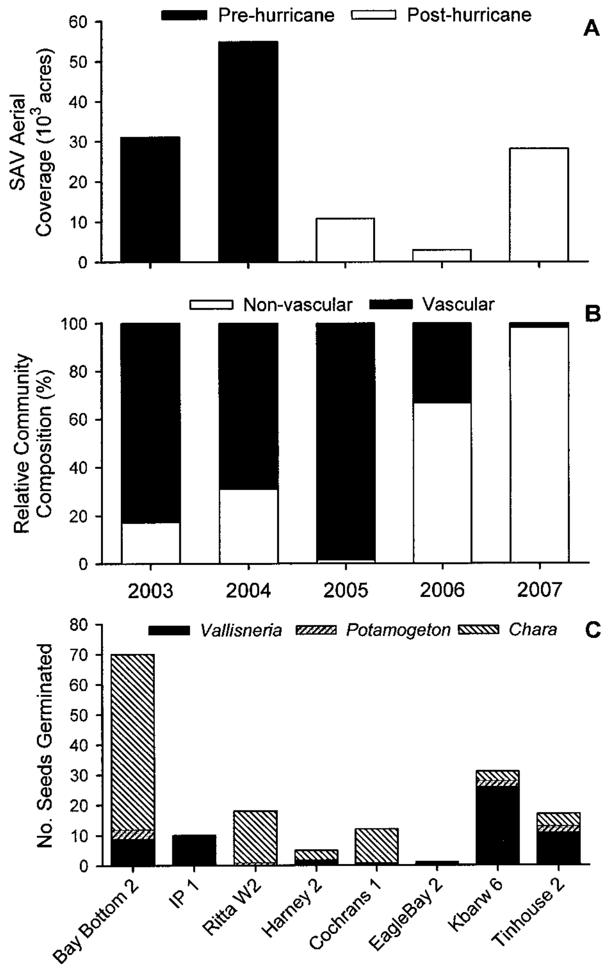

Fig. 9. Response of submersed aquatic vegetation (SAV) in Lake Okeechobee to hurricanes: **(A)** Acreage of SAV cover based on annual surveys conducted in August and/or September of each year **(B)** the percent of coverage of vascular and non-vascular SAV species in the annual surveys and **(C)** the number of germinating plants in sediment cores collected from various nearshore transects.

(Chimney 2005). This led to the dramatic decline in SAV coverage (Fig. 9A). The percent coverage of non-vascular SAV species also declined (Fig. 9B year 2005). Hurricane Wilma uprooted approximately 90,000 m^3 of plants that led to further declines in SAV coverage (Fig. 9A year 2006) and a reduction of the percent coverage of vascular SAV species (Fig. 9B year 2006).

The optimal water level for SAV recovery (3.7 m NGVD; Havens et al. 2005) was reached in the summer of 2006 (Fig. 7D). However, Secchi transparency remained low (Figs 5B and 6B), which potentially delayed SAV expansion. Viable propagules of vascular SAV species were found at many transect sites (Fig. 9C).

Phytoplankton

Algal blooms (defined as chlorophyll-*a* concentrations $>40\,\mu g\ l^{-1}$, [Walker & Havens 1995]) occurred in all regions of the lake in 2004 and 2005. After Hurricane Wilma, only one algal bloom occurred: in the littoral region in May 2006. The large variation of chlorophyll-*a* associated with these blooms was reflected in standard deviations greater than 100 percent of the littoral-region means in 2005 and 2006 (Fig. 6C). Chlorophyll-*a* concentrations were higher in this region after the hurricanes. However, because of the high annual variation, only increases after Hurricanes Frances and Jeanne (2005) were significantly different from pre-hurricane levels. In the nearshore region, chlorophyll-*a* decreased after the hurricanes, but only the years after Hurricane Wilma were significantly different from both pre-hurricane years. In the offshore region, chlorophyll-*a* concentrations were significantly lower in all post-hurricane years.

For both offshore and nearshore sampling locations, the average yearly biovolume of phytoplankton was highest in 2003 and declined in each year thereafter (Fig. 10A). The biovolumes of diatoms, Chlorophytes, Cryptophytes and Cyanobacteria in the pre-hurricane years 2003 and 2004 were not significantly different from each other, despite the visibly lower values in 2004. Comparisons made between the pre-hurricane 2004 data and the post-hurricane years revealed significantly less Cyanobacteria and Chlorophytes in the nearshore region, while all divisions with the exception of Chlorophytes in 2005 had reduced biovolumes in the offshore region ($p < 0.05$). For most years, diatoms and Cyanobacteria were the dominant phytoplankton groups (Fig. 10B). The percent biovolume of diatoms increased to over 60 % in the nearshore region and over 80 % in the offshore region after the hurricanes, while the percent biovolume of Cyanobacteria declined.

The major heterocystous Cyanobacteria genera included *Cylindrospermopsis*, *Anabaena* and *Aphanizomenon* that were observed in most years and in both regions of the lake (Fig. 10C). In 2005, *Lyngbya*, a non-heterocyst, and *Cylindrospermopsis*, dominated the nearshore Cyanobacteria biovolume, while *Cylindrospermopsis* and *Anabaena*, dominated the offshore Cyanobacteria biovolume. In 2006, *Planktolyngbya*, a non-heterocyst, was the dominant Cyanobacteria in the offshore region while both *Planktolyngbya* and *Anabaena* made up the majority of Cyanobacteria in the nearshore region.

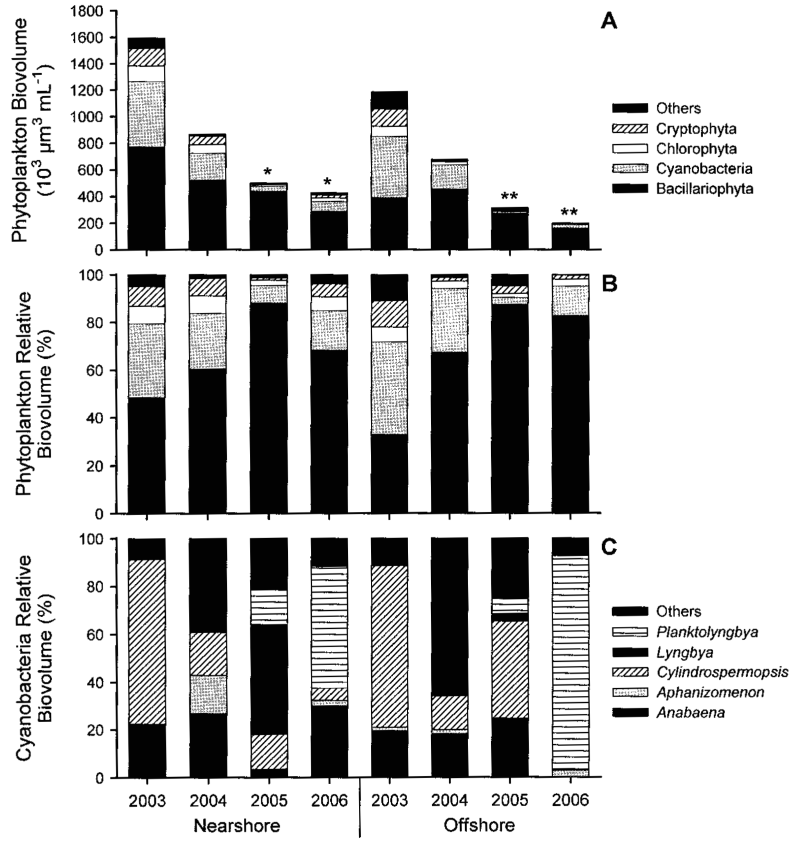

Fig. 10. Average biovolume estimates in the offshore and nearshore regions of Lake Okeechobee for **(A)** total biovolume of phytoplankton by division (* – significantly different ($p < 0.05$) from 2004 except for Cryptophytes and Bacilliarophytes (diatoms); ** – significantly different ($p < 0.05$) from 2004 except for Chlorophytes in 2005), **(B)** percent biovolume by divisions and **(C)** percent biovolume of Cyanobacteria genera.

Discussion

Sediment

We contend that the comparatively rare event of Hurricane Frances caused a dramatic change in sediment structure that has inhibited the return of Lake Okeechobee to pre-hurricane conditions. Although this hurricane was not the strongest recent storm to move over the lake, it exposed the system to high winds for over four days (Table 1). These winds not only resuspended a tremendous amount of solids, but also generated a thick layer of unconsolidated sediment that was much more easily resuspended by subsequent wind events. Evidence that this layer exists is documented in the ^{210}Pb and water-content profiles (Figs 3 and 4) as well as the significant change in the relationship between water-column TSS and wind speed (Fig. 5D). This easily resuspended sediment potentially has led to increased sediment-water exchanges of P and solids, which have maintained high levels of nutrients and low light conditions over the post-hurricane years throughout most of the lake.

The sediment water-content profiles also suggest that following homogenization of the upper sediment column, there has been a gradual consolidation and dewatering, but that sub-surface strata (2–15 cm) – which were more compact than the surface (0–2 cm) prior to the hurricanes – have still not returned to their pre-disturbance state (Fig. 4). Further sediment dewatering and compaction should occur, provided no additional hurricanes affect the area, thereby continuing to reduce the potential for resuspension.

Loads and nutrients

The increases of nutrients (especially P) and TSS in the water column of Lake Okeechobee immediately following the 2004 and 2005 hurricanes were expected based on prior experience with Hurricane Irene in 1999 (Havens et al. 2001a). Internal and external loading during the storms and the increased sediment resuspension after the storms contributed to the two- and four-fold increase in water-column TN and TP concentrations, respectively, from August to December 2004 (Fig. 8B, D). Similar to TP and TN, internal and external loading also contributed to the increase of water-column SRP and DIN shortly after the hurricanes (Fig. 8A, C). In addition, decomposition of uprooted aquatic plants may have contributed additional nutrient inputs in the months immediately after the hurricanes.

In the post-2005 hurricane period, we expected a gradual return of water quality to pre-hurricane conditions as was observed by Havens et al. (2001a) following Hurricane Irene. However, to date this recovery has only slowly begun. Two years after Hurricane Wilma, water quality in Lake Okeechobee remains significantly different from the pre-hurricane period with the exception of TN in the nearshore and TN and DIN in the offshore region (Fig. 8C, D).

We propose that reduced nutrient uptake by SAV and phytoplankton maintained high water-column SRP concentrations after Hurricanes Frances and Jeanne. This hypothesis is based on laboratory experiments, which showed that nearshore phytoplankton and bacterioplankton and littoral SAV communities sequestered the majority of available P (Havens et al. 2001b). Under light-limited conditions, P uptake was reduced resulting in higher SRP in the water column. The concentrations of SRP after Hurricanes Frances and Jeanne were an order of magnitude or greater than those reported by Havens et al. (2001b) for non-hurricane years. While increased SRP flux from the sediments after the hurricanes could be a factor in maintaining high water-column SRP concentrations (Fig. 8A), a similar result for DIN would be expected. However, DIN levels declined (Fig. 8C). The most logical explanation for these two different results is the low uptake of SRP and the removal of DIN through denitrification (see below). The subsequent decline of water-column SRP and TP concentrations in 2007 may be related to improved light conditions as water levels declined and SAV coverage increased (Fig. 8A, B).

The water-column concentrations of N species have returned more rapidly to pre-hurricane conditions. Unlike P, this nutrient can be removed from and released to the atmosphere by N-fixation and denitrification, respectively. Both of these processes are significant in Lake Okeechobee (Messer & Brezonik 1983, Phlips & Ihnat 1995). Because of the reduced Cyanobacteria biovolume after the storms, we propose that N-fixation was limited and that denitrification in the sediments or at the sediment-water interface largely contributed to the reduction of DIN in the water column.

SAV

Even though water levels declined to an optimal level by 2006 (3.7 m NGVD, Havens et al. 2005), SAV regrowth was delayed until 2007, and then it was almost exclusively musk grass (*Chara* spp.). These results mirror previous findings that showed the dominance of *Chara* in the first year of optimal SAV conditions (Havens et al. 2004). Because viable propagules of vascular SAV species were found at many transect sites (Fig. 9C), we predict further recovery of the SAV community in the near future, provided no hurricanes affect the area and lake levels remain within an optimal range (James & Havens 2005).

Phytoplankton

Low light penetration not only delayed regrowth of SAV in the lake, it also appeared to have affected the phytoplankton community adversely. Low light conditions in Lake Okeechobee's offshore region have led to dominance by small-celled Cyanobacteria such as *Oscillatoria* and *Lyngbya* (Phlips et al. 1997). Using canonical correlation analysis, Havens et al. (1998) supported the observations of Phlips et al. (1997) by finding a strong negative relationship between Secchi transparency and *Lyngbya,* which is a low-light adapted genera (Loeb & Reuter 1981, Roberts & Baylen 1988, Havens et al. 1996b). When Secchi transparency is higher in Lake Okeechobee, *Anaebena circinalis*, *Aphanizominon flos aquae*, and *Microcystis* occur in greater abundance (Havens et al. 2003).

The post-hurricane period, which was typified by greater turbidity and lower Secchi transparency throughout the lake, was unfavorable for bloom-forming heterocystous Cyanobacteria (Mur & Schreurs 1995, Scheffer et al. 1997, Phlips et al. 1997). The overall reduction of Cyanobacteria biovolume and the dominance by small-celled species of *Lyngbya* and *Planktolyngbya,* is consistent with these observations. The abundance and dominance by *Cylindrospermopsis*, an exotic N-fixing Cyanobacteria that has invaded lakes in Florida (Chapman & Schelske 1997), appears to play a role similar to *Oscillatoria* and *Lyngbya* (Havens et al. 2003) and is consistent with small Cyanobacteria dominating in these increasingly turbid waters.

The only time after the 2004 hurricanes that algal blooms occurred on Lake Okeechobee was from August to October 2005. During this period, *Microcystis* blooms occurred in the lake and other water bodies throughout south Florida (Zhang et al. 2007). This dominance pattern ended with Hurricane Wilma, and no major algal blooms have been observed through the end of 2007. The poor environmental conditions for Cyanobacteria including low light levels, low water-column stability (Zhang & Prepas 1996), high bottom shear stress (Moisander et al. 2002) and high DIN levels (Phlips et al. 1997), continued throughout most 2005 and 2006 and provides the rational for dominance by phytoplankton other than Cyanobacteria, especially diatoms. This pattern was consistent with past studies that showed diatoms out-compete Cyanobacteria under turbulent and light-limited conditions (Litchman 1998).

Has there been a change to an alternative stable state?

In light of the increase in sediment-water exchanges that occurred after Hurricane Frances and the persistently high P and TSS water-column concentrations and low Secchi transparency throughout the lake after the storms, might this be an example of a change to an alternative stable state caused by a dramatic event (*sensu* Scheffer et al. 1993)? In the offshore region, post-hurricane changes do not fit the definition of a classic change of state, as this region has simply moved further along a continuum of increasing turbidity and nutrients. In the nearshore region, the areal extent of the SAV community has varied dramatically over the years, alternating from high–water, turbid, plankton-dominated conditions to low and clear-water SAV-dominated conditions (James & Havens 2005). The increased turbidity in this region after the 2004 hurricanes, attributed to the movement of sediment from the offshore region, has potentially made the turbid state in this region more stable, as observed in the slow regrowth of vascular SAV species. This change potentially could delay recovery of the lake as management activities move forward. The drought that followed in 2007 also has led to negative consequences by dewatering regions of the lake where SAV had begun to regrow. Once water levels return to normal conditions, the possible switch to an alternative stable state in the nearshore region can be re-evaluated.

Management of ecosystem recovery

Excessive P loads have been a major concern for the ecological health of Lake Okeechobee for decades (Havens & James 2005). A number of projects and programs have been initiated within the Lake Okeechobee Watershed (SFWMD et al. 2007) to reduce P input to a Total Maximum Daily Load of 140 t P per year (Florida Department of Environmental Protection 2001) by 2015.

The Lake Okeechobee Water Quality Model (LOWQM) (James et al. 2005) has been used to forecast responses to load reductions in the lake (Blasland Bouck & Lee Inc. 2003). Lake responses are predicated in part on the burial of sediments to the point where they no longer interact with the water column. In LOWQM simulations, James et al. (2005) assumed that sediments deeper than 6 cm were permanently buried and not subject to reintroduction to the system. Due to the depth to which sediments were disturbed after the hurricanes (Fig. 3), this assumption must be reconsidered. It now appears that estimates of the time required for recovery of the lake as internal P loads diminish may be lengthened. However, despite the effects of hurricanes on Lake Okeechobee described in this paper, we fully expect that P load reductions will lead to improved lake conditions (Cooke et al. 2005, Jeppesen et al. 2003).

Reduced water levels also should contribute to improving habitat conditions in the lake. To help manage lake stage within a more ideal range, plans have been developed to store excess water from the lake in reservoirs and deep injection wells through the Comprehensive Everglades Restoration Plan (www.evergladesplan.org). These projects should improve conditions in the lake that promote SAV growth (Havens 2002).

Lake management recommendations

Shallow coastal lakes that are vulnerable to anthropogenic and climatic events (Havens et al. 2007) may experience similar deleterious changes in their ecology as a consequence of a (potentially) higher frequency of hurricanes in the future (Goldenberg et al. 2001, Webster et al. 2005). For Lake Okeechobee, these changes are attributed primarily to increased resuspension of flocculent sediments that influenced water quality, phytoplankton and SAV. Such changes in other vulnerable lakes could potentially delay the benefits of restoration activities related to water or nutrient management. Our results suggest that sediment conditions be evaluated in vulnerable lakes to determine the role they could play in response to extreme weather events. While direct mitigation of sediments may not be feasible, management of water levels, as are being pursued for Lake Okeechobee, could help maintain healthy SAV beds and improve water quality conditions.

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References

APHA, 1998: Standard Methods for the Examination of Water and Wastewater. – American Public Health Association, American Water Works Association and Water Pollution Control Federation, Washington, D. C.

BEM & University of Florida, 2007: Lake Okeechobee Sediment Quality Final Report. – South Florida Water Management District, West Palm Beach.

Blasland Bouck & Lee Inc., 2003: Evaluation of Alternatives for the Lake Okeechobee Sediment Management Feasibility Study. – Report in partial fulfillment of contract C-11650. South Florida Water Management District, West Palm Beach, FL, pp. 252.

Brezonik, P. L. & Engstrom, D. R., 1998: Modern and historic accumulation rates of phosphorus in Lake Okeechobee, Florida. – J. Paleolimnol. **20:** 31–46.

Chapman, A. D. & Schelske, C. L., 1997: Recent appearance of Cylindrospermopsis (Cyanobacteria) in five hypereutrophic Florida lakes. – J. Phycol. **33:** 191–195.

Chimney, M., 2005: Surface seiche and wind set-up on Lake Okeechobee (Florida, USA) during Hurricanes Frances and Jeanne. – Lake Reserv. Manage. **21:** 465–473.

Cooke, G. D., Welch, E. B., Patterson, W. P. & Nichols, S. A., 2005: Restoration and Management of Lakes and Reservoirs. – CRC Press, Boca Raton, FL, pp. 598.

Donnelly, J. P., Bryant, S. S., Butler, J., Dowling, J., Fan, L., Hausmann, N., Newby, P., Shuman, B., Stern, J., Westover, K. & Webb III, T., 2001: 700 yr sedimentary record of intense hurricane landfalls in southern New England. – Bull. the Geol. Soc. Amer. **113:** 714–727.

Engstrom, D. R., Schottler, S. P., Leavitt, P. R. & Havens, K. E., 2006: A re-evaluation of the cultural eutrophication of Lake Okeechobee, Florida using multiproxy sediment records. – Ecol. Appl. **16:** 1194–1206.

Fisher, M. M., Reddy, K. R. & James, R. T., 2001: Long-term changes in the sediment chemistry of a large shallow subtropical lake. – Lake Reserv. Manage. **17:** 217–232.

Florida Department of Environmental Protection (FDEP), 2001: Total Maximum Daily Load for Total Phosphorus Lake Okeechobee, Florida. – Submitted to U. S. Environmental Protection Agency, Region IV, Atlanta, GA.

Goldenberg, S. B., Landsea, C. W., Mestas-Nuñez, A. M. & Gray, W. M., 2001: The recent increase in Atlantic hurricane activity: causes and implications. – Science **293:** 474 – 479.

Havens, K. E., 1995: Particulate light attenuation in a large subtropical lake. – Can. J. Fisher. Aquat. Sci. **52:** 1803–1811.

– 2002: Development and application of hydrologic restoration goals for a large subtropical lake. – Lake Reserv. Manage. **18:** 285–292.

– 2003: Submerged aquatic vegetation correlations with depth and light attenuating materials in a shallow subtropical lake. – Hydrobiologia **493:** 173–186.

Havens, K. E., Aumen, N. G., James, R. T. & Smith, V. H., 1996a: Rapid ecological changes in a large subtropical lake undergoing cultural eutrophication. – Ambio **25:** 150–155.

Havens, K. E., East, T. L., Meeker, R. H., Davis, W. P. & Steinman, A. D., 1996b: Phytoplankton and periphyton responses to *in situ* experimental nutrient enrichment in a shallow subtropical lake. – J Plankton Res. **18:** 551–566.

Havens, K. E., Fox, D., Gornak, S. & Hanlon, C., 2005: Aquatic vegetation and largemouth bass population responses to water–level variations in Lake Okeechobee, Florida (USA). – Hydrobiologia **539:** 225–237.

Havens, K. E., Hanlon, C. & James, R. T., 1995: Historical trends in the Lake Okeechobee ecosystem. V. Algal blooms. – Arch. Hydrobiol. Suppl. **107:** 89–100.

Havens, K. E., Harwell, M. C., Brady, M. A., Sharfstein, B., East, T. L., Rodusky, A. J., Anson, D. & Maki, R. P., 2002: Large-scale mapping and predictive modeling of submerged aquatic vegetation in a shallow eutrophic lake. – The Scientific World **2:** 949–965.

Havens, K. E. & James, R. T., 1999: Localized changes in transparency linked to mud sediment expansion in Lake Okeechobee, Florida: ecological and management implications. – Lake Reserv. Manage. **15:** 54–69.

– – 2005: The phosphorus mass balance of Lake Okeechobee, Florida: implications for eutrophication management. – Lake Reserv. Managem. **21:** 139–148.

Havens, K. E., James, R. T., East, T. L. & Smith, V. H., 2003: N:P ratios, light limitation, and cyanobacterial dominance in a subtropical lake impacted by non-point source nutrient pollution. – Environm. Pollut. **122:** 379–390.

Havens, K. E., Jin, K.-R., Iricanin, N. & James, R. T., 2007: Phosphorus dynamics at multiple time scales in the pelagic zone of a large shallow lake in Florida, USA. – Hydrobiologia **581**: 25–42.

Havens, K. E., Jin, K.-R., Rodusky, A. J., Sharfstein, B., Brady, M. A., East, T. L., Iricanin, N., James, R. T., Harwell, M. C. & Steinman, A. D., 2001a: Hurricane effects on a shallow lake ecosystem and its response to a controlled manipulation of water level. – The Scientific World **1:** 44–70.

Havens, K. E., Phlips, E. J., Cichra, M. F. & Li, B.-L., 1998: Light availability as a possible regulator of cyanobacterial species composition in a shallow subtropical lake. – Freshwat. Biol. **39:** 547–556.

Havens, K. E., Sharfstein, B., Brady, M. A., East, T. L., Harwell, M. C., Maki, R. P. & Rodusky, A. J., 2004: Recovery of submerged plants from high water stress in a large subtropical lake in Florida, USA. – Aquat. Bot. **78:** 67–82.

Havens, K. E., Steinman, A. D. & Hwang, S.-J., 2001b: Phosphorus uptake by plankton and periphyton in relation to irradiance and phosphate availability in a subtropical lake (Lake Okeechobee, Florida, USA). – Arch. Hydrobiol. **151:** 177–201.

Hoyer, M. V., Bachmann, R. W. & Canfield, D. E., 2008: Lake management (muck removal) and hurricane impacts to the trophic state of Lake Tohopekaliga, Florida. – Lake Reserv. Manage. **24:** 57–68.

James, R. T., Bierman, V. J., Jr., Erickson, M. J. & Hinz, S. C., 2005: The Lake Okeechobee water quality model (LOWQM) enhancements, calibration, validation and analysis. – Lake Reserv. Manage. **21:** 231–260.

James, R. T. & Havens, K. E., 2005: Outcomes of extreme water levels on water quality of offshore and nearshore regions in large shallow subtropical lake. – Arch. Hydrobiol. **163:** 225–239.

James, R. T., Jones, B. L. & Smith, V. H., 1995a: Historical trends in the Lake Okeechobee ecosystem II. nutrient budgets. – Arch. Hydrobiol. Suppl. **107:** 25–47.

James, R. T., Smith, V. H. & Jones, B. L., 1995b: Historical trends in the Lake Okeechobee ecosystem III. water quality. – Arch. Hydrobiol. Suppl. **107:** 49–69.

Jeppesen, E., Jensen, J. P., Søndergaard, M., Hansen, K. S., Møller, P. H., Rasmussen, H. U., Norby, V. & Larsen, S. E., 2003: Does resuspension prevent a shift to a clear state in shallow lakes during reoligotrophication? – Limnol. Oceanogr. **48:** 1913–1919.

Jin, K.-R. & Ji, Z.-G., 2004: Case study: modeling of sediment transport and wind-wave impact in Lake Okeechobee. – J. Hydraulic Engineer. **130:** 1055–1067.

Jin, K.-R., Ji, Z.-G. & Hamrick, J. H., 2002: Modeling winter circulation in Lake Okeechobee, Florida. – J. Waterway, Port, Coastal and Ocean Engineer. **128:** 114–125.

Jin, K.-R., Ji, Z.-G. & James, R. T., 2007: Three dimensional water quality modeling of a large shallow lake. – J. Great Lakes Res. **33:** 28–45.

Litchman, E., 1998: Population and community responses of phytoplankton to fluctuating light. – Oecologia **177:** 247–257.

Littell, R. C., Miliken, G. A., Stroup, W. W. & Wolfinger, R. D., 1996: SAS System for Mixed Models. – SAS Institute Inc., Cary, NC., pp. 633.

Liu, K. & Fearn, M. L., 2000: Reconstruction of prehistoric landfall frequencies of catastrophic hurricanes in northwestern Florida from lake sediment records. – Quatern. Res. (Orlando). **54:** 238–245.

– – 2002: Lake sediment evidence of coastal geologic evolution and hurricane history from Western Lake, Florida: reply to Otvos. – Quatern. Res. (Orlando). **57:** 429–431.

Loeb, S. L. & Reuter, J. E., 1981: The epilithic periphyton community: a five lake comparative study of community productivity, nitrogen metabolism and depth distribution of sanding crop. – Verh. Internat. Verein. Limnol. **21:** 346–352.

Lowe, E. F., Battoe, L. E., Coveney, M. F., Schelske, C. L., Havens, K. E., Marzolf, E. R. & Reddy, K. R., 2001: The restoration of Lake Apopka in relation to alternative stable states: an alternative view to that of Bachmann et al. (1999). – Hydrobiologia **448:** 11–18.

Messer, J. & Brezonik, P. L., 1983: Comparison of denitrification rate estimation techniques in a large shallow lake. – Water Res. **17:** 631–640.

Moisander, P. H., Hench, J. L., Kononen, K. & Paerl, H. W., 2002: Small-scale shear effects on heterocystous cyanobacteria. – Limnol. Oceanogr. **47:** 108–119.

Mur, L. R. & Schreurs, H., 1995: Light as a selective factor in the distribution of phytoplankton species. – Water Sci. Technol. **32:** 25–34.

Phlips, E. J., Cichra, M., Havens, K., Hanlon, C., Badylak, S., Rueter, B., Randall, M. & Hansen, P., 1997: Relationships between phytoplankton dynamics and the availability of light and nutrients in a shallow sub-tropical lake. – J. Plankton Res. **19:** 319–342.

Phlips, E. J. & Ihnat, J., 1995: Planktonic nitrogen fixation in a shallow subtropical lake (Lake Okeechobee, Florida, USA). – In: Aumen, N. G. & Wetzel, R. G. (eds): Ecological studies on the littoral and pelagic systems of Lake Okeechobee, Florida (USA). – Arch. Hydrobiol., Advanc. Limnol. **45:** 191–201.

Presley, S. M., Rainwater, T. R., Austin, G. P., Platt, S. G., Zak, J. C., Cobb, G. P., Marsland, E. J., Tian, K., Zhang, B., Anderson, T. A., Cox, S. B., Abel, M. T., Leftwich, B. D., Huddleston, J. R., Jeter, R. M. & Kendall, R. J., 2006: Assessment of pathogens and toxicants in New Orleans, LA following Hurricane Katrina. – Environment. Sci. Technol. **40:** 468-474.

Richardson, J. R. & Harris, T. T., 1995: Vegetation mapping and change detection in the Lake Okeechobee marsh ecosystem. – In: Aumen, N. G. & Wetzel, R. G. (eds): Ecological studies on the littoral and pelagic systems of Lake Okeechobee, Florida (USA). – Arch. Hydrobiol., Advanc. Limnol. **45:** 17–39.

Roberts, D. A. & Baylen, C. W., 1988: Patterns of epipelic algal distribution in an acidic Adirondack lake. – J. Phycol. **24:** 146–152.

Scheffer, M., Hosper, S. H., Meijer, M. L., Moss, B. & Jeppesen, E., 1993: Alternative equilibria in shallow lakes. – Trends Ecol. Evolut. **8:** 275–279.

Scheffer, M., Rinaldi, S., Gragnani, A., Mur, L. R. & van Nes, E. H., 1997: On the dominance of filamentous Cyanobacteria in shallow, turbid lakes. – Ecology **78:** 272–282.

Schottler, S. P. & Engstrom, D. R., 2006: A chronological assessment of Lake Okeechobee (Florida) sediments using multiple dating markers. – J. Paleolimnol. **36:** 19–36.

Schwimmer, D. R. & Frazier, W. J., 1994: Lake-sediment record of late Holocene hurricane activities from coastal Alabama: Comment and reply. – Geology **22:** 285.

South Florida Water Management District, Florida Department of Environmental Protection & Florida Department of Agriculture and Consumer Services, 2007: Lake Okeechobee Protection Program, Lake Okeechobee Protection Plan Evaluation Report. – South Florida Water Management District, West Palm Beach, FL., pp. 61.

South Florida Water Management District (SFWMD). 1999: SFWMD Comprehensive Quality Assurance Plan – 1999. SFWMD, West Palm Beach, FL.

Stoermer, E. F., Andresen, N. A. & Schelske, C. L., 1992: Diatom succession in the recent sediments of Lake Okeechobee, Florida, U. S. A. – Diatom Res. **7:** 367–386.

U. S. Environmental Protection Agency (USEPA), 1983: Methods for Chemical Analysis of Water and Wastes. – 600/4/79/029. U. S. EPA Office of Technology Transfer, Washington D.C.

Walker, W. W., Jr. & Havens, K. E., 1995: Relating algal bloom frequencies to phosphorus concentrations in Lake Okeechobee. – Lake Reserv. Manage. **11:** 77–83.

Webster, P. J., Holland, G. J., Curry, J. A. & Chang, H.-R., 2005: Changes in tropical cyclone number, duration, and intensity in a warming environment. – Science **309:** 1844–1846.

Zhang, J., James, R. T., Ritter, G. & Sharfstein, B., 2007: Chapter 10: Lake Okeechobee Protection Program – State of the Lake and Watershed. – In: Redfield, G. W. & Efron, S. (eds): 2006 South Florida Environmental Report. – South Florida Water Management District, West Palm Beach pp. 10-11 – 10-102.

Zhang, Y. & Prepas, E. E. A., 1996: Regulation of the dominance of planktonic diatoms and cyanobacteria in four eutrophic hardwater lakes by nutrients, water column stability, and temperature. – Can. J. Fisher. Aquat. Sci. **53:** 621–633.

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